Breeding Behaviour of a tropical bird: a study of the Blue-throated Bee-eater (*Merops viridis*) using a relational database and DNA fingerprinting

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ABSTRACT

The breeding behaviour of the Blue-throated Bee-eater was studied at two colonies in Peninsula Malaysia during 3 breeding seasons, with particular emphasis on pair behaviour, mixed reproductive strategies and nestling competition. This is the first study of vertebrate social behaviour and ecology to contain the documentation of a relational database. This was designed to store and manipulate all data obtained from regular captures and biometric measurements of adults and nestlings and from observations of adults. DNA fingerprinting was used to establish the true genetic relationships between nestlings and their social parents: most nestlings were genetic offspring (72%). Nestlings were classified as illegitimate offspring using 95% confidence intervals of the band sharing coefficient and number of unexplained nestling bands as criteria. Very few if any nestlings were sired by an extra-pair male (fewer than 5%). Behavioural evidence of strong cooperation between pair members throughout the breeding season supports the DNA fingerprinting results of no confirmed case of offspring fathered by extra-pair males (extra-pair offspring; EPO). The Blue-throated Bee-eater probably has a near monogamous mating system. Most illegitimate nestlings had been 'dumped'. They were either the result of intra-specific nest parasitism (INP; 7%) or of 'quasi' parasitism (the offspring of the pair-male and an extra-pair female; 7-12%). INP by relatives of the hosts could have explained some intermediate band sharing coefficients. Anti-INP behaviour was demonstrated when experimentally 'dumped' eggs were almost always expelled before the onset of laying, but never afterwards. DNA fingerprinting showed that relatives may roost together and that related males may nest close together. Compared with other colonial Bee-eaters, *M. viridis* had low levels of helping-at-the-nest and EPO, but similar or higher levels of INP.

The high nestling mortality in Blue-throated Bee-eaters was explained by a combination of three hypotheses, some of which were tested by experiment. (1) *Insurance*: extra-eggs are needed to counter hatch failure. (2) *Brood reduction* (including *resource tracking*): in times of food constraint, the later-hatched nestlings in asynchrously hatched broods starve. (3) *Anti-INP hypothesis*: these later-hatched nestlings are eliminated because they are likely to be illegitimate. Hatching failure was about 1 in 3 eggs overall. Help from the male allows an early onset of incubation which results in asynchronous hatching. Nestling hunger was shown to be a proximate factor affecting runt mortality both directly through competition and indirectly through nestling aggression. The demise of runts was delayed when conditions improved. Blue-throated Bee-eater broods are severely limited by food. Under this severe brood size constraint, breeding females may increase reproductive output by 'dumping' their last egg. This leads to the high frequency of INP observed in Blue-throated Bee-eaters. An early onset of incubation also gives the first-laid egg(s) a temporal developmental advantage over subsequently 'dumped' parasitic eggs. The 'dumped' nestlings are eliminated by starvation and siblicide, which may itself be an adaptation to INP to eliminate of unrelated nestlings.

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CHAPTER 1 - INTRODUCTION

Individuals maximize fitness by evolving behavioural strategies that increase particular components of fitness (Gustafson, 1986; Trivers, 1985 and 1972; Hamilton, 1964; Fisher, 1958). A variety of such behaviours is found especially in the social biology of breeding birds. Components of fitness for individual birds during breeding are mate choice, encounter rate of mates, fertilization rate (for males), timing of laying, securing a nest site, predator avoidance, parental effort and the survival of eggs, nestlings and parents. Table 1.1 shows behavioural options for breeding birds to maximize each of these. Below, I briefly introduce the aspects of breeding behaviour on which this study aims to focus.

1.1 Coloniality

The availability of food resources during breeding is a limiting factor for many birds (e.g. Emlen and Wrege, 1991; Perrins and Birkhead, 1983; Murton and Westwood, 1977, Medway and Wells, 1976; Lack, 1954). Breeding systems have evolved in response to a combination of resource distribution, predation pressure and phylogenetic constraints (Davies, 1991; Emlen and Oring, 1987; Fig. 1.1). If resources are defendable, territoriality often follows, and occasionally males can keep multiple females, each on a different territory (e.g. Davies, 1991). If, on the other hand, resources are unpredictable in time and space, such as insect food, breeding in colonies may be advantageous to birds (Shields *et al,* 1988; Møller, 1977 d; Shields and Crook, 1977; Hoogland and Sherman, 1976).

Coloniality may enhance an individual's chance to meet with a partner ('encounter rate'; Table 1.1). At the beginning of the breeding season, both sexes may return to a previous breeding site and meet their breeding partner there for example. Breeding colonies may thus become established, and by breeding colonially the chances of meeting not only a member of the opposite sex, but a good quality mate ('mate choice'; Table 1.1), might increase for individual breeders (Vehrenkamp and Bradbury, 1984). Each of these behaviours may enhance the chances of having a successful breeding attempt.

Table 1.1: Components of fitness and options of behaviours for individual birds to increase them (Adapted from Vehrenkamp and Bradbury, 1984).

Component of fitness	Indi-vidual	Options for increasing component
mate-choice	M+F	- choose good quality mate to pass its genes on to offspring - chose mate compatible in age or size - choose mate of good condition/ ability/ experience to provide care
encounter rate	M+F	- assemble at breeding grounds to meet with previous or new partner - stay paired during the winter
fertilization rate	M	- exclude other males by guarding partner or increasing copulation rate - behavioural and physiological adaptations (sperm plug, sperm removal)
timing of laying	M+F	- help to dig or induce partner to dig - arriving early
nest site for eggs	M+F	- return to nest site of the previous year if successful - dig burrow and defend it - steal burrow
	F	- 'dump' eggs
Predator avoidance	M+F	- synchronize breeding at colonies to swamp predator (see below) - breed solitarily so as not to attract predator attention
egg survival	M+F	- help to incubate
	F	- 'dump' eggs in host clutch (INP)
parental effort	F	- avoid partner siring EPO
	M+F	- use colony as 'information centre' to forage more efficiently - desert eggs or chicks: partner has to increase effort (but may desert too)
	chicks	- begging behaviour
nestling survival	M+F	- invest in care - recruit helper to provision young - reduce competition for food by breeding solitarily
adult survival	M+F	- defer breeding if conditions are unfavourable (and help relatives) - dilute risk of predation by living in groups

M male
F female

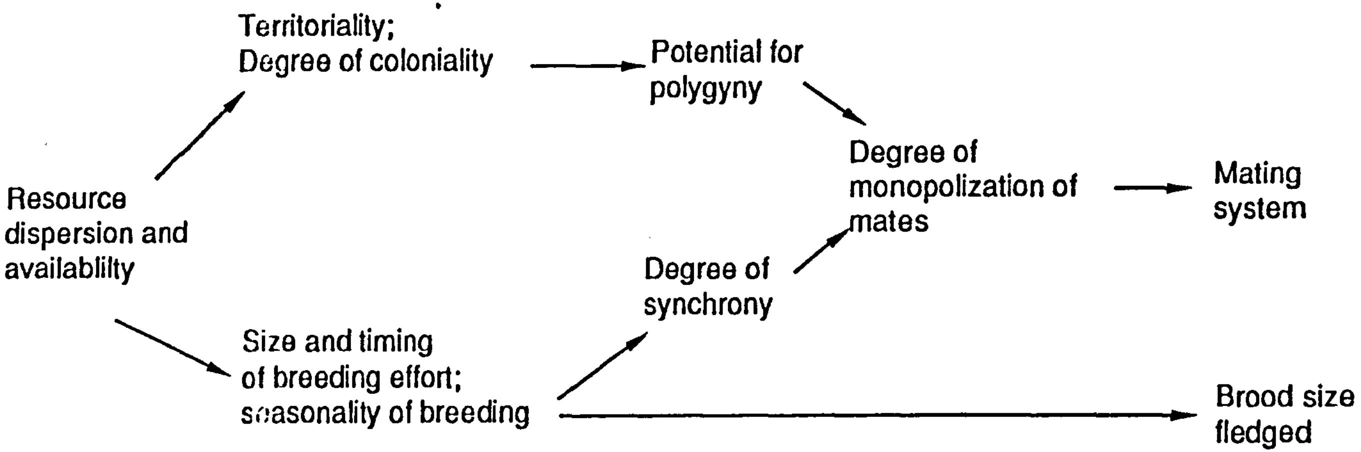


Figure 1.1: Relationship between resource dispersion and breeding system (adapted from Emlen and Oring, 1977; and Davies, 1991). x -> y = x determines y.

Coloniality may also enable birds

(1) to detect predators faster or more efficiently and evict them by mobbing or vocalization (Hoogland and Sherman, 1976; see also Wilkinson and English-Loeb, 1982);

(2) to 'flood' potential predators with synchronized fledging of their broods so that each bird has a lower probability to be predated ('selfish herd' effect; Watt and Mock, 1987; Hamilton, 1971); or

(3) to forage more efficiently by using the colony either (a) to reduce travel distances to unpredictable food resources (Horn, 1968; but see Brown *et al*, 1992) or (b) as an 'information centre' (Ward, 1965; Brown, 1988; but see e.g. Templeton and Giraldean, 1990, and Stutchbury, 1988; Bayer, 1982).

Alternatively, there may not be any direct benefits associated with colonial nesting, but a shortage of suitable nesting areas may crowd the birds together (Shields and Crook, 1987; Wittenberger and Hunt, 1985), or they may simply aggregate at arbitrary but traditionally settled sites (Shields *et al*, 1988; Siegel-Causey and Kharitonov, 1990). They may do this despite potential disadvantages, such as:

(1) conspicuousness of breeding colonies promises great rewards which attracts predators;

(2) competition amongst the colony members for mates, nests, nest sites or food (Shields *et al*, 1988; Hoogland and Sherman, 1976; Snapp, 1976); and

(3) ready transmission of ectoparasites (e.g. Hoogland and Sherman, 1976; Poulin, 1991) which can significantly increase chick mortality (Shields and Crook, 1987), and poses a problem especially in hole-nesting species (Møller *et al*, 1990).

Costs and benefits of coloniality have been examined mainly for hirundines which nest on the whole in large colonies. They feed on small insects, which have particularly patchy distribution, and they depend on regular food intake for survival and successful breeding - like Sand Martins or Bank Swallows *Riparia riparia*, Cliff Swallows *Petichelidon pyrrhonota* and Barn Swallows *Hirundo rustica* (Brown and Brown, 1991, 1989, 1988 a and b, 1986; Shields *et al*, 1988; Møller, 1987 d; Shields and Crook, 1987; Watt and Mock, 1987; Hoogland and

Sherman, 1976). Coloniality is furthermore obligatory in Cliff Swallows and Sand Martins (i.e. they are not found nesting solitarily). Fewer studies examine species with less patchily distributed food, which depend less on a regular food supply for survival, or which typically nest in colonies of smaller sizes.

1.2 Mate choice

Mate choice is linked to fitness in both sexes (Jones and Hunter, 1993; Komars and Dhinsda, 1989; Partridge and Halliday, 1984; Petrie, 1983 a and b), but the interests of males and females in the choice and number of mates do not necessarily coincide. Within each species, the mating system can be viewed as the outcome of a conflict between male and female reproductive interests (Davies, 1991; Wittenberg and Tilson, 1980). Mate choice and the mating system are affected by sexual selection. This occurs when one sex is a limiting resource for the other sex, whose members compete for mates (Emlen and Oring, 1977). Males have the capacity to produce vast numbers of gametes and are thus not physiologically constrained to a limited number of offspring (Trivers, 1972; but see Chapter 5). The limiting factor for males is then the access to mates. Males can aim to increase their reproductive success by enticing or forcing more than one female into copulating with them. Unless a skewed sex ratio ensures that each male has sole access to several females to fertilize, males compete with each other for females (intrasexual selection) and guard their females from other potential suitors (mate guarding; see Birkhead and Møller, 1992).

The reproductive success of females on the other hand is thought to be limited by resources (Emlen and Oring, 1977), since they have only a few eggs which could be fertilized with few matings (e.g. Davies, 1991). They should therefore choose males that can provide either good resources (either in a good territory, or as paternal help), or 'good genes' to the offspring, or both. Females may actively select a fit male as a mate to sire her offspring (Intersexual Selection; e.g Harvey and Bradbury, 1991; Partridge and Halliday, 1984). Females may try to monopolize, and compete with each other for access to, high quality males (e.g. Hunter *et al*, 1993; Petrie, 1992 a; Veiga, 1992 and 1990; Petrie, 1983 a and b).

The main body of research on mate choice and sexual selection to date has focused on dimorphic species where only the male is ornamented or brightly coloured (Holder and Montgommery, 1993; Andersson, 1992; Götmark, 1992; Petrie, 1992 b; Zuk *et al*, 1992; Hedrick and Temeles, 1989; Brodsky, 1988; Anderson, 1982; see also reviews by Jennions, 1993; Harvey and Bradbury, 1991; Cherry, 1990; Järvi *et al*, 1987). Little work of mate choice has been done on monomorphic species with high level of pair cooperation, with the notable exception of Choudhury and Black (1994) and Choudhury *et al* (1992) who investigated assortative mating and mate choice in a monomorphic species with life-long pair-bond (Barnacle Geese *Branta leucopsis*), and Jones and Hunter (1993) research on the Crested Auklet *Aethia cristatella*, where both sexes are ornamented (the crest), is the first study to show experimentally not only that female Auklets actively chose males with a larger ornament, but also that males preferred females with a larger ornament. More work is needed on mutual mate choice and pair formation in monomorphic species to help understand the evolution of mating systems.

1.3 Mixed reproductive strategies

A further cost of social breeding is the risk of becoming a victim of intra-specific nest parasitism or of cuckoldry by extra-pair copulations (Møller and Birkhead, 1993; Petrie and Møller, 1991; Davies, 1988). Individuals lead variable lives according to their ability and circumstances. Each individual may have to choose between behaviours according to likely costs and benefits of the strategies supported by these behaviours. This can lead to mixed reproductive strategies either of individuals or (if some individuals practice one behaviour, and some follow a different strategy) at the population level. In preference to incubating her eggs and feeding her young herself, for example, a female may lay some or all of her eggs into the clutch of another female, if the cost of rearing each egg outweighs the risks entailed by the cuckoo (Yamauchie, 1993; Yom-Tov, 1980; Table 1.1). Colonial nesting increases the opportunity for such egg 'dumping' or intraspecific nest parasitism (e.g. Davies, 1988), but whether this is a benefit or a cost of coloniality depends on whether a bird 'dumps' eggs on conspecifics or whether it is a victim of egg 'dumping'. The same is true for the opportunity for extra-pair copulations (EPCs). In colonies, an increased number of conspecifics increases the number of potential partners and thus the opportunity for extra-pair copulations (Møller and Birkhead, 1993) and the potential for polygyny (Morton *et al*, 1989; Emlen and Oring, 1987; Fig. 1.1).

Observations and genetic evidence of EPCs or 'occasional polygyny' (Davies, 1991) in species that had previously been classed as strictly monogamous has been accumulating rapidly in the last 10 years (reviewed by Birkhead and Møller, 1992; Birkhead *et al*, 1987; Møller, 1986). With the use of genetic (or DNA) fingerprinting which has the power to identify illegitimate offspring within families, mixed reproductive strategies have been recognized as commonplace and are known to be an important strategy in many mating systems. High frequencies of extra-pair fertilizations (EPFs) have been emerging from genetic fingerprints in some species (e.g. Westneat, 1990; Morton *et al*, 1990), up to 65% of nestlings in Splendid Fairy-wrens *Malurus splendens*, for example (Brooker *et al*, 1990, as reviewed by Birkhead and Møller, 1992). Again, most studies of mixed reproductive strategies have focused on cuckoldry of males by other males, including a large body of literature on mate-guarding by males against being 'cuckolded' by other males; the subject is even termed 'sperm competition' (see review of Birkhead and Møller, 1992). Traditionally, EPCs have been viewed mainly as opportunistic polygyny where monogamous (or sometimes unpaired) males try to enhance their reproductive output through extra-pair offspring. In breeding colonies, the rôle left to the females seemed to have been a passive one, namely to control their partner's EPC attempts by breeding synchronously, which reduces the time-span during which fertile females are available (e.g. Emlen and Oring, 1987; Fig. 1.1), and during which the male's primary concern it is to guard the female and not to seek EPCs (Birkhead and Fletcher, 1992). Monogamy has thus been viewed as being forced on males by essentially female strategies.

More recently, however, evidence of females choosing extra-pair males to father some of their nestlings (which could perhaps be coined 'opportunistic polyandry'?), has been put forward (e.g. Kempenaers *et al*, 1992; see also Dunn *et al*, 1994, and for non-avian animals Hardy, 1994, and Madsen *et al*, 1992). More importantly, females have been shown to choose *not* to participate in EPCs (e.g. Mills, 1994; Birkhead and Møller, 1993; Björklund *et al*, 1992; Wagner, 1991), and, indeed, the most recent research suggests that female cooperation is probably needed in most species for successful copulations both within and outside the pair bond (e.g. Sheldon, 1994). In accordance with mutual mate choice, monogamy may be the best option also for the male. If EPC attempts are wasted effort for males and, at the same time, a high degree of cooperation between pair members improve fledgling success, monogamy is the best option for both partners and not just a female strategy imposed on uncooperative males for whom a better strategy would be to 'cheat' at every opportunity to increase their reproductive output. The view that males may increase their net reproductive output by concentrating their paternal care on pair-offspring is the interpretation of some of the most recent genetic and observational evidence of studies of long-lived altricial birds where parental help of the male is essential for fledging nestlings (in particular Mills, 1994; see also Decker *et al*, 1993). To conclude, the original proposition by Lack (1968), that most birds are monogamous probably because monogamy is beneficial for *both* pair-members, cannot be reconsidered without genetic evidence also from monomorphic altricial species in which both pair-members are expected to benefit from a monogamous mating systems.

Egg 'dumping', or intraspecific nest parasitism (INP), involves the deposition of one or more eggs into a nest of the same species by a female which is not the resident breeding female. It has been reported for many bird species (reviewed e.g. by Yamauchie, 1993; Davies, 1988; Evans, 1988; Yom-Tov, 1980). If a female can produce and lay more eggs than the number of eggs that can be raised successfully by laying or transferring eggs into the clutch of another pair, she could increase her reproductive output (Brown and Brown, 1988) or reduce the cost of parental care (Bulmer, 1984): several species with INP are altricial (Davies, 1991; Payne, 1977; Hamilton and Orians, 1965). Spreading eggs across different nests can insure against nest-failure in an unpredictable environment. Cliff Swallows seem to select superior neighbours as hosts: nest failure was lower in nests that contained transferred egg(s) than in those that did not (Brown and Brown, 1988). In many species, females known to 'dump' eggs have no nest or permanent mate, or are disrupted breeders (Pinxten *et al*, 1991 a; Evans, 1988; Yom-Tov, 1988; Emlen and Wrege, 1986; Andersson, 1984), or they have been fertilized by a male who is paired to a different female (Brown and Brown, 1991). This was possibly observed for White-fronted Bee-eaters *Merops bullockoides* (Emlen and Wrege, 1986). Egg dumping may be particularly frequent if nest sites are limited (Horn and Rubenstein, 1984). Research on mixed reproductive strategies has focused more on extra-pair offspring (EPO) than INP which has until recently been assumed by most studies to be a 'best-of-a-bad-job' strategy of failed breeders or, at best, to offset nest-failure (e.g. Yom-Tov, 1980). In the past few years, however, INP has emerged as a possible large cost of coloniality: high levels of INP sometimes lead to very high mortality of eggs (Wrege and Emlen, 1991). Recent work moreover suggests that INP may be part of a sophisticated mixed reproductive strategy in some birds, practised by breeding females who have their own nest, (Jackson, 1993; Lyon, 1993 a and b; see also Petrie and Møller, 1991).

1.4 Sibling competition

Finally, resource abundance affects the size of the breeding effort (Fig. 1.1), both proximately (i.e. if not enough food is available, success is reduced) and ultimately as a selective force. Clutch size depends on the availability of food: the optimal clutch size is that which maximizes the number of chicks that can be fledged without any of them being under-nourished (Partridge, 1992; Lack, 1954). If siblings compete for limited resources, and in species where the food supply is unpredictable or generally low, it may be adaptive for nestlings not only to beg to influence parental effort but to practice siblicide in order to sustain a satisfactory growth rate (Table 1.1). In these species, nestling aggression and siblicide should thus be favoured (O'Connor, 1978 a). Nestling hunger elicits fighting between nestlings (see review in O'Connor, 1978 a), and siblicidal behaviour is a common observation in pelicans, boobies, cranes, grebes, herons, gulls, owls and many species of raptors (Drummond and Chavelas, 1989; Sutherland, 1989; Evans and McMahon, 1987; Forbes and Ankney, 1987; Mock *et al*, 1987; Hahn, 1981; O'Connor, 1978 a), where it often results in obligate nestling mortality (Forbes and Yrdenberg, 1992; Edwards and Collopy, 1983; Stinson, 1979).

Nestling aggression may or may not be an adaptive strategy to aid brood reduction in conditions where broods are under food constraint. Few studies have concentrated on the proximal factors influencing siblicide, including Mock *et al* (1987) who established experimentally that the food amount has a proximate rôle in nestling aggressive behaviour. Drummond and Osorno (1992) showed that the place in the hierarchy influences nestling competition and that once a chick has adopted a dominance status, the outcome of agonistic interactions is predictable.

In smaller birds, hatching asynchronies are widespread, in particular in altricial species (e.g. Magrath, 1990 and 1989; Sutherland, 1989; Mead and Morton, 1985), but less well-known are the mechanisms of sibling competition and the rôle of food. Sibling aggression against co-nestlings and indeed siblicide may be much more widespread amongst birds with hatching asynchrony than is presently realized. Experimental evidence and observational data are lacking on the proximate factors affecting nestling aggression and on how food availability affects chick mortality. A notable exception is McRae *et al* (1993) who systematically observed nestling competitive behaviour (mainly begging and 'jostling' for a favourable position) of American Robins *Turdus migratorius*. Similar observations are needed of siblicide behaviour.

1.5 Bee-eaters

Social breeding provides each bird with a wide range of social contacts beyond the pair bond. This gives Barnacle Geese, for example, the chance to select the most compatible partner for a life-long pair-bond (Choudhury and Black, 1994). The opportunity for multiple social contacts has implications the study of which has produced some of the most interesting work in the field of behavioural ecology. This is nowhere more apparent than in the bee-eaters.

Bee-eaters (Meropidae) feed on large flying insects (e.g. Fry, 1984), which often are patchily distributed, are highly mobile and relatively unpredictable in time (Fry, 1984; Emlen, 1982 a; Dingle and Khamala, 1972). Bee-eaters are highly skilled hunters, catching insects while in flight, often by sallying from a perch. Their eyesight is well developed, and they can see insects flying past from a great distance (Fry, 1984). All species are brightly coloured and highly vocal, with contact calls, and even the more solitarily bee-eater species living in forests show gregarious behaviours and have a generally social habit (Fry, 1984). The species of Bee-eaters that have been studied extensively, like the European Bee-eater *Merops apiaster*, the White-fronted Bee-eater and the Red-throated Bee-eater *M. bullocki*, are colonial and nest in self-dug burrows along river-banks in the tropics (Emlen, 1990; Lessells, 1990; Dyer, 1983). White-fronted Bee-eaters live in closely-knit family units, sometimes called 'clans', and bee-eater family members hunt together and dig nests close to each-other (Lessells *et al*, 1993; Hegner *et al*, 1982; Hegner and Emlen, 1987). Bee-eaters are on the whole apparently monogamous, but colonial bee-eaters commonly recruit relatives as 'helpers-at-the-nest' (see below in this section). The three species of Bee-eaters mentioned above all live in highly seasonal, semi-arid African or Southern-European savanna type habitats, are all highly colonial and highly cooperative. European Bee-eaters are inter-continental migrants, whereas White-fronted and Red-throated Bee-eaters are sedentary (Fry, 1984).

Bee-eater food distribution is probably more even than for hirundines because their insect food is larger (Emlen, 1982 a). White-fronted Bee-eater nestlings are able to retard growth in times of food shortage (Emlen *et al*, 1991), so regularity of food supply is not as important as it is for breeding hirundines who are immediately vulnerable to variations in the food supply: they may interrupt laying after a day of bad weather (e.g. Alves, 1993). If bee-eaters depend less on the regularity of their food supply, then selection pressures that led to coloniality in hirundines are probably different from those shaping colonial breeding in Bee-eaters.

Bee-eaters lend themselves naturally to a study of mutual mate choice and pair formation. Not only is parental help of the male required, but in bee-eaters parental care often includes additional helpers who increase the reproductive output of the pair. Young birds reproduce less well (Curio, 19983). If the cost of breeding is thus too high in terms of the 'adult survival' component of fitness, an animal may defer breeding to a more advanced age (Table 1.1; Vehrenkamp and Bradbury, 1984), in particular if the breeding system is such that the animal can meanwhile increase its inclusive fitness by 'helping' close relatives in their breeding effort (Emlen, 1984). Cooperative breeding, where either parental care is provided by individuals additional to the breeding pair (helping) or breeding individuals raise their offspring communally, is reported for many animals (see Emlen, 1984; Owens and Owens, 1979; Rood, 1978, for example), especially for colonially nesting birds (see reviews by Emlen, 1984; Skutch, 1961). 'Helping-at-the-nest' is the provisioning, digging or nest-defence at any one burrow by any adult that is not a member of the breeding pair. Helpers are common in bee-eaters, such as the White-fronted Bee-eater (Emlen and Wrege, 1994; 1992; 1991; 1989; 1988; Emlen, 1982 a), the European Bee-eater (Jones *et al*, 1991; Lessells, 1990; Lessells and Krebs, 1989) and the Red-throated Bee-eater (Crick and Fry, 1986; Dyer, 1983; Crick *et al*, 1987)..

The details of the highly intricate social system of bee-eaters and their reproductive strategies have only very recently started to be unravelled with the advance of new analytical methods and tools such as DNA fingerprinting, in European Bee-eaters (Jones *et al*, 1991; see also Lessells *et al*, 1993) and optimal modelling of decision-making based on economic theory, in White-fronted Bee-eaters (Emlen, 1994; Emlen and Wrege, 1994).

1.6 Blue-throated Bee-eaters

Blue-throated Bee-eaters *Merops viridis* are monomorphic and apparently monogamous (e.g. Fry, 1984), but both sexes have elongated central streamers of variable length, which are a potential ornament. They are altricial and have helpers-at-the-nest (P.T. Green and D.M. Bryant, pers comm). In conjunction with a pronounced hatching asynchrony and high nestling mortality, Blue-throated Bee-eater nestlings have a mandibular 'hook' which is apparently used to inflict wounds on each other (Bryant and Tatner, 1990). They dig burrows nearly horizontally into flat ground, so their nests are easier to access than those of bee-eaters digging into sand cliffs, so that nestlings can be taken out regularly to monitor mass loss and growth rates. They are found in open country, but in contrast to the large colonies of bee-eaters found in the seasonal African and Southern European savannas introduced above, Blue-throated Bee-eaters live in relatively moderately sized colonies (topically 50-200 pairs) and can sometimes be found nesting solitarily. Coloniality in Blue-throated Bee-eaters is therefore not obligatory. They are neither sedentary nor do they migrate over long distances, but they migrate locally in South-east Asia and are the only breeding bird of Peninsula Malaya doing so (Medway and Wells, 1976). South-east Asia lacks the strong seasonality of the East-African savanna and Southern Europe. Although they are also open-country birds, Blue-throated Bee-eaters live in a less seasonal environment and have a slightly different ecological status from other open-country bee-eaters. This may be reflected in their breeding system, which has not been studied before in detail.

1.7 Thesis

Blue-throated Bee-eaters are particularly suitable for this study, which is concerned with the social behaviour of breeding birds. Little is known about costs and benefits shaping coloniality for birds nesting in moderate size colonies or for whom colonial nesting may be non-obligatory as in some hirundines. Mate choice has been under-studied in monomorphic species or species with ornaments in both sexes which might hold the key to a better understanding of the evolution of mating systems. This is particularly relevant in altricial species where parental help of the male is needed to improve the breeding success of both pair members. Altricial species often hatch asynchronously, setting the scene for a nestling size hierarchy to develop in which nestling competition might result in selective starving of the later-hatched runts. Details of this competition are not clear for birds with non-obligatory brood reduction, especially with respect to siblicide, for which Blue-throated Bee-eaters have apparently evolved a specialist weapon.

Such behaviours as might be employed by individuals, and the component of fitness they each affect, are the subject of this study of the Blue-throated Bee-eater. I aim to describe and quantify the behaviour of two populations of colonially breeding Blue-throated Bee-eaters by observation and experiment, in particular studying

(1) mixed reproductive strategies using DNA fingerprinting and

(2) nestling mortality due to starvation and siblicide.

Whenever I relate to other research work, the relevant literature is cited in reverse chronological order, and alphabetically within each year. Latin names of organisms are given at the first mention only. Abbreviations are explained at first mention and sometimes again thereafter. A list of abbreviations is found in Appendix 1.

Thesis structure

This chapter has related the background and set the context with respect to other work as well as summarized the aims of this study. The sites of the two study colonies in Peninsular Malaya are described in Chapter 2, where I also detail those methods which are applicable to more than one of the results chapters (Chapter 4-7). Each of these chapters has its own methods section detailing those methods which were used only to obtain the results presented in that chapter.

I developed a relational database and document its usefulness for data storage and manipulation in studies such as this (Chapter 3). Although commercial 'packages' are commonly used for specific designs for companies and projects, there is no current database design that could be easily adapted for data storage for studies of vertebrate behaviour and ecology. My work includes the first documentation of the design, implementation and use of such a database. Data storage and retrieval was therefore sometimes more time-consuming and more complex than necessary for the analysis, because it was imperative to manipulate most of my data in the database, both as a trial of the implemented database and for the documentation of its use.

In Chapter 4, the study species is introduced and the general breeding ecology, behaviour and environment (habitat, climate and weather) are described. Next, I examine pair behaviour in Blue-throated Bee-eaters, and the evidence for its adaptiveness to Bee-eater-specific life-style and environment, with particular emphasis on pair cooperation and behaviour relevant to the mating system (Chapter 5). These are investigated in the chronological order of the breeding season, starting with arrival and pair formation, through digging, to nestling provisioning. In Chapter 6, mixed reproductive strategies are examined further with DNA fingerprinting and an egg 'dumping' experiment to illuminate anti-egg-'dumping' behaviour. Finally, I investigate nestling growth and mortality and the role of sibling competition. I look in particular at behavioural and morphological adaptations and use both experiment and observation to investigate mechanisms of sibling competition (Chapter 7). The most important implications of my findings are discussed in the final chapter (Chapter 8).

CHAPTER 2 - STUDY SITES AND GENERAL METHODS

The study was conducted at two different colonies, the sites of which are introduced here. The methods relevant to the study in general are described in this chapter.

2.1 Study sites

The two study sites are situated on Peninsula Malaysia, at Sungai Buloh (SB) near Kuala Lumpur in the state of Selangor and on the Nam Heng Complex (NH) in South Johore, near the Johore capital Johore Bahru and Singapore (Fig. 2.1).

The Sungei Buloh colony had been an established colony for decades. The birds here were first studied by D.R. Wells and Lord Medway (the Earl of Cranbrook) in the 1960s. They are featured in Medway and Wells' (1976) account of the birds of Malaya (Medway and Wells, 1976). In the early 1980s, D.M. Bryant, C. Hails and P. Tatner conducted their studies at this colony. More recently, P.T. Green based his research at the Universiti Malaya on the Blue-throated Bee-eaters of Sungei Buloh. During the 1988 breeding season, he regularly captured breeding adults and wing-tagged most of the 400+ birds breeding there.

The main colony in the compound of the manager's residence at the Rubber Research Institute (RRI) consisted of about 2000m^2 of short-cropped, well-maintained 'lawn' surrounding the bungalow; the compound was very open except for a few solitary trees and telephone wires which were used as perches by the Bee-eaters (Fig. 2.2). Below about 10-20cm of top-soil, the substrate was sandy and well-drained. The compound was protected by a bamboo hedge and security guards. During later years, the garden was planted with some additional shrubs; at the same time, the mowing of the lawn became less regular. In the 1991 season, the management changed and the garden was neglected.

In 1989, SB was my only study site. Because the number of breeders at Sungei Buloh dropped dramatically at the beginning of the study, I progressively changed study sites to Nam Heng (below). In 1990, I conducted work at both colonies, but in 1991, there were less than 10 birds at the main colony at SB and I worked exclusively in Nam Heng.

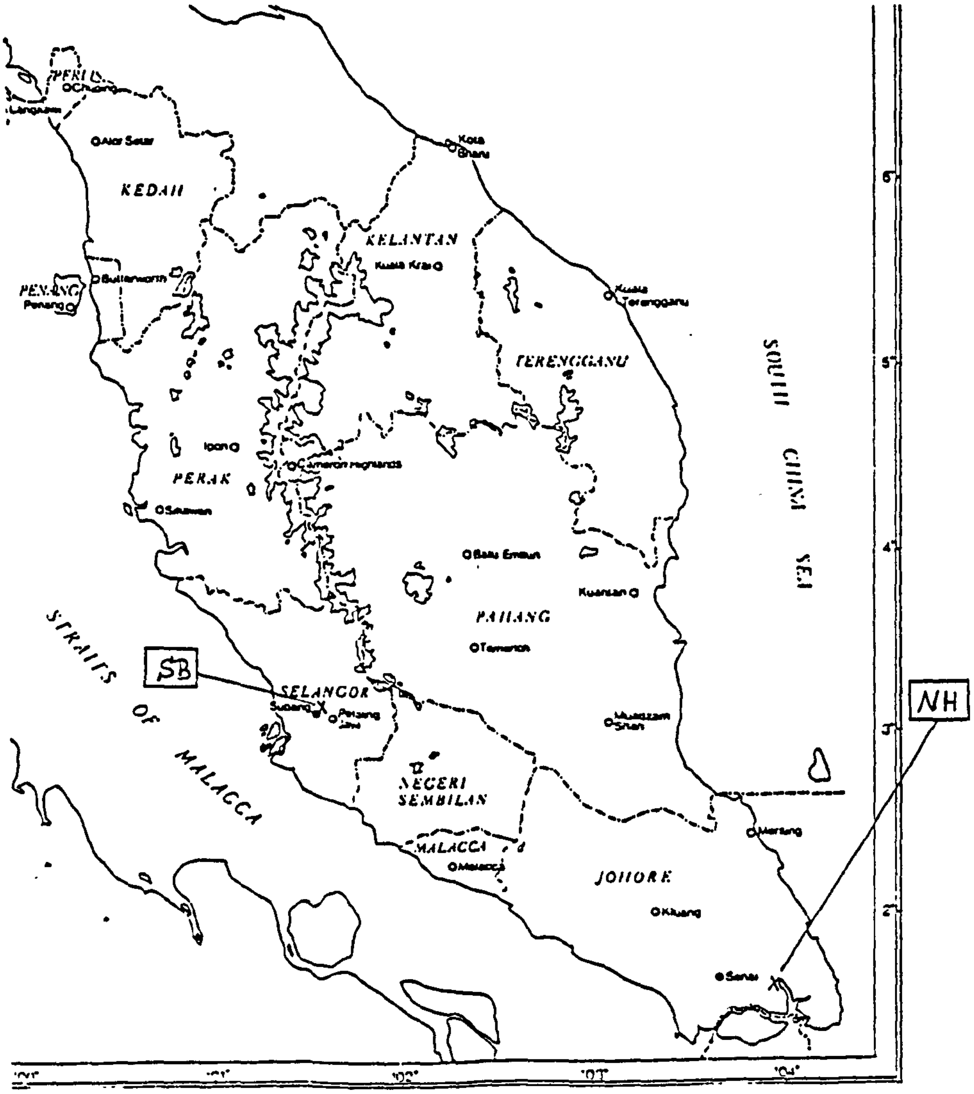


Figure 2.1: Map of the Peninsula Malaysia, with the two study sites, SB and NH. 2,000,000 : 1

Figure 2.2: The study site at Sungei Buloh (SB), Selangor, in the Rubber Research Institute (RRI). The main colony site was located in the manager's compound. The lawn was cut regularly once per month, a telephone wire and single bushes or trees provided perches for Bee-eaters, and the compound was surrounded by a hedge.

The Nam Heng colony (NH) was situated on part of a golf-course in the heart of a large oil-palm estate, the Nam Heng Complex, immediately adjacent to the Johore River, and lined with mangroves (Fig. 2.3). On the opposite side of the colony lies the estate manager's bungalow. Both study colonies are thus effectively protected from access by the general public by the security that is extended to estate managers' compounds. NH was a well-established breeding colony (R. McLane, pers comm) similar to Sungei Buloh, but was very secluded and was only brought to our attention in June 1989 by a letter from the manager of the Nam Heng Complex.

In NH, the birds burrowed into a slightly sloping piece of 'lawn', again regularly mowed, with sandy soil beneath a 10-20cm layer of earth. Trees and telephone-wires surrounded the colony and were used as perches by the birds. Visibility here was extremely good, with no obstructions to the scanning eye.

The study colonies Sungei Buloh and Nam Heng in different years are referred to as colony-years, which are abbreviated to SB89, SB90, SB91, NH90 and NH91. (For a listing of abbreviations, names and variables see Appendix 1). The main colony was sub-divided by natural landmarks into 'sub-colonies', and these into 'sub-locations' which could be scanned comfortably during behavioural observations.

2.2 Behavioural observations

Recording of behavioural observations should be carried out according to rules that define which individuals and times are selected for observation (e.g. Martin and Bateson, 1986). I therefore conducted preliminary observations at the beginning of the first field season, during which I selected suitable sampling and recording strategies. During preliminary observations, I found that the activities of adult Blue-throated Bee-eaters at the colony were concentrated on the site of the main colony, where most birds present could be clearly seen. Birds spent long intervals sitting on clearly visible perches so that they could be identified with a telescope (Fig. 2.4). Only a few tagged birds were usually present at the main colony at any one time, mostly between none and 5 and rarely more than 10. Each individual tended to use the same one or two favourite perches, and once these were identified by the observer, the

Figure 2.3: The study site at Nam Heng (NH), Johore, on the golf-course of the Nam Heng Complex, essentially a palm-oil plantation. Adjacent to the colony site is Johore River (Sungei Johore) with its mangrove islands. The lawn was mown and perches were provided by trees and telephone wires.

<u>Figure 2.4</u>: Observations were carried out from a car using a telescope to read wing-tags. Sungei Buloh study site.

behaviour of all marked birds at any one sub-colony could be observed more or less simultaneously. The behaviour of marked adults (marking methods are described later) was recorded according to which types of records provide the best trade-off between detail and completeness of records. This depends both on the specific circumstances at the study colony and on the questions asked. During each observation period, I decided to aim for observations to be as continuous as possible, but to keep records of observations flexible so that they could be used in different combinations so as to answer different types of questions. In the following, I discuss the types of recordings made and their assumptions and describe the central unit of observation I chose.

2.2.1 Continuous observations and scans

Continuous observations commenced soon after arrival at a particular sub-colony and were ended usually before the onset of observer fatigue (see section 2.2.3). I usually aimed at between 1 and 2 hours of observations, both to include rarer behaviours like sexual interactions and so as to be able to calculate rates, of visits to broods, for example. Sub-locations for observations were chosen to provide a comfortable field of view, so that all nests and perches could be seen by the observer without the turning of the head.

To obtain a complete record of all birds present at the sub-colony, scans were conducted. Scans, as defined in Altman (1974) as 'instantaneous sampling of groups', were made by a second observer, or outside the continuous observation periods. In a scan, the observer started noting birds present at the same end of the sub-colony each time, completing the scan in as short a time as possible (1-5 minutes). Scans record how many of all birds present are tagged or carry food. In general, bird numbers were low enough to guarantee completeness of records within one-minute intervals (see above), but occasionally too many birds were around, so that some may have been included twice and some missed out because they moved. To avoid such double-counting, I concentrated in those cases on scans of the presence of individuals.

2.2.2 Sightings

Within continuous observations, the central unit of observation was 'sightings' of focal birds. Focal birds for any one sighting were defined as being either:

(a) of a known identity (tagged), or

(b) at a marked nest, or

(c) associated with (within one bird-length of) a marked bird, or

(d) engaged in an interaction with another Blue-throated Bee-eater, or

(e) tail-flickering (see Chapter 4).

Apart from the identity of the focal bird and its behaviour (activity), for each sighting I also noted perch-location and whether the focal bird carried or manipulated food (in which case the insect was identified as closely as possible and its relative size noted). The focal bird could be close to one or more associates whose identities were also noted.

Martin and Bateson (1986) argue that the accuracy of records requires as short an interval between observations as possible, but that the observer error increases with short intervals. I decided that one-minute sightings at roughly 5-minute intervals provide a compromise, with relatively short intervals that still allow the appropriate detail to be recorded comfortably.

During 'continuous observations' at any one sub-colony (see 2.2.1), sightings for all birds with the above specifications were included to split continuous observations into instantaneous samples of behavioural recording. Each focal bird was watched for up to one minute, in a scan of 'instantaneous sampling' (Altman, 1974). In 'instantaneous sampling', synchrony of records is assumed (Altman, 1974). Thus, instead of recording the time of a sighting for all focal birds present during each scan of one-minute sightings (e.g. first sighting of focal bird 1 at 10:30, of focal bird 2 at 10:31, bird 3 at 10:32; second sighting of bird 1 at 10:35, bird 2 at 10:36 and of bird 3 at 10:37 etc), the sightings for each focal bird were recorded as if they were observed in the *same* minute, for each complete scan once in about every five minutes during 'continuous observations' (e.g. first sighting of focal bird 1 at 10:30, of bird 2 at 10:30 and bird 3 at 10:30, second sighting of bird 1 at 10:35, of bird 2 at 10:35 and of bird 3 at 10:35). The term 'continuous observation' thus refers to the state of observations for the observer and should not be confused with 'continuous recording' as termed e.g. by Martin and Bateson (1986), which refers to collection of consecutive data points. Continuous observations are closely equivalent to 'instantaneous sampling' in continuous scans.

Behaviours like 'eating' or a bout of 'tail flickering' were often much shorter than one minute. If more than one behaviour occurred during any one sighting, then I noted either (a) all behaviours or (b) the rarer behaviour. For example, if the bird was mostly sitting on the wire (most common behaviour) but preening (less common) for some of the time (at least about 10 seconds), only preening was recorded, but if it was preening and eating, or bashing an insect and then eating it, both behaviours were recorded. If, as was the case very occasionally, a bird performed more than two behaviours in any one minute sighting, then the two rarest were recorded. If sightings were to be translated into real time therefore, durations of common behaviours would be under-estimated and durations of rarer behaviours over-estimated, and I therefore did not calculate the duration of any one behaviour. For any sexual interaction observed, the sexes as displayed were recorded, and for any agonistic interaction the identity of an 'attacker' and 'attacked', who 'won' and the perch owner previous to the interaction were noted. These recordings were made whenever I saw an interaction and were therefore not used to calculate absolute frequencies or rates (see e.g. Altman, 1974).

2.2.3 Sources of error for analysis and interpretation of observations

A potential source of error is that scans and continuous observations assume that observations were complete, i.e. that all birds in the sub-colony falling into the definitions were recorded. Scans and continuous observations may not always be complete for any of the following reasons:

(a) observer fatigue

(b) some birds aim not to be seen by potential predators (e.g. when flying off directly when emerging from a nest) and such behaviour is therefore easily missed; if birds behave towards the observer as a potential predator, this may be particularly the case where the observer is positioned close to the birds.

(c) Observations may be generally less complete if birds are far from the observer, since birds closeby are generally easier to notice and observe.

According to Altman (1974), the onset or the end of a particular observation period may not be biased depending on consciousness of behaviours or characteristics of the birds themselves. Behaviours recorded during such biased observation periods cannot be used for quantitative assessment. In this study, the selection of observation periods and scanning times was *ad libitum*. We cannot be certain that selection of observation periods was unbiased. For example, if scans were made mostly when bird numbers were high, then behaviours that are performed at high bird densities (e.g. interactions) might be over-represented in scans. If a conspicuous behaviour by a bird with a bright tag was more likely to trigger an observation period, then conspicuous behaviour for birds which were newly tagged in May 1989 (when I used the brightest tags, orange) could have been over-estimated.

On the whole in this study I do not think that serious bias was introduced for the following reasons:

1. Quantitative assessments in this study rarely involved absolute rates or frequencies, other than very general feeding rates which would probably be under-estimated with any sampling method. Instead, my data were used to compare behaviours between different circumstances, such as association between pair members in different seasons, in which case only relative quantity differences over different seasons are used.

2. Whether a bird was included in an observation or not depended on entirely pre-defined concepts, i.e. whether it had a tag or was at a nest, and whether or not it was involved in conspicuous behaviour. Sightings were consciously biased *for* conspicuous behaviour (like interactions and association), and the results were interpreted accordingly.

3. I usually started an observation period 3-5 minutes after I arrived, as soon as field book, binoculars and telescope were in place, regardless of what was going on at the colony. Observations finished after 1-2 hours, depending on fatigue. Observer alertness, however, may have depended on temperature and humidity.

In addition to continuous observations where nest feeding visits may have been missed, focal nest watches were made with a telescope. Not only were these exceedingly difficult to maintain, but I doubt whether they produced more reliable rates. This is because birds moved into burrows very swiftly and inconspicuously, and movement is more easily missed in a narrow field of view than when it covers the entire sub-colony, when each bird can be observed and anticipated to swoop down from a perch nearby, which is usually seen quite easily.

2.3 Breeding biology

To obtain general information on breeding stage and success, nests were examined regularly. The methods employed are given below.

2.3.1 Accessing and monitoring of nest

Blue-throated Bee-eaters lay their eggs into underground nest chambers found to be about 0.3-0.7m deep at the end of tunnels 0.9-2.1m long which they burrow themselves at the beginning of the season (Fig. 2.5; see methods in this section). Initially, efforts were made to use a specially built optical scope to examine the content of Blue-throated Bee-eater nests without digging into the nests. The burrows were not straight, however, and there were problems with lighting, so that I eventually abandoned this approach. Thus each nest had to be dug up and re-sealed for monitoring its contents, with minimum disturbance to the broods inside. Nest chambers were entered from the back through a pit of 30-50cm in diameter which was dug into the soil behind the nest chamber (Fig. 2.5). The location of the back of the nest chamber was estimated by carefully inserting a palm-leaf base into the burrow entrance right through to the other end of the nest chamber, which gave an indication of how long the tunnel was and the direction of curvature. After digging the pit, one person made a tapping noise with the palm leaf base against the back of the chamber from inside the burrow, while the other person listened for a hollow sound in the pit-wall with a stethoscope. Having located the sound, a careful incision (of less than 10cm in diameter) could be made to reveal the nest-chamber without any damage to its contents. After each inspection, the incision to the nest chamber was re-sealed with a curved piece of plastic wash-up bowl, and most of the soil was filled back into the pit. The initial entry into a nest took about 10 to 20 minutes, depending on the shape and length of the tunnel, and each subsequent visit took less than 10 minutes.

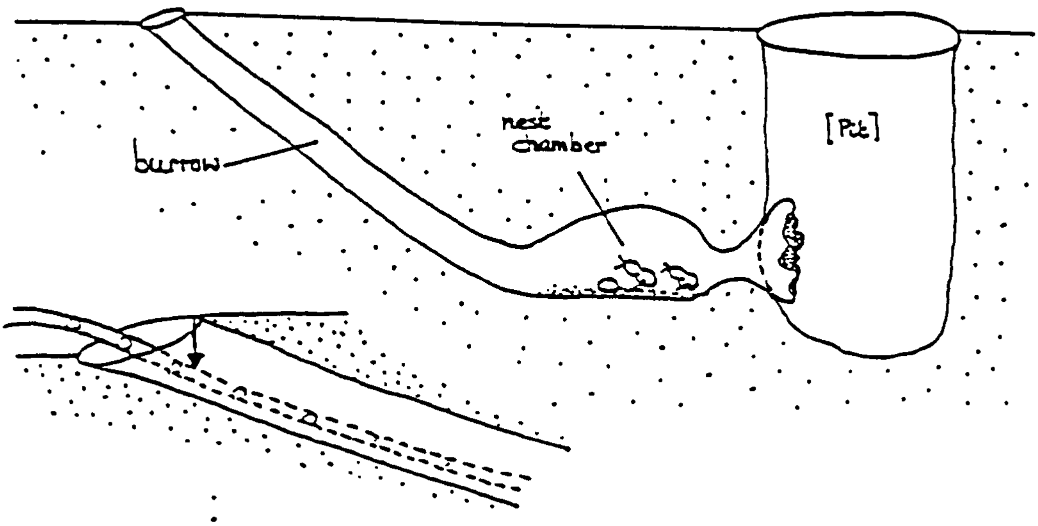


Figure 2.5: Diagram of a Bee-eater burrow, dug by the birds. At the end is a nest chamber with fine, loose sand at the bottom where the eggs are laid. Inset: burrow length was measured against the top ridge of the burrow entrance. Burrows were entered through the back by digging a pit of 30-50cm diameter behind the estimated location of the nest chamber. The hole in the nest chamber was sealed with a piece of plastic wash-up bowl and the pit re-filled with sand between inspections.

Nests were visited once every 2 or 3 days for regular monitoring, but during the first breeding season, many nests were dug only once or twice during the whole season. The very first nest we dug had eggs and was deserted subsequently, so that in 1989 I expected desertions if nests were dug before hatching. This did not happen in practice during the early season in 1990.

2.3.2 Measuring burrow length

Burrow length was measured with a plastic hose-pipe marked every 5 cm which was inserted into the burrow until the end or nest chamber had been reached. The hose-pipe was allowed to 'curl' around the nest-chamber for an additional 10-15cm, until there was a reasonable amount of resistance, without squashing anything inside the chamber (eggs or chicks) that might be in its way. The reading of hose-pipe length at a standard level (the top ridge of the burrow entrance, Fig. 2.5) was taken as the length of the burrow, including any 'curling' in the nest-chamber. Burrows were measured every 2-4 days during the digging phase until several similar measurements indicated that the nest chamber had been excavated and the burrow had been completed.

2.3.3 Determination of nest contents

Each time a nest was visited, its contents was noted as: number of live chicks, number of dead chicks with an estimate of how long ago the chick(s) perished and comments, number of eggs, number of addled eggs (coloured off-white and smelling bad, or damaged). Comments were also recorded, including the clutch temperature (see Chapter 5), whether a brooding adults had been disturbed, and any un-eaten food items.

The fate of a brood can usually be inferred as follows:

1. Breeding success in terms of numbers of chicks fledged could only be determined for those nests that had been regularly monitored during the later part of the nestling period. Chicks of near-fledging-age at the last visit (fully feathered and mobile) that went missing without trace (no evidence of dead chicks in the nest) were assumed to have fledged. Some of these were seen at the colony at a later date, but most did not spend much time at the colony, so

that their fate could not be confirmed but had to be assumed. For nests in which chicks were not of near-fledging-age at our last visit, no success rate was noted.

2. Eggs which did not hatch were either addled, predated or expelled. The term addled refers to an egg that was either broken before hatching or rotting (see above) but does not distinguish between infertile eggs and those with embryos.

3. If all chicks died in the nest in quick succession, the parents were assumed to have deserted the nest (uncommon).

4. If the whole clutch of eggs or brood of chicks was missing without trace from one nest visit to the next and without any evidence of expelled eggs nearby, the nest was assumed to be 'predated'. Although most nestlings probably died of starvation and part of their corpse was found later, they sometimes decomposed within days, so that the fate of unaccounted nestlings could not be clearly established in all cases. Predation on part clutches or part broods could therefore not be clearly established although unaccounted nestlings were rare and the rate of part-clutch or part-brood predation was probably low.

2.4 Catching and processing

Adults and nestlings were regularly handled, ringed and measured. Different characteristics were measured for nestlings and adults respectively, and, because they grow, nestlings were measured more frequently. Adults were marked individually for identification in the field. The methods used for trapping, handling, measuring and marking of birds are detailed in this section.

2.4.1 Catching and handling of adults

Three methods were used to catch adult birds:

1. Breeding Blue-throated Bee-eaters usually sleep in their burrows, and sleeping in a burrow associates birds with nests for recording purposes. Adults were usually caught at their burrows

with a net-trap which consisted of a piece of mist-net attached to a metal frame (Fig. 2.6 a). The centre of the net was suspended from a metal hook. The contraption was placed over the burrow entrance and pegged down, with the hook out of sight from within the burrow, usually late at night or before dawn, to catch adults after sleeping in the burrow. The birds were trapped in the net when leaving the burrow. Many birds sleeping in the burrow were not captured unless they left the burrow in the first 2h after dawn, because nets were taken down early so as to minimize disturbance. Occasionally, birds were caught during the day, for example, when entering their nest during incubation. If the bird stayed in the burrow for about 10 seconds or longer, the net was placed over the burrow exit while the bird was inside the burrow.

2. During digging, I sometimes used a 'decoy loop' to try to trap adults (Fig. 2.6 b), which is a locally made bird trap consisting of a series of about 30 small loops of green nylon fishing line connected to each-other and each attached to a small bamboo peg which is inserted into the soil. The loops are virtually invisible when pegged-out, except for the roll on which they are stored (see Fig.). The bird steps into one of the loops which tighten when it tries to step out again, usually catching the bird by its leg. This method is very work-intensive and was only used to catch birds which did not roost in their burrows. In practice, only one bird was actually caught with this method, while trying to enter its burrow.

3. During the first field season, I tried mist-netting to catch birds before they started roosting in the burrows, but since the colony sites had no canopy within which to conceal the nets, the birds were using the mist-nets as perches and only occasionally flew into the net. During the early season, disturbances might further cause desertion, so I abandoned mist-netting.

Birds were extracted from nets within a few minutes of becoming trapped and immediately transferred to clean, 20x30 cm 'bird bags' to avoid stressing the birds, for 5 minutes to about 2 hours awaiting processing. Altogether, 3 adults died while in the net or during processing. One bird died during processing as a direct result of handling; once a net-trap was mistakenly left on a nest which was thought to have been deserted and a bird was trapped and died, and once a bird died in the net immediately after being trapped, for no apparent reason other than exhaustion and probably not as a direct result of capture (see Chapter 5).

Figure 2.6: Two methods of capturing adults. (A) net-trap: a piece of mist-net attached to a metal ring is suspended on a metal support and pegged over the burrow exit. The bird is caught when it attempts to leave the nest. (B) The 'decoy loop' (see text). When pegged-out, the 30 or so loops are as good as invisible in the grass, only the contraption on which the loops are hooked when not in use is seen here.

2.4.2 Measurements of adults and chicks

Each time an adult was captured or a chick was taken out of its nest, measurements were taken. Chicks grow and were therefore measured each time, but for adults, size measurements which were not expected to change were only taken once per season. Some measurements were taken for both chicks and adults, whereas some were unique for adults or unique for chicks. Measurements were generally taken as described in the BTO Ringer's Manual (Spencer, 1984) and similar P.T. Green's measurements for the SB colony in 1986-1988 (pers comm), so as to be able to compare measurements after correcting for ringer. In addition, birds were bled (Chapter 6), usually the first time they were captured, but occasionally not enough blood had been taken and they were bled again at a subsequent capture. Chicks were bled when they were about 1 week or older because younger chicks cannot be bled easily.

In the following, I describe the different measurements of adults and nestlings, starting with those that were taken for both adults and nestlings, followed by measurements taken only of adults and finally measurements taken only of nestlings. Each measurement is listed under the name it was referred to during the recording of the measurements.

Measurements of both adults and chicks

BILL: bill length to the nearest 0.1mm in mm from the end of the nostril to the tip of bill, measured with dial callipers using the *side* of the calliper tips.

BW: bill width in mm to the nearest 0.1mm at the outer nostril, measured by sliding the callipers from the bill tip towards the skull, stopping at the outer edge of the nostril and pushing close until the callipers just begin to 'stick' slightly.

COND1 (condition): qualitative thickness of the pectoral muscle. Scored from 0 to 5 at integer intervals (see Fig. 2.7). 0 = nearly no pectoral muscle, 1 = muscle concave on either side of keel, 2 = muscle slightly below level with keel, 3 = muscle and keel level, 4 = muscle slightly convex on either side of keel, 5 = thick muscle, convex on either side of keel.

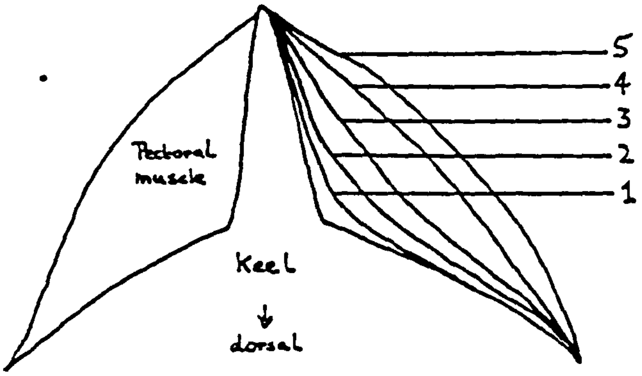


Figure 2.7: Scoring condition by assessing the thickness of the pectoral muscle.

Eyes: colour of eyes. R (red), LR (light-red), B (brown), BR (brown-red) or RB (red-brown).

HB: head-and-bill length in mm to the nearest 0.5mm, measured by sliding one tip of the callipers along the nape until it rested against the back of the skull, then sliding the other calliper tip down the crown and forehead of the bent head to the bill tip, taking the measurement as the calliper tip slid off the bill tip.

KEEL: keel length in mm to the nearest 0.1mm. This measurement is particularly affected by slight variations in the amount of pressure applied to the callipers. Therefore, the mean of two successive measurements was taken. Nestling keel length was not measured in their first week after hatching, because the keel is too soft for a reliable measurement.

Mass: mass of adult in g. Measured to the nearest 0.1g by constraining the bird in a plastic cone weighing 0.5g (this mass was subtracted from the bird mass noted) and clipping the bag to a 'Pesola' balance.

Mites: infestation with feather mites. Scored as follows with increasing infestation: none, 1 egg, 1 adult, few eggs, few adults, few eggs and adults, medium eggs, medium adults, many eggs, many eggs and adults.

TAIL: tail length without streamers in mm to the nearest 0.5mm. The distance from the root of the tail to the tip of the longest tail feathers, excluding the central streamers, was measured with an 'unstopped ruler' which was slid under the tail until it rested against the root of the tail (see Ringer's Manual, 7.4.e).

TARSUS: length of the tarso-metatarsal bone in mm to the nearest 0.1mm, taken by resting one calliper tip behind the depression of the intertarsal joint and then sliding the other calliper tip along the bent tarsus to the base of the last complete scale of the bent toe joint (see Ringer's Manual 7.4.d and fig. 22 f therein).

WING: Wing length in mm to the nearest 0.5mm. A 'stopped ruler' (see e.g. Spencer, 1984) was slipped under the naturally flexed, unspread wing which was then flattened against the ruler, with pressure on the coverts and straightening the bastard wing (Spencer, 1984), to remove all curvature, and with out-stretched primaries. The longest primary was measured. This measurement corresponds to that described in the Ringer's Manual 7.4.b.iii and is described there in great detail (Spencer, 1984).

Measurements of adults only

BRIGHT: strength of throat colour and contrast from green to blue. Scored from 'not bright' (very faint coloration and nearly no contrast between blue and green of throat; Fig. 2.9 a), 'not to medium bright' (little contrast, slightly less faint colour), 'medium bright' (medium contrast and medium strong colour, sometimes light-green and light-blue), 'medium to bright' (more contrast and stronger colour; Fig. 2.9 b), 'bright' (deep green and blue coloration and strong contrast, usually not very light green and blue) to 'very bright' (exceptionally deep coloration and contrast). For analysis, these scores were converted to integer steps (0 to 5).

BROWN: extent of brown on crown, nape and down the mantle. Scored from 1 to 5 at integer intervals. 1 and 2: not extending far down the mantle, barely reaching folded wings (see Fig. 2.8 a); 3: extending to wings (see Fig. 2.8 b); 4: extending down the mantle slightly over the folded wing; 5: extending well over the folded wing.

Cloaca: size of cloaca when captured may help to sex birds or may indicate if birds have copulated or laid an egg recently. In the last field season, cloaca size was noted before the birds were placed in the 'bird-bag' until processing, because we noticed that cloaca size changed sometimes after capture and prior to processing. Scored in integer intervals, 0 to 5. 0: cloaca small and round (pin-head size); 5: cloaca swollen with an oval opening (see Spencer, 1984).

GREEN: amount of green feathers on the crown. Scored 0 to 5 at integer intervals. 0: no green feathers amongst brown on the crown; 1: a few green feathers; 2: more than 5 green feathers; 3: about one-quarter green feathers; 4: half of feathers are green; 5: all feathers on crown are green (fledgling coloration).

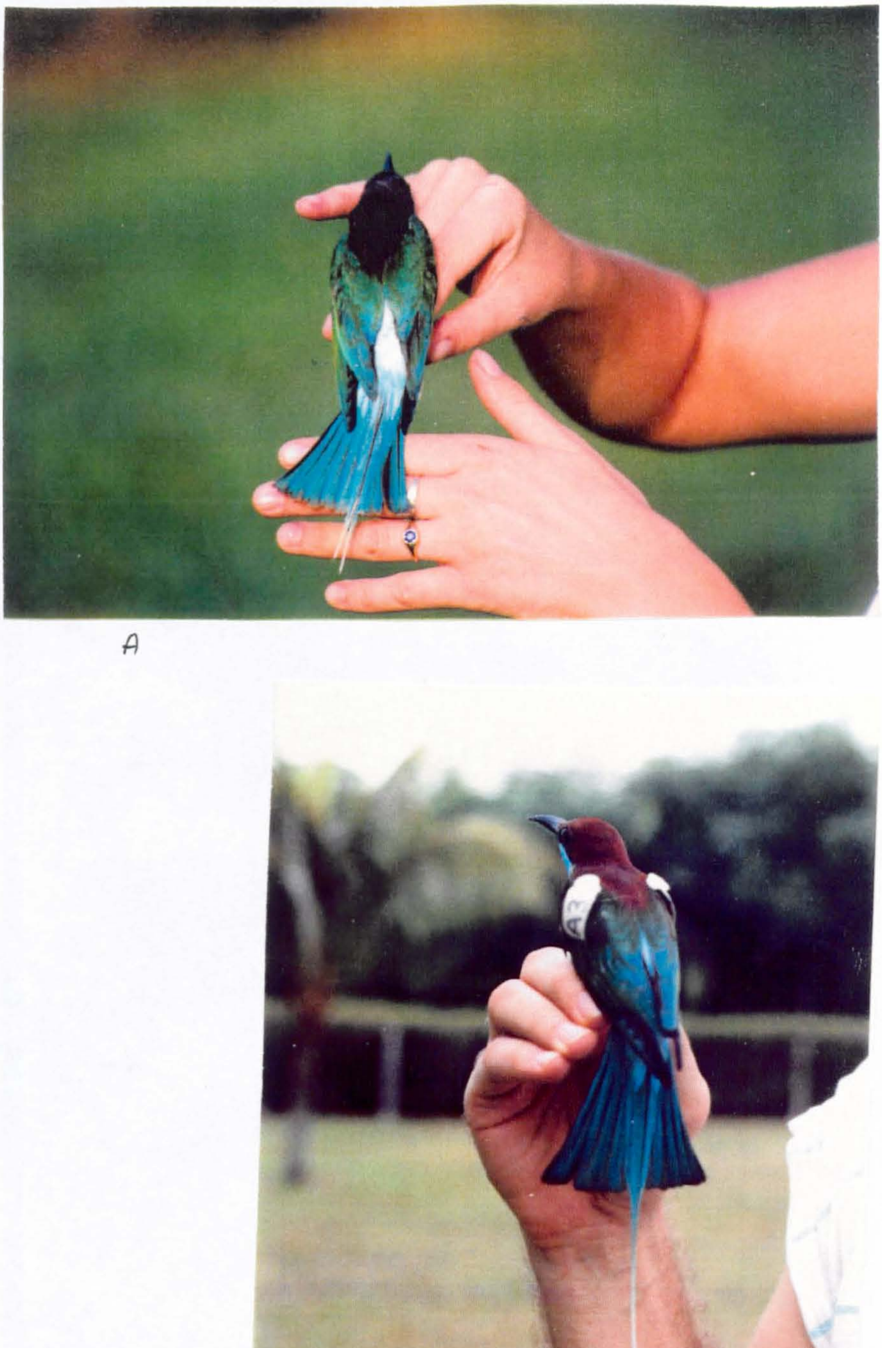


Figure 2.8: Two examples of the extent of brown on the nape and of streamer condition (IA): the bird in (A) has a score for BROWN of 2 and abraded streamers, the bird in (B) has BROWN score 3 and intact streamers with tassels.

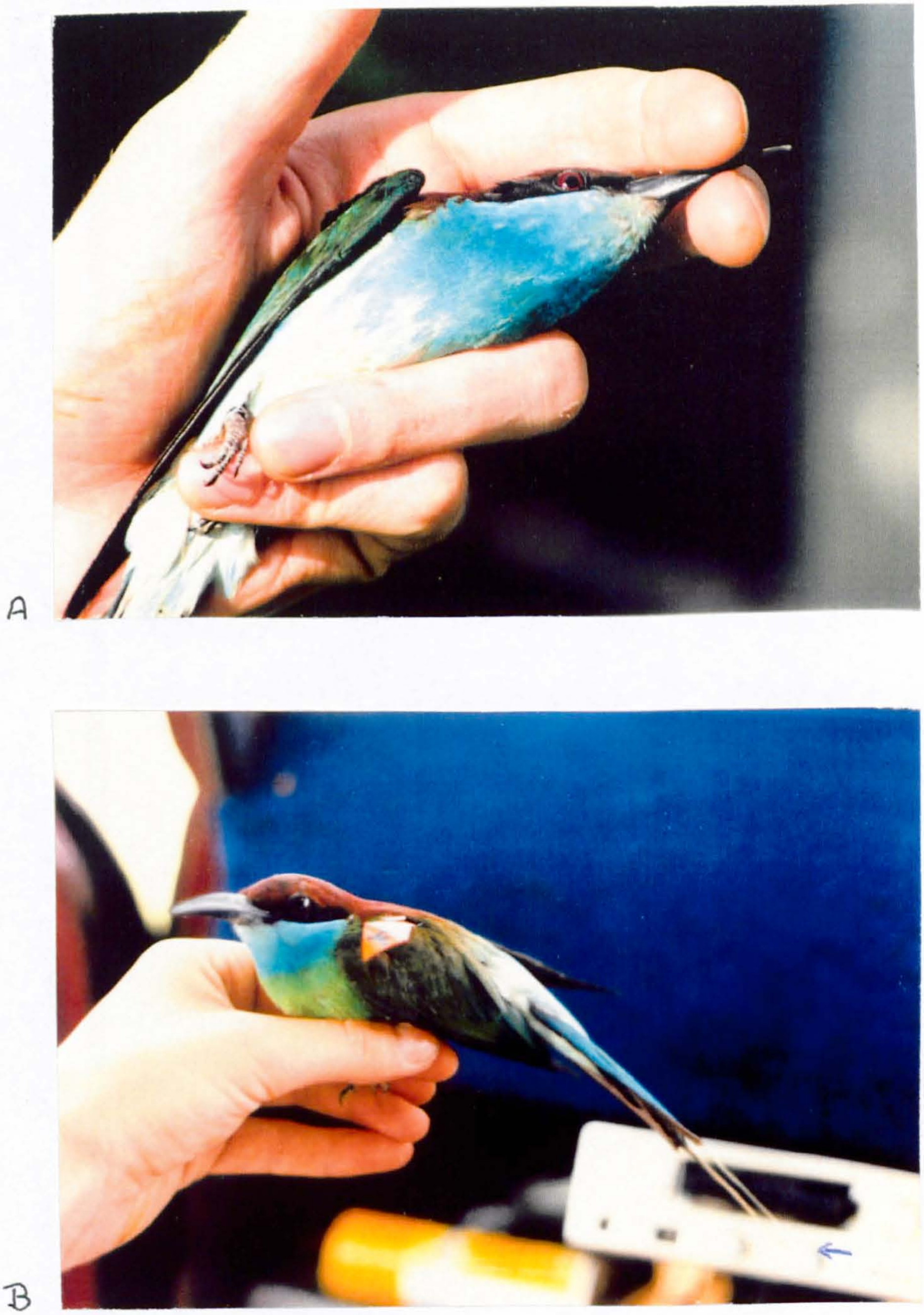


Figure 2.9: **Throat colour intensity and contrast of green and blue: the bird in (A) has dull coloration and nearly no contrast in colour, BRIGHT = not-bright. The bird in (B) has bright coloration and quite strong contrast, BRIGHT = medium-bright to quite bright.**

Head: abrasion of head feathers, recorded as integers from 0 to 5. 0: no abrasion; 1: very little abrasion; 2: moderate abrasion; 3: medium abrasion (Fig. 2.10); 4: more than medium abrasion; 5: very abraded.

IA: condition of streamers: intact with tassels (I; Fig. 2.8 b), abraded (A; Fig. 2.8 a) or newly grown after moult (N). Only intact streamers have the original length.

Ovary: qualitative extent of abdomen, indicating swelling of the ovary and oviduct, scored from -5 to 5 in integer intervals. -5 = 'stretch marks' (see Spencer, 1984), 0 = flat, 5 = egg palpated.

TS: Tail plus streamers in mm, to the nearest 0.5mm. From the root of the tail to the tip of the central streamers, measured with an unstopped ruler which was slid under the tail until it rested against the root of the tail.

Measurements of chicks only

Abdomen: extent of abdomen. Scores: 'empty' if flat and with no food; 'yolk' if 0-2 days old and not yet fed, 'bulge' if extremely taut, 'full' if moderately replete.

Hook: presence and sharpness of the mandibular hook, scored as 0-5 in integer steps: 0 = no hook, 1 = hook present but not sharp (soft or very blunt), 2 = hook present, but not sharp, 3 = hook sharp, 4 = hook very sharp, 5 = hook unusually large and very sharp.

Pins: qualitative extent of feather sheaths, from the naked chick to fully feathered: no sheaths, some sheaths out, all out, some feathers, most sheaths visible, some visible, fully feathered and no sheaths visible.

TF: The length that the tail feathers extend out of their sheaths, in mm to the nearest 0.5mm.

Wounds: total number of scabs and wounds, as visible on naked or near-naked chicks during the first week after hatching.

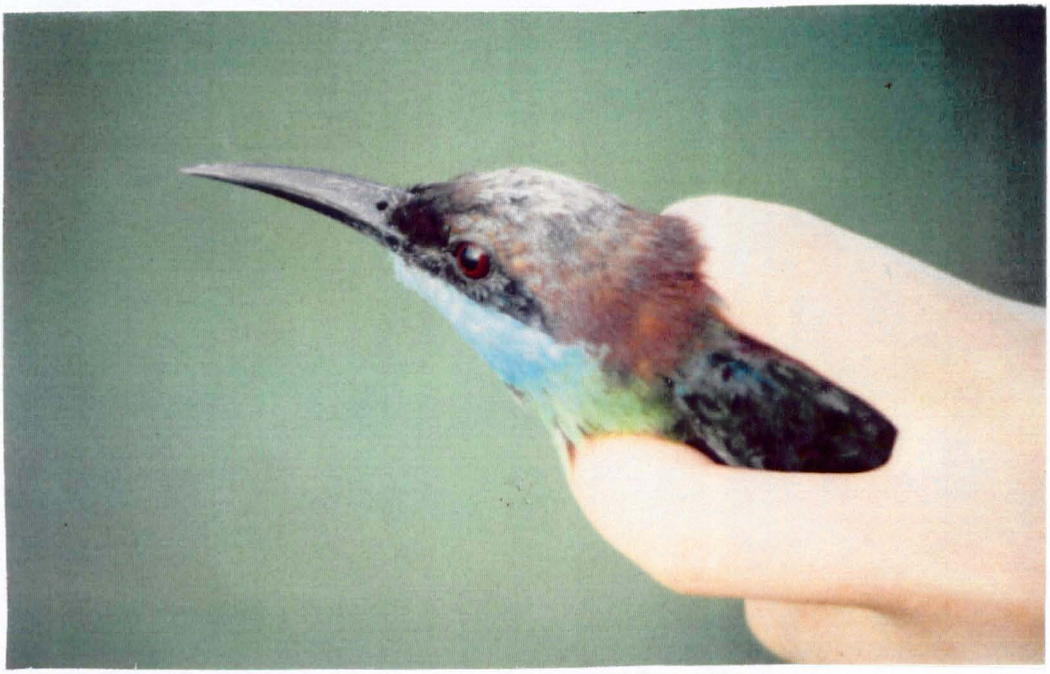


Figure 2.10: Abrasion of the feathers on the crown due to digging, scored as 'Head', between 0 and 5. This bird had a score for Head = 3 (quite abraded).

2.4.3 Individual marking of adults

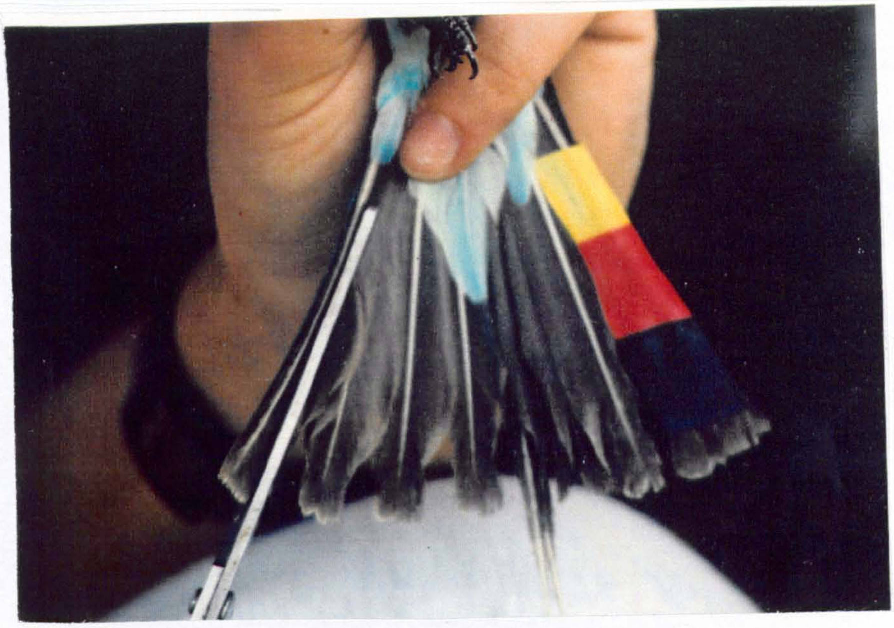
Bee-eaters have very short legs so that the traditional colour rings for marking adults individually are not visible in the field and were therefore not suitable here. Several alternative marking methods were tried successfully in other studies of Bee-eaters, such as body harnesses designed to last over more than one season (H. Crick, pers comm; Crick and Fry, 1987). Lessells and co-workers used acrylic paints applied to the tail feathers (C.M. Lessells, pers comm). In this study, I used several methods:

1. The marking method that had been used on the Blue-throated Bee-eaters of SB previous to this study were patagial wing-tags of thin UV-fade-resistant plastic (Fig. 2.11). This method provided the most durable marks, the only ones that might last from one season to the next and was therefore the only means with which pre-nesting observations of individuals could be made. Colour fading between seasons was minimal because the colours were UV light resistant. I also tested this resistance by keeping identical sets of strips of tag material for each colour (1) continuously in full sun-shine outside and (2) wrapped-up indoors during one complete breeding season. No colour change due to exposure was detected 6 months later. Colours on tags from the previous season could therefore be identified usually without error. There was the possibility of a detrimental effect of patagial wing-tags on survival or breeding success (which is investigated in Chapter 4), so that alternative methods had to be explored.

2. Another method of marking used was non-toxic paint applied to the head or nape or, on a few occasions, Tippex painted on the head, sometimes in conjunction with other methods. The paint and Tippex wore off after about 3 weeks so that it had to be renewed frequently which was not always possible.

3. I also used adhesive tape applied to the tail feathers (Fig. 2.12), as described by Best (1990): two outer tail feathers on each side of the tail were first clipped and then taped together in different colours (Fig. 2.12 a and b). The taped tails could be distinguished both when the bird was facing the observer on the perch (Fig. 2.12 c) and when sitting at the burrow, from the back (Fig. 2.12 d). Most birds preened off the tape from the feathers, or

Figure 2.11: Patagial wing-tag



A

B

Figure 2.12 A and B: Taping of two outer tail-feathers on either side of the tail. (A): first, the feathers were trimmed to give maximum adhesiveness. (B) Adhesive tape was attached on both sides (upper and lower) of the tail feathers, using three different colour tapes. The edges were trimmed to the original width of the feathers.

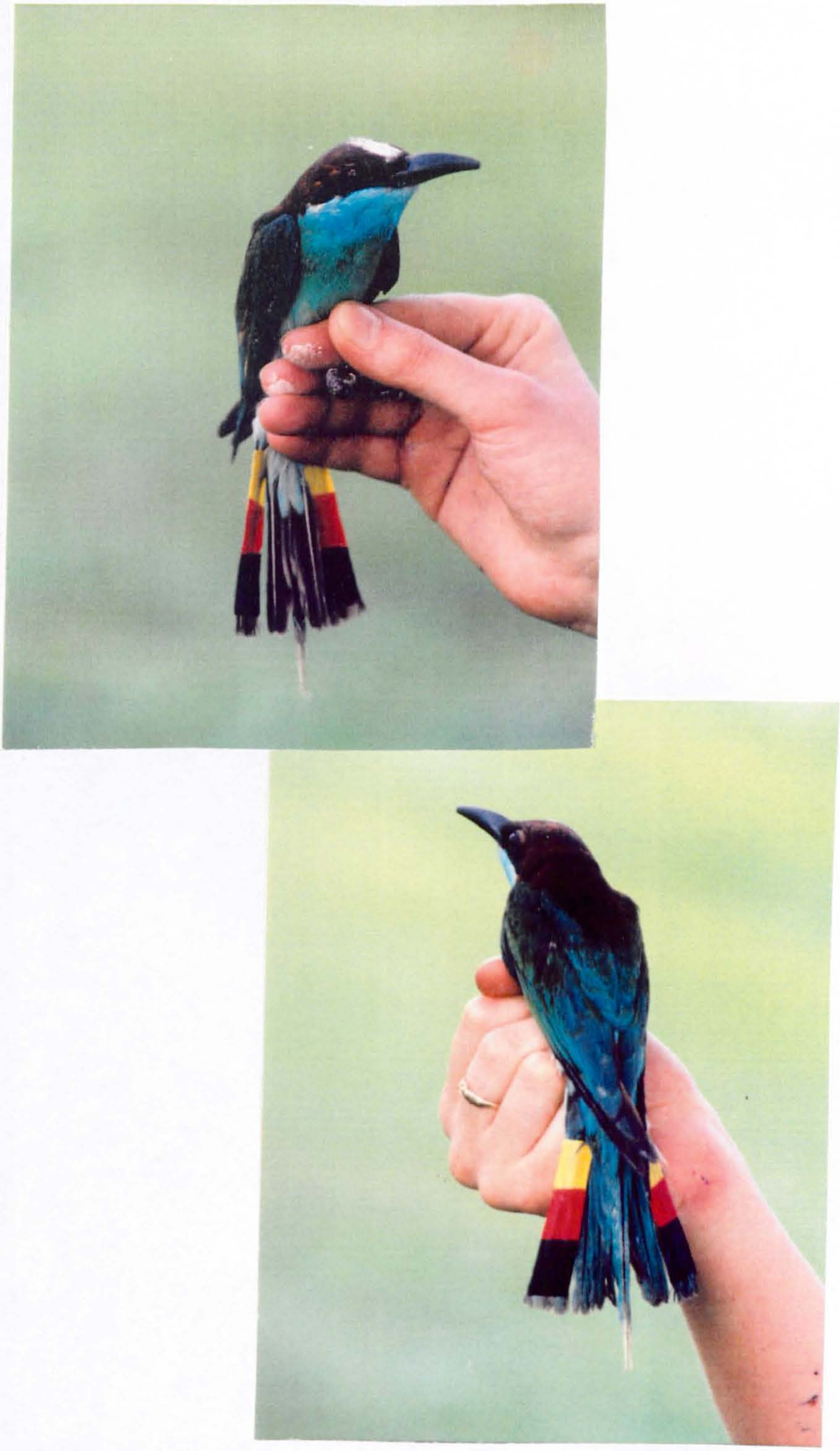


Figure 2.12 cont. - C and D: The taped tail-feather marking can be seen clearly from the front and the back. To facilitate finding marked birds when scanning a site with binoculars, tail-marked birds were marked with a dot of Tippex on the head to mark it out clearly as an identifiable individual.

even broke off taped feathers at the base or pulled out all or some of the taped feathers within 1 to 3 weeks of the tagging, which again rendered this tagging method unsatisfactory.

2.5 Data and statistics

The data collected in the field as described above were entered into datafiles which were read into database tables. These data were then retrieved from the database either to update secondary data columns such as nestling age or breeding dates, brood sizes etc, or they were used directly for statistical analysis. Data storage and handling are described in detail in the next chapter.

For parametric statistical tests, data were tested for the assumption that they are normally distributed. Except if looking for interactions, most parametric tests are quite robust, such as Analysis of Variance and Linear Regression Analysis (Norusis, 1988); their parametric assumptions are satisfied by near-normality. To test if a particular dataset is normally distributed, it is usually sufficient to look at the distribution of data, or at the sorted data plotted against their normal probability scores (NPSs; Zar, 1984). Normally distributed data should have a straight-line relationship and correlate highly with their NPSs (Norusis, 1988). The correlation coefficient can be used for unbiased judgement on normality. Depending on the sample size N, the null hypothesis that the dataset is normally distributed is rejected if the correlation coefficient falls below a critical value r (Minitab Inc (1989): MINITAB reference manual, release 7, U.S.A, p 4-8). At probability $p < 0.05$, these are:

N	r
4	0.8734
5	0.8804
10	0.9180
15	0.9383
20	0.9503
25	0.9582
30	0.9639
40	0.9715
50	0.9764
60	0.9799
75	0.9835

Parametric tests were only used if data were expected (1) not to be heteroscedastic (i.e. their variances depending on their value) and (2) to be independent conceptually. The latter was also ensured for χ^2 tests. For χ^2 tests with 4 cells, I always used Yates' Correction or else the Fisher exact test (unless stated otherwise).

The probability p of a result having been obtained by chance was given throughout this study as summarized in Table 2.1. For $p < 0.10$ (or, in a few cases < 0.2), p was given as 'smaller than'. For $p > 0.10$ (or, in a few cases > 0.20), p was given as 'greater' than the nearest 0.10. Usually, significance was allocated in cases where $p < 0.05$ (but a 'trend' was mentioned where $0.05 < p < 0.10$ or, in very few cases, $0.05 < p < 0.20$). Significance was sometimes given as * ($0.01 < p < 0.05$ exclusive), as ** (if $0.001 < p < 0.01$) or as *** (if $p < 0.001$).

Multivariate analyses, in particular Principal Component Analysis (PCA) and discriminant function analysis, were conducted in the following chapters. In PCA, several correlating variables are combined into a series of factors or principal components (PCs) that are not themselves correlated to each-other (orthogonal). The first principal component (PC1) holds most of the information and has the highest percentage of variation explained by the PCs. In this study, PCAs were used to summarize size variables, making use of the fact that if size variables are used in the PCA, PC1 usually reflects overall size (e.g. Loughheed *et al*, 1991), wheras shape is deflected into the second or third PC (PC2 or PC3). In Chapter 4, for example, I compared the size and shape of adults in the two different colonies by using size variables. by using principal component (PC) scores. Instead of comparing the relative constituents of each PC (PC loadings) between colonies, I used the same PC for for all birds of both colonies and then compared the scores the same multivariate factors for the two colonies. In Chapter 5, PCA was used to compare body size between pair members. Again, the same PCs were used without first assessing if PCs have different constituents in males and females. In Chapter 7, PC1 of nestling size variables was used as the growth vector, a measure of relative nestling size (O'Connor, 1978 b). Gilliand and Ankney (1992) aged nestling Great Black-backed Gulls *Larus marinus* with various size measurements, of which PC1 was the best predictor of age. When used for ageing growing organisms, PC1 should be a combination of measures that highly correlate with age (see Chapter 7). The PCAs used in each chapter are briefly introduced in the relevant methods sections.

Table 2.1: **Equivalent notations used in this study for the probability p that a result has been obtained by chance.**

p	level given		result classified as
$p < 0.001$	$p < 0.001$	***	(highly) significant
$p < 0.01$	$p < 0.01$	**	(highly) significant
$0.01 < p < 0.05$	$p < 0.05$	*	significant
$0.05 < p < 0.10$	$p < 0.10$	(ns)	not significant
$0.10 < p < 0.20$	$p > 0.10$	ns	not significant
$0.20 < p < 0.30$	$p > 0.20$	ns	not significant
$0.30 < p < 0.40$	$p > 0.30$	ns	not significant
⋮			
$0.90 < p < 1.00$	$p > 0.90$	ns	not significant

CHAPTER 3 - DATABASE DOCUMENTATION

3.1 Introduction

Data are the basis of all research in behaviour and ecology. Despite their central role, much of the data for research are still stored in large, inflexible data files which are inefficient for access and retrieval. Data storage and management has been lagging behind the increasingly sophisticated techniques of data exploration and statistical analysis. Recently, the use of more powerful and sophisticated database management systems has become more widespread, and biologists are just beginning to explore the use of relational database management systems (DBMS's). Here I document the design and implementation of a relational database (DB) for the data collected for this study. The implementation is based on the DBMS ORACLE. Central to the documentation of the database is the *conceptual analysis*, or *data model*, which specifies what the database is to contain and represent (Whittington, 1987; Ullman, 1988). For internal consistency of the database structure and consistency of the data themselves it is necessary to first model the data on a conceptual level and base the database implementation on this conceptual data model. A consistent, logical data model provides the background for the efficiency and power of relational databases. It also serves as a documentation to make the implemented DB usable and understandable.

In the following account, I will give a description of conceptual modelling and the way it was applied to this study. I then describe the updating, manipulation and retrieval of data for analysis or exploration with the help of examples from my database implementation in ORACLE. This is followed by a discussion of improvements both achieved and still needed in order to fully utilize the power and flexibility of relational databases to manage the data required for research in behavioural ecology.

3.2 Conceptual analysis of the Bee-eater data

In this section I first give a brief introduction to the design of databases and introduce the notations used in this chapter. I then describe the data model before discussing some design decisions.

3.2.1 Introduction to conceptual analysis and terminology

There are three levels of designing a relational database (see Whittington, 1987; Ullman, 1988). These are:

(1) conceptual design, which describes the meaning of the data in terms of concepts such as birds, nests, and behaviours, and the relationships between them;

(2) logical design, where the emphasis is on how this information is to be organized correctly, and on the validation of the design; and

(3) physical design, which describes the implementation of the logical design and re-organizes it for efficient performance into tables and columns, introducing keys and indices for access speed and space considerations.

The notation and terminology used here are based on entity-relationship-attribute (ERA) modelling as reviewed and explained in detail, for example, by Whittington (1987). ERA modelling has become the principal data model used in relational database systems (Whittington, 1987). In the following I shall briefly introduce the basic terminology of ERA modelling with illustrations from the database itself (for a comprehensive review of the theory see e.g. Ullman, 1988), before describing the data model for the Bee-eater database.

The objective of a conceptual analysis is to describe the meaning and to construct a model of the part of the real world which is specified in the data (called the *universe of discourse* in IT jargon). The data are described in terms of their inherent structure, using a formal notation to provide clear guidelines for the design of the database. The *universe of discourse,* and thus the data themselves, are organized into *entities,* their *types* (ETs) and *attributes,* and *relationships* between entities. An entity can be a physical object like a nest or a bird, or an abstract concept, such as a sighting of a bird at a certain time and day, or a schedule classifying sightings into observation types. Entities are classified into entity types (ETs): bird O6B seen on the 22nd of April, 1989, at 10.20 is an entity of type 'Sighting'; 1989's nest no. 20 at the Sungai Buloh colony is an entity of type 'Nest'. ET names (Sighing, Nest, etc) start with a capital letter. This notation is adopted throughout this chapter.

Entities have attributes, which are their characteristics. Entities of the same type are characterized by the same attributes: each nest has a number in any particular year, and an exact location; birds have rings and sometimes wing-tags, and they are either male or female and of a particular age. There is a way to identify each entity uniquely, for example each nest identified by year, colony and nest number; each bird is identified by its ring. In the physical design, such identifers are called *keys* and can consist of one or more columns. Sometimes, artificial keys (such as codes) are introduced, mainly to make cross-reference more convenient. For example, in the DB implementation each nest has a code associated with it, which includes the year, colony and nest number.

Entities can be associated with each other by logical relationships. There is a relationship between a Nest and a Sighting, for example, if the Sighting is made at a Nest. Relationships are classified in turn into one-to-one, one-to-many, many-to-one and many-to-many relationships. The above 'Sighting made at Nest' relationship, for instance, is a many-to-one relationship because, assuming that each bird only visits one nest in any one-minute Sighting, each Sighting can be made at only one Nest, but each Nest can have many Sightings made at it. Furthermore, relationships do not necessarily apply to all entities of one or the other ET. For example, not every Sighting is made at a Nest, it may be made on a perch location instead, and not every Nest needs to have Sightings made at it. Sightings do not necessarily occur always at a nest, and similarly not all nests have Sightings at them. Fig. 3.1 illustrates most of the parts of the conceptual analysis which I have discussed so far. Each entity type is represented by a box (rectangle). The notation for relationship types is a line connecting the corresponding ETs (Nest and Sighting, in the example), with a single end for a 'one' and a forked end for a 'many' relationship type.

The logical design as described by Whittington (1987), is the next step before the database implementation, which is described in the physical design. The role of the logical specification is mainly to test for inconsistencies in the conceptual design. Whittington (1987) introduces a further set of notations for the logical design: Entity Types become *relations* which need to be *normalized.* This is done by checking for anomalies with a succession of 4 to 5 rules called *normal forms.* The main aim of the logical design is to structure the information logically correctly in order to avoid redundancy and inconsistencies so as to facilitate access, update and maintenance of the database. Data that are dependent must be updated together, and related information which is used together should be stored together. Similarly, data that are related but independent must not be made dependent in the model (e.g. Nest and Location: Locations exist without nests).

In the physical design, ETs, or relations, are translated into *tables* and attributes into *columns*. Each entity in an ET becomes an entry or record in a table, which is uniquely identified by its *key*. Additional columns are included at this stage for cross-references which implement relationships between ETs. Corresponding concepts between the Conceptual, Logical and Physical Designs are shown in Table 3.1.

In the following, I describe ETs and relationships of the conceptual design of my DB. I concentrate on the conceptual and physical designs, with only a brief validation with a logical design, but not using all the formal rigour of the normal forms. This should be done in a commercial database design for group users or long-term projects, but for this study it was more important to concentrate on the implementation and the use of the implemented database, after the conceptual specification. The logical design is contained in the 'Conceptual design decisions' in the following account. In the implementation, which is described in the physical design, additional columns had to be introduced into the physical ETs to cross-reference the information.

3.2.2 Description of the data model

The part of the world about which data have been collated is called the Universe of Discourse (see above). The Universe of Discourse to be modelled in the database design consists of the colonies of Bee-eaters and all data that may be collected to study their social system, with strong emphasis on data collected during my own 3-year study. The Universe of Discourse falls naturally into two sections: one type of data identifies and describes physical entities, such as the birds (adults or chicks), nests and broods inside the nests, and their measurements. The second part of the data consists of observations of these birds and their behaviour and of related information, like weather data (Fig. 3.2). The Universe of Discourse thus consists of the observations and measurements collected as data as well as the derived entities Chick,

Figure 3.1: Example of two Entity Types (ETs) and a one-to-many relationship: Each Sighting can only be made at one nest, but more than one Sighting can be made at each nest.

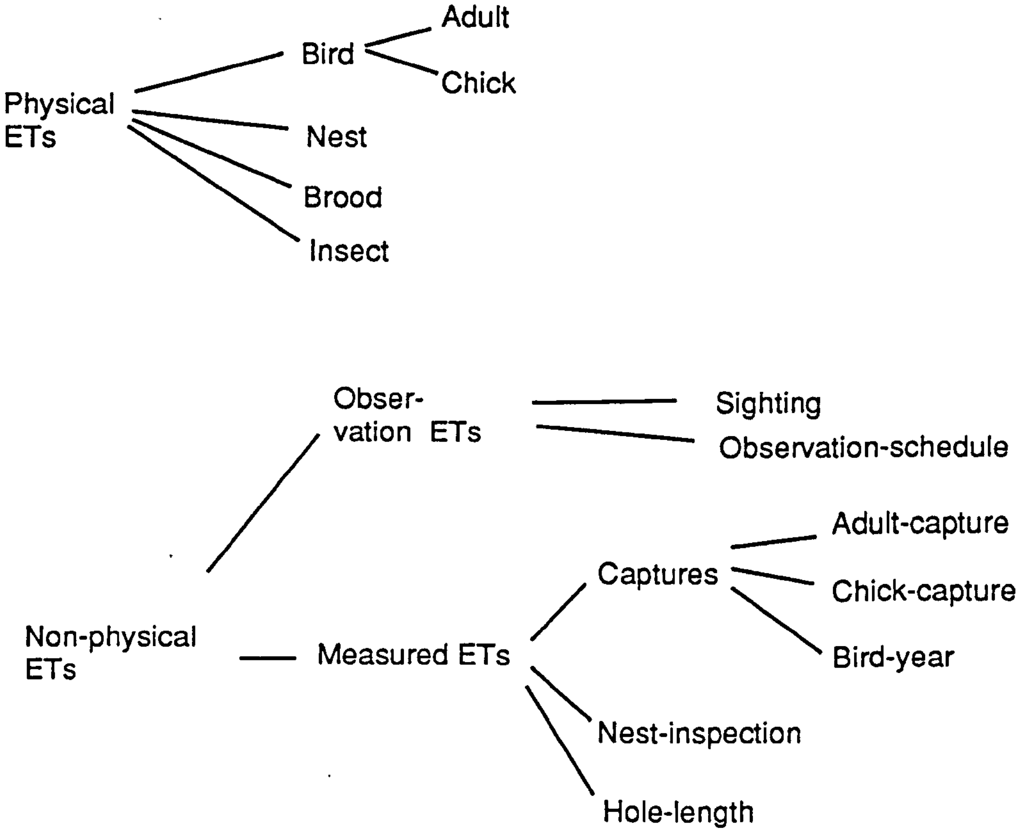


Figure 3.2: An overview of the Entity Types and the Universe of Discourse, described with 'Isa' relationships. Sighting, for example 'is a'n observational ET, each of which 'is a' non-physical ET.

Table 3.1: Corresponding concepts between Conceptual, Logical and Physical designs

Conceptual Analysis	Logical design	Physical design
Entity Type	Relation	Table
Attribute	Attribute	Column
Identifier	Key	Key
Entity		Entry or record
Relationship		Cross-reference (additional column)

Adult, Brood and Nest. Measurement definitions and methods are described in detail in Chapter 2. The ETs and their relationships are described in more detail in the following sections. For an overview of the Universe of Discourse and ETs see Figs. 3.2 and 3.3.

Entity types of the conceptual model

In the following, for each ET I give a brief description and a list of its attributes, before explaining the ET and its significance in more detail. ETs are underlined, and values are given in brackets.

Adult: Identification of adult birds and information that does not change throughout an adult's life.

Attributes:

- Ring: the bird's metal ring, e.g. SO0523
- Tag: the bird's colour mark (wing-tag, tail-tape or paint), e.g. O6B
- Sex: (Male, Female)
- Sexing Method: the method by which the sex was determined, e.g. mating observation

Each adult or sub-adult Blue-throated Bee-eater (first year or above) that was caught at the colony is represented, provided that the bird was either ringed, tagged or both. The bird's sex is noted, and there is a code stating how the sex was determined, for example, by mating observation, egg palpation or discriminant function score (see Chapter 2). Sex and Sexing Method can be updated with information from observations (for instance, courtship feeding), or from a discriminant function analysis, for birds which were classified reliably (with 95% certainty) as male or female (see Chapter 5). Information that may vary between years, such as body size and dimensions, can be found in the ET Bird-Year, and changing information about adults, like body mass and condition, in Adult-capture (Fig. 3.4 a).

Bird-Year: The information on body size and plumage for adult birds which is not expected to change within one season.

Attributes

- Date: date of first capture within the season, e.g. 23-MAR-89
- Status: if the birds was suspected to be a breeder or not: (Breeder, Helper, Non-Breeder)
- New/ Recovery: if the bird was caught previously: (New, Recovery)
- Ringer: who measured the bird: (LDS, AC, PTG, LB, PW)
- Keel length: in mm, e.g. 29.4

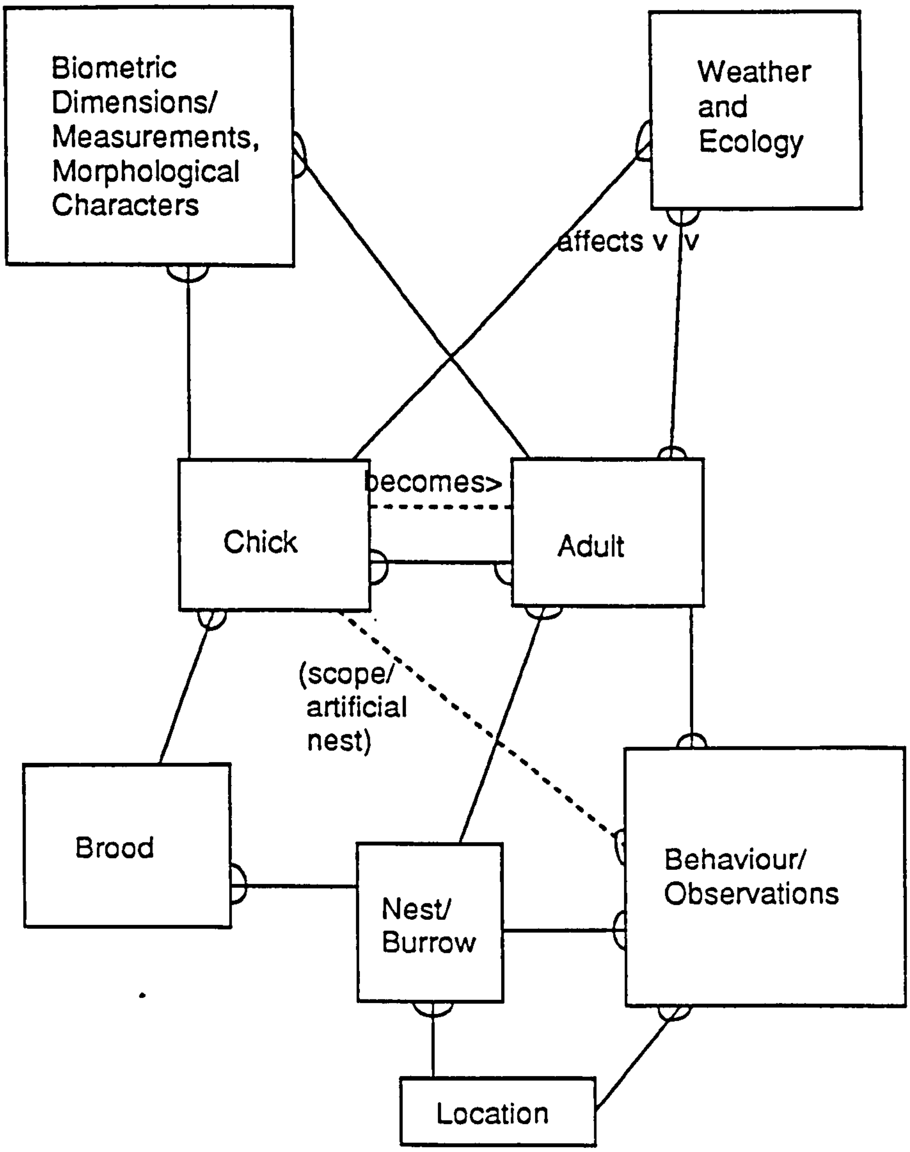


Figure 3.3: An overview of the data model. Entity Types are represented by boxes, and relationships between them by lines. Arrows ^ v > < are given to show the direction of a relationship, e.g. Broods are in Nests (and not vice versa). The 'many' side of one-to-many relationships is represented by a fork. See text for further details and explanations of terms. Relationships not dealt with in Table 3.2 are given in this figure.

(Figure 3.4)

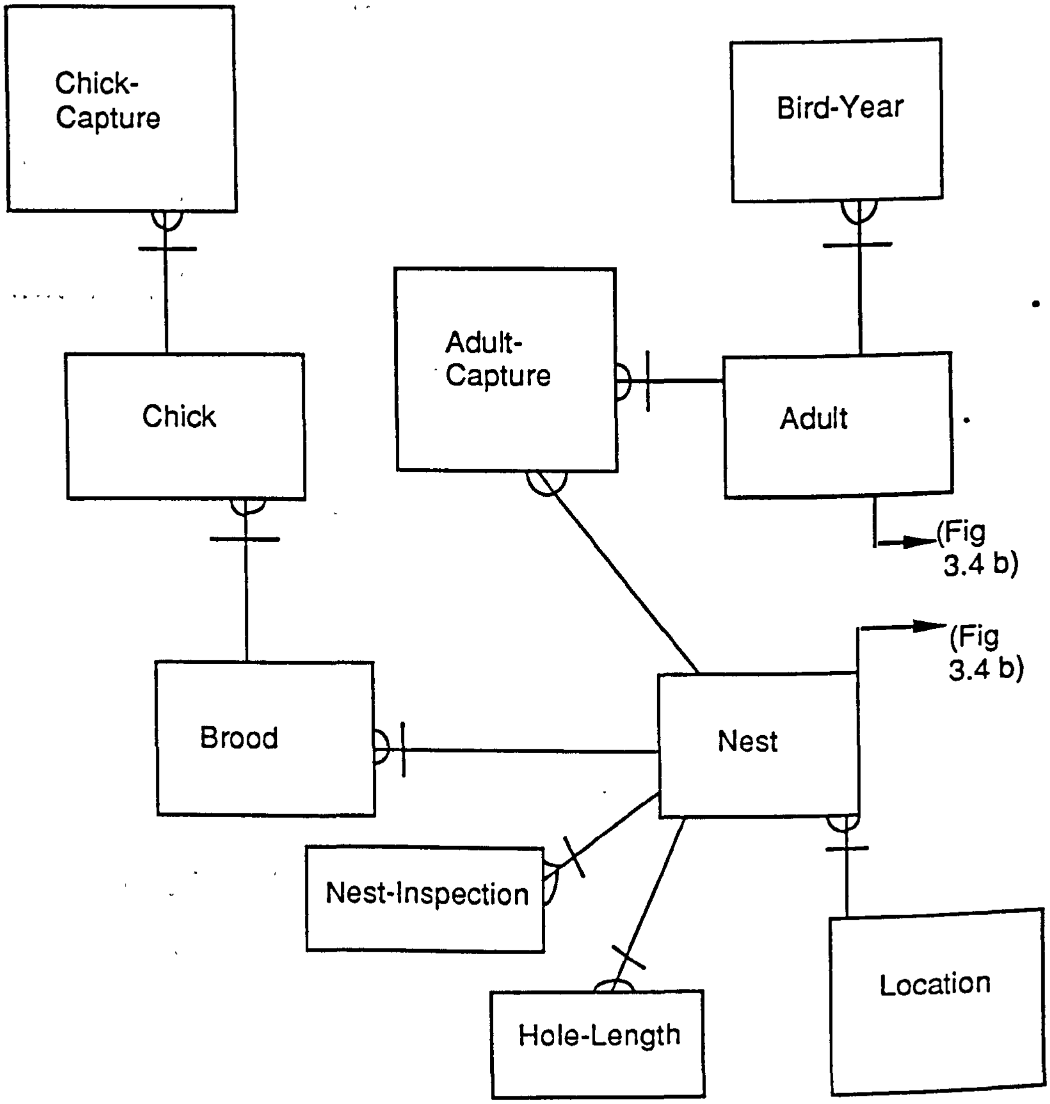


Figure 3.4 a: Conceptual specification of the Bee-eater data. Real' entity types and measurements. Representation as in Figure 3.3; see text for explanation of terminology.

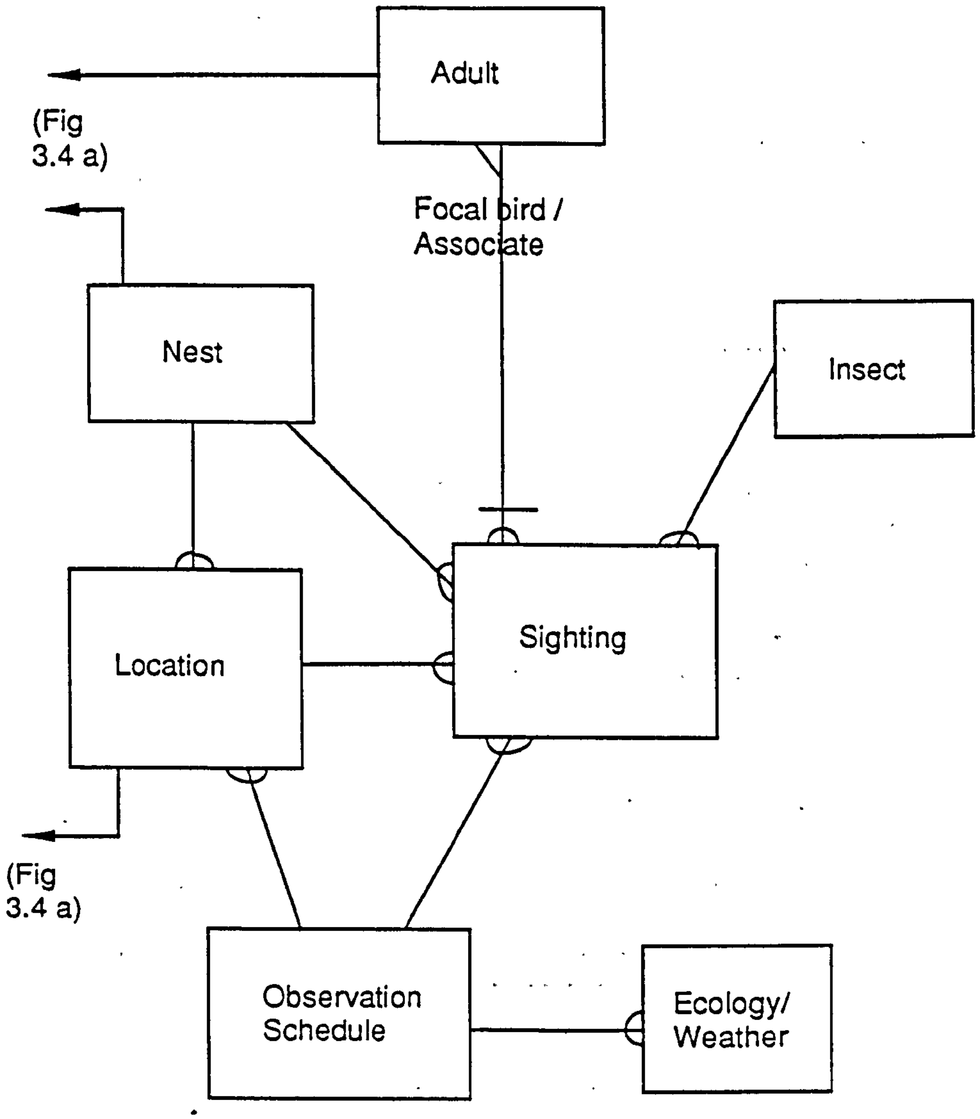


Figure 3.4 b: Conceptual specification of the Bee-eater data. Observational data. Representation as in Figure 3.3; see text for explanation of terminology.

- Wing length: in mm, e.g. 112
- Tarsus length: in mm, e.g. 10.7
- Head and Bill length: in mm, e.g. 57.8
- Bill length: in mm, e.g. 27.3
- Bill width: in mm, e.g. 7.1
- Tail length: without streamers in mm, e.g. 78
- Brown: extent of brown on nape, 1 (little) - 5 (large)
- Green: amount of green feather on head, 0 (none) - 5 (many)
- Eyes: colour of the eyes, e.g. red, brown, red-brown etc

Measurements that are recorded once a season only for each Adult are kept in Bird-year. This ET relates only to Adult and Adult-capture when they were first captured each season (Fig. 3.4 a).

Adult-capture: Information for adult birds which is expected to change within one season, including blood samples taken at capture.

Attributes:

- Date-time: date and time of capture and processing, e.g. 23-MAR-89 09:20
- Recapture: if the bird was newly caught or had been caught previously (New, Recapture)
- Ringer: who measured the bird, e.g LDS, AC, PTG, LB, PW
- Tag-condition: the condition of the colour mark when caught, e.g faded
- Blood taken: amount of blood taken, per 1mm capillary tube, e.g. 1.5
- Tubes: tube numbers, e.g. 167,168,169
- Ovary: palpation of egg, 0 (flat) - 5 (egg palpated)
- Cloaca: size of cloaca when captured, 0 (small) - 5 (large)
- Condition: thickness of the pectoral muscle, 0 (thin) - 5 (thick)
- Tail-Streamer: Tail plus streamers in mm, e.g. 135
- Streamers: condition of streamers: (intact, abraded, new)
- Mass: mass of adult in g, e.g. 32.3
- Mites: amount of infestation with mites, e.g. few eggs
- Bright: throat brightness, 'not bright' to 'very bright'
- Head: extent of abrasion of the head feathers, 0 (not abraded) - 5 (very abraded)

Every time an Adult is captured at a nest or in a mist net, measurements which change during the season and the amount of blood taken for DNA fingerprinting are noted in Adult-capture. Each Adult-capture entity corresponds to the data from one capture, of one bird.

Chick: This is the birth record of the colony. All nestlings found are 'registered' here, including their identification and information that does not change during their lifetime.

Attributes:

- Chicknumber: order in the hatching sequence (1=first)
- Ring: *either* its ring, *or* its toe marking (if very young), e.g SO9878, or rh-last
- Hatchday: date of hatching, if known, e.g. 13-AUG-89
- Qualifier of Hatchday: method by which the hatch date was established (see Chapter 2): direct observation or from growth curves
- Day died: date on which chick perished, if it did, e.g. 20-AUG-89
- Qualifier of day died: method by which day died was established (see Chapter 2), e.g. direct observation, inferred from parts of the corpse found etc.
- Exactness of the 'Day died' estimate, in number of days (±), (0,1,2,3,...)
- Experiment: name of any experiment it was part of, and its role, e.g. fed chick in experimental nest of feeding experiment, unfed chick in... etc

If a chick is ringed, the ring number identifies each chick uniquely, as for adults. (Otherwise identification is via the chick's relationship with Nest, Brood and colony as well as year, see below). Chicknumber does not necessarily reflect the actual position in the hierarchy but the position as found the first time the nest was inspected. The parents of any Chick are in Adult. Note that here, 'parents' is defined socially. Data from DNA fingerprinting, which can provide genetic relationships between Adults and Chicks, are excluded here for simplicity. Chicks which return to the colony as breeding adults are recorded in Adult if they have been ringed as nestlings.

Hatchday and Daydied (and qualifiers) are updated either from observational ETs such as Nest-inspection (see below), or from growth curves which were used to estimate age and re-calculate hatch date. Experiment is updated after the allocation of nests and chicks to experiments is made.

Chick-capture: contains information about chicks which changes during the season, such as growth data, and calculations related to the current state of brood reduction in its nest.

Attributes:

- Date-time: date and time of capture, e.g. 21-JULY-90 14:40
- Recapture: if the bird was newly caught or had been caught previously, (New, Recapture)
- Dead: whether the nestling was dead when it was found or alive, (Dead, Alive)
- Blood taken: amount of blood taken, per 1mm capillary tube, e.g. 0.7
- Tubes: tube identification number(s), e.g. 120

- Abdomen: extent of abdomen, e.g. bulge, full, empty, yolk
- Tail Feather length: in mm, e.g. 4
- Pins: description of stage of feather sheaths, e.g. all still, some, most
- Condition: thickness of the pectoral muscle, 0 (thin) - 5 (thick)
- Keel length: in mm, e.g. 12.4
- Wing length: in mm, e.g. 18
- Head and Bill length: in mm, e.g. 27.8
- Hook: presence and sharpness of the hook, e.g. 0-5 (large and very sharp)
- Wounds: number of scabs and wounds, e.g. 3
- Mass: mass of chick in g, e.g. 8.1
- Mites: amount of infestation with mites, e.g. few adults
- Age: day after hatchday (0), e.g. 7
- Place: actual place in size hierarchy (usually = chicknumber), e.g 2
- Mass Disadvantage: difference in mass compared to elder sibs (see Bryant and Tatner, 1990) in g, e.g. 12.3

Chick-capture is the equivalent of Adult-capture for chicks. Chicks grow, however, so that most body size measurements, which stay the same for adults and are thus stored in Bird-year, change from capture to capture for Chicks. Therefore, some attributes of Adults, for example Brown and Bright, are not relevant for Chicks, and there are some additional attributes typical for Chicks, such as Wounds and Hook. Each Chick-capture is uniquely identified by a reference to the Chick (Fig. 3.4 a) and the date of the capture. Most attributes are updated, as in Adult-capture, during processing, but Mass Disadvantage and Age are updated with queries. Place and Chicknumber are the same, if the size hierarchy keeps the same places as the hatching hierarchy, otherwise Chicknumber = Place at hatching. Place changes when nestlings move up in the hierarchy when an elder sibling fledges, or, on rare occasions, if an elder sib dies.

<u>Brood</u>: all general breeding information for each brood is summarized here from the raw data. Attributes:

- Broodnumber: first or second brood in the nest, e.g. 1
- Start-date: first egg date, or first date of any records of clutch or brood, e.g. 13-MAY-91
- Qualifier of Start-day: how start-day was determined (see Chapter 2), e.g. hatchday
- Success: number of fledglings, or any other info, e.g. chicks
- Min Eggs: minimum number of eggs that must have been laid, e.g. 2 if two chicks were found
- Total Eggs: size of complete clutch, e.g. 4
- Min Chicks: minimum number of chicks that must have hatched, e.g. 2 if one live and one dead was found

- Total Chicks: size of complete brood, e.g. 3
- Experiment: name of the experiment the brood was part of, and its role, e.g. experimental nest of feeding experiment, control nest of the feeding experiment, experimental nest in hook experiment
- Fingerprint: record of whether fingerprint data are available, e.g. (F, no entry)

Brood includes data concerned with the onset of incubation (first egg) and provisioning (first hatched), and breeding success at different stages (no. eggs, no. hatched, no. fledged). In most cases, Brood is the same as Nest, i.e. entities are identified uniquely by the colony, year and the nest number, except in nests where the first brood was followed by a second. For each Brood, breeding success, onset of laying, number of eggs and chicks are summarized. The first day that a couple of adults is caught or observed is used as a starting date of the brood, if no better measure (first egg date) is available, either from back-calculations from chick ages or from Nest inspection directly. Min Eggs and Total Eggs are the same if clutch size is known, and similarly, Min Chicks and Total Chicks have the same value if brood size is known. If clutch size is not known, Total Eggs is null (no entry), but whether or not eggs were laid is obtainable from Min Eggs; the same is true for Min Chicks and Total Chicks, and brood size. Brood is a derived ET, and summarized rather than updated in the field.

Nest: Identification and location of each burrow.
Attributes:

- Nestnumber: e.g. 121
- Year: e.g. 1991
- Microlocation: grid-location in Nam Heng e.g G4
- Substrate: of excavation, e.g. (sand, earth)
- Length: total length in cm, e.g. 185

Contains the exact location of a nest, and defines it with Nestnumber, colony and year. Nests are not re-used between seasons, because they collapse between seasons. Breeders attend to the Brood at the Nest, and Nest-watches are made here. Each nest can potentially have a succession of two or more pairs using it, so one or more broods can be in each nest. Nestnumber implies colony, since nests in Sungai Buloh were designated a number between 1 and 99, whereas Nam Heng nests were numbered 100 and upwards.

Hole-length: length of each burrow at different times during the digging phase.
Attributes:

- Date: of measurement, e.g. 23-JUN-91

- Re-measured: 'new' burrow, or re-measured, e.g. (N, R)
- Length: (see Chapter 2) in cm, e.g. 184
- Curls: 'curling' of the measuring hose indicates that there is a nest-chamber at the end of the burrow, and that the actual length is less than recorded.

During the digging phase of the breeding season, repeated measurements of numbered burrows are taken, for instance to estimate digging rates. Hole-Length is identification dependent on Nest, i.e. it is identified by date and its relationship to Nest (see Fig. 3.4 a, and below).

Nest-inspection: information on nest contents collected during nest inspections.
Attributes:

- Date-time: of inspection, e.g. 13-MAY-90 12:30
- Eggs: number of fresh eggs, e.g. 3
- Spoilt: number of spoilt eggs (broken or old and smelling bad), e.g. 1
- Dumped: information on artificial egg added to the clutch (D), not present, previously added egg (NP) or not added or missing (0)
- Chicks: number of live chicks, e.g. 2
- Dead: number of chicks of which remains were found, e.g. 1
- Maggots: amount of maggots (to estimate Day Died in Chick), e.g. lots
- Food: list of items of un-eaten food, e.g 2 dragonflies, 1 cricket
- Comments: other text comments, e.g. eggs lukewarm, flushed incubating adult

Each time a nest is inspected, one entity is added. This ET contains raw data which can be used to update Brood and Chick. Nest-inspection is identification dependent on Nest.

Location: Defines the study colonies and subcolonies into areas.
Attributes:

- colony: Sungai Buloh or Nam Heng
- location: sub-colony of the main colony, or another sub-colony, e.g. rh, rh-, NH Garden
- sublocation: further sub-division of the main colony into e.g. rh-end, rh-top, lh-2
- microlocation: further sub-division. In Nam Heng: grids, e.g. B3; in Sungai Buloh: e.g. rh-end-tree or rh-end-wire.

The ET relates Microlocation, Sublocation and Location within a colony. Sungai Buloh was sub-divided into 'right hand' (rh) and 'left hand' (lh) in one direction (location), and into 'end', 'mid','top','top-top' (main colony; for example 'lhtoptop'), continuing outside the compound with the main colony, on compounds in front, with '-1','-2','-3' etc, for example 'rh-1'. The main colony at Nam Heng was subdivided into grids (A1-D4), and sub-colonies (location) or foraging grounds were named according to the estate where they were found (NH, REM) and area (garden, river etc). Sub-colonies are defined in Location for each colony, which are used in Nest, Sighting, Observation-Schedule etc. The ET Location is used for investigating year-to-year return rates from captures, distances between pair members in sightings and for defining nests.

Ecology: Information on any aspect of the physical or organic environment collected during observation periods.
Attributes:
- Date: of record, e.g. 23-MAY-90
- Start-time: time in hours (24), to the nearest minute, e.g. 14:20
- Duration: in minutes, e.g. 120
- Type: type of ecological record scored, e.g. cloud cover
- Score: a score defined by the type of record, such as extent of cloud cover on a 0-5 scale; e.g. 4

All ecological data (such as sun index, cloud cover, rain) or any other relevant information (disturbances, for instance) made during any type of observation or at any time during the season are collected in this ET. The basic structure allows for a wide variety of data to be entered here. Ecological records can then be related to any observation by Date and Start-time. The Type of ecological record defines exactly how this should be done, e.g. records on rainfall may be more important for observations on the same day, whereas cloud index or disturbance is measured for the duration of observations (see physical design). This ET is identification dependent on Location (Fig. 3.4 b), because different observers could take different ecological information at the same time at different locations.

Insect: Assigns absolute size to insects according to species and relative size.
Attributes:
- Type: species or family name, e.g. butterfly, honey-bee, wasp
- Relative Size: size for each insect type on a 0-6 scale, e.g. 4
- Absolute Size: size that can be used to compare all insects, e.g. 3

Any Insect-type which was sized is assigned an absolute size in this ET. A 'large dragonfly', for example, is a 'medium size insect' (absolute size), compared to a 'large bee' which is a 'large insect'. Absolute size is coded from 1 to 7 (from very small to very large, see Appendix 2).

Observation schedule: Classifies Sightings into types of observations according to how they were collected.

Attributes:

- Date; of observations, e.g. 13-MAR-90
- Start-time: hour (24) and minute of the start of an observation period e.g. 13:50
- End-time: as start time, observation period ended, e.g. 15:00
- Observer: initials of the observer (as ringer above), e.g. LDS
- Type: type of observation, e.g. continuous, nestwatch etc

The Observation schedule is used to classify observations. For each observation period, the Observation schedule records the observer, the arrival and departure times of the observer, the particular sublocation and date of the observation, and the type of observation made. Continuous observations, nest-watches, pair-watches and sightings are observation types (see Chapter 2).

Sighting: A one-minute observation of one bird and its activity, associates and location.

Attributes:

- Date-time: of sighting, e.g. 12-MAY-89 12:24
- Activity: behaviour of the focal bird (see text)
- Observer: initials of the observer, e.g. LDS

Sightings are made

- of a known bird anywhere, any time,
- of any bird (known or untagged) that is seen at any one marked burrow,
- of an unknown bird that is associated with another bird and is involved in an interaction (sexual, agonistic, etc), or
- of an unknown bird that is part of a pair that is watched over several minutes.

Sighting is a record of one focal bird seen at a specific time (one minute). A Sighting contains information about what the bird did (Activity) and any information about any food the focal bird carried (relationship with ET Insect, see Fig. 3.4 b, and below). A Sighting can be an observation in its own right or be part of different types of observations, as specified by Observation Schedule (Fig. 3.4 b; see below). If an untagged bird was seen at a nest, it was identified with an ID number. ID numbers are multiples of 100 (100: first bird, 200: second etc). These ID numbers are chosen to avoid confusion with *amounts* of birds in column Associate. Groups of Sightings that are made in successive minutes have consistent ID numbers: the ID number of each bird holds across minutes for all sightings in the group. Thus, for instance, birds taking turns during digging at the nest can be identified in Sightings in successive sightings at the same nest, and sexual or agonistic behaviour can be recorded consistently for each bird during the whole interaction, even if these were unmarked. An Associate is defined as being within an estimated bird-length (25-30 cm) of the focal bird during any part of the minute of observation. If there is no bird within one bird-length of the focal bird, Associate takes the value 0. An Associate of the focal bird can be tagged or untagged. Untagged Associates can have an ID number (100, 200, 300, ...), if the Sighting is part of a pair observation or an interaction. The amount of associates (which is recorded if the birds are not interacting and not at a nest) is an integer number, usually between 1 and 3 or 4. Tagged Associates or those with ID numbers are also focal birds in Sighting because both birds may behave differently: A may 'sit' next to B, but B may 'preen' next to A. Each Sighting therefore is uniquely identified by a combination of the Day-time and Identity. The Associate can take different roles, depending on the type of interaction that a Sighting may represent. An Associate of a sexual interaction is the mating partner, whereas an Associate of a bird in an agonistic interaction is either the opponent, or a 'guarded mate' (defined as being another bird that is within one bird-length of either of the opponents during any time of the clash).

Relationships of the conceptual model

Relationships are the second central notion of the conceptual design, containing most of the information on data structure. They specify how entities are connected, i.e. their inherent, logical associations and links. Understanding how connected information is distributed amongst entities is important when considering how the information can be accessed. For clarity, the relations are split into two groups which are shown in Fig. 3.4. a and b. Relationships are explained one by one, referring to Fig. 3.4 and to Table 3.2.

Table 3.2: List of direct and indirect relationships of the conceptual database design

ET1 is related to ET2	type of relationship
Adult is parent of/feeds Chick	indirect
Adult is measured by Adult-capture	direct
Adult is measured by Bird-year	direct
Adult lives in/ is caught at Nest	indirect
Adult raises Brood	indirect
Chick measured by Chick-capture	direct
Chick hatches in Brood	direct
Brood raised in Nest	direct
Nest situated in Location	direct
Nest measured in Hole-length	direct
Nest-inspection made of a Nest	direct
Adult observed by Sighting	direct
Adult is associate in Sighting	direct
Sighting is made at a location	direct
Sighting is made at a Nest	direct

Adults

The central ET is Adult. Adults have relationships to their captures, measurements and sightings, i.e. to the ETs Bird-year, Adult-capture and Sighting. Adults also have indirect relationships with other ETs (Table 3.2): Adults are the parents of Chicks, and Adults feed Chicks. For design simplification I shall assume that adults are the genetic parents of the chicks they feed (see design decisions below), so that these relationships are identical. Both these relationships, 'parent of' and 'feeds' are indirect relationships, via Brood, Nest and Adult-capture: Adults are measured in Adult-capture at Nests, and Nests contain Broods which in turn contain Chicks. The identity of a Chick's parents therefore has to be established via the relationship of Adult with Adult-capture, Nest and Brood. Another relationship between Chick and Adult is Chick 'becomes' Adult (Fig. 3.3). This relationship was ignored because of low return rates of chicks (see design decisions below).

Captures

Each Adult is 'caught at' one Nest and can be caught at more than one nest per season and in different nests in different years. Each Nest can also have more than one Adult. This many-to-many relationship is resolved by Adult-capture. Any one Adult can be caught more than once within one season, so that for each Adult there are several Adult-captures per season. Similarly, each Chick is usually measured repeatedly before it fledges. Because each Adult-capture measures only one bird, but each bird was re-captured many times, both the relationships between Chick and Chick-capture and between Adult and Adult-capture are one-to-many relationships. Adult-capture is identification dependent on Adult, and each Chick-capture is similarly identified by one Chick.

Chicks

Several Chicks make up a Brood, but each Chick hatches in only one Brood (one-to-many relationship). Chicks are identification dependent on their natal Broods, which in turn are identification dependent on the Nests in which they are raised. Nestnumber, broodnumber, year, colony and chicknumber defines each Chick uniquely, including unringed young chicks.

Nests

There are many nests in each Location, and each Nest is in one Location, by which it is partly defined, which makes Nest identification dependent on Location. Burrows are measured with Hole-Length which is a measure taken repeatedly for most Nests during the digging phase of the breeding season. Nests were inspected regularly throughout incubation and the nestling season. There are thus one-to-many relationships between the ETs Nest and Hole-Length, and Nest and Nest-Inspection respectively, which both depend for identification on Nest. By relating Location and Observation-shedule, it is possible to establish which nests were within the vicinity of any observation period (in Obs_Sched), for example to list all nests within an observed Sublocation.

Sightings

Sighting, the central unit of behavioural observations, is made of Adults, on which Sightings are identification dependent for the identity of the focal bird (Fig. 3.4 b). Any bird associating with the focal bird is also an Adult, so that Sighting and Adult have a two-to-many relationship. Sightings are made at Locations or at Nests, and can be part of any type of observation defined by Observation-Schedule. Each Sighting can be part only of one period specified in Observation schedule, which in turn has many Sightings (one-to-many relationship). Sightings of continuous observations are defined as all those that lie between the start and end times in Observation Schedule by the same observer. This relationship between Observation schedule and Sighting is realized through the date, part of which is equal to Day in Observation-Schedule, and through the time, part of which is between Start- and End-Time.

Ecology

Ecology affects both chicks and adults (see Fig. 3.3), but the only aspect of this effect which is included in the database design is the indirect effect on the behaviour (e.g. feeding rates; for other effects of ecological aspects see design decisions). For this, Ecology is connected to Sightings through Observation schedule (Fig. 3.4 b). For each Observation schedule, there can be more than one entity of Ecology (one-to-many relationship). Ecology is identification dependent on Location, because ecological data can be collected simultaneously for different locations. Each entity of Ecology is made in one Location, but each Location can have a succession of Ecological records for different days and times (one-to-many relationship).

3.2.3 Conceptual design decisions

Many of the ideas included in the original design proved to be too complicated and impracticable in the implemented database. This was partly due to the fact that the data that were expected in this study were different from the data which it was possible to collect, because of unforseen changes in the study set-up. The original design was to deal with data of the same set of individual birds returning year after year to the same colony. Return rates were poor, however, since I had to change study colonies, so that the data I did collect were less relevant to individuals than I had expected. To retain data consistency, I tried to adjust the conceptual design rather than make changes only in the physical implementation. This resulted in many conceptual design changes during the course of the study, as the data collection developed. The most important of these are described below. This section which describes the conceptual specifications of the database, is concluded with a brief validation of the design according to the logical rules mentioned above.

Since Blue-throated Bee-eaters have extreme hatching asynchrony and brood reduction (Chapter 7; Bryant and Tatner, 1990), laying and survival should perhaps have been recorded for each egg and chick and transferred into ETs Egg and Chick, and Chick_Death respectively. The ET Egg would have included the laying sequence, per brood and egg laid. No consistent laying records were available for the nests investigated in the current study, however, and so there was no need for a relationship between laying and hatching sequence in ETs Egg and Chick. Instead, the number of eggs laid, and the date of the first egg laid, are summarized in Brood. Logically, Chick-Death should be a separate ET, because not all chicks die, but for simplification, chick deaths were instead included in Chick-captures in the attribute Dead, and also in Nest-Inspection, where an additional note was made of how long ago each dead chick was estimated to have perished (attribute Comments). This was less laborious in data manipulation at the time, but also less satisfactory for the analysis, as dates of chick deaths were not in easily available format, and the fate of each nestling in any particular brood had to be inferred separately. Similarly, an ET Adult-Death should contain all deaths of known adults or adults at known nests, where they were found, how and when they were likely to have died, and how certain was the information. Instead, some of this information was stored in attribute Dead in Adult-capture to avoid having to use difficult and lengthy queries for too little information. Only very few nestlings at the study colonies were re-captured as adults. The relationship 'chicks become adults' (see Fig. 3.3) was therefore ignored. The original expectations of high return rates would have meant that this relationship is important and should then have been included. In addition, the attribute Hatchday in ET Adult was dropped.

Genetic relatedness between Chicks and Adults who attend to them, were obtained from DNA fingerprinting results for a few broods and could be inserted into an additional ET, determining whether each attending Adult is the Chick's genetic or foster parent. The ET would contain the relatedness and a qualifier by which the relatedness was determined. It would be identification dependent on both Chick and Adult. Since for most chicks, genetic parentage was not established, however, such detail was not included here.

Observations of chicks with an endoscope inserted through the burrow, or in the artificial nest (see Chapter 7) could have been included too (Fig. 3.3). Since I had no endoscope, and the experiments in the artificial nest were analyzed separately from the remaining data, I did not include observations of chicks in the database design.

For observations of interactions (greetings, sexual and agonistic interactions) of two or more birds, ETs additional to Sighting were originally designed, where additional information which is particular to each type of interaction could be allocated, and where the relevant information from Sighting could be summarized. The ETs were called Flicker, Sexual-Interaction and Displacement. Each entity of these ETs would contain one complete interaction, whether it lasts one minute or half an hour. Displacement, for example, contained how severe the attack was overall, how long it lasted, which type (aerial, open bill, etc), who initiated it and who won (if there was a winner), whether the initiator was defending a perch, mate, food item or nest against an intruder, or if it was attacking another bird's resource. If more than 2 birds were involved in a clash, each match between two would be in a separate entity of Displacement. During this study, however, most interactions were observed in 1989 and separate ETs were not needed for my dataset.

3.2.4 Verification of the conceptual specifications

The following validation rules are met by the conceptual data models:

- Entity type names are unique: Each ET described above has a unique name.
- Attribute names are unique within each ET.
- There are no superfluous (unrelated) ETs. Each ET is connected to at least one other by a relationship (see Fig.s 3.2 a and b).
- There are no 'hanging' relationships, no superfluous relationships, no open-ended relationships and each relationship type is between two entity types. The many-to-many relationships (in Fig. 3.3) are resolved (Fig. 3.4 a and b).

3.3 Physical design

Most changes to the database that were felt necessary during the study were made to the conceptual design (see above). Therefore the physical implementation remained close to the conceptual design. Tables thus corresponded mostly to entity types, and column names to attributes, but I used abbreviated names for tables, and some value columns are coded to save space. Below is a summary of the changes made with respect to the conceptual design. First, the tables of the physical design are listed, in particular columns which were added to accommodate relations between ETs. This is followed by a description of the general changes in the Physical design decisions. A summary of the value sets are in Appendix 3.

3.3.1 Tables and columns

The changes made in the Physical Design in tables and columns, to the conceptual ETs and attributes, are listed below. This includes in particular, additional columns needed for cross-reference between tables, using the relationships then means joining tables on the additional column(s). For example, by adding the column Ring to the key in Adult_Capture and

Bird_Year (see below), these two tables can be cross-referenced with each-other and with table Adult. Identification dependent ETs use these introduced columns as 'foreign keys', i.e. these columns become part of the key used to uniquely identify a record in the table (which corresponds, in most cases, to an entity, or an individual of the ET). The key of Adult_Capture, for example, is comprised of Ring and Date, Ring being the foreign part of the key. Cross-references implement the relationships of the conceptual design.In the following, for each table a list of columns are given. Column names are in capital letters, and their corresponding attributes in brackets where different. Table names are underlined and key columns are highlighted in bold typescript.

Adult: **RING**, TAG, SEX, QUALS (Sexing Method).

Table Adult remained the same as ET Adult, except for the attribute Hatchday (see below). Each individual Adult record is of one individual bird, which is identified by its unique Ring. Each Tag from Sighting is assigned its unique Ring here, so that table Adult is referred to whenever cross-reference between observational data of marked birds (where each bird is identified by its Tag) and capture data (where individuals are identified by Ring) is needed.

Bird_Year: **DAY**, **RING**, R_N (New/ Recovery), BREEDER (Status), BROWN, GREEN, KEEL, TARSUS, H_B (Head and Bill length), B_W (Bill width), B_L (Bill length), EYES, WING (Wing length), T_L (Tail length), RINGER.

The Ring of the bird which is measured in table Bird_Year was added to the key. Ring can thus be used for cross-reference between the tables Bird_Year and Adult and therefore implements the relationship between Adult and Bird-year. Each record in Bird_Year is identified uniquely by the combined key Ring and Day (Fig. 3.5). Strictly speaking, only the year component of Day is needed for this. Ringer was added to each record so as to be able to control for inter-ringer-differences.

Adult_Capture: **DAY_TIME**, NESTID, TAG, **RING**, NR (Recapture), TAGCOND (Tag condition), BLOOD (Blood taken), BLOODTUBES, OVARY, CLOACA, COND (Condition), TS (Tail and streamer length), IA (Streamer condition), WT (Mass), MITES, BRIGHT, RINGER, HEAD, NESTNO.

Table Adult_Capture corresponds to ET Adult-capture, but has the additional columns Ring, Tag and NestID. Ring relates Adult_Capture to table Adult. Strictly speaking, Tag is superfluous, but more intuitive than Ring for the identification of individual birds. It can also be used to cross-reference directly to Sighting with column Tag. NestID contains the relationship to Nest. Each Adult_Capture is identified by the combined key Ring and Day_Time. Since each Adult is only ever captured once each morning, the time component of Day_Time is not needed for unique identification and could have been stored in a different column (as in Nest_Entry below). Time of day is important, however, for interpreting measurements like Mass, Cloaca etc in Adult_Capture. Column Nestno contains duplicate information to make easier cross-reference with some tables (see below, physical design decisions).

Chick: **NESTID, CHICKNO**, HDAY, QUALD (Qualifier of Hatchday), EXACTD (Exactness of Hatchday), COMMENTS, EXPT (Experiment), DDAY (Day died), QUALDD, EXACTDD.

Table Chick is the same as ET Chick, with the additional column NestID for cross-reference to Brood.

Chick_Capture: **DAY_TIME, NESTID, CHICKNO**, RING, N_R (Recapture), D_A (Dead), BLOOD, BLOODTUBES, ABDOMEN, TF (Tail feathers), PINS, COND (Condition), KL (Keel), HB (Head and Bill length), HOOK, B_L (Bill length), EYES, WOUNDS, WT (Mass), MITES, WING (Wing length), DAYX (Age), DAY0 (Hatchday), PLACE, DAYX_WING, MD (Mass disadvantage).

This table is cross-referenced to Chick by Chickno and NestID, which are added to the table Chick_Capture. Each Chick_Capture is referred to uniquely by NestID, Chickno and Day_Time. Various columns were added during data analysis, to simplify access and avoid excessive joining of tables, for example MD (mass disadvantage), day0 (hatch date, used to calculate age), dayx (age calculated from hatch date) and dayx_wing (age calculated from wing growth curve).

Brood: **NESTID, ADULT1, ADULT2, ADULT3, START_DAY,** QUALST (Qualifyer for Start day), END_DAY, QUALE, SUCCESS, MINEGGS, TOTEGGS, MINCHICKS, TOTCHICKS, NESTNO.

Table Brood contains the additional columns NestID and Adult1, Adult2 and Adult3 (for attending pair- and extra-pair members). Experiment role is retained in Chick and dropped from table Brood. Attribute Broodnumber was also dropped, because most nests only had a single brood. For the 2-3 nests each year which were re-used by late breeders, brood number is added to the code NestID (see below). NestID covers the relationship between ETs Brood and Nest. Each Brood is uniquely identified by NestID. Column Nestno contains duplicate information to make easier cross-reference with some tables (see Adult_Capture and below, physical design decisions).

Nest: **NESTID,** NESTNO, YEAR, SUBLOC, SUBSTRATE, FGLOC (Micro-location).

Here, the code NestID (e.g. 12-89 or 168-91-2) is specified, with the key columns Nestnumber, Year, Subloc and FGLoc. It consists of the nest number (e.g. 12 or 168) and year (e.g. -89 or -91). Colony is contained inherently both in Subloc and in nest number (up to 99 Sungai Buloh, and Nam Heng from 100, see below), and Broodnumber is added to NestID for the few Nests with more than one successive broods (i.e. -1 or -2, e.g in 168-91-2). Therefore, instead of 4 columns in a combined key, column NestID becomes the single key. This is a good simplification, both to uniquely identify each record of Nest and for cross-references from other tables.

Hole_L: **DAY, NESTID,** LENGTH, N_R (Re-measured), CURL.

Table Hole_L is the same as ET Hole-length, with NestID added, which contains the relationship to ET Nest in the conceptual design. Each burrow was measured once a day or less, so that Nest_ID and Day are the key columns of Hole_L.

Nest_Entry: **DAY-TIME, NESTID,** EGGS, SPOILED, DUMPED, CHICKS, DEAD, MAGGOTS, FOOD, NEST, COMMENTS.

Table Nest_Entry is equivalent to ET Nest-inspection plus NestID for cross-referencing with table Nest. An inspection of one nest is a record in Nest_Entry and uniquely identified by NestID, Day and Time.

Location: **COLONY, LOC, SUBLOC, PGLOC** (Micro-location).

Table Location is equivalent to ET Location. Each record specifies a micro-location within either study colony, by sub-location and location within the colony. The combined key of Location thus consists of columns Colony, Loc and Subloc. Column name PGLoc stands for Perch-Grid Location and is equivalent to the column names 'perchloc' in Sighting (e.g. rhendwire) and FGLoc ('f-grid-location') in Nest (e.g. B4). The relationship between ETs Location and Observation-schedule is implemented with the column Subloc.

Ecology: **DAY, START_TIME,** DURATION, **INDEX_TYPE,** SCORE.

Table Ecology stayed the same as ET Ecology. Different types of ecological measurements taken were e.g. Cloud Cover, Disturbances and Sun Index. This table could have been expanded to include a variety of ecological data, but this was not necessary for the present study. Each record in Ecology is uniquely identified by Day, Start_Time and Index_Type. Cross-referencing is achieved through Day and Start_Time. Table Ecology relates to observations through the table Obs_Sched.

Insect: **I_TYPE, I_SIZE,** ABS_SIZE, NSIZE.

Table Insect corresponds to ET Insect, with the added columns I_Type and I_Size to deal with the relationship to Sighting. Abs_Size contains each size in character type, 'very small' to 'very large'. Once all prey items were sized in Abs_Size, this was translated into number codes 1 (for very small) through 7 (very large) in an additional numerical column NSize. This is the main use of the table Insect, since most of the information on insect sizes is also duplicated in Sighting for ease of access (see above, design decisions).

Obs_Sched: **DAY, SUBLOC, START_TIME,** END_TIME, **OBS,** OTYPE.

Table Obs_Sched corresponds to ET Observation-Schedule. The columns Subloc, Day and Start_Time act as the combined key of Obs_Sched. Subloc is used for cross-reference to table Location, and columns Day, Start-time and End-time implement the relationships to Sighting and Ecology.

Sighting: DAY_TIME, PERCHLOC, BIRD_ID, ASSOCIATE, ACTIVITY, I_TYPE, I_SIZE, OBS.

The ET Sighting is identification dependent on ET Adult for the focal bird, which is added as a column named Bird_ID to table Sighting. From ET Adult also comes the identity of associates (in added column Associate; Associate = 0 if there is no other bird within one bird-length of the focal bird). They both link to table Adult's column Tag, which is assigned its unique Ring in Adult. From table Adult, all capture tables can be reached via column Ring. Column Perchloc specifies the relationship of ET Sighting with either ET Location or ET Nest: Perchloc contains either a Micro-location, like 'rhendwire' or a nest number. Each individual Sighting is defined by columns Bird_ID and Day_Time.

3.3.2 Physical design decisions

In the physical design, changes are made to the conceptual ETs and attributes in tables and columns which were listed above. All ETs became database tables, and attributes their columns (see previous section). Columns for cross-reference between tables are added to express relations between ETs in the conceptual design. These were in particular Ring (or Chickno) and NestID, which allow cross-referencing between records of the same individual bird or nest respectively in different tables.

While using the database, is became apparent that to split data into different tables to attain data consistency makes both data entry and data retrieval very time consuming. Updating several tables at once is tedious, and queries quickly get very complex if they involve several links ('joins'; see below). They can take a long time to 'de-bug' - even if structurally correct - and they take a long time to run. I had to save time and take short-cuts. This was necessary in this study, but it is strongly advised against, since it can seriously affect data consistency which is important for automated retrieval and maintenance of the database.

The easiest short-cut is to add columns to tables. This carries the cost of rendering the physical design open to inconsistencies because it duplicates information. Calculations which were used frequently or belonged only in one table were added to these tables as columns, for example. The mass disadvantage for nestlings at any one capture (see Chapter 7) was added to table Chick_Capture, although this is duplicate information which could, and should, be calculated from existing columns in Chick_Capture, which is very complicated and involves several steps, however.

Column names that were often used in conjunction with a particular table were added to that table, for convenience of use and to make querying easier. One such column is Nestno which contains the attribute Nestnumber only, rather than the full code NestID. Nest numbers rather than NestIDs were used in observations (Sightings), and complicated cross-references to table Nest would be necessary every time one wants to link observational records at known nests to any other breeding information. For instance, to relate feeding rates to breeding data, it was much easier to add Nest as an extra column e.g. to tables Brood and Adult_Capture, extract the year from dates in these tables (Start_Day and Day_Time) to refer to each nest uniquely, and then select records from Sighting for each nest (in Perchloc). A similar advantage of duplicating information arises from the necessity of using both rings and tags (markings) to identify individual birds, depending on whether the context is measurements or observations. This means that cross-reference between observational and dimensional data of birds is through table Adult, which is complicated to program. Instead, column Tag was added to Adult_Capture, and Adult1 to Adult3 to Brood (which also contains information of tag marking). Sightings can then be directly cross-referenced to Adult_Capture and Brood by its column Bird_ID. The information in columns Adult1 to Adult3 in table Brood is closely linked to the other information in Brood, like breeding success etc, and is referred to in retrieval queries regularly. Attending adults can be found by cross-reference from Brood to Adult_Capture and then reducing the multiple records returned. Queries would be more awkward in this structure however, and savings in storage space are not an important consideration for the present study (see below). It was decided therefore to store the information on the identity of attending adults in Brood itself.

Attribute Hatchday was dropped from table Adult in the physical design because there were too few returns of nestlings, so that the age of most adults was not known.

In order to cater better for the majority of cases, I had to leave exceptions out of the database design, introducing deviations in the logical relationships between entity types. For example, only very few adults were helpers, so there is no special allowance in the design for this. This introduces problems for cross-references. The fact that more than 2 adults can attend to a brood, for example, means that the attending adults of each Brood can not easily be cross-referenced from Adult_Capture. I worked around that by updating adult1-3 in table Brood by hand.

Initially, only the Sungai Buloh colony was monitored, but during the course of the study it became necessary to collect data from a second colony, Nam Heng (see previous chapters). Instead of including a column 'colony' in each table key, Nests from 1-99 were assigned to Sungai Buloh and nests numbered 100 and above to the Nam Heng colony. Since most nests only contained one brood, Brood and Nest could be combined into one table, where the few nests with more than one broods would have duplicate information regarding nest location. This could have been done in a further step of refining the conceptual design, or at this stage in the physical specifications. Instead, I left the two tables separate since this design did not interfere significantly with my queries. In the next section I report the next and final step in the database design: the implementation of the design by data entry and transfer into the database and using the database with queries.

3.4 Implementation and using the database

The conceptual design was changed continually as the database was being used, to accommodate changes in data collected at the conceptual level and thus retain data consistency wherever possible. Once a column is added to a table, it cannot be deleted easily in SQL, and some columns included in the original design therefore stayed in the database implementation simply because it would have been too work-intensive to clean up the database after adjusting the conceptual model to the data that were being collected. The structure of implemented tables was therefore different to the physical design structure, because some had additional columns which are not reported here. As this has mainly an effect on storage space, however, it should not be important for our purposes.

3.4.1 Data collection and entry

Most data were collected in the field in field-books (first two field seasons) and later on customized data sheets (last field season). It was then entered into the computer. Most of the observational data were assumed to have been collected at the same time for any one minute, at any one sub-colony (see Chapter 2). To ensure consistency and to facilitate the updating process, they were entered into the database together, using the 'pipedream' software facility of 'suspending activities' of the Z88 portable computer. Several spreadsheets (each containing a database table) can be kept open and updated simultaneously, and jumping between the different suspended tables is quick (one keystroke to get back to the menu, one more to get into another table, at the place where data entry was left off when 'suspending' it last) and easy (choosing the table name in the menu is by highlighting it, for example). From the Z88 portable computer, files were transferred via the Z88 import-export facility 'pclink' to an IBM compatible computer as a worksheet file for the Quattro spreadsheet, where they were edited into the standard format as specified by the database dictionary (see above, and Appendix 3) and transferred to the mainframe Unix computer at Stirling University, where the database was implemented.

Original data were read into the database, first into temporary tables with control programs which can only fill character columns. From the temporary tables, the database tables were filled with insert queries specifying other data formats (numeric and date) where required. Data which were derived from other data rather than collected in the field was updated as available, either record-by-record (e.g. Sex and QualS in Adult with results from the discriminant function analysis) or with update queries from tables that contain raw data. The update of Hatchday in Chick and Dayx and DayD in Chick_Capture was done with queries. Adult_Capture and Bird_Year were updated together at the first capture of each adult per season. The database was implemented in ORACLE/ SQL. Below I shall first introduce very briefly some of the features of the query language SQL relevant for database querying and then give an example from the database of how queries are conceived and formulated.

3.4.2 Query language SQL

SQL (or, as originally, 'SEQUEL'), is the main query language for relational databases (Ullman, 1988). It is used to create tables, store information in tables, change information in tables, to retrieve information from tables, and to format the retrieved information for reports. Here I only introduce data retrieval in SQL. More detail on any aspect of SQL and SQLplus can be obtained for example from the SQL User Guide, Version 2.0, Oracle Corporation, 1986. Data were retrieved from tables by formulating a *select statement*, which takes the basic form:

```
SELECT column list
FROM table list
WHERE certain conditions are met  (logical expression)
```

This specifies which data we want to see (SELECT), which tables we need to access (FROM) and about which entities we want information (WHERE), i.e. not all information is of interest. The conditions in the WHERE clause are specified with the use of *comparison operators*, such as

=, <, >, in (list), between ... and ..., like, is null.

These are grouped into phrases of values and operators, called *logical expressions*, which may be evaluated into a single value, e.g.

Tag = 'O6B'   or: chickno > 2

in their simplest form. It is in the more complicated conditions where the power of SQL can be demonstrated. Negative conditions are possible (e.g. WHERE NOT chickno = 1), several logical expressions can be used at the same time, connected by logical operators like AND

and OR. Sub-queries can be nested into the WHERE clause, which is where cross-references between tables are made. Cross-referencing in database query languages is called *join*ing.

Joining tables in SQL

The join operation is a common constraint. It is an artificial constraint introduced by data structuring, and it allows us to pretend that the data SELECTed is all in one table, so that splitting data in the design becomes irrelevant for its retrieval. The join operation is best explained with an example. All terms used in example queries relate to the physical data model, and the data values specified relate to data entries in the database itself. Here is an example for a join operation: to compare streamer length of males and females, statistical summaries are calculated for two subsets of data, namely birds with intact streamers for males and females separately. This can be phrased as:

```
Calculate mean, SD and N of streamer length
for sexed birds with intact streamers,
for each sex separately.
```

Birds are sexed in table Adult, and the streamer measurements (TS) are in Adult_Capture. I_A specifies if steamers are intact (I) or abraded (A). For each sex, a separate query is formulated. In the query, columns are referred to in the format Table.Column, which is necessary since columns can have the same name in different tables. For females, the SQL query is:

```
SELECT Adult.Sex, mean(Adult_Capture.TS),
     SD(Adult_Capture.TS), count(Adult_Capture.Ring)
FROM Adult_Capture, Adult
WHERE Adult.Ring = Adult_Capture.Ring
AND Adult_Capture.I_A = 'I'
AND Adult.Sex = 'F'
```

(This query is listed, with examples of selected summaries, in Appendix 4.3.b.i.) The join operation is found in the first condition:

```
     Adult.Ring = Adult_Capture.Ring.
```

Note that *joins* can involve more than one column per table and that more than two tables can be *joined* in one query. The operation joins rows in table Adult_Capture with rows in table Adult by common values in the corresponding columns, both called Ring. Thus, for each capture of each individual bird, the information for that bird in Adult (its sex and how that was obtained, mainly) is added to each capture record of that bird. It is then possible to select only those birds of interest (females with intact streamers) and the information needed (calculations concerning streamer lengths). Below I give an examples of a query derivation.

3.4.3 Algorithm of an example query

Our example investigation is a comparison of the return rates of males and females. To do this, we count all birds in the database which were sexed and which have returned to the colony between study seasons. We can formulate this as an algorithmic expression as follows:

```
Find males and females separately,
for birds for which the sex is known,
and which have records in any two different years
```

The sex of birds is recorded in table Adult, and each bird has one record in Bird_Year for each season in which it was caught at the colony. It is necessary to assume that all adults which returned were caught. This was the case at Sungai Buloh in 1989 and 1990 and at Nam Heng in 1990 and 1991. We also assume that data were entered exactly once into Bird_Year consistently, each year a bird was captured. The algorithm can then be made more specific:

```
Find males and females separately
for birds for which Sex in Adult is either 'male' or 'female'
and for which there is more than one records in Bird_Year
```

This algorithm can be expressed in an SQL-like query, which includes tables Adult and Bird_Year:

```
SELECT bird-ID, sex and count of records in Bird_Year
FROM Bird_Year and Adult
WHERE the sex of records in Adult is either 'male' or 'female'
  AND the identification of the bird is the same in Adult and
      Bird_Year
  AND the count of records in Bird_Year is greater than 1
```

The SQL query which can be executed in the database is similar to the above:

```
SELECT Bird_Year.ring, min (Adult.sex), count (Bird_Year.ring)
FROM Bird_Year, Adult
WHERE (Adult.sex like '%M%' OR Adult.sex like '%F%')
  AND Bird_Year.ring = Adult.ring
GROUP BY Bird_Year.ring
HAVING count (Bird_Year.ring) > 1
```

Note that in SQL, the constraint involving counts is specified in the 'GROUP BY...HAVING' command. Note also that SQL is not case sensitive, so it is not important whether queries are written in upper or lower case.

3.4.4 An example session of exploring data in the database

Databases are useful and at their most powerful when combining and exploring data 'on screen'. The purpose of such exploration can be to see if there are enough data for a particular analysis, to explore a few ideas, or simply to browse through the data by viewing additional data to follow through a train of thought triggered by the data that were already retrieved. The following is a documentation of a simple exploratory 'session' (see Appendix 4.12 for a listing of queries and selected records). Fig. 3.5 shows a summary of the following exploration:

I want to explore throat brightness and streamer length, both of which are morphological characters that seem to vary a lot between individuals in the field, more than other plumage scores or size variables. I first of all want to look at birds with very long streamers, so the aim is to select those birds with the longest streamers, ideally around 5 or 10 birds. In SQL, I can do this by trial and error with an 'educated guess', since I know how long streamers usually are, and gradually narrow down the constraint from > 130cm to > 150cm by editing the query each time (Fig. 3.3, First Path, start). Alternatively, I can ask for a maximum streamer length and widen the constraint from there, but again I have to edit the query with a new amount each time. Eventually, with the constraint > 150cm, the database counts 8 records which I select.

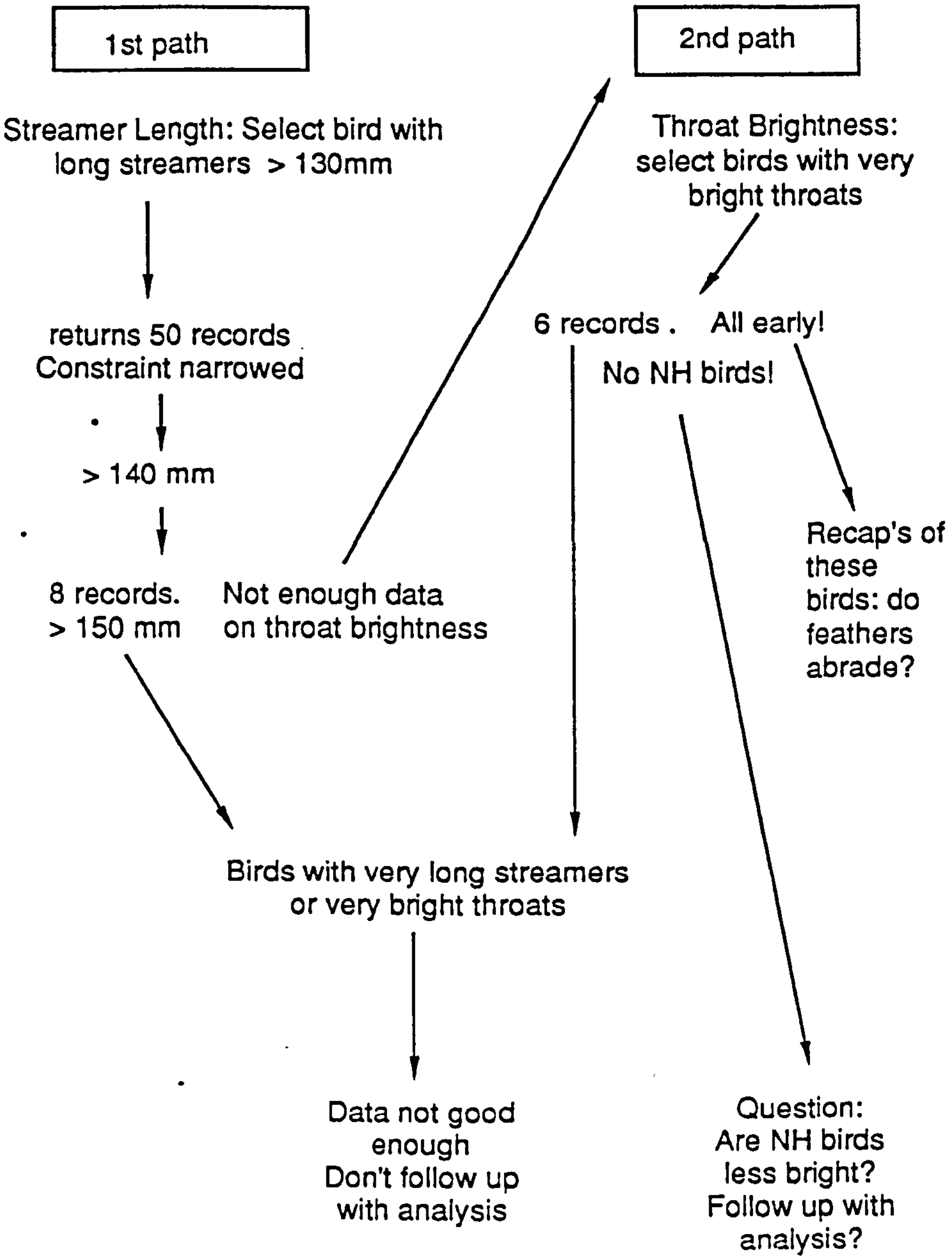


Figure 3.5: Flow diagram of the sequence in which questions were asked and queries made in the example session, to explore streamer length and throat brightness and the possibility that they might be linked (see text for details).

One of the birds with very long streamers also has a very bright throat, but the record for throat brightness for the birds with the longest streamers is incomplete. I decide to change the angle of the query and start again, this time with birds that have very bright throats (Fig. 3.3, Second path, top). Six records are returned from Adult_Capture which have 'very bright' throats. Most of these records are from the earlier season, before or during laying (mean first egg date is 13th May, see Chapter 4). Streamer feathers break and abrade during digging (pers obs), and the same might be true for throat feathers, which might account for the loss of throat brightness during the season. However, two of the 6 records selected refer to the same bird. These two records were taken a month apart. Looking at these 6 records I would like to know whether throat brightness in these birds stays the same throughout the season. To select all recapture records for each of the 5 different birds, I should use the 6 returned records either to create a *view* (a kind of temporary table used in ORACLE) with which to 'join' Adult_Capture (by ring number) to retrieve additional records for these birds, or join Adult_Capture with itself, using a long and tedious program based on the query already created. Either would be too complicated for the current investigation, so I prefer to create a query asking for all records for each of the ring numbers returned in the previous SELECT. In the selected records, 2 of 3 recaptured birds had a lower score for BRIGHT later in the season. I decide to investigate this further with a larger dataset (see Chapter 5).

Getting back to the original investigation, I ask: Do birds with very bright throats have long streamers? I now retrieve birds that have *either* long streamers, *or* very bright throats, editing a previous query. All streamers are more than 100mm long, and only one bird has a throat that is not 'very bright', but the dataset is incomplete, with missing throat brightness or streamers that are already abraded, and therefore do not give a good enough idea about the original length. I therefore decide not to follow up the initial question with an analysis.

In the records returned with the first 'bright throat' query, I noticed that nearly all birds that have very bright throats are from 1989. I may have been inconsistent when scoring, especially since I did not manage to produce a colour template against which to score throat brightness, but I remember noticing in the field that the birds at the Nam Heng colony, which was studied mainly in 1991, were more dull in general. I decide to take the matter up again (Fig.

3.3). This exploration thus triggered a formal comparison of plumage colour between colonies, which is something I had not considered on the onset of the study.

The original question yielded some interesting ideas to follow up and it gave a feel for how much data are available for a formal investigation. The number and complexity of queries, however, was considerable, which requires that the investigator is comfortable with programming in SQL and knows exactly how the data are coded.

3.5 Experiences with using a relational database

3.5.1 Using the database in the study of Blue-throated Bee-eaters

Relational databases are at their most powerful when data from different areas of research can be brought together for exploration, updating or retrieval for analysis. In the present study, I used the database for all these purposes. Example queries are given in Appendix 4. Below are listed some of the advantages and disadvantages of using relational databases both in general and during my study.

3.5.2 Advantages

Potential advantages of relational databases which are not so relevant for the database documented here include: (1) Data are securable with a password and set-protection commands, but (2) can be made accessible to other people who are using the same DBMS. (3) Quick data access: even large tables are searched quickly. (4) Multiple keys for ordering and cross-referencing are available. (5) Savings of storage and memory space. Below, I detail the advantages of relational databases most relevant to this study.

Data can be combined on a logical basis

In a statistical analysis package with powerful data manipulation abilities such as the Statistical Package for the Social Sciences (SPSSX), it is possible to add columns to one data file from another data file (this is the facility 'match files' in SPSSX). Spreadsheets like

Lotus-123 or Quattro have operators which can add or subtract values of two files while joining them, but the process of joining is similar to the statistics packages, and in both cases, joining files quickly reaches the limits of software packages. It is very difficult for example, to add environmental data (stored in one file) or catching records (in another file) to observations in another data file, because the data files have different time-scales and overall structure. In relational databases the inherent, logical relationships between data are taken advantage of, so that adding an environmental variable to observations, for example, involves only a single query (e.g. see Appendix 4.11). In relational query language, the conditions of selecting cases for inspection are efficient and versatile and reach across tables. Therefore, data can be combined for analysis with extreme flexibility.

Defined dependencies between attributes

The main benefit of having well-defined dependencies between attributes is automated updating: the values in a column can be calculated and updated using values of other columns, which may be in other tables, in a query. Updating columns with queries is usually much less laborious than updating by hand or reading-in new data. In this study, columns were derived in several cases. Hundreds of nestling ages (DayX), for example, were updated from hatch day in Chick_Capture records, with a simple query (in Appendix 4.4). Unsexed birds were sexed with an update query, if their values for the discriminant function score S fell within the 95% certainty limits for either sex, after calculating S for each bird from their biometric measurements with another query (see Chapter 5 and Appendix 4.5-7).

Simultaneous access to various files

Tables in relational databases can be compared to traditional storage files. In traditional files, however, at most one file can be accessed at any one time, making cross-references between files impossible. With relational databases, the 'join' operation described above allows cross-references between different files of different structure.

Flexible angle for retrieval

In studies with a rigid experimental design or where large datasets are available, data structure is either arranged previously to data collection, or data are input or laboriously selected and formatted once and for all, to suit one major analysis. In the present study, however, or in exploratory work, the sample sizes for some of the analyses are so low that a different sub-set of the data has to be retrieved separately for each angle of the investigation. For example, to investigate the correlation of hatching rate with fledging success, I had to retrieve a different dataset than for the effects of timing of breeding on fledging success, because hatching success *as well as* the first-egg-date were not available for all broods with known fledging success. To retrieve these two different datasets, I simply had to change aspects of the WHERE clause of one query and run it again. In most cases, retrievals of similar datasets for different analyses were therefore very easily done in the database.

3.5.3 Disadvantages and improvements on the database

In order to be able to use the database, users have to know its structure. For this it is essential that a database is well-designed and well-documented, like the Bee-eater database presented here. Without the information in sections 3.2 and 3.3, this database is almost impossible to use. Many factors interact to determine the structure of a database, so that the database structure seldom reflects the structures of the real world. These factors include storage space, access time, compatibility with other systems, control over access in a multi-user environment and data integrity (Stader and Inder, 1993). If emphasis in the database design is on data consistency to avoid redundancy, for example, information that conceptionally belongs together is split into a complicated array of different entity types and physical tables. The user has to know how these tables interrelate.

Secondly, SQL (and other formal programming languages available for formulating queries) can be so complicated and user-unfriendly that many queries which are possible are nevertheless too complicated to formulate for the average user, so that the real power of the database and its flexibility remains unexploited. In particular, few researchers will be prepared to spend hours de-bugging a query unless they really need to retrieve a specific dataset for analysis. The explorative use of a relational database, which is really where the database's main strength lies, is consequently often not utilized. The idea of treating data that are stored in different tables as if they were stored together (by using the *join* operation, see above) works in theory, but each additional constraint adds potential 'bugs' to each query.

Thirdly, the database programmer has to know the codes for values in columns. The value set used for entry into the database was changed and updated as more data accumulated, abbreviations were not always adhered to, and general inconsistencies within value sets were quite common. Because query constraints in the WHERE clause are dependent on particular column values, this makes programming in SQL even more awkward. For example, for calculations involving the onset of breeding, only Start_Days that were determined fairly accurately should be selected from table Brood, which is coded as 'hatch date' in QUALD in Chick. This information is sometimes listed as 'value sets' in the database documentation. Each user therefore has to be an expert both on the internal structure and design of the database, and on the programming language of its implementation.

To avoid these shortcomings of relational databases, it should be made possible to access data with the least possible knowledge about the physical structure in which they are stored (i.e. tables and columns), to offer requests to the users rather than to leave the programming of queries up to them, and to provide users with values to choose from.

One such solution is provided by an intelligent database access tool called Smart DataBase Access (SDBA), developed at AIAI, University of Edinburgh (Stader and Inder, 1993). SDBA was connected initially to a database used by exploration geologists. A prototype connection between SDBA and this Bee-eater database has been implemented, as reported in Stader and Stader (submitted). Originally I had hoped that SDBA would be available for querying the Bee-eater database routinely. This, however, was not possible for logistic reasons and because SDBA itself is not yet a product but a demonstrator system.

ORACLE/ SQL produces a very limited set of statistical summaries. At present, data have to be retrieved by 'spooling' the retrieval session into a print file, which is edited 'by hand' and then read into a statistical package like SPSSX. This whole process proved to be one of the most time-consuming activities in the whole of data handling and analysis.

3.6 Conclusions

As part of the study of the breeding behaviour of Blue-throated Bee-eaters, I designed, implemented and used a relational database to store and manipulate data for analysis. I documented the conceptual analysis of the data for the database design, its physical design and the database implementation. I showed how the database is used and pointed out its advantages and draw-backs, suggesting improvements to take full advantage of the database's flexibility for data retrieval and exploration.

I hope to have demonstrated how powerful - and how complicated - the use of a database can be, and that (1) without the right motivation and time for designing and prototyping, relational databases are more than a small project such as this can handle, but that (2) with proper input, a relational database can make a great difference for accessing the information that is stored in data. Relational databases are therefore useful in long-term studies where, without a relational database, a lot of the data that accumulate are underexplored simply because its organization is not flexible and the tools for retrieval not powerful enough. Given a user-friendly application, such as SDBA, to facilitate the use of the relational databases, they are very powerful tools of data storage and retrieval for exploration, analysis or presentation.

CHAPTER 4 - GENERAL ECOLOGY AND SOCIOBIOLOGY

4.1 INTRODUCTION

This chapter starts with a description of aspects of (1) the breeding ecology of the Blue-throated Bee-eater, (2) its social behaviour and (3) the structure of breeding colonies, such as the extent of 'helping-at-the-nest' and birds returning to their colonies and morphological differences between birds of the two colonies. These descriptions provide a background of breeding biology for the Blue-throated Bee-eater for the following chapters, Chapters 5 to 7, which investigate details of the mating system and nestling development.

4.1.1 Climate, weather and habitat

The breeding seasons of birds have evolved in response to temporal and spatial changes in food abundance (Lack, 1954; Crick *et al*, 1993). In the tropics, where day length is relatively constant throughout the year, seasonal changes of flora and fauna are linked not so much to day length as to climate patterns like rain seasons and droughts (Hegner and Emlen, 1987; Emlen, 1982 a; Dingle and Khamala, 1972; Lack, 1954). In this chapter, one of my aims is to illuminate the climate experienced by Blue-throated Bee-eaters and their habitat in the past and present in Malaya, and the patterns of drought and rain which affect the two study colonies. Although the rains in Malaya are not very seasonal, Dale (1974 a) lists four main seasons of two monsoons and two transitional periods (Table 4.1). Different parts of the Peninsula vary particularly in rainfall patterns. Dale (1974 a) divides Malaya into five 'rainfall regions'. In Selangor, and the Sungei Buloh colony, which lies in the West region, rain occurs mainly during the transitional periods, peaking in April and in October-November, with July (and February) as the driest months (Dale, 1974 a). Selangor is affected mostly by intermonsoonal rains of the south-west monsoon. South-east Johore, as part of the east-coast is the main target for the north-east monsoon and its long, hard rains (Dale, 1974 b). Here, the driest months may be earlier than in Selangor, starting in April, and the wettest month in inland stations is January (Dale, 1974 a). The south-west experiences more evenly distributed rainfall (Dale, 1974 a) and shorter dry spells (Dale, 1974 b). The Nam Heng colony in South Johore is situated between the east and south-west regions and may experience climate similar

Table 4.1: **The four seasons in Malaya (after Dale, 1974 a)**

season	duration	main characteristics
North-east monsoon	Nov/ early Dec - March	north-easterly winds, mostly < 25 mph
Transitional season	4-5 weeks: April(South) or May (North)	weak or variable winds or calm
South-west monsoon	(May-) June - Sept/ Oct	south-westerly winds, often subordinate to local winds
Transitional season	Oct/ early Nov	weaker winds

to that of Singapore which is transitional (Dale, 1974 a). Overall, there is therefore seasonal variation in rainfall and drought in Malaya, which is likely to affect the temporal distribution of insect food, and with that the breeding-season, of the Blue-throated Bee-eater.

Original Malaya comprised mainly Lowland and Montane tropical forest habitats and significant areas of Mangrove. Open country represented a fourth habitat type but was limited to small clearings in the forest, river edges or dunes at the east coast (Medway and Wells, 1976). Much of Malaysia's original forest has been replaced by monoculture plantations of rubber and oil-palm, and open-country habitat has been increased by artificial sites such as tin-mines and parks or suburban gardens and settlements, collectively covering as much as 50-60% of the flat lowland in the 1970s (Medway and Wells, 1976). This number has probably increased to 80-90% in the early 1990s and is highest for the Johore in the South (D.R. Wells, pers comm). On Peninsula Malaysia, Blue-throated Bee-eaters nest in open habitat, on short pasture with good visibility, such as the fringes of large rivers, suburban gardens or parkland and disused tin mines (Medway and Wells, 1976). They dig burrows in sandy substrate either on vertical banks (pers obs; D.R. Wells, pers comm) or on flat ground, as at the two study colonies. During breeding, they rely on nearby shrubland, forest edge, secondary growth around plantations, swampy and riverine habitats, and perhaps the forest canopy (Waugh and Hails, 1983) for a consistent abundant supply of aerial insect food.

Differences in breeding success at the colony level between years or localities could be a reflection either of differences in seasonal climate or of overall habitat quality. For example, the increase of monoculture plantations near colonies may reduce insect availability, or overgrowing resulting from neglect may reduce the suitability of a particular parkland for nesting. Habitat deterioration through the years would result in reduced productivity at any one colony, either in numbers of returning breeders, or in the success of breeding attempts.

Bee-eaters are known not to hunt in heavy rain (e.g. Fry, 1984), so that prolonged dense rain interferes with their feeding. Variations in rainfall duration between years or areas are common in Malaya. Dale (1974 b) reports a variation of the number of raindays per year of ±40% of the average at any one meteorological station. In Malaya, 'orographic' rain during the monsoons is characterized by heavy and extensive showers, and a common type of rain, 'convectional' or 'instability' rain, which is attributable to differential heating and cooling of the ground in unstable equatorial air temperatures at lower latitudes, and has heavy showers which last 1-6 hours, typically localized to 1-24 square miles (Dale, 1974 a). Between stations, large variations in rainfall are therefore common even in the absence of topological differences (Dale, 1974 a).

Insect populations in the seasonal tropical savanna of East Africa are known to be affected by droughts, which in turn produce food stress for Bee-eaters (Emlen, 1982 a). In a study by Dingle and Khamala (1972), insect biomass and numbers increased dramatically in samples taken during the long rains, showing that insects breed seasonally with the rains in the East-African Savanna. The authors argue that the drop in insect abundance, which correlates highly with avian breeding seasons in that area, is sufficient to trigger migration and breeding seasonality amongst insectivorous birds. Blue-throated Bee-eaters rely mainly on dragonflies (Odonata; Bryant and Hails, MS; Fry, 1984). In the savanna, dragonflies are more common in wet weather than in dry conditions (Fry, 1984), but in Malaya, the climate is generally much more humid and less seasonal, and insects may indeed be favoured, and not decimated, by dry spells (cf Fogden, 1972; Hails, 1982).

Hunting success depends on insect availability which is in turn affected by climate. Out of several meteorological effects measured by Bryant and Hails (MS), the only climatic variables that influenced the proportion of Blue-throated Bee-eaters carrying food, were rain and 'sun index': Blue-throated Bee-eaters were more likely to carry food in sunny conditions than in cloudy weather. In my investigation of hunting success I have therefore focused on the effect of local sun intensity (i.e. cloud cover and time of day, see Methods below).

4.1.2 Philopatry, survival and returns

The evolution of gregarious breeding such as in Bee-eaters depends on a high level of allegiance of individuals to their colony site both in space and from season to season: nestlings should return to their natal nest location and previous breeders should return in the following years. In European Bee-eaters, often both sexes return to the natal breeding colony, but females decamp and join the 'clan' (family group) of their male partner (Lessells *et al*, 1993). Paired males in European Bee-eaters are thus more likely to have un-paired male or female relatives close-by, whereas paired females are less likely to have unpaired relatives nearby, apart from unpaired chicks. Extra-pair 'helpers at the nest' (see below, 4.1.4) are often male relatives of one or both members of the breeding pair (e.g. Lessells, 1990). Returns of nestlings and past breeders were investigated in this study with respect to sex and return micro-site. 'Helping at the nest' is introduced elsewhere (section 4.1.4).

Kinkel (1989) reports that in a colony of Ring-billed Gulls, wing tags had both short- and long-term adverse effect on potential breeders. Return rates of tagged birds to the colony were low even four years later. Furthermore, those that did return arrived later than birds without tags; pair bonds were broken more frequently, and more than half of the tagged females that returned were rejected by the males, their social status seemingly affected by the tag. I investigated the effects of patagial wing tags on return rates of Blue-throated Bee-eaters.

4.1.3 Mate and site fidelity

Mate and site fidelity may be directly related to the breeding success of the previous season. Alternatively, pairs may stay together regardless of their immediate breeding success, for example if pair cooperation is so important overall for breeding success, that it pays to stay with a partner even if initially the success is not very high, or if in some years the breeding effort fails. Birds with successful broods in previous year(s) may be expected to breed together again in following seasons. Pairs of Kittiwakes *Rissa tridactyla* improve their breeding success with successive seasons of staying together (Coulsen, 1966). Conversely, if mate fidelity depended mainly on breeding success of the previous season, then divorce would be adaptive if reproductive success is low in the previous year and likely to increase with the new spouse. For example in Oystercatchers *Haematopus ostralegus*, divorce between seasons is more likely after low hatching success (Harris *et al*, 1987). If a bird is widowed or divorced while rearing young in the middle of the breeding season, it may seek another partner. Gjershaun (1989) reports that widowed breeding females of Pied Flycatchers *Ficedula hypoleuca* solicited visiting males into mating with them even after their fertile period.

Birds may return to a particular site or patch of the lawn (sub-colony) where they may meet with the mate of the previous year (see Tenaza, 1971), and re-establish the pair-bond as a consequence of site-allegiance, provided both partners return. This hypothesis can be tested for Blue-throated Bee-eaters by comparing maps of nest-locations and known occupancy between years. If pairs re-nested at their previous location, the site-allegiance hypothesis would be favoured, whereas if pairs were still together but did not return to their micro-site, the alternative hypothesis, that the pair bond is stronger than site allegiance, would be true. This finding would not mean that 'site' does not enter into the choice of breeding burrows or where to dig: it is possible, for instance, that the birds recognize 'bad' sites that were flooded in the previous year, or that they are out-competed by other pairs or groups if their site of the previous year was a 'good' site, perhaps in the centre of the colony (see Tenaza, 1971).

4.1.4 Helping at the nest

Cooperative breeding generally allows all participants to benefit directly from the combined effort that may, for example, reduce predation rate (Ford *et al*, 1988). In 'helping' on the other hand, the distribution of benefits is more subtle. The 'helped' individuals may benefit (1) by increasing their reproductive success in terms of number of young produced (Emlen and Wrege, 1988; Russell and Rowley, 1988; Emlen, 1982b) or in terms of growth rate of the nestlings (Dyer, 1983); (2) by decreasing the energy stress that provisioning puts on the parents especially during periods of food shortage (Reyer and Westerterp, 1985) and reducing mortality of the breeding adults (Lessells and Avery, 1987) or at least of the female (Rowley, 1986). Auxiliary birds can also help to guard the nest against cuckoldry (Payne *et al*, 1988) and predators (Stacey and Ligon, 1987, their table 6). The parents of helpers often recruit their previous offspring or other related, failed breeders through manipulation (Charlesworth, 1978; Emlen and Wrege, 1989; Emlen, 1982b).

There are also benefits of helping to the helper itself (for review of the hypotheses see Emlen and Wrege, 1989). Helping may benefit the helper who may gain breeding experience or inherit a territory or other breeding space. In spite of being fertile and therefore potentially able to raise their own brood, young breeders are often less successful than older birds

(Emlen, 1982a and 1984), for instance because they are less experienced in foraging (Heinson *et al*, 1988; Ford *et al*, 1988). In Red-cockaded Woodpeckers *Picoides borealis*, young males have a particularly low breeding success, and most helpers are male (Walters *et al*, 1988). Youngsters may have evolved to choose to stay with their parents from whom they can learn how to raise a brood successfully (Emlen, 1982b and 1984), or helping may be the better evolutionary strategy for a young bird in conditions that do not favour dispersal and breeding of young adults which are often subordinate (Emlen, 1982a and 1984). One such environmental constraint to dispersal is habitat saturation due to a limited resource (Koenig, 1981; Walters *et al*, 1988), and helpers may benefit from staying in their natal group by inheriting a territory (Rowley, 1981). This could be an 'incentive' for staying, even if there is no obvious saturation but instead some territories are better than others (Stacey and Ligon, 1987). Emlen (1982a) argues, that for White-fronted Bee-eaters, environmental constraints due to drought can have the effect of a 'limited resource' for 'helping' to increase. Lessells and Avery (1987; see also Lessells, 1990) put forward that a biased sex-ratio (towards males) may also result in more males being recruited as helpers (which in turn may affect the sex ratio itself; Emlen, 1986). Helping can also strengthen social relationships between helpers and the nestlings that are being helped (Emlen and Wrege, 1989). These may eventually be of direct benefit to the helper, either through the principle of there being strength in numbers against other family units (Ligon, 1978b), or because the helper in turn may later recruit the younger birds that it had helped to raise, in a reciprocal helping system (Emlen, 1984). In the extreme case, helpers may therefore even negatively influence long-term productivity of parents by competing with them for future helpers.

Helpers may also benefit indirectly, through inclusive fitness. Helpers in Bee-eaters are usually closely related to the resident male or female or their brood (e.g. Emlen and Wrege, 1988; Lessells, 1990; Jones *et al*, 1991). Where 'attendance' at the nest has been reported for non-relatives, the third party harassed the parents rather than 'helping' them (Crook and Shields, 1987), or the helpers' investment was significantly lower than when relatives were being helped (Reyer, 1984). The relationship between helpers and helped emerging as most common from the literature is that helper(s) are the young from an earlier brood of the pair they help (Russell and Rowley, 1988; Walters *et al*, 1988; Emlen, 1982a). Often these previous offspring have attempted to breed but failed (e.g. Emlen, 1982a; Emlen and Wrege, 1989; Lessells, 1990). Helping may thus be in the interest also of the helper through kin selection (e.g. Lessells, 1990). If the cost to the helper of not breeding, in terms of its own lifetime reproductive success, is balanced by the benefit of its action to its parents and their new clutch, because they are close relatives of the helper (Reyer, 1984), then the benefit to the helper is in terms of its inclusive fitness only (Emlen and Wrege, 1989; see also Milinski, 1978).

In this study, I recorded evidence for more than 2 birds tending a nest, with the aim to investigate the incidence and, if possible, the context of 'helping'.

4.1.5 Summary of aims

In this chapter, I investigate the general breeding biology, ecology and social biology of the Blue-throated Bee-eater, including (1) general breeding data such as breeder numbers, clutch size, hatching and fledging success, first-egg date and nestling period (2) habitat, climate and weather and their effect on the breeding season and hunting success of the Blue-throated Bee-eater, in particular solar radiation and rainfall; (3) aspects of general colony use linked to migration and the use of wing tags, such as arrival times, philopatry and return rates; (4) differences in morphology between the two colonies; and (5) some aspects typical of Bee-eater social behaviour not directly connected to pair behaviour (which is described in Chapter 5), such as the description of calls, greeting behaviour, helping at the nest and klepto-parasitism.

In the following section I introduce the methods relevant only to the results section of this chapter, which follows in section 4.3. For general methods see also Chapter 2.

4.2 METHODS

The methods used for researching aspects of general ecology and sociobiology include methods for breeding biology, habitat and foraging site survey, measurement of climate and weather, and of hunting success, return rates, arrival times, interference of marking methods, population differences in morphology and the incidence of helping. In the descriptions, the study colonies Sungei Buloh and Nam Heng are referred to in different years as colony-years, e.g. SB89 and NH91. For a listing of abbreviations and names see Appendix 1.

4.2.1 Aspects of the breeding biology

Information on eggs, hatchlings and fledglings was only available for nests at SB90, NH90 and NH91. For the analysis of fledging success, I included only those nests for which brood sizes were available.

The onset of laying (date of the first egg of the clutch being laid = Day0) was expressed as 'days after 7th April' which is the onset of laying of the earliest pair ever observed during this study (e.g. onset of laying on 8th April: day0 = 1). Day0 was either directly observed (if nests were inspected on successive days) or calculated from hatch day estimates if available: 26 days were subtracted from estimated hatch dates for the first two hatchlings (see Chapter 7). If both eldest nestlings were unaged, I did not attempt to age the clutch and excluded it from analysis involving the onset of laying. Hatch dates were estimated from age and wing length curves of first and second hatched nestlings which usually grow unrestrictedly, in their first week (see Chapter 7).

4.2.2 Habitat and foraging sites

The areas surrounding the two breeding colonies at Sungei Buloh and Nam Heng were frequently and regularly surveyed for foraging Blue-throated Bee-eaters. These areas included most of the estate in Sungei Buloh surrounding the colony, the forest and glades nearby SB, and plantations and villages in and near Nam Heng Complex. At Sungei Buloh, I covered the same route by car every few days, stopping at the same places for the same number of minutes, at different times of day, all through the breeding season and the adjacent pre- and post-breeding season in 1990. Phil Whittington spent 1-4 hours every day or two, covering most of the NH and neighbouring REM estate by car looking for Bee-eaters. To locate the birds, we made use of the fact that hunting and loafing Bee-eaters use conspicuous perches during the breeding season and their far-carrying calls can be heard very clearly. A large proportion of the Bee-eaters in the surveyed area could be discovered by driving slowly with open windows, stopping whenever a call was heard or to scan the edge of a tree-line for perching birds.

4.2.3 Climate and weather

The sample of potentially relevant climatic data given here is subject to availability from local weather stations. Meteorological stations closest to the two study colonies include 3 types of station: the principal stations of Subang and Senai airports, the climatological stations 'Universiti Malaya', 'Hospital Kota Tinggi' and 'R.R.I. Kota Tinggi', and the rainfall stations 'R.R.I. Sungei Buloh' and 'FELDA Sungei Tiram' (Table 4.2). The SB colony is about 2km from the RRI Sungei Buloh rainfall station and less than 10km from Subang Airport (Fig. 4.1), but the NH colony is quite far from the nearest station, half-way between Sungei Tiram and Kota Tinggi, with Senai Airport even further away (Fig. 4.2). Rainfall may be particularly localized, with data even sometimes differing greatly between adjacent stations (Dale, 1974 a), so that weather conditions at NH might have been mis-represented by the stations. Nam Heng weather is probably intermediate between that recorded at the stations in nearby Senai, Kota Tinggi and Johore Bahru (Fig. 4.1). Principal stations record a wide variety of climatological data, including solar radiation, whereas climatological stations cover a limited range and rainfall stations record rainfall and little else. For this study, the time during which rain falls was considered to be more relevant than the *amount* of rainfall, because dry spells are included in the former, and because Bee-eaters do not forage during heavy rainfall (see below). The number of hours during which it rained during daylight was not available, so the number of days on which it rained was used instead. Weather data used here include local cloud cover and sun index, total and mean radiation and raindays. A *rainday* is defined as a period of 24 hours, commencing 08:00 Malaysian Standard Time (MST), on which 0.1mm or more rainfall was recorded. Throughout the breeding season, half-hourly records on cloud

Table 4.2: **Meteorological stations near the two study colonies.**

Station	Latitude	Longitude	Height above M.S.L (m)	Type of station
Sungei Buloh Colony	3°07'N	101°34'E		
Kuala Lumpur International Airport (Subang)	3°07'N	101°33'E	16.5	Principal
Universiti Malaya, Kuala Lumpur	3°07'N	101°39'E	104.0	Climatological
R.R.I. Sungei Buloh	3°10'N	101°34'E	33.8	Rainfall
Nam Heng Colony				
Johore Bahru International Airport (Senai)	1°38'N	103°40'E	37.8	Principal
Hospital Kota Tinggi	1°44'N	103°54'E	9.1	Climatological
R.R.I. Kota Tinggi	1°44'N	103°55'E	15.3	Climatological
FELDA Sungei Tiram	1°34'N	103°53'E	35.0	Rainfall

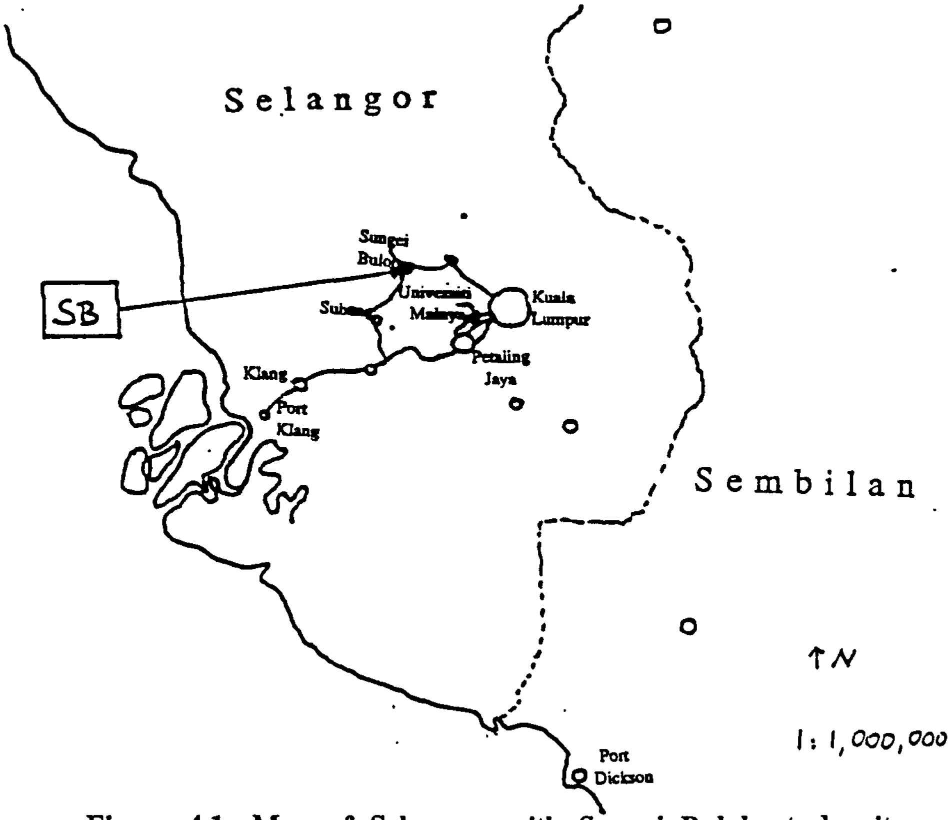


Figure 4.1: Map of Selangor, with Sungei Buloh study site and meteorological stations

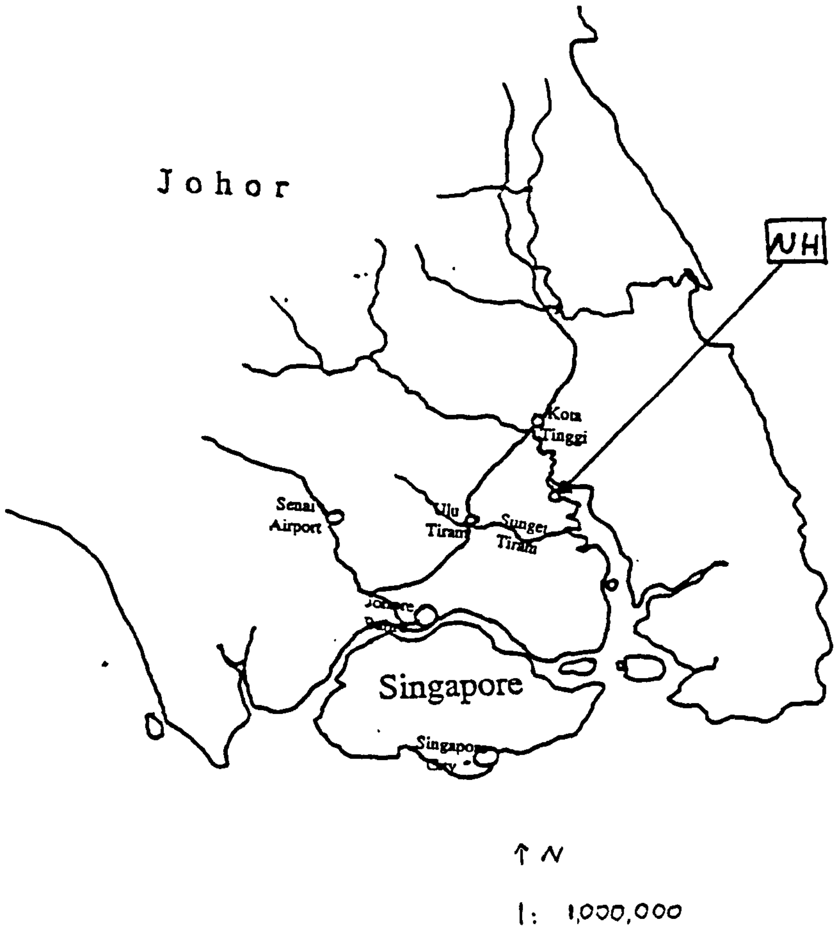


Figure 4.2: Map of South Johore, with Nam Heng study site and meteorological stations. Johore Bahru, Kota Tinggi, NH = Nam Heng, Sungai Johore, Sungai Tiram, Singapore, Ulu Tiram, Senai Airport.

cover and of the related sun index were made at the colony during behavioural observations. *Cloud cover* was scored as follows: 0 = full sun, no clouds, 1 = one or two single clouds (10-20% cloud cover), 2 = sun intermittently obscured by few clouds (30-40% cloud cover), 3 = half cloud cover (50-60%), 4 = nearly full cloud cover (70-80%) and 5 = no sun, full cloud cover. *Sun index*, the most important variable amongst those tested by Bryant and Hails (MS) which influenced feeding rates, was scored as follows: 1 = full sun and no obscuring cloud, between the times 9:00-15:00 (the part of the day with highest sun intensity); 2 = full sun and no obscuring cloud, before 9:00 or after 15:00 (when sun intensity is less), 3 = sun intermittently obscured by cloud during any time of the day, 4 = sun largely obscured by cloud during any part of the day, 5 no sun and full cloud cover during any part of the day. Sun index is highly correlated with solar radiation (Bryant and Hails, MS).

4.2.4 Feeding success

The effect of sun intensity on feeding success was assessed in two ways: (1) using sun intensity as in Bryant and Hails (MS) and (2) combined cloud cover and the hour from 12 noon (HRFR12) in multi-variate analysis. HRFR12 was calculated as absolute * (12 - hour of observation), so for observations between 12:00 and 12:59, HRFR12 = 0; observations within 11:00-11:59 and 13:00-13:59; HRFR12 = 1, 10:00-10:59 AND 14:00-14:59 = 2 etc. Feeding success was investigated using behavioural observations which were made in scans and sightings. Sightings were made in intervals of about 5 minutes within each observation period (see Chapter 2). Sightings were not statistically independent of each-other, because sightings of the same birds were made repeatedly for each value of sun index scored. Therefore, the influence of sun intensity on feeding was tested statistically with scans. Each scan can be assumed to be independent of other scans, since birds arrived and departed between scans so that a different subset of the population was present in each scan. Scans included the general population, whereas sightings were of marked individuals only (Chapter 2), which were all breeders.

4.2.5 Return rates

Adults returning to the colony are defined as those birds which have more than one record (per ring) in table Bird_Year (see Chapter 3). Birds were first captured in 1986 (by P.T. Green) and 'returned' in the seasons between 1987 and 1991. Adults of known breeding success were captured extensively only at SB89, SB90, NH90 and NH91. Returning breeders could therefore be identified from only one set of successive seasons each at SB and NH. A sample query of how returning birds were retrieved from the database is given in Appendix 4.1.

4.2.6 Arrival times

When they first arrived at the colony, most birds had either lost their tags or had not yet been tagged, so that arrival of individuals could not be investigated in general. A reasonably large number of wing-tagged birds, however, returned with tags intact in SB89, so arrival patterns were investigated for birds in this colony-year.

4.2.7 Interference of wing tags

The investigation of the effect of wing tags on return rates was based at NH90 and NH91. Birds were either ringed and wing-tagged or ringed and not tagged, and some of the untagged birds were marked with paint. I investigated the effect of wing tags on return rates. Returns of birds that had been ringed but not tagged were compared with returns of birds with tags (regardless of whether they had lost the tags). I always used both pair members in the same group, because the partner's reaction to tagging may have influenced a bird's likelihood to return (see Discussion below). As much as possible, I randomized the assignment of pairs to the 'tagged' and 'not tagged' group. For the main study, however, wing tags were used for as many birds early in the season as possible, because they were much easier to identify in the field than other marks and do not fade or break during the season. Wing tags are therefore also the most likely marking method to have any damaging effect on the birds, which is why I examined the effect of wing tags and not of other marking methods like tail-taping initially.

4.2.8 Population differences

I compared plumage, size and 'shape' of birds at SB89 with those at NH91. Overall size is often best expressed by the first principal component (PC1) of a Principal Component Analysis (PCA) using measurements of body dimensions (e.g. Lougheed *et al*, 1991). I used the PC1s of those size PCAs in Chapter 5 in which PC1s carried more than 60% of the variance in size. These were PCAs with variables (1) wing and keel lengths (WING, KEEL), (2) wing and head-and-bill lengths (WING, HB) and (3) wing length and bill width (WING, BW). 'Shape' is usually considered to be contained in further PCs (e.g. Lougheed *et al*, 1991). To include these further PCs, I conducted a PCA including *all* size variables apart from streamer length (TS), and used PC2 and PC3, which explained similar amounts of variance in biometric measurements. I used one data record for each bird, containing the mean value for all measures from 1989 (which only contained birds from Sungei Buloh) or from 1991 (where only birds from Nam Heng were processed), so that birds from different populations were also from different years.

4.2.9 Helping

The incidence of helping was determined from catching records (more than 2 birds caught at one burrow on any one day) and from observations at nests where the breeding pair was clearly identified by individual tags or taped tails.

4.3 RESULTS

Using the methods described in the previous section (4.2) and in Chapter 2 (general methods), the following results were established concerning general breeding biology; habitat, climate and weather; returns of breeders and philopatry; population differences in morphology; aspects of social behaviour; helping; and predators and ectoparasites.

4.3.1 General breeding biology

This section is comprised of general breeding data such as number of breeders at different colony-years, clutch size, hatching and fledging success, predation rates, nestling period and onset of laying. These results will be referred to whenever breeding data are required in following chapters (5-8).

Numbers of breeders

The numbers of nests recorded at the two colonies in different years are summarized in Table 4.3. In the first season, the total number of burrows with a nest chamber was underestimated because I missed the earlier breeders. The same is true for breeding records at NH90, where only a sub-sample of the colony was monitored. In the 1991 season I did not catch any adults at SB. Most pairs dig and occupy a single burrow. Some birds dig more than one burrow and some pairs take over burrows that were already dug, but in general, breeding numbers are reflected by the number of burrows with chambers. There was a decline in numbers overall at SB, especially between the last two seasons, from 20 to only 5 nests with a brood. NH was probably at least as crowded in 1990 as it was in 1991, holding in any season many more birds than SB during this study. For NH, the 100 burrows and 150 breeders in 1991 were probably typical for the colony, whereas SB declined from 400 breeders at 200 nests in 1988 (P.T. Green, pers comm) to only a few birds in 1991.

Clutch size and hatching success

At 59 nests with an average clutch size of 3.7 ± 1.5 (standard deviation, SD; range 1-7 eggs per clutch), 2.1 ± 1.5 (range 0-4) nestlings hatched. Of these 59 nests, 2 were from 1989, 15 from 1990 and 39 from 1991 (Fig. 4.3). Fifteen clutches (all but one from NH91) did not hatch any chicks. They were therefore either totally infertile, or deserted before clutch completion or during incubation. The latter is more likely, since desertion of clutches was very common in some colony-years (pers obs). Since desertion would bias hatch rates, these 15 clutches were excluded from the hatching success statistics. The remaining 44 clutches (which hatched at least one chick) had a mean size of 3.9 ± 1.1 (range 1-7) eggs (Table 4.4), from which 2.8 ± 1.0 (range 1-4) chicks hatched (Table 4.5). In these 44 broods, a total of 171 eggs was laid, of which 128 (74%) hatched. Clutch size did not vary significantly between colonies (2-way Analysis of variance ANOVA; $F = 0.299$, $p > 0.5$) or between years ($F = 0.651$, $p > 0.5$). Similarly, hatching success (using an arcsine transformation for proportions in the 2-way ANOVA) did not differ between colonies ($F = 0.110$, $p > 0.7$) or years ($F = 0.195$, $p > 0.8$). Thus, the null hypothesis that there is no difference in clutch size or hatching success between colonies or years is retained. This conclusion risks a 'Type 2 error' where real differences are not detected due to small sample sizes, in particular for SB89, NH90 and SB91. All probabilities were higher than $p = 0.5$ however, and with an overall sample size of 44, any consistent effect of year or colony should have been detected. I therefore conclude that it is permissible to pool clutch sizes and data on hatching success from different sites and years.

Of 229 eggs in 62 clutches of known sizes (including predated and expelled clutches, see Chapter 2.4.2 for definitions), 93 eggs (40.6%) in 43 clutches did not hatch and 38 (61.3%) had all or some eggs addled (Table 4.6). Fig. 4.4 shows the proportion of eggs hatched for different clutch sizes. Medium-large clutches (3-4 eggs) suffered fewer losses from addled eggs and thus had better hatching success than smaller or larger clutches. Hatching success had a tendency to be lower for clutches of more than 4 eggs (Non-parametric ANOVA; $\chi^2 = 3.363$, $p= 0.067$, $N=27$). As expected, brood size increased with absolute clutch size (Spearman correlation coefficient $r= 0.377$, $p<0.005$, $N=58$), but the number of eggs in excess of those that hatched (clutch size minus brood size for each nest) was negatively correlated

Table 4.3: Numbers of breeders at NH and SB 1989-91

	SB 1989	SB 1990	SB 1991	NH 1990	NH 1991
Total number of burrows completed (with chamber)	> 31[a]	20	12	> 33	101
Total number of nests where adults were caught	> 31	12	9	> 55	97
Total number of adults attempting to breed at burrows (caught)	> 41	30	> 0	> 61	142
Total number of broods	> 20	20	5	> 30	81

[a] >: Counts are obtained by nest visits and captures and are underestimates because of incomplete records

Table 4.4: Clutch size means (±SD) for the colonies NH and SB in 1989, 1990 and 1991. None of the differences was significant (see text)

	1989 mean	N	1990 mean	N	1991 mean	N	total mean	N
SB	5.0 ±0.00	2	4.3 ±1.07	14	4.0	1	4.4 ±1.00	17
NH	-	0	4.0 ±0.00	2	3.6 ±1.04	25	3.6 ±1.01	27
total	5.0 ±0.00	2	4.3 ±1.00	16	3.6 ±1.03	26	3.9 ±1.06	44

Table 4.5: Means of hatching success (chicks hatched per eggs laid) for the colonies NH and SB in 1989, 1990 and 1991. None of the differences was significant.

	1989 mean	N	1990 mean	N	1991 mean	N	total mean	N
SB	0.70	2	0.69	14	0.50	1	0.68	17
NH	-	0	0.63	2	0.79	25	0.78	27
total	0.70	2	0.68	16	0.78	26	0.74	44

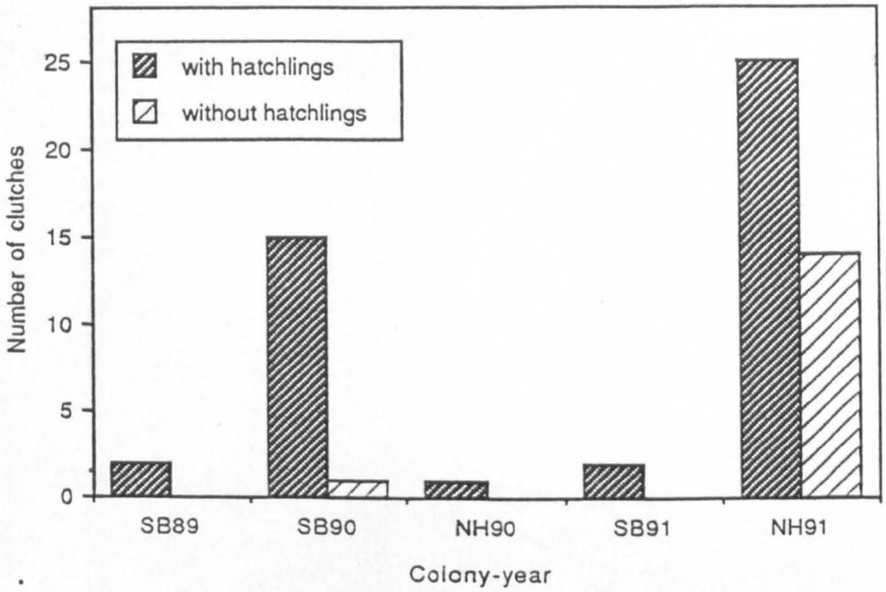


Figure 4.3: Number of monitored clutches with and without hatchlings, at colony-years SB89, SB90, NH90, SB91 and NH91.

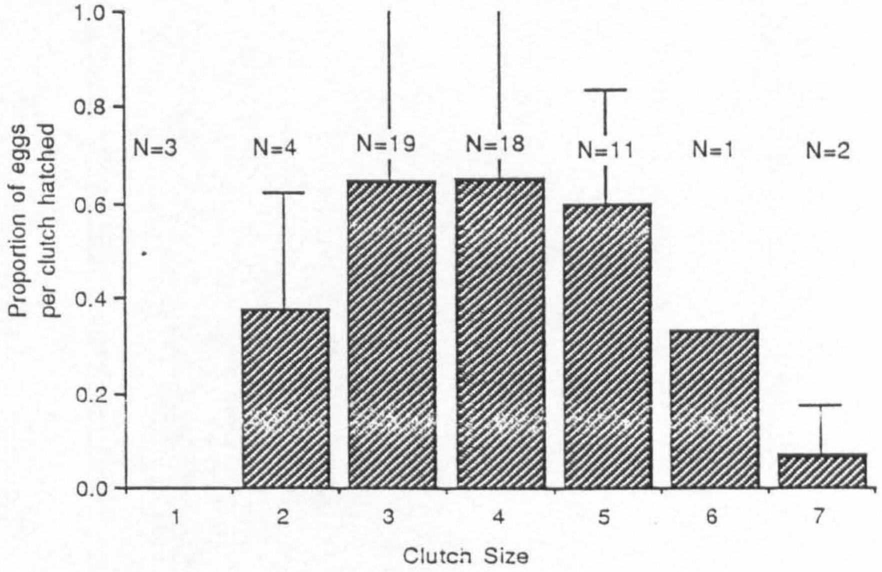


Figure 4.4: Mean hatching success (+SD) for different clutch sizes. These are significantly different: Kruskal-Wallis non-parametric ANOVA, $\chi^2 = 10.296$, $p < 0.05$, N = 58)

with brood size (Spearman correlation coefficient r= -0.695, $p < 0.001$, N=58). This meant that small broods often came from large clutches, while large broods hatched from clutches of intermediate size. There were 16 clutches in which all eggs hatched, out of 58 (27.6%) or, excluding deserted nests, out of 44 clutches (36.4%); all clutches with all eggs hatching had either 3 or 4 eggs. Thus, hatching rates are compatible with those found previously (1981 and 1985) at SB by Bryant and Tatner (1990). Clutches of 5-7 eggs probably hatch fewer chicks than clutches of 3-4 eggs (Fig. 4.4). Smaller clutches, of 2 eggs, on the other hand, cannot hatch more than 2 chicks by definition, and losing one is a higher proportion for these. Clutches of 3 or 4 eggs therefore hatched the most chicks and, furthermore, were the only clutch size from which all eggs hatched. The most successful clutch size both for percent hatching success and the absolute number of chicks hatching was therefore an intermediate 3 or 4 eggs. For broods of less than 5 chicks, 3-4 eggs was also the most frequent clutch size.

Predation rates

Only 2.2% of eggs (N=229) and 3.2% of complete clutches (N=62) were predated (Table 4.6). The predation rate on broods of chicks was 7% (4 of 55). In each colony-year, a similarly low number of nests (0-2) was recorded as predated, regardless of the total number of monitored nests, which varied from 3 to 37 (Table 4.7). The numbers of nests predated was respectively 0 of 3, 1 of 4, 1 of 11 and 2 of 37 nests. Apart from SB89 (only 3 nests monitored out of more than 40 nesting attempts, see Table 4.3), the relative number of nests monitored in each colony-year corresponded to the relative colony sizes (cf Table 4.3), the probability of being predated thus varied for nests in different colony sizes from 5% (large colony, NH91) to 25% (small colony, SB90). Predation rate per nest is therefore lower in larger colonies. These predation rates, however, may be under-estimates, because only whole clutches or broods were considered as predated, whereas it is likely that single eggs or single chicks were also predated occasionally (see Chapter 2).

Fledging success

The number of nests that fledged one or more chicks, varied between 2 out of 2 (in NH90) and 18 out of 32 (in NH91) of clutches (Table 4.7 a) and between 3 out of 3 (NH90) and 26 out of 35 broods (Table 4.7 b). The proportion of successful nests (1 or more chicks fledged) did not vary between SB90, NH90 and NH91 (χ^2 tests, Table 4.7). In Table 4.8 fledging success is given per year and colony. (Note that SB89 is added here, so that total numbers do not agree with those in Table 4.7 b). Most of the successful nests had only one nestling. I compared two aspects of overall fledging success between the colony-years in a series of 2-way χ^2 tests (to include Yate's correction), testing each colony in Table 4.8 with the other colonies combined, to increase sample sizes. Overall fledging success (nests with and without fledglings) did not vary significantly between years or colonies (Table 4.9). Considering, however, that sample sizes were very small, the percentage of nests with 2 or 3 fledglings may be lower in NH91 and higher in SB90 than in the other colony-years. Since the number of nests with more than one fledgling tended to be greater in SB90 and smaller in NH91 than in other colony-years, while the proportion of successful nests with fledglings was not affected by colony-year differences, it seems that the number of fledglings was more seriously affected between different colonies and years than the incidence of fledging itself.

Most nests fledged one chick only (56%), and only 19% of nests with chicks fledged more than one chick. The number of fledglings seems only slightly related to brood size (Fig. 4.5). There was no significant difference in brood size at hatching between (a) unsuccessful nests, (b) those that reared only one fledgling and (c) those that fledged more than one chick (non-parametric ANOVA; $\chi^2 = 4.568$, $p>0.1$, $N=31$). If post-hatch failure due to nestling starvation was random with respect to brood size, any such difference would have been masked. Only broods of 3 and 4 nestlings fledged more than 1 chick (Fig. 4.5). This brood size difference was nearly significant if compared with broods that fledged a single chick ($\chi^2 = 3.806$, $p= 0.0511$, $N=22$), indicating that broods of 3-4 hatchlings fledged more chicks than broods which were smaller at hatching. No nest with 2 nestlings fledged both, but one brood of 3 fledged successfully. Some broods of all sizes failed, and the only brood size that perhaps fledged more chicks than average were broods of 4 ($\chi^2 = 3.196$, $p= 0.074$, $N=31$). All other comparisons of fledgling numbers and brood size showed no significant differences.

In summary, in most clutches 3 chicks hatched, but only one chick fledged. Broods of all sizes can fail, but only large broods (3-4 chicks) fledged more than 1 nestlings. It seems that the optimum brood size to produce the most fledglings is 4, as these have nearly significantly

Table 4.6: The fate of all eggs which did not hatch. Less than half of all eggs (40.6%) did not hatch from nearly 70% of the broods, because most broods had one or more addled eggs.

fate	% of eggs	% of broods
spoilt	34.5%	61.3%
expelled	3.9%	4.8%
predated	2.2%	3.2%
total not hatched	40.6% (N = 229)	69.3% (N = 62)

Table 4.7: Number and proportion of nests (a) with eggs and (b) with chicks that produced fledglings

Nests fledging 1+...	SB90	NH90	NH91	total
(a) ...out of clutches (nests with eggs)	6/9(10)[c]	2/2(3)	18/32(38)	56% (47%) 24/43(51)
(b) ...out of broods (nests with chicks)	9/10(11)	3/3(4)	26/35(37)	79% (74%) 38/48(52)

(a) χ^2 (SB90, NH90, NH91) = 1.690, p>0.4 (ns), N=43
(b) χ^2 (SB90, NH90, NH91) = 2.007, p>0.3 (ns), N=48
[c] () = inclusive of nests that were predated

Table 4.8: Number of chicks fledged in nests with hatchlings. There was no significant difference between colonies or years (see Table 4.9)

Fate	SB89	SB90	NH90	NH91	total
Fledged 1	2 (67%)	5 (46%)	2 (50%)	22 (60%)	31 (56%)
Fledged 2	1 (33%)	2 (18%)	1 (25%)	4 (11%)	8 (15%)
Fledged 3	0 (0%)	2 (18%)	0 (0%)	0 (0%)	2 (4%)
Successful	3 (100%)	9 (81%)	3 (75%)	26 (71%)	41 (75%)
All starve	0 (0%)	1 (9%)	0 (0%)	9 (24%)	10 (18%)
Predated	0 (0%)	1 (9%)	1 (25%)	2 (5%)	4 (7%)
Unsuccessful	0 (0%)	2 (18%)	1 (25%)	11 (29%)	14 (25%)
Total	3 (100%)	11 (100%)	4 (100%)	37 (100%)	55 (100%)

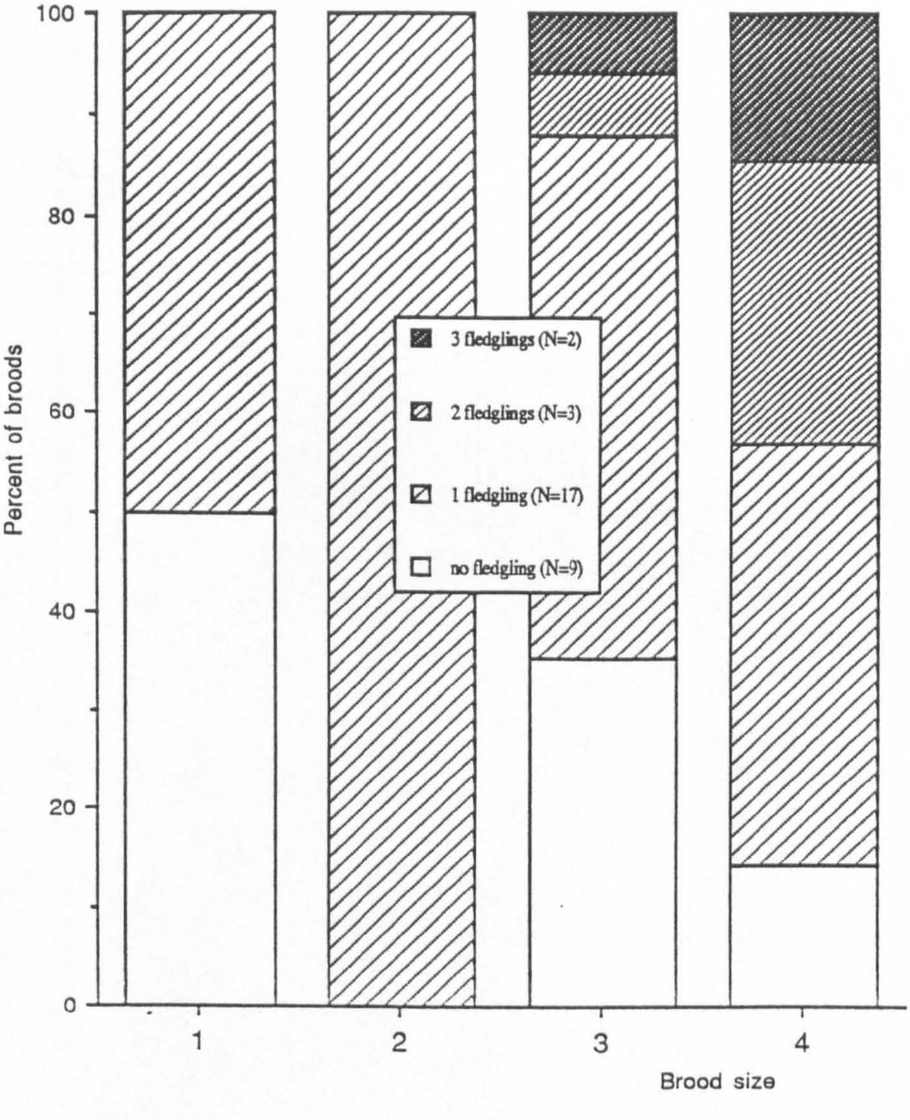


Figure 4.5: Percent of successful (1-3 fledglings) and unsuccessful (0 fledglings) broods compared to their brood size. (N for Brood size 1 = 4, N for Brood size 2 = 3, N for Brood size 3 = 17, N for Brood size 4 = 7; overall N = 31).

higher fledging success than broods of 1-3 chicks combined. In order to get a brood of 4, 4 eggs should be laid; more eggs do not guarantee higher hatchling success. Most birds, however, hatched 3 chicks rather than 4. The observed optimum brood size of 4 was therefore larger than the most frequent brood size of 3.

Nestling period

Nestling period is the time from hatching to fledging that a chick spends in the nest. The nestling period was estimated from nestling age at fledging. Nestling age was determined as in Chapter 7, from an age-size curve specific for its place in the nestling hierarchy, and the estimate obtained at the earliest date of capture before the age of 14 days (usually much earlier, see Chapter 7). A chick was assumed to have fledged when it disappeared from the nest without trace between two visits after the age of 22 days (see 2.4.2). For 3 nestlings, the exact fledging day was determined by daily checks as 29, 30 and 31 days (mean = 30). The fledging day of a further 12 chicks was known within 2-5 days; for these the mean of the middle day was 31 (± 2 days, SD). For 4 chicks, the nestling period was at least 33, 34, 40 and 40 days, and 4 more were known to have fledged after less than 26, 27, 29 and 29 days respectively. The mean nestling period was therefore 30-31 days, ranging from 26 to 40 days.

The mean onset of laying (Day0)

The first egg date (Day0) was calculated for most nests from nestling hatch dates, which were in turn calculated from age-size curves (Chapter 7; and previous sub-section). To evaluate how good these estimates were to establish Day0, I visited 32 broods during laying and noted all eggs appearing between any two visits, and compared direct laying observations with estimates made subsequently from hatch dates. All observations on laying dates were incomplete because I could not visit nests daily, so that for most nests only an estimate of the first egg date was available. For most broods, the estimate of Day0 from hatch dates fell within this period within which the first egg date was (N=26, 81%). For 3 broods (9%) the estimate from hatch day estimates was too early (by at least 1, 1 and 3 days respectively), and for another 3 broods (9%) the predicted onset of laying fell at a later date than within the observed period (by at least 1, 3 and 9 days). Most estimates of Day0 were thus acceptable, and there was no directional bias in estimates of Day0 from hatch dates.

This evaluation of the estimates of the onset of laying from hatch date estimates assumes that an egg is laid every day or two (in 2 broods, more than one egg appeared per 2 days, as would be the case when eggs are dumped, see Bryant and Tatner, 1990), and that later eggs may sometimes appear at intervals of more than 2 days (N = 3 broods). This can create a bias of the estimates of Day0. Egg 'dumping' by intra-specific nest parasites (see Chapter 6) could create bias in the calculations to age chicks (Chapter 7), which again would bias Day0 calculations, except that Day0 was usually calculated from the first hatchling, and 'dumped' eggs do not normally hatch first (see Chapter 6).

Day0 was determined mostly from hatch dates for a total of 89 broods at colonies SB and NH between 1989 and 1991. The mean Day0 for all broods across colonies and years was 13th May (day 36), ranging from 8th April (day 1) to 13th July (day 97) when the first broods are fledging, showing a roughly normal distribution with most pairs laying near the mean day0 (Fig. 4.6). Yearly means show a trend to become earlier between 1989 and 1991, and NH birds tended to lay about 9 days before pairs at SB (colony means; Table 4.10). A nine day difference in the onset of laying between colonies was probably an over-estimate, however, since they co-vary with yearly differences: the earlier records from 1989 with later Day0s were all from SB, whereas the laying dates from 1991 were from NH. In 1990, NH birds were 4 days earlier than SB pairs, with a mean Day0 of 14th May (day 37) compared to 18th May (day 41). Similarly, part of the apparent advance in laying date over the years was probably due to changing study site from the generally later laying SB in 1989 to the earlier laying NH in 1991. None of these differences was significant, however (two-way ANOVA of Day0 between years and colonies; all $p >> 0.05$). Therefore, the 13th May was used as average first egg date for the complete study in all further analysis.

Fledging success and first egg date

Early breeders (determined by their first egg date) were no more likely to fledge one or more nestlings in any of the 3 study seasons, except perhaps in NH91 where Day0 in nests with

Table 4.9: Fledging success between colonies and years
2-way crosstabulation statistics (incl Yates correction) for data in Table 4.8. Each colony-year was compared to the rest (pooled)

	colony-year	χ^2	p
(a) general fledging success	SB89	0.129	0.719
(no versus 1 or more chicks fledged)	SB90	0.054	0.816
	NH90	0.000	1.000
	NH91	0.509	0.297
(b) proportion of nests that fledged	SB89	0.000	1.000
0-3 chicks	SB90	1.718	0.190(*)
	NH90	0.000	1.000
	NH91	2.754	0.097(*)

Table 4.10: Means for date of first egg laid (Day0) for colonies and years and per fledging success per year. Dates are given in 'days after 8th April inclusive', day 1 = 8th April , ± SD, N= number of nests. 0 fledged = nests in which eggs hatched but no chick fledged (including predated broods), 1 fledged = 1 chick fledged, 2 fledged = 2 chicks fledged.

	1989	1990	1991	Colony means
SB	25th May (day 48 ± 8) N=4	18th May (day 41 ± 22) N=12	-	20th May (day 43 ± 19) N=16
NH	-	14th May (day 37 ± 13) N=19	10th May (day 33 ± 22) N=54	11th May (day 34 ± 20) N=73
Yearly means	25th May (day 48 ± 8) N=4	16th May (day 39 ± 17) N=31	10th May (day 33 ± 22) N=54	13th May (day 36 ± 20) N=89
0 fledged	-	13th May (± 14) N=4	15th May (± 22) N=23	
1 fledged	19th May N=1	21st May (± 20) N=10	5th May (± 21) N=20	
2 fledged	-	11th May (± 20) N=2	8th May (± 6) N=3	

at least one fledgling was 6th May (± 4.6 days, N=23), and Day0 in nests which had chicks but fledged none was 15th May (± 4.1 days, N=23, including predated broods; t=1.45, p = 0.155). The means per year are summarized in Table 4.10 (bottom).

4.3.2 Habitat, climate and weather

Habitat and foraging sites at Sungei Buloh

On the grounds of the Rubber Research Institute (RRI), the vegetation predominantly consisted of rubber plantations (Fig. 4.7). Maps of the RRI grounds and surrounding areas were not available. In Malaysia maps are often military classified material. I never heard or saw any Bee-eaters in the closed canopy of mature rubber tree plots. In the remaining plantations, rubber trees were of different ages and sizes, interspaced with small islands of mixed vegetation and with open spaces near small lakes or rivers or where young rubber trees were growing. Some foraging Bee-eaters were found in such areas, especially edges and clearings near pools and ditches. They were in groups of 3-6, perching on the taller trees around the edges of open spaces, hunting and loafing or calling. No tagged birds were found, but on two occasions I noticed rings on foraging birds, which had probably been caught previously at the colony. Since most breeders at SB90 were tagged, these ringed foraging birds could have been past breeders which returned to the colony in 1990 but did not breed. Although some of these birds could have been breeding solitarily nearby those hunting grounds, there were other indications of the presence of a population of non-breeding 'floaters'. Early-on in the season, groups of birds visited the colony on occasions. I caught some of these birds by mist-net in 1989 and tagged them (see Chapter 2), but none of them stayed to breed.

The built-up areas near the Sungei Buloh colony were rural: established *kampongs* (villages) and recently cleared areas of forest where more village houses were built. There were some rubber and oil-palm plantations. Some lowland forest nearby was still intact but disturbed and under a lot of logging pressure, increasingly so from 1989 to 1991, when chain-saws could be heard in some part of the forest nearly every day. In the forest adjacent to the RRI plantations, there were several established glades and open spaces of secondary forest, where

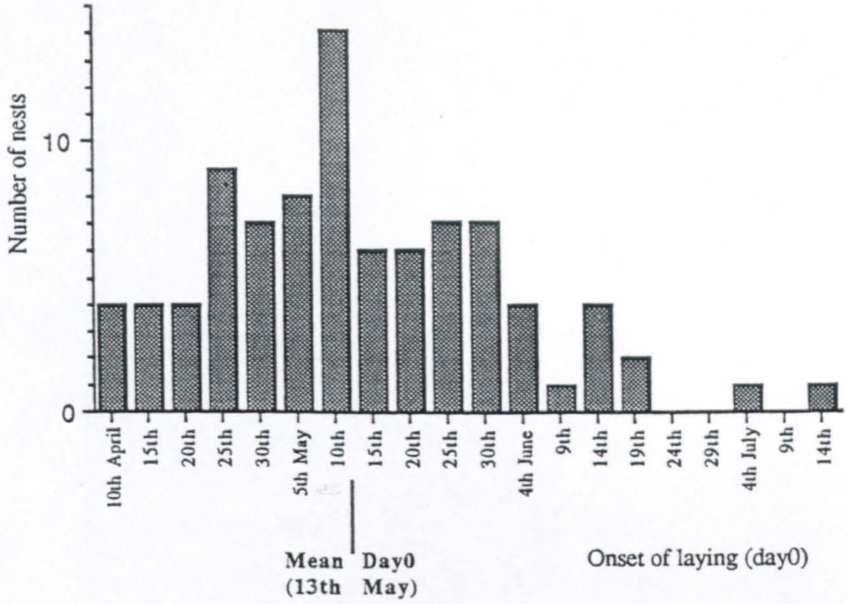


Figure 4.6: The distribution of the onset of laying (first egg date; Day0; see text)

Figure 4.7: Mature Rubber trees in a plantation at Sungei Buloh, Selangor, Malaysia.

I found Bee-eaters on occasion after the breeding season, but never any foraging Bee-eaters during the breeding season, despite regular visits.

Habitat and foraging sites in Nam Heng

The Nam Heng Complex and most of the neighbouring estates were nearly exclusively oil-palm monocultures. Old oil-palm (Fig. 4.8 a) support little else apart from rodent pests (rats *Rattus* spp and squirrels *Sciurus* spp) and their predators (Barn Owls *Tyto alba*; Duckett, 1976). Bordering some of the oil-palm plots were rubber trees, remnants of secondary rainforest or mangrove forest. Nam Heng lies on the Johore River, which at that point is a slow-flowing stream bordered with established mangrove. Immediately opposite the colony lies an island with undisturbed mangrove forest, and the Bee-eaters were sometimes seen flying off in that direction. I did not have the opportunity to visit the island to investigate whether it constituted a major foraging site. Several areas near the NH colony where Bee-eaters were hunting were identified (see Fig. 4.9). *REM Swamp* had secondary forest, a pool of water with adjacent swamp-like conditions (and plenty of dragonflies) and some remnant rubber trees; *REM Rubber* was on the edge of a plot of rubber trees, and *REM Clearing* encompassed a large area of several hectares of recently burnt oil palms (this remains a common method to clear old plots for re-planting; the other method is poisoning of old trees) and scanty vegetable plantation, with banana palms, rubber trees and oil palms at the edges on which the birds perched (Fig. 4.8 b). The three areas *REM Swamp*, *REM Rubber* and *REM Clearing*, were situated on the REM estate neighbouring Nam Heng Complex (Fig. 4.9). Bee-eaters were also seen in *NH Garden*, which is the area around the detached houses where we were accommodated in Desa Dua (Fig. 4.9). *NH Garden* had small areas of short-cut 'lawns' like that of the colony sites, and with wires and single trees on which birds could perch, but with plantations on either side of the roads. Occasionally, sightings of Bee-eaters were made at *NH River* and *NH Village* (Fig. 4.9), which were both relatively open areas without the typically dense oil-palm. As in Sungei Buloh, these sites all lacked dense vegetation such as established monoculture (i.e. old oil palm or old rubber trees), which were largely avoided by the Bee-eaters. The sites also had good visibility in common and perches at the edge, from which the Bee-eaters can survey for passing insects.

Figure 4.8 a: Mature oil palms (15-20 years old) of the Nam Heng Complex plantation.

Figure 4.8 b: REM clearing, one of the foraging areas of *M. viridis* within 5km of the colony, where non-breeding birds tagged at the colony were occasionally found hunting.

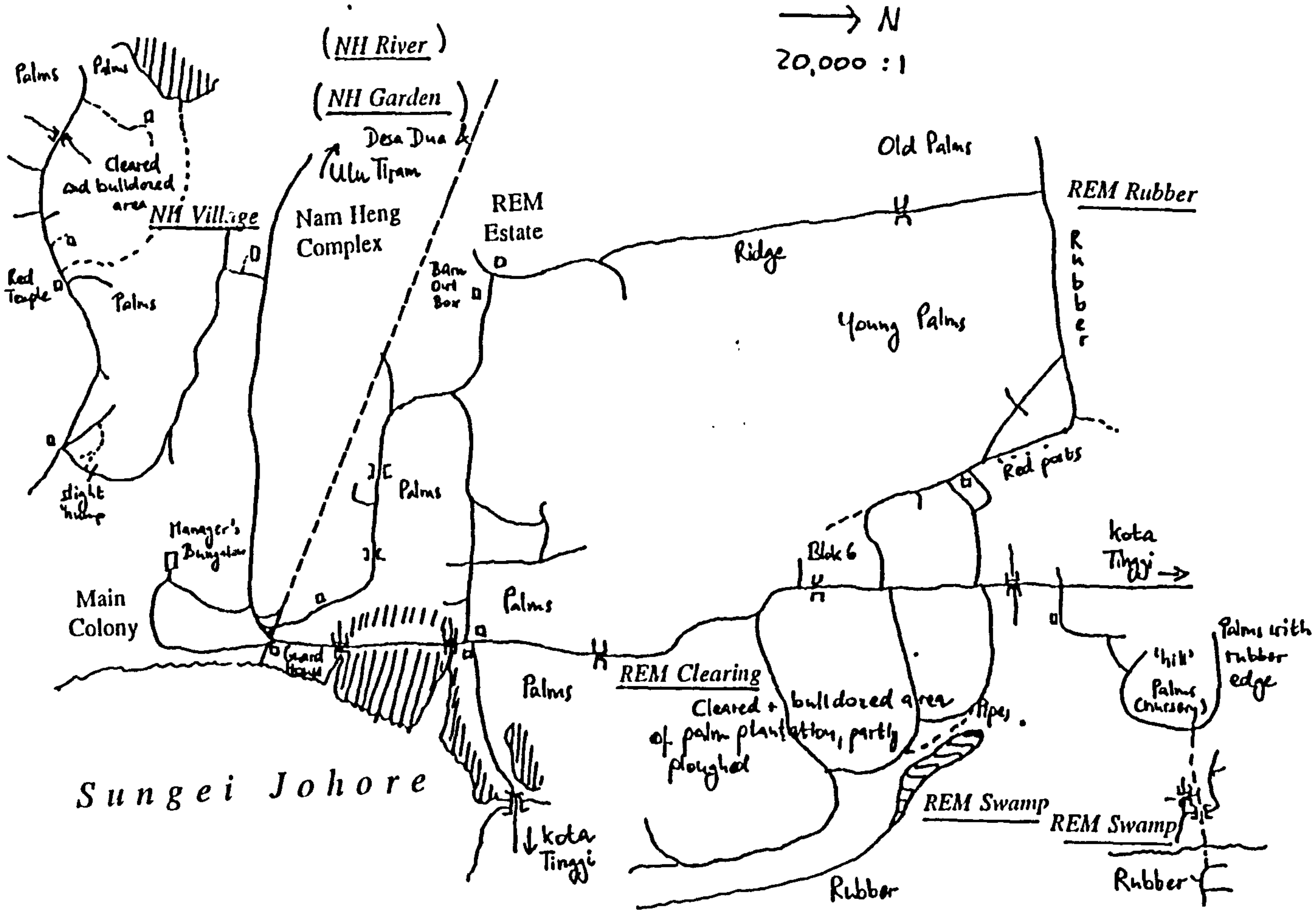


Figure 4.9: Map of Nam Heng complex and the neighbouring REM estate showing the NH main colony site and foraging areas of Blue-throated Bee-eaters (some of which were marked in the colony).

//// remnant mangrove;][bridge; | road; ¦ track; □ bulding.

The total number of Blue-throated Bee-eater sightings made at foraging sites was 377. Forty-nine of these were of 9 identified birds with readable tags on 6 different days between 18th June and 3rd July 1991. Six of those 9 birds were foraging at the rubber plantation in the REM estate (*REM Rubber*) and one each at the sites *NH River*, *REM Swamp* and *REM Clearing* (Fig. 4.9). All birds were only seen during one observation period each; except one bird which was seen at *REM Rubber* on two successive days. It was therefore impossible to establish whether these birds were feeding in home-ranges or territories, or whether they opportunistically followed each-other or patches of insects within a colony home range. All of the 9 birds were first tagged in 1991. Four birds were probably feeding chicks at the colony during the time when they were seen hunting (all at *REM Rubber*). Two of them were probably members of the same pair (the identity of one of the partners was not clearly established), and both were spotted hunting at the same site but on different days. One of these four chick-feeding adults was feeding a recent fledgling from a known burrow at the colony, which, judging from the breeding record, was the first of two. One further bird had fledged its nestlings before it was spotted hunting at *REM Rubber*, i.e. it was a post-breeder. The three other birds were probably failed breeders - the nest of one of them had not been investigated, probably because no activity had been recorded there for several weeks. Two of these were seen at *REM Rubber*, one at *REM Clearing* and one at *REM Swamp* respectively. If breeders (including post-breeders and failed breeders) and floaters hunt at different sites, then *REM Rubber* was the only 'breeder' site, whereas *REM Clearing* and swamp were possibly 'floater' sites. In *NH Garden*, we regularly saw an unmarked pair feeding one or two fledglings during late June and early July. These birds did not have rings and were therefore probably not from the main colony, but were nesting either solitarily nearby or at the 'fringes' of the NH colony, where fewer of the breeders were ringed. Bee-eaters were found nesting solitarily on two occasions, near *NH Village* in 1991, and near the main colony at SB in 1989, about 100m into a young oil-palm plantation. These birds were not caught and therefore not ringed or tagged and their nests were not investigated.

Climate and weather

There were some overall similarities across years in seasonal rainfall not only between different stations near the same colony, but also between the two study colonies. After a particularly dry spell in January and February with very few raindays, the Bee-eater breeding season started off particularly wet: some of the wettest weather occurred during April and May, during digging, laying and incubation. This was particularly so in SB91 (both Subang and Sungei Buloh rain patterns), and in Kota Tinggi near NH, in 1989 and 1990, all of which had over 20 raindays in April and May (Figs. 4.10 a and b). In June and July, most stations near both colonies had only about 10 raindays per month on average (Figs. 4.10 a and b). Kota Tinggi recorded more raindays in general. At the stations relevant for the SB colony, the lowest number of raindays occurred in February, and in June/July during nestling rearing. In Sungei Buloh, September had 15-20 raindays, a sharper increase than at Nam Heng, where the number of raindays stayed below 15 per month for most of the time (Kota Tinggi excepted). SB89's rain pattern was very 'even': the early season in April and May was not wet, but June had more raindays than usual, followed by an early start to the wetter season in August. SB91 on the other hand had strong rains in the wet season (April/May) followed by dry conditions in June. NH90 did not have consistent rain days between its weather stations, even if Kota Tinggi is excluded. Sungei Tiram had quite a wet start to 1991. There were therefore large variations in the number of raindays per month between colonies and years. The local difference in raindays between weather stations near the same colony furthermore implies that Bee-eaters could be selecting favourable 'weather patches' on a daily basis.

Bee-eater breeding seasons were not strikingly sunny at either colony (Figs. 4.11 a and b). Mean daily and total monthly solar radiation during the breeding season for different seasons during the study period show the high values for Senai 1990 in March, and consistently low radiation in Senai 1989 (Figs. 4.12 a and b). Subang was perhaps generally slightly sunnier than Senai during the Bee-eater breeding season. Data from Senai Airport may, however, be not very relevant to the NH colony. In Singapore, which is of similar distance to NH as Senai (Fig. 4.1), Chia (1974) showed not only a larger amount of daily sunshine from March until August (his fig. 6.3), but also a pattern where a 'window' of the highest amount of sunshine appears in March to April, between 08:00 and 10:00 a.m. (his fig. 6.5). This may be the window exploited by breeding Bee-eaters.

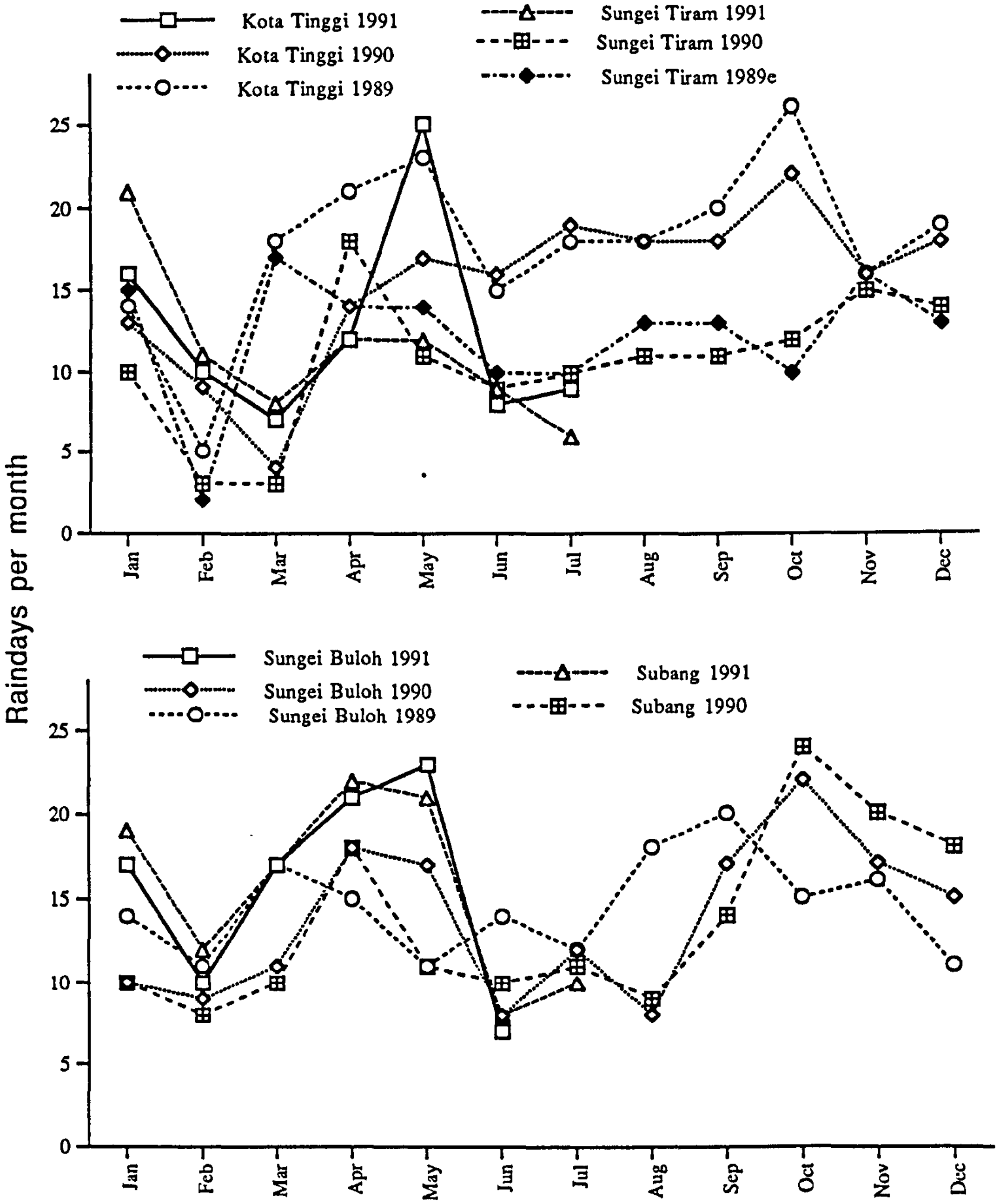


Figure 4.10: The number of raindays (defined as a period of 24 hours, commencing 08:00 Malaysian Standard Time (MST), on which 0.1mm or more rainfall was recorded) per month, as distributed throughout the year, for the 3 years of this study as available, at weather stations nearby the study colonies. (a) Nam Heng and (b) Sungei Buloh. This is to give a general picture of seasonal similarities and differences at the two study colonies and at the weather stations near each of them.

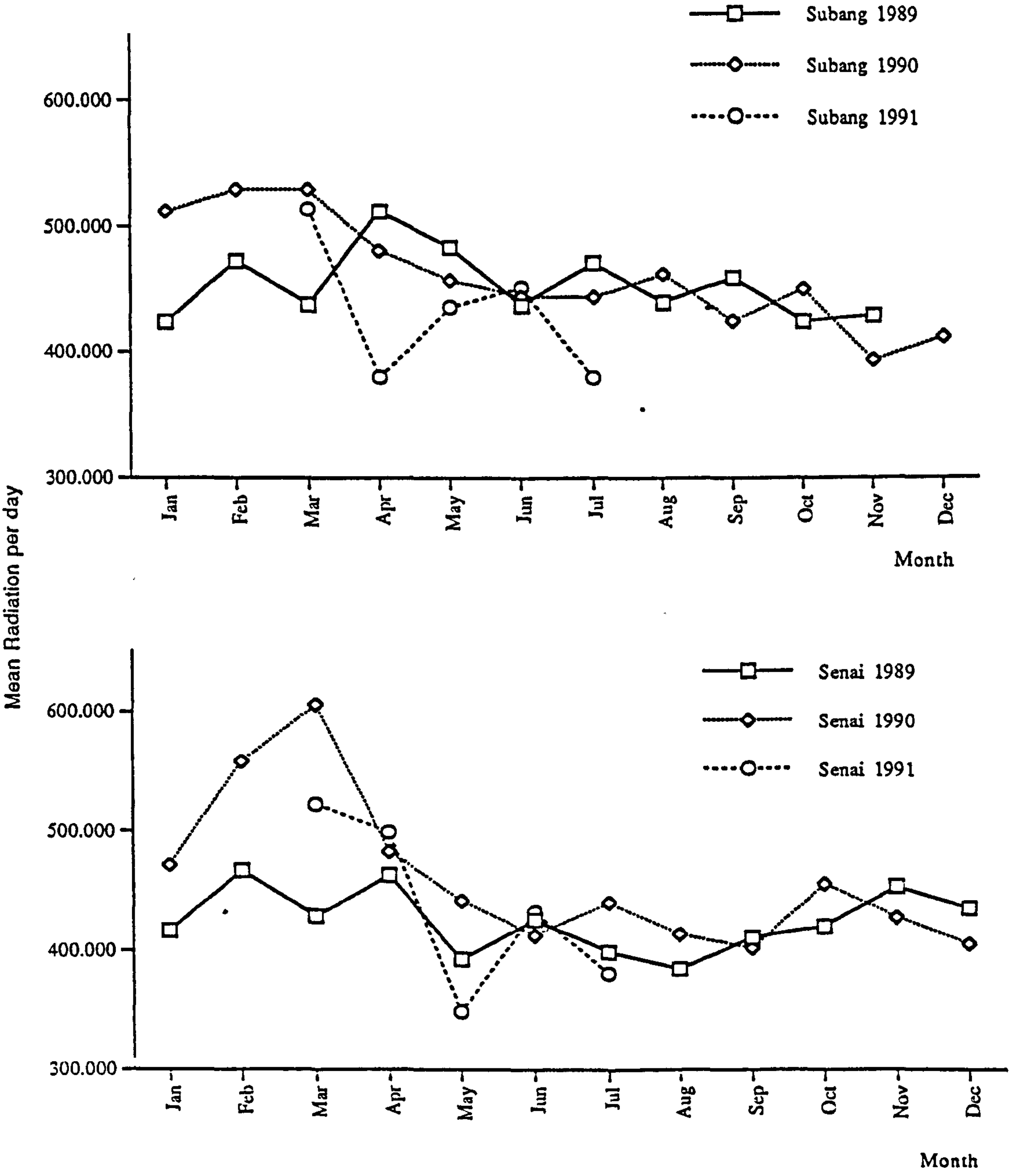


Figure 4.11: Mean solar radiation per day (in $mWcm^{-2}$; time measured in hours) for each month throughout the year, for the 3 years of this study as available, at weather stations near (a) Sungei Buloh (Subang Airport) and (b) Nam Heng (Senai Airport).

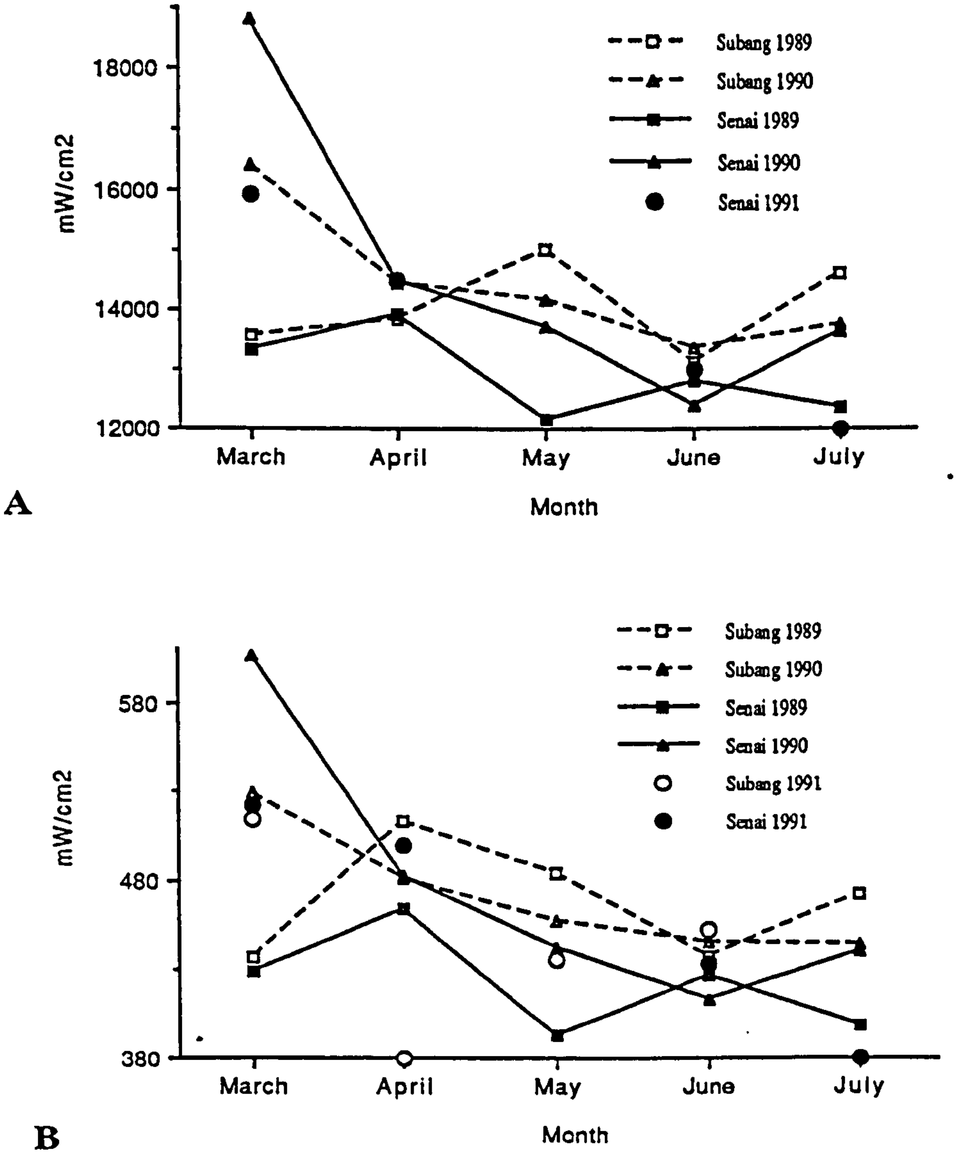


Figure 4.12: Mean daily (a) and total monthly (b) solar radiation for each month of the breeding season, at weather stations near the Sungai Buloh (Subang Airport) and Nam Heng (Senai Airport) study colonies.

Weather and hunting success

In the majority of individual sightings, breeders did not carry any food, but if they did, then it was mostly when sun intensity was not high (Fig. 4.13). The proportion of breeders carrying food appeared to be lowest in medium cloud cover (Fig. 4.14, Table 4.11 a). In 278 scans, the proportion of birds with food at the colony did not change consistently either with sun index or with cloud cover and hour from 12 noon (HRFR12) in any of the months May to July (Fig. 4.15, Tables 4.11 b and 4.12). In July, proportionally more breeders carried food overall than in the months before (Fig. 4.14, Table 4.11 a), probably reflecting the general breeding stage of the colony, i.e. all breeders were provisioning, most of them for big chicks. July, however, included more late breeders than June, which was the main month for nestling feeding. In June, the highest proportion of breeders carrying food was for low scores of cloud cover (Fig. 4.16). The proportion of birds carrying food tended to decrease with cloud cover, for scans (linear regression of arcsine-transformed proportions, $R^2 = 2\%$, $p = 0.094$, $N=69$). The proportion of birds carrying food was higher in the morning and afternoon, for the general population (scans; Fig. 4.17 a and b).

Of the Sightings with food, 12.4% were of dragonflies and ‘antlions’ (no distinction was made between these), on which Blue-throated Bee-eaters specialize (Bryant and Hails, MS; Fry, 1984; Avery and Penny, 1978). I have seen large congregations of dragonflies at the forest edge, the type of habitat where Bee-eaters seemed to hunt preferentially (see above), and some dragonflies may mass-fly high up on bright days along forest rivers (D.R. Wells, pers comm - nothing is known of dragonfly behaviour in the open country). I looked at the times of day and cloud cover of when dragonflies and ‘antlions’ were preferentially taken (Fig. 4.18 a and b). I did not discriminate between insect types taken in scans, so these results were not tested statistically, but again the proportion of dragonflies and ‘antlions’ taken tended to decrease roughly proportionally to cloud cover and tended to be lowest around mid-day as well as after dawn. Thus, the general feeding pattern and the pattern of specialist food taken both point towards greatest feeding activities being during mid-morning and in the afternoon, and under low to intermediate cloud cover.

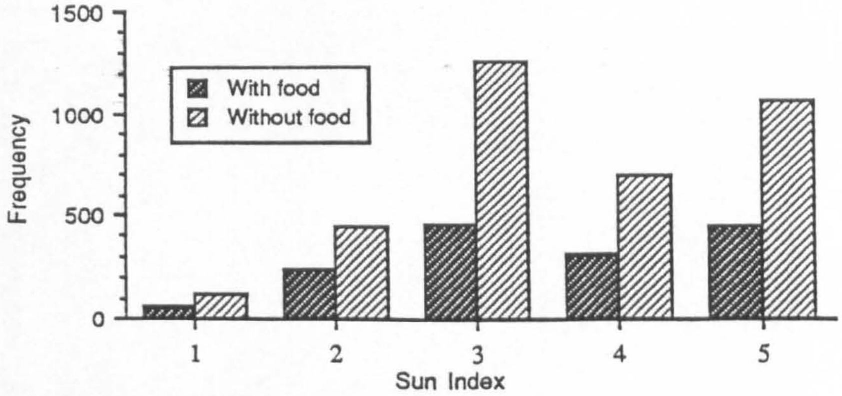


Figure 4.13: Frequency of birds seen with and without food for different values of Sun Index (1=cloudy, 5=sunny near midday, see text)

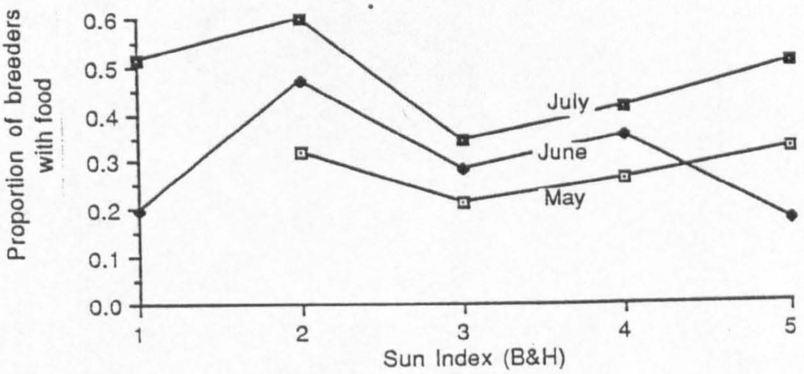


Figure 4.14: The proportion of breeders (in sightings) seen with food for different values of Sun Index (1=cloudy, 5=sunny near midday, see text), in different months at NH91.

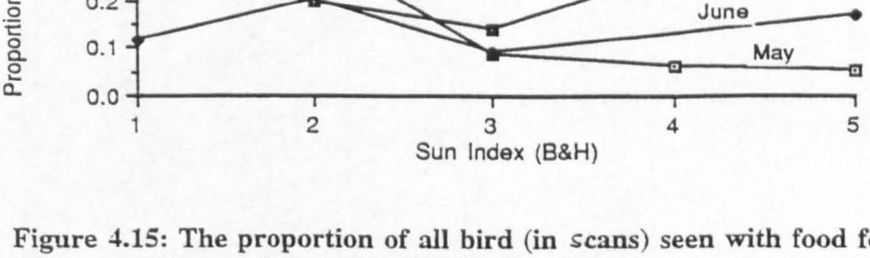


Figure 4.15: The proportion of all bird (in scans) seen with food for different values of Sun Index (1=cloudy, 5=sunny near midday, see text), in different months at NH91

Table 4.11 a: Summaries for the proportion of birds carrying food at any one minute, in different environmental conditions (sun index) and times of season, from sightings of tagged birds (means and se; N)

Sunindex/ Month	1	2	3	4	5	Total
May	- - (0)	0.318 ±0.039 (98)	0.210 ±0.037 (100)	0.260 ±0.037 (128)	0.323 ±0.030 (168)	0.284 ±0.017 (546)
June	0.197 ±0.056 (38)	0.469 ±0.041 (123)	0.282 ±0.022 (335)	0.354 ±0.074 (37)	0.173 ±0.027 (166)	0.290 ±0.015 (720)
July	0.516 ±0.061 (51)	0.600 ±0.074 (32)	0.342 ±0.022 (410)	0.412 ±0.030 (218)	0.502 ±0.036 (157)	0.404 ±0.015 (894)
Total	0.380 ±0.046 (89)	0.427 ±0.027 (253)	0.300 ±0.014 (914)	0.344 ±0.020 (460)	0.331 ±0.019 (502)	*

* could not be computed in SPSSX, and since it is not statistically useful, I did not try to compute it by hand

Table 4.11 b: Summaries for the proportion of birds carrying food in different environmental conditions (sun index) and times of season, from scans of all birds present at a sub-colony (means and se; N)

Sunindex/ Month	1	2	3	4	5	Total
May	- - (0)	0.310 ±0.099 (12)	0.088 ±0.023 (19)	0.061 ±0.045 (8)	0.055 ±0.025 (19)	0.119 ±0.027 (58)
June	0.117 ±0.073 (5)	0.202 ±0.055 (36)	0.091 ±0.040 (17)	- - (0)[a]	0.167 ±0.098 (11)	0.161 ±0.034 (70)
July	0.269 ±0.059 (26)	0.200 - (1)	0.141 ±0.032 (61)	0.260 ±0.045 (43)	0.232 ±0.086 (19)	0.209 ±0.024 (150)
Total	0.244 ±0.051 (31)	0.229 ±0.047 (49)	0.122 ±0.022 (97)	0.229 ±0.040 (51)	0.148 ±0.042 (49)	0.178 ±0.276[b] (278)

[a] : no data for June with Sunindex = 4; [b]: SD given for overall total

Table 4.12 Regression of sun index on the proportion of birds carrying food and ANOVAs of the proportion of birds carrying food with HRFR12 and cloud cover, separately for May, June and July)

tests of promotion of birds carrying food with ...	May			June			July		
	R^2/F	p	(N)	R^2/F	p	(N)	R^2/F	p	(N)
sun index[a]	15%	0.002	(58)	0.1%	0.753	(69)	0%	0.970	(150)
cloud cover and	3.193	0.051		0.607	0.659		2.131	0.081	
HRFR12	3.948	0.002		0.575	0.773		1.102	0.366	
(interaction term)[b]	3.758	0.005		0.041	0.997		1.676	0.093	

[a] linear regression analysis of arcsine-transformed proportions

[b] ANOVA (criss-cross design) of arcsine-transformed proportions

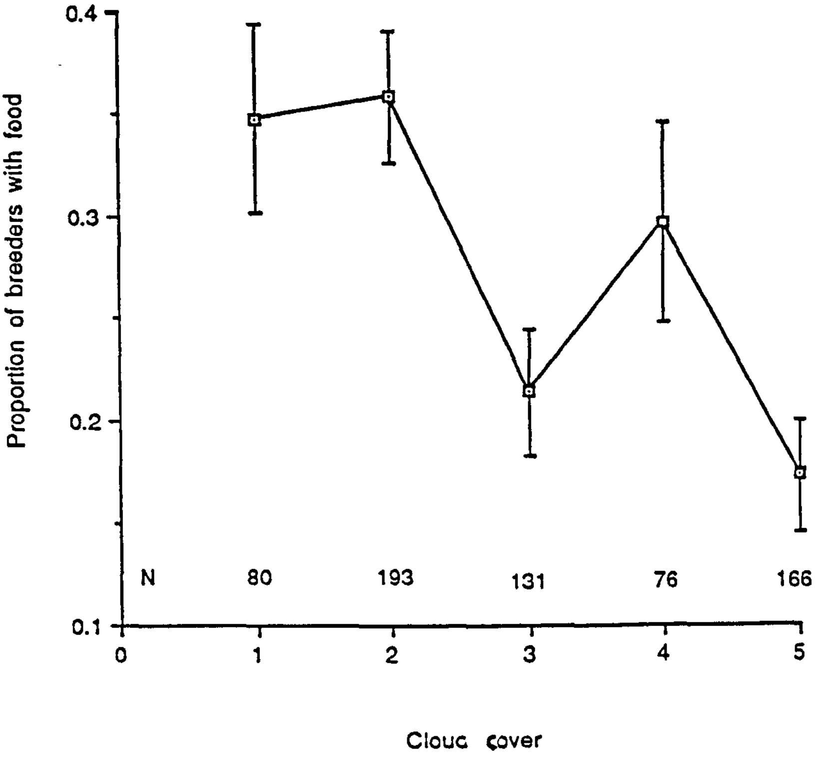


Figure 4.16: The proportion of breeders (in Sightings) with food, for different values of cloud cover (1=sunny, 5=overcast, see text), during the main provisioning period (June) at NH91. (For times of day see Figure 4.17)

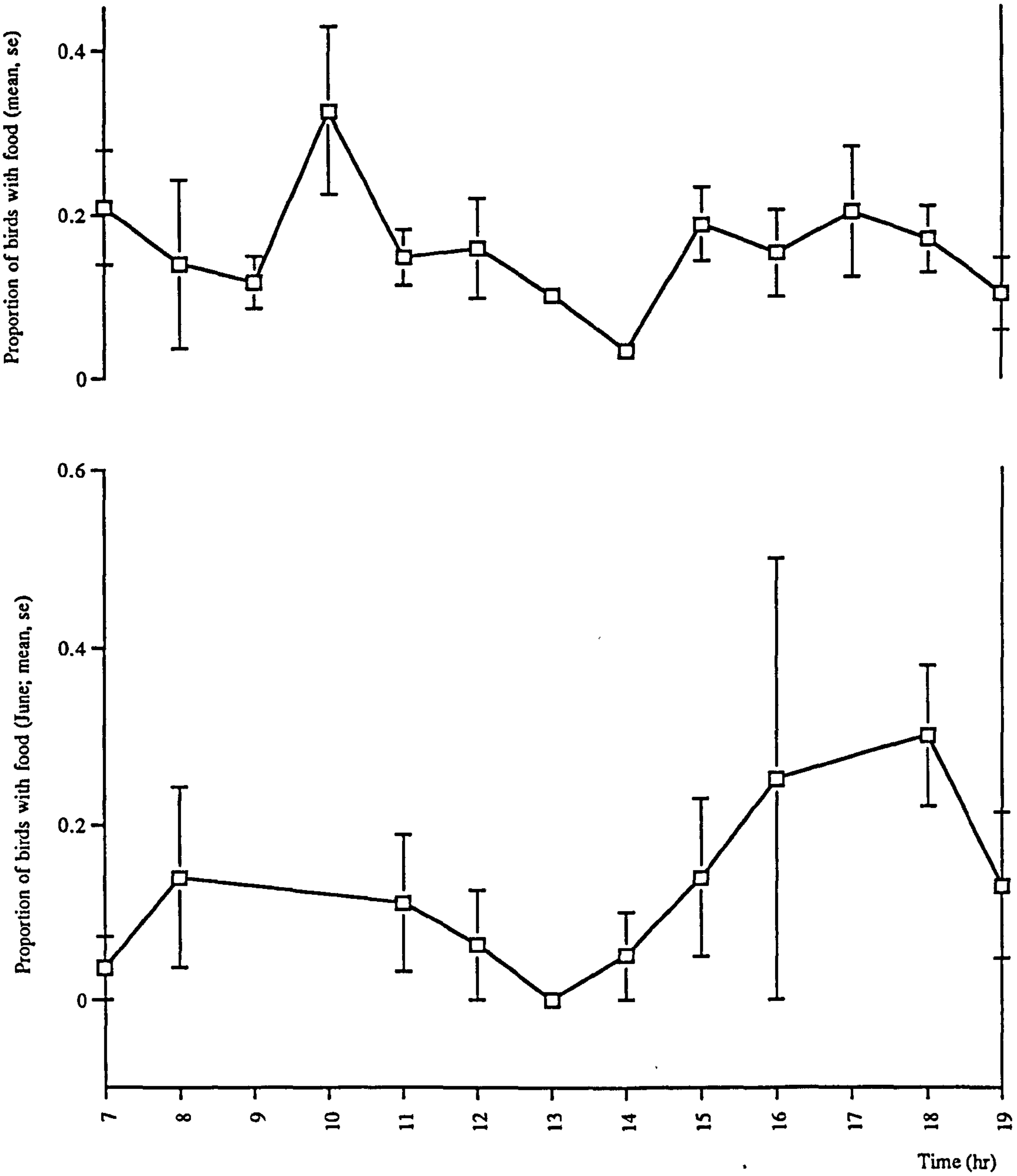
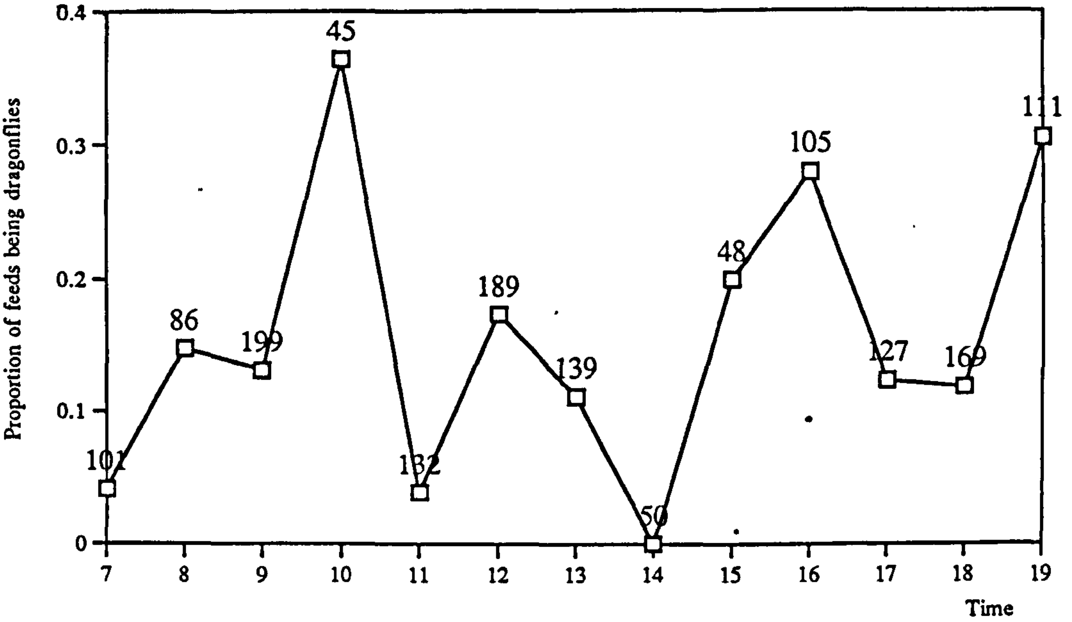


Figure 4.17: The proportion of all birds (breeders, and non-breeders; in Scans) carrying food at different times of day, (A) during May to July and (B) during the main provisioning period (June) only, at NH91. Time is in minutes, grouped by previous hour (see text).



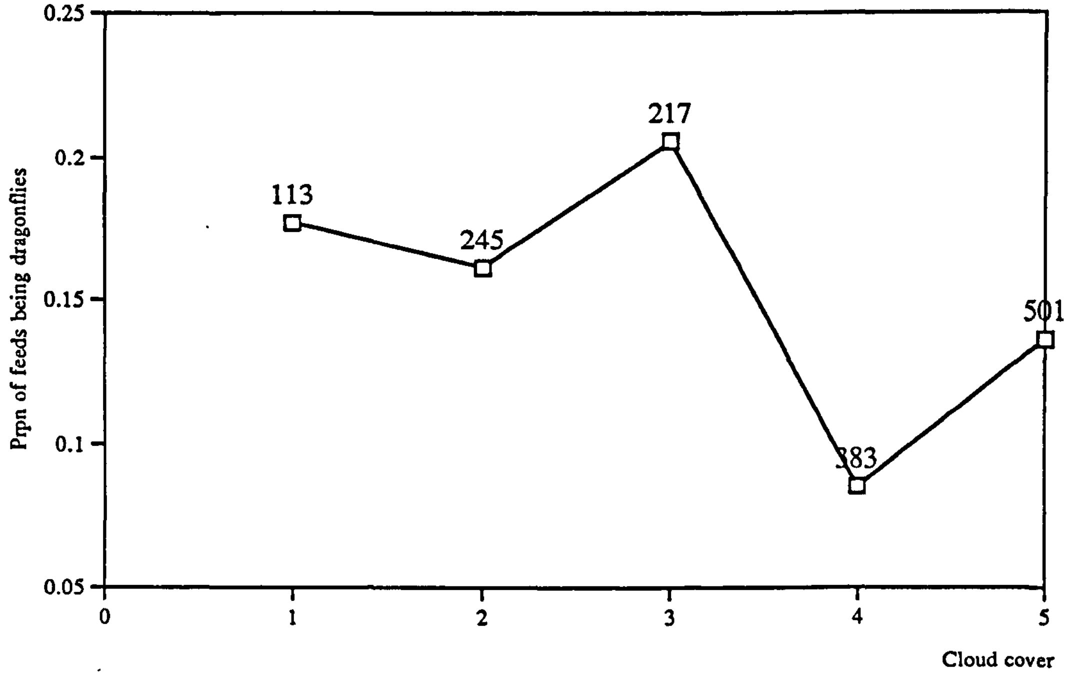


Figure 4.18: Dragonflies as a proportion of the total number of bee-eater food items, (A) for different times of day (in minutes, grouped by previous hour, see text) and (B) by Cloud cover (1=sunny, 5=heavy overcast, see text). The total number of observations (Sightings with any food item) are given above each point.

4.3.3 Returns of breeders and philopatry

In all, 26 breeding adults returned to the colony in a subsequent season. Of these, 17 were sexed as females and 9 as males (see Chapter 5 for sexing of adults). In total, 108 males (43.9%) and 138 females (56.1%) were sexed, which, for 26 returns, translates to 14.6 females and 11.4 males expected amongst the returns. The number of males and females in the sample of breeders returning to the colony did not differ significantly from the numbers of females and males expected (χ^2= 0.900, df=1, p > 0.60). Of 14 adults with known breeding success that were captured in two successive seasons, all had at least one chick and, where known, at least one fledgling in the first season (prior to return). In the second season however, 7 of these 14 returns failed to hatch chicks and 7 raised chicks to fledging. Hence, whether or not the birds returned was apparently dependent on the actual breeding success of the previous season, but birds that returned to the colony did not necessarily do well.

For 3 pairs that returned intact as pairs and 8 individual birds pairing with a new partner, the distance of the nest of the second season with respect to the nest in the previous season was estimated to the nearest 1m (nests are spaced at roughly 0.3 - 10m between nests). All birds returned to within 10m of their nest in the previous season except for one bird which changed to a different sub-colony (Fig. 4.19). I caught birds regularly at most sub-colonies, so it is unlikely that birds were missed simply because they changed sub-colony. The three intact pairs (one-quarter of all returns) re-nested within about 1m of their previous nest. Most adult breeders thus returned to their particular micro-site at the same sub-colony, very close to their previous nest. Where the mate was available, pair members stayed together (or re-pair) in successive seasons. Three pairs attempted to breed with the same partner in two successive seasons (see above). Four returning birds changed partners between years, but their previous partners had not returned. There is thus no evidence of divorce. Two returning birds had probably been ‘helpers’ in the first season at successful nests and returned with a partner, probably both without raising chicks in the second year. For the remaining returning birds I could not establish whether a change of partner had occurred from one season to the next. To conclude, the number of males and females returning is not significantly different from that expected from overall capture rates. Where both partners from a previous breeding pair returned, they remained as a breeding pair again in the following season, and returned to the

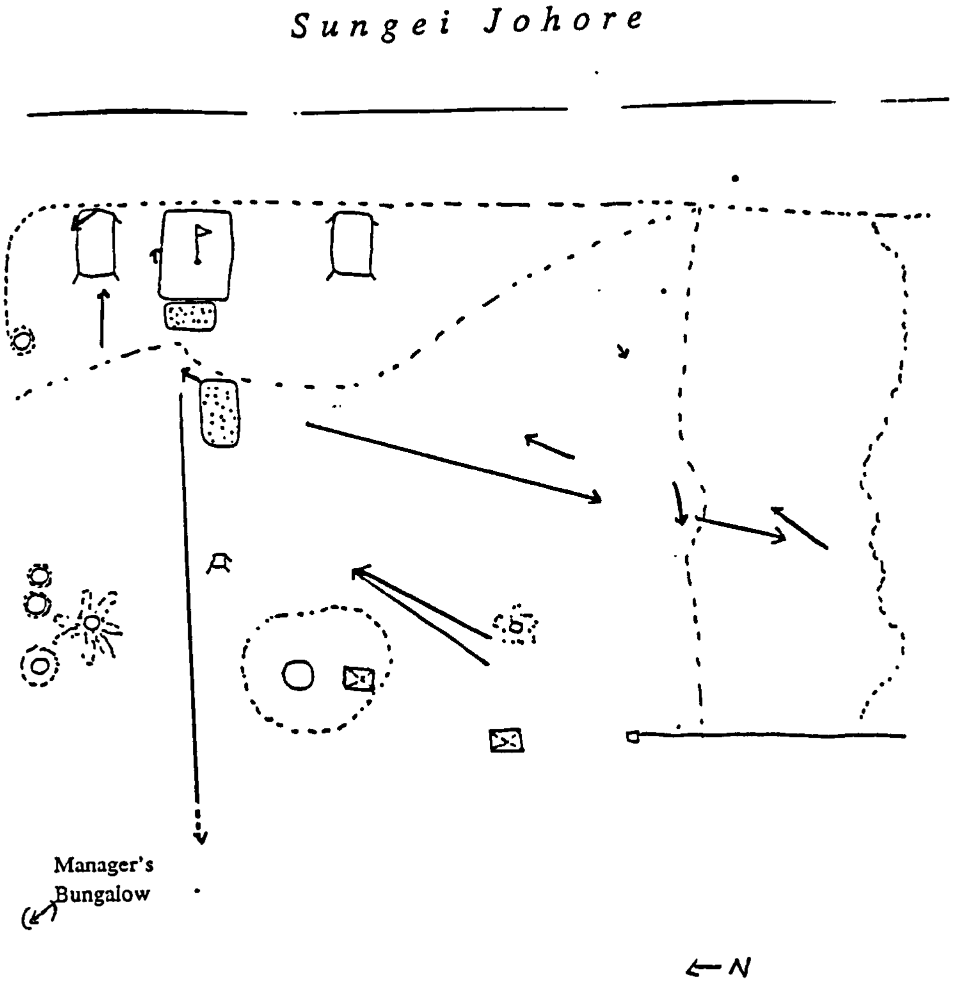


Figure 4.19: Map of Nam Heng, main colony, indicating the location and distance moved between 1990 and 1991 (arrow) by the burrow of each returning bird. Scale = 1:200, or 0.5cm = 1m. Each arrow is *from* the nest site of one bird in 1990, *to* its nest site in 1991; thus the length of the arrow corresponds to the sistance moved between successive breeding seasons. (One bird moved to a different sub-colony in 1991, indicated by dotted end of arrow)

micro-site of their last breeding attempt. Return rates were so low, however, that both partners returned for only 3 pairs from one season to the next. The high rate of re-mating between seasons without apparent divorce suggests that return rates were low, unless many of the previous breeders, including the 'missing' partners, joined the floater population nearby.

Of all adults captured at a colony, 8 had been ringed as nestlings and had returned to the colony to breed. Of these, only 3 were sexed: two males and one female (Table 4.13). Although this shows that nestlings of both sexes did return to the colony, it is not possible to determine which sex disperses more frequently or further afield. Seven out of 8 returning birds were classified as first-hatched amongst their siblings in their broods or came from broods of one. Only one of the 8 returns was a second-hatched chick from a brood where the two eldest nestlings fledged. Where known, the returning nestlings came from clutches started close to the mean Day0, so that in terms of recruitment into the breeding population, 'intermediate' broods seemed more successful than either early or late broods. Two out of 8 chicks (25%) were caught as breeders for the first time in their *second* year. It is possible that in the interim year they either bred elsewhere or were not caught, but equally likely these birds did not breed in their first year, or they 'helped' but did not sleep in their host's burrow so that they were not caught (see Chapter 2). Most chicks returned to their natal sub-colony, close to where the parental nest had been (Table 4.13). The only bird nesting in a different part of the colony from where it hatched was the only identified female. Perhaps therefore females disperse further from their natal micro-site within the colony than males, as in other Bee-eaters (see Discussion below).

Arrival pattern and colony use

In the first 2 weeks (19th March to 1st April) after the first birds were seen at SB89, 25 different tags were noted, of which 16 were seen only on a single day during those 2 weeks (6 of which within 2 days of 1st April, indicating that they had just arrived), 4 on 2 and 5 on 3 different days. The majority of early arrivals, therefore, paid only occasional visits to the breeding colony. In 45 scans during these 2 weeks, a total of 55 out of 229 birds were tagged, i.e. 1 in 4 birds. Four times the number of different tagged birds present, i.e. 4 * 25 different tags = 100 birds, had arrived from the wintering grounds before or on the 1st of April, assuming that all wing-tags were recorded in any one scan and that tagged and un-tagged birds visited the colony at similar frequencies. These 100 birds may have included 'floaters' which apparently only visited the colony at the beginning of the breeding season.

Do wingtags interfere with survival?

Thirty-five birds (members of 23 pairs), were ringed and wing-tagged in NH90, and 30 birds (from 19 pairs) were only ringed in NH90. Less than 10% of tagged birds returned in NH91 compared with 50% of the untagged (Table 4.14 a). The returns of birds marked with paint were compared opportunistically. Of 5 birds which were painted in 1990 at NH (included in the untagged sample, Table 4.14 a), only 1 returned (20%), compared to 56% of birds with rings only (no tags and no paint), which was not significantly different, however (Table 4.14 b). Wing tags therefore dramatically reduced return rates of adult breeders. This could not be shown for paint marking, probably because the sample of paint-marked birds was too small.

4.3.4 Population differences in morphology

Of all plumage characteristics (see Chapter 2 for definitions), only the extent of brown on the nape (BROWN) was significantly different between SB89 and NH91. The brown napes of the birds at NH extended further down their backs than at SB (Table 4.15 a). In NH91, birds had shorter streamers, but because streamers abraded during the season, this was probably due to the fact that catches there were later in the season than at SB89. Two lines of evidence suggest that size was only slightly different between colonies, but that birds at NH had on average a different shape to those in SB. Firstly, size measures differed in opposite directions: values of wing length (WING), bill width (BW) and perhaps keel length (KEEL) were larger for NH birds, whereas SB birds had larger values overall for head-and-bill length (HB), bill length (BL) and tail length (TL). KEEL was not significantly different, and the PC1 of WING and KEEL was only just significantly different at the 5% level (Table 4.15 a). Secondly, the PC1 ('size') of the PCA with all size variables was still not significantly different between SB and NH, whereas both PC2 and PC3 ('shape') were highly significantly different between birds from the two colonies (Table 4.15 b). Although there were no birds at all with very bright throats (BRIGHT = 6) at NH, there was no significant difference overall between throat

Table 4.13: Philopatry. Details of birds that were ringed as nestlings and returned to the colony as breeders.

Ring	Sex	C'no[a]	Brood (chick)[b]	Day0	location (chick br)	Brood (adult)	location (ad br)	Dist[c] (chk-ad)
0461		1	25-89	12 May	rhtop	12-90	rhtop	17m
0472	M	1	6-89		lhtoptop	6-91	lhtop	34m
0478		1	5-89	15 May	lhtoptop	40-90	lhtoptop	3m
0484	M	1	28-89	7 June	rhmid	37-90	rhmid	7m
0487		2	34-89		rhmid	13-90	rhmid	8m
06534	F	1	14-89		rh-1	15-91	rhtoptop	>65m
5453		1	141-90	10 May	C4	155-91	C3	4m
5487		1	184-90		B2	143-91	C3	14m

[a] C'no = chick number in hatch sequence
[b] Broods 1-99 were at the SB colony, broods 100+ at the NH colony.
[c] Dist (chk-ad) = distance between chick and adult broods

Table 4.14 a: Number of returns of tagged and untagged birds from 1990 to 1991 at the Nam Heng colony

	1990	1991	returns
Tagged	35	3	8.6%
Untagged (some painted)	30	15	50.0%

χ^2 (Yates Correction) = 5.8, $p < 0.02$

Table 4.14 b: Number of returns of colour marked and unmarked birds from 1990 to 1991 at the Nam Heng colony

	1990	1991	returns
Painted	5	1	20.0%
Ringed only (Unpainted)	25	14	56.0%

χ^2 (Yates Correction) = 1.3, $p > 0.20$

Table 4.15: Morphological differences between the Nam Heng and Sungei Buloh populations. Data are based on means of repeat measurements for any one bird.

A

Direct measurements and those principal components 1 (size) which explained more than 60% of the variance in size between birds.

Character	SB89 *	NH91 *	Test	Statistic	p
BRIGHT	3.0 (1.0-6.0; 48)	3.0 (1.0-5.0; 129)	M-W	-1.2718	0.2035
BROWN	2.0 (1.0-3.0; 37)	3.0 (1.0-4.0; 125)	M-W	-6.2849	0.0000
GREEN	1.0 (0.0-5.0; 56)	0.0 (0.0-3.0; 124)	M-W	-1.6406	0.1009
TS	122 (83-172; 54)	110 (84-160; 134)	M-W	-3.7340	0.0002
KEEL	29.7±0.16 (96)	30.0±0.12 (135)	Stud's t	-0.84	0.403
WING	111±0.4 (56)	113±0.3 (126)	Stud's t	-2.79	0.006
HB	57.3±0.31 (54)	55.4±0.25 (125)	Stud's t	4.40	0.000
BILL	31.7±0.61 (56)	28.3±0.16 (126)	Stud's t	5.33	0.000
BW	7.03±0.047 (56)	7.31±0.027 (126)	Stud's t	-5.51	0.000
TL	80.5±0.42 (56)	79.1±0.23 (126)	Stud's t	3.21	0.002
PC1 (WING, KEEL)	(54)	(124)	Stud's t	-2.04	0.042
PC1 (WING, HB)	(54)	(124)	Stud's t	0.95	0.346
PC1 (WING, BW)	(54)	(124)	Stud's t	-5.29	0.000

*: means±se (N) for size variables (normally distributed), or medians (min-max; N) for plumage variables; N. PC scores are not meaningful and therefore no means given here

M-W = Mann-Whitney-U test, statistic = Z

Stud's t = Student's t-test, statistic = t

PC1: First Principal Components for size variable combinations with the highest Eigenvalue (see Table 4.15 b)

B

Difference between Sungei Buloh and Nam Heng birds, in Principal Components 1-3 from a PCA with all body size measures (KEEL to TL, in A), to demonstrate size (PC1) and shape (PC2 and 3) differences between colonies. PC4 explains only 9.8 % of the variance, PC5 9.3 % and PC6 6.0 %. There is therefore a 'cut-off' point between PC3 and PC4, and PC4-6 are not likely to represent 'shape'. N=260 birds

PC	Eigenvalue	% variance	t	p
1	2.21879	37.0	1.25	0.214
2	1.18261	19.7	7.37	0.000
3	1.08905	18.2	-6.23	0.000

brightness at the two colonies (Table 4.15 a; also cf Chapter 3, section 3.4.2). More birds had 'bright' throats, and 'very bright' throats, at SB than at NH (Table 4.16).

4.3.5 Aspects of social behaviour

I observed the following aspects of social behaviour which have not been recounted before for the Blue-throated Bee-eater: kleptoparasitism, calls and tail flicker. These behavioural aspects are described in this section.

Kleptoparasitism

Bee-eaters sometimes stole food items from other birds rather than hunting for insects themselves, a behaviour which is called kleptoparasitism. They did this by waiting for returning nest-feeders and intercepting them when they arrived and tried to enter their burrow. I only observed kleptoparasitism in NH90, a dense colony, on a few occasions during the main nestling feeding season (June). A bird would sit at its own burrow entrance without food and intercept and chase other birds descending to burrows nearby with food, attempting to grab the item from them and feed it to its own nest. This was successful in several instances, but at other times the incoming feeder managed to enter its own burrow with the food despite being subjected to several intense chases. One single pair or bird (unmarked, at nest 185-90) was the aggressor in all successful attacks. On one occasion, however, this pair was chased itself by another kleptoparasitic Bee-eater, but the chased bird gave the food item to its partner which came to its aid and successfully fed it to their young. Single birds specializing on kleptoparasitic feeding strategy have also been reported occasionally for Red-throated Bee-eaters (Fry, 1984). Although kleptoparasitism was not observed frequently (only during a few days, and only at NH90), it may nevertheless have an impact on feeding rates both of the specialist kleptoparasites and of the victims. Pair cooperation could then be a very efficient deterrent.

Table 4.16: The number of birds with very bright throats (BRIGHT = 6) and very bright or bright throats (BRIGHT = 5 or 6) at Nam Heng and Sungei Buloh. These data also include breeders from both colonies, for 1990.

Colony	Very Bright throats	Others (less bright)	Very Bright and Bright throats	Others (less bright)
Sungei Buloh	3	63	11	55
Nam Heng	0	170	6	164

Fisher's exact test: $p = 0.02116$ $p = 0.00115$

Table 4.17: The infestation rate of feather mites in different colonies (SB89 was not scored. SB90 was the smallest colony, NH90 and NH91 probably of roughly similar size, i.e. large colonies. N = 195 adults.

Colony	Number without Mites	Number with Mites
SB90 (small colony)	6	2
NH90 (large colony)	34	5
NH91 (large colony)	82	66

$\chi^2 = 15.575$, $p < 0.0005$

Calls of *M. viridis*

The following calls were distinguished and described in notes either directly in the field or when listening to tape-recordings taken in the field. The contact calls 3-6 were very similar in description but could be distinguished with good repeatability in the field. The description of sounds is in bold type-script, and a dash indicates that there is no clearly detectable break between repeats.

1. Longcall: loud, intense far-carrying **'blüüü-blüüü-blüüü-blüüü'** (German pronunciation of 'ü', sounds vaguely like a broad Scottish pronunciation of 'oo' in 'good'). The call is uttered either in flight or from perch, with the body including the bill stretched and pointing vertically in a typical 'longcall' posture (cf contact call, Fry, 1984, for Red-throated Bee-eaters). This call is probably a long-distance contact call, perhaps advertising the colony site. It is uttered either alone or in groups; if one bird calls most birds nearby will join in.

2. Alarm call: sharp, but not very far-carrying **'tik-tik-tik-tik'** (see also Fry, 1984, for red-throated Bee-eater).

3. Chirp: a single **'chypp'** ('y' as in 'myth') or **'chüpp'**, sharp and short but not loud. The sound coincides with the *closing* of the bill. It is uttered from perch, in regular intervals which are longer than for other calls. This call is a contact call during digging. I could probably not hear any calls by the digging bird inside the burrow, but Hahn (1982) reports that *M. apiaster* calls in duet during digging, prompted by the digging bird with a vocalization very similar to nestling begging.

4. Low Chirp: **'bik bik bikik bik'**, lower and less throaty than Chirp and at higher frequency, but similar in context and sound.

5. Purr/ Cooe: low **'bu-ée bu-ée bu-ée'** (accent is on the letter which is stressed) or **'kíyuu kíyuu kíyuu'** ('y' as in 'you') or **'kíyou'**, sometimes more throaty **'glu-é'**. This is a low contact call during digging or immediately preceding digging (possibly in anticipation or as encouragement), uttered by the vigilant partner on a perch or sitting near the burrow.

6. Sharp Cooe/ Cooee: a Cooe that becomes louder and faster **'bué bué bué'** or **'glué'** or **'ghué'** (the 'gh' is a slightly throaty sound, like the Greek letter γ (gamma) or a very soft 'ch' of the scottish 'loch') or even **'kyou'** ('y' as in 'you', 'ou' as on loud) or **'píuu'** (the latter sounds a little like the alarm call 'tik'). The vowel at the end represents a diph-tong pronunciation, and a lowering of the 'voice'. The call is uttered by the vigilant bird from a perch during long bouts of digging.

7. Trill: continuous chirping sound, like a very loud cicada, **'trr-trrrr-trrr-trrrr'**, very distinct, from nestlings of about 1 week of age until after fledging. This is a begging call of nestlings and fledglings, in reply to adult's feeding call (see 8).

8. Feeding Call: sharp, drawn **'tlek. tlek. tlek.'** (full-stop indicates regular intervals), very distinct, uttered by adults arriving at nest during provisioning. Always elicited a response by nestlings when 'played-back' to them on cassette tape (see Chapter 7).

Tail flicker: greeting

Like other Bee-eaters (Fry, 1984), Blue-throated Bee-eaters use their tail to 'greet' conspecifics. This behaviour is used regularly between pair members and other birds, and may occur during sexual interactions and courtship-feeding. This behaviour may involve either or both of two different tail movements: tail-fanning (Fig. 4.20 a) and the characteristic 'flicker' (Fig. 4.20 b). Occasionally, birds may tail-flicker even if no conspecific is nearby, in which case it is associated with the Longcall described above and can probably be interpreted as a kind of 'intention behaviour' similar to intention movements, which are made out of context or are not completed (e.g. Fry, 1984).

4.3.6 Helping

During the three study seasons at the two colonies, captures were made at 231 nests. Both adults were captured at 123 of these (more than half), but there were only 7 incidences where 3 birds were either caught at one nest on the same morning (at nests 160-90, 165-90, 201-91) or caught within the same week (at 149-90, 127-91, 171-91, 184-91). There were no

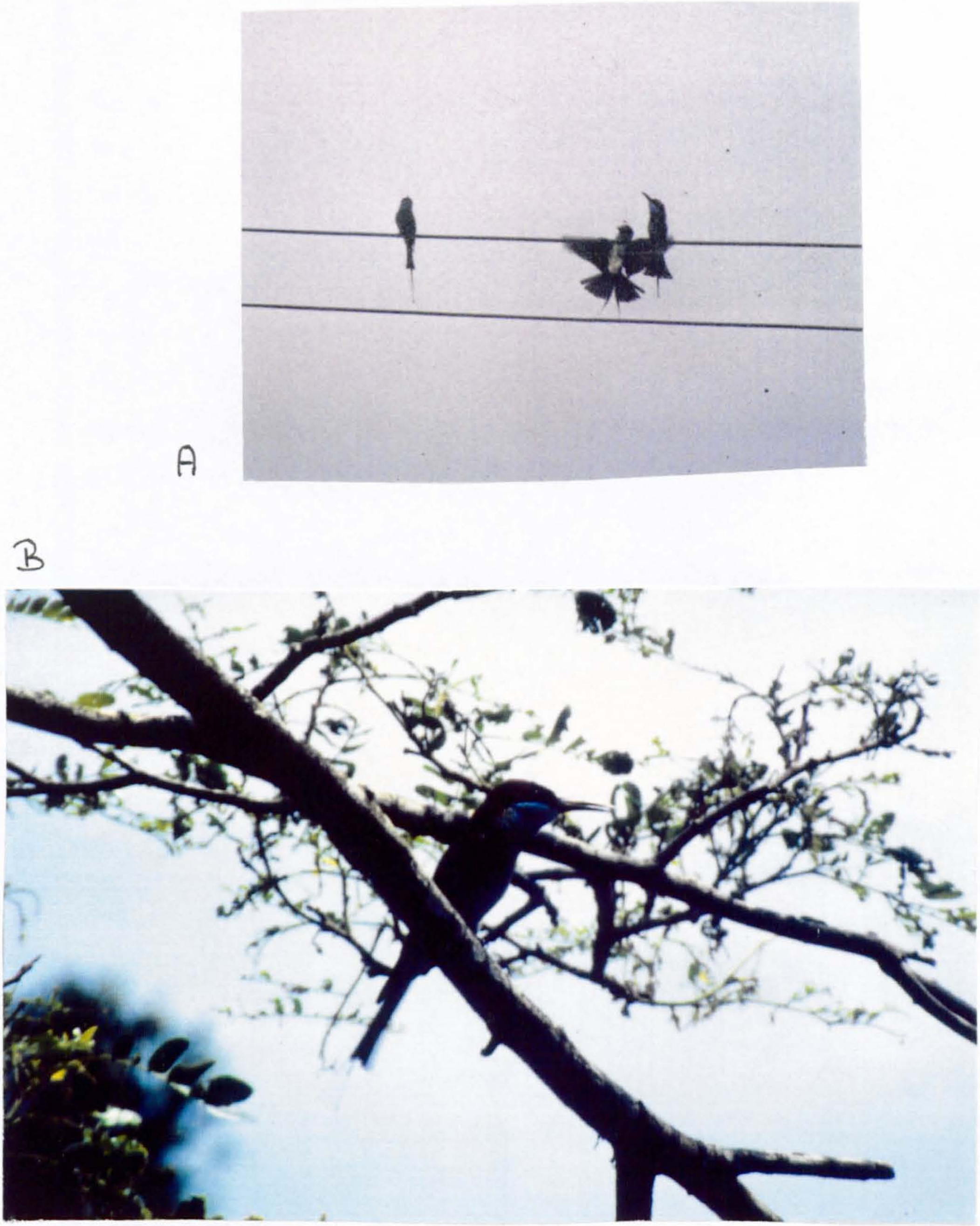


Figure 4.20: Tail Flickering (a) in the context of greeting an arriving bird: the perched bird on the right is fanning its tail. In the second picture (b), the 'flicker' movement of the tail and streamers is captured by the camera as a blurr.

consistent observations for any of these birds, either because they were not tagged (149-91, 165-90), or because the markings were not clearly identifiable (for birds with taped tails, at 171-91, 184-91 and 201-91), or because they did not visit the nest during observations (165-90). In one case (127-91), one bird was caught earlier than the other two and was observed only once making a brief visit to the burrow during the incubation by the other two, to whom it had probably lost its burrow rather than being their helper. At nest 171-91, the third bird (RPB) was a breeder at the neighbouring nest 170-91 and not closely related (r=0.25 or less) to the brood in 171-91. The two burrows ended within 20cm of each-other and it is possible that RPB swapped burrows either because of an error in 'microlocation', or out of convenience; the latter could, however, arise only if neighbours tolerate each-other in their burrows, perhaps because they are related (see Chapter 6) and, as established above, RPB was not a relative. Thus, birds that could have been helpers were roosting in only 5 out of 123 nests, less than 5%.

Although during prospecting more than 3 birds were occasionally seen to descend together to the ground (Fig. 4.21), there were never more than 3 birds were captured on any one day at any one burrow. There was an incidence where 3 different birds were observed at one burrow (17-89), but the complete clutch was expelled from that nest, so that the observations are best explained as a take-over attempt rather than helping.

There were two possible helpers which were not captured but observed frequently. The two birds are X6W, marked by P.T. Green, and A4G, captured for the first time in early 1989. I describe their recruitment to illustrate helper-recruitment in the Blue-throated Bee-eater. X6W was seen first on 20 March 1989, so it arrived early. It was seen associating with many birds, greeting them and long-calling at the colony all through the early breeding season (Focal observations of X6W are listed chronologically through the season in Appendix 5.1). It spent a lot of time at the colony, where it was observed during most observation periods. It was first seen to visit its host nest 31 once on 4 May. On 31 May, it flickered into empty space, carrying an insect - similar to soliciting behaviour that males exhibit towards a female. Fry (1984) reports that in Red-throated Bee-eaters, where males feed ('allofeed'; see Chapter 5) their female partners prior to copulation, male helpers also allofeed the breeding female, which would explain the above observation as 'intention behaviour' by X6W. On 1 June, X6W inspected the nest. Two weeks later, on 15 June, it provisioned young at the same nest. During this time it was not associating with the breeders at 31, or with any other birds.

A second helper, A4G, was seemingly recruited late in the season, when the nestling(s) were already large enough to wait at the entrance for provisioning adults. It was observed feeding a chick at nest 9-89 (the breeding pair was 33O (female) and 40O (male)). A4G provisioned 9 insects of varying small sizes (absolute sizes 1-4) on one day, 2 July, when the pair female was present but not provisioning. The pair female was seen provisioning on 12 and 15 June, 5 insects of size 3-6. The pair male was seen only once, dropping off a large insect (size 6) on 1 July (Appendix 5.2).

In conclusion, helping was confirmed to occur in Blue-throated Bee-eater colonies. During this study, however, it was a rare occurrence, and never more than one helper was observed at a nest. A frequency of helping of less than 5%, suggested by the dawn nest captures, could not be confirmed by observations at nests because insufficient numbers of breeders were individually identifiable, particularly at NH.

4.3.7 Predators and ecto-parasites

Predation rates were generally low at 0-2 clutches or broods per colony-year (see above, section 4.3.1). Predators of nests were not identified, but a Black Cobra *Naja melanoleuca* and Scorpions (Scorpionida) were found in Bee-eater burrows (D.M. Bryant, P. Tatner, pers comm), although it is not known whether scorpions are predators or just enter a burrow on occasion. Ants (Formicidae) were abundant in some burrows, in particular at SB. They prey particularly on the contents of damaged eggs and possibly on dead or dying chicks. Adult mortality amongst White-fronted Bee-eaters is thought to be mainly due to raptor predation (Hegner and Emlen, 1987). Brahminy Kites *Haliastur indus* were common in Nam Heng and they breed during the late Bee-eater breeding season (pers obs), but a tame juvenile Kite visiting the Bee-eater colony regularly did not elicit any alarm calls or anti-predator behaviour.

In Ginting, on Penang Island in the northern part of Peninsula Malaya, the greatest threat to Bee-eaters apart from rat-snakes, birds of prey, young monitor lizards (*Veranus* sp.) and, possibly, house cats, is from humans who interfere with their burrows or destroy their colony sites (Charles, 1976; Kumar, 1987). The main sites of both my study colonies were situated in areas without access to the general public, but nests were destroyed by village children just outside the main colony site (Fig. 4.22).

Mite (Acari) infestation (Figs. 4.23 and 4.24) varied in different colonies, and the birds at colony NH91 were the most heavily infested with mites (Table 4.17). The infestation, however, was different at colonies that were of similar size (NH90 and NH91; M-W test, $Z=-3.4514$, $p < 0.001$) but not between a small colony (SB90) and either of the large colonies (SB90 and NH90, $Z = -0.6858$, $p > 0.40$; SB90 and NH91, $Z = -1.4403$, $p > 0.10$). It can thus be said that adults at NH had significantly heavier mite infestation in 1991 than birds at that colony in 1990, and mite infestation was independent of overall colony size. Parasitic pathogens are common in gregarious Bee-eater species that breed colonially (Fry, 1984). Fry *et al* (1969) and Fry (1984) review the occurrence of several species of harvest- and feather mites (*Neoschogastia sp., Neocheyletiella sp., Meromenopon meropis*) on Bee-eaters. They cause epidermal swellings and lesions. Hippoboscid flies *Ornitophila metallica*, fleas and feather lice as well as endoparasitic flatworms, microfilarians and blood-cell protozoans were also recorded as occurring on Bee-eaters by Fry *et al* (1969). Flies similar to the hippoboscid flies were also encountered in the plumage of *M. viridis* in this study.

Figure 4.21: During the early season, often several birds 'prospect' for a suitable nest-site together. During this stage, only few birds are tagged so that their identity cannot be established.

Figure 4.22: Village children are the main danger to breeding Blue-throated bee-eaters nowadays. Burrow entrances are blocked, so that the broods, and sometimes the adults, perish inside. Sometimes whole nests are dug up, sometimes to collect eggs which are eaten. On Penang Island, interference from children at the nearby school had helped to destroy a strong colony. These photographs were taken on the fringes of the Sungei Buloh colony, which is not protected from the public, unlike the main colony inside the manager's garden.

Figure 4.23: Feather mite eggs (head of an fledgling, moistened with water to show the infestation, which is of medium extent)

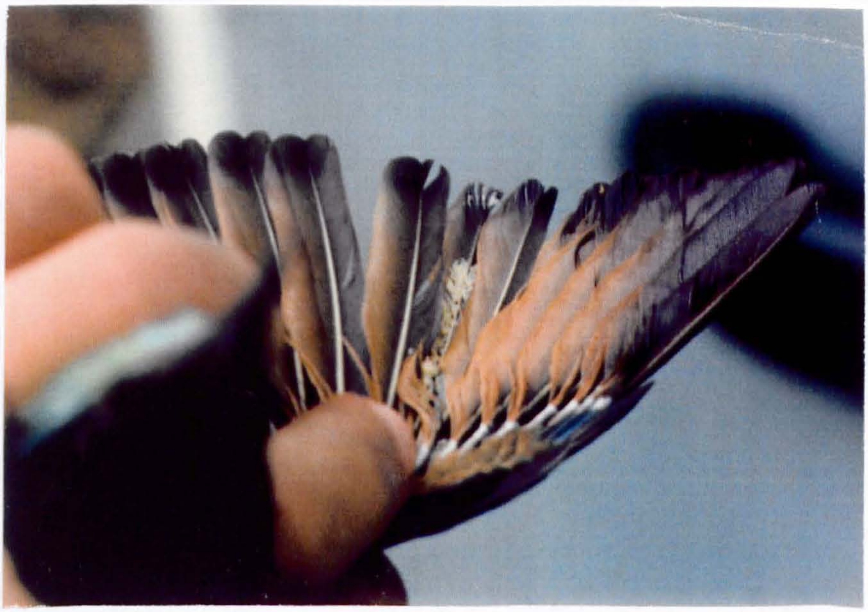


Figure 4.24: Feather mite eggs on fledgling bird wing (medium infestation)

4.4 DISCUSSION

4.4.1 Breeding season, insect food and the effect of climate and weather

Breeding in birds corresponds by and large to the season during which optimal food availability can be exploited for feeding young (Murton and Westwook, 1977). Whereas in temperate areas breeding seasons are limited mainly by cold weather (Perrins, 1970), in tropical environments the relationship between climate and breeding is often less clear-cut (e.g. Emlen, 1982 a; Fogden, 1972). In tropical rainforest habitats, the food supply is considered to be the main factor controlling avian breeding seasons (Keast, 1985), both proximately and ultimately (by acting on nutritional state, Medway and Wells, 1976). This is considered likely also for the insectivores of Malaya (Medway and Wells, 1976). Fogden (1972) showed that the breeding season in insectivorous rainforest birds in Sarawak/Malaysia coincides with abundance in insect populations which build up after highly seasonal leaf production (see also Medway and Wells, 1976), despite relatively non-seasonal rainfall patterns. Fogden (1972) also showed that the lean season (cf insect abundance) is avoided for both breeding and moulting.

Although geographically the area studied by Fogden (1972) is close to the Peninsula Malaysia, Fogden considered rainforest birds, whereas Blue-throated Bee-eaters are found in open-country grass-land habitats. In the bushed grass-land of East-Africa, home to the White-fronted Bee-eater, wet weather just before breeding increases insect abundance, and the amount of rain in the month prior to breeding poses an environmental constraint strong enough to increase cooperative breeding in these Bee-eaters (Emlen, 1982 a). In the following I discuss how climate and weather affect Blue-throated Bee-eaters in their breeding effort and season.

Climate and weather during the study period

Some of the variation in weather and climate observed in the Blue-throated Bee-eater study area is probably seasonal. In the West and South Peninsular Malaysia, January and February are generally the months with longest dry spells (Dale, 1974 c). This is in agreement with the lowest number of raindays found in these months during the study period (1989 to 1991). The rain peak in April and May is intermonsoonal, before the south-east monsoon which is particularly marked on the west coast (Dale, 1974 b). Flooding of nests has been reported during these months for the SB colony, causing desertions and nestling mortality (P.T. Green, pers comm). Some of the weather data and its variation, however, may not be representative of the weather at the study colonies (see Methods above). Kota Tinggi station is the most easterly of the stations monitored, and Nam Heng is situated to the west of Kota Tinggi. More raindays were recorded in general for Kota Tinggi during this study, which is more typical of east-coast weather (Dale, 1974 d) and thus not immediately representative of NH.

Climate and other factors affecting return rates, numbers and success at SB and NH

There was marked variation between years in both the timing and the amount of rainfall in the study areas. Emlen (1982 a) reports similar conditions and observes that for White-fronted Bee-eaters, unexpectedly late rains in an unpredictable environment result in a high rate of unsuccessful breeding attempts (and, ultimately, in high recruitment of helpers, which Emlen explains according to the environmental constraints model, although there are no limited 'territories' as such). In Table 4.18, I summarize the general trends of weather and breeding data presented in this chapter, to see if such constraints were evident in this study. The birds at SB89, for example, may have been under particular pressure, because the rains were less pronounced in the early season but particularly frequent during provisioning. Although not much is known of their breeding success and some chicks returned in subsequent years, it is possible that low numbers in the following year (SB90) were due to adverse breeding conditions in SB89. Those birds that did breed in SB90, however, had comparatively high numbers of fledglings per brood, and weather conditions were not particularly adverse. The small size of the colony (as SB90 was) may be the reason for birds to have high breeding success (Sasvári and Hegyi, 1994) - for example if there is less competition for food in smaller colonies.

Since I could not demonstrate a direct relationship between the variation in weather and general breeding data, I cannot rule out that other factors, such as disturbance of habitat or of the colony, override the effects of weather. In SB91, for example, weather conditions were

Table 4.18: Summary of weather and breeding success in colony-years

Colony -year	Weather	Breeding success
SB89	Dry laying season, wet nestling season, early end of dry nestling season. Intermediate to high radiation	Low numbers of breeders. Few data on breeding success. Some chicks recruited.
SB90	Intermediate pattern of raindays, late onset of rains after provisioning period. Intermediate radiation	Very low number of breeders. Trend of high fledging success (number of fledglings)
SB91	Wet laying season, with low radiation, dry provisioning season	Breeder number close to nil. No data on breeding success
NH90	Very dry pre-laying season with very high radiation, wet in April, not very dry thereafter	Large numbers of birds. Few data on breeding success. Some chicks recruited
NH91	Dry laying season with medium to high radiation, dry nestling season with medium to low radiation,	Large number of birds. Many early desertions, trend of low fledging success (number of fledglings

favourable during the main season, but by that time the colony may have been reduced to extremely low numbers for other reasons. The main factor responsible for high desertion and low return rates may have been interference from research for this study, in particular the use of patagial tags (see below, 4.4.3). In NH91, on the other hand, the season with high early desertions, less harmful marking methods were used on most birds but numbers nevertheless have decreased dramatically to less than about 30 pairs in 1992, and fewer than that in 1993 (T. Liong, manager of Nam Heng Complex, pers comm). It is possible that interference from golfing or severely increased insecticide spraying on Nam Heng Complex from 1991 onwards have played a part in this decrease.

Breeding season, weather and foraging

Climate and seasonality may ultimately limit Blue-throated Bee-eater breeding success by affecting the abundance of its insect food. This is reflected in their hunting success, which is influenced by weather. There are two ways in which weather and climate can affect Bee-eaters - either directly by interfering with their foraging or nesting effort, or indirectly by acting on food abundance. Both aspects are discussed in the following.

The breeding season of Blue-throated Bee-eaters on the Malay Peninsula is from April to August, peaking in a mean first-egg-date in early May. This corresponds loosely to the breeding season of 244 other insectivores and partial insectivores in Malaya (cf Medway and Wells, 1976). The incidence of breeding of all of these species peak in March/April around a unimodal curve (Medway and Wells, 1976, chapter 1, fig. 2). Medway and Wells (1976) link the breeding season of the Malayan insectivores to insect abundance in Malaya, which is cyclic throughout the year, following vegetation growth (also Fogden 1972, see above). In East African savanna, most insectivorous birds breed similarly at the end of the long rains, when insect abundance (number of species, individuals and biomass) is dramatically increased (Dingle and Khamala, 1972; see also Wrege and Emlen, 1991; Brown and Britton, 1980).

In a study by Hails (1982) conducted at one of the weather stations for the SB colony (Universiti Malaya, see Table 4.2), insect abundance was not particularly high just before or during the main rain season (Fig. 4.25). Hails trapped mainly those insects available to

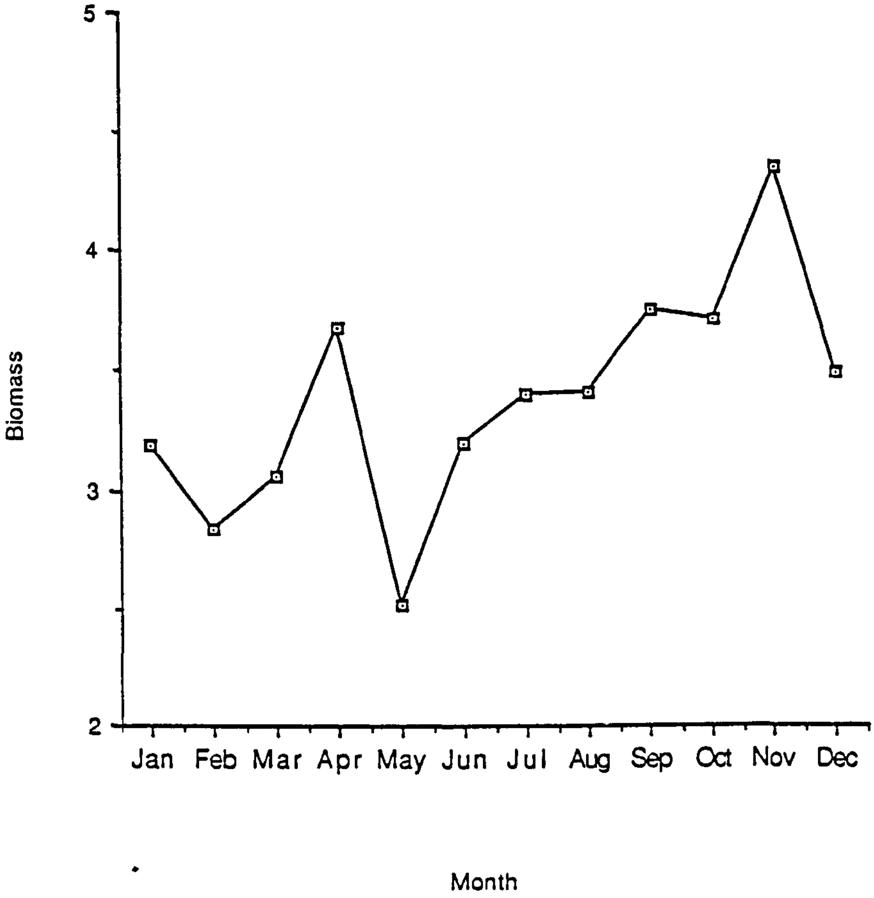


Figure 4.25: Biomass of insects caught in suction trap throughout two sample years at Universiti Malaya, open habitat near the Sungei Buloh study colony (from Hails, 1982).

Hirundines and did not measure abundance of the mainly large taxa taken by Meropidae, so his samples are not strictly relevant. Emlen (1982 a) mentions unpublished data which indicate that White-fronted Bee-eaters may time their breeding to coincide with high insect abundance at a colony in Eastern Africa, but that the relationship between insect abundance and rainfall may be complex and differ between seasons. Although Malaysia is not as strongly seasonal as African savanna (see e.g. Keast, 1985), insectivorous birds in Malaya are nevertheless thought to be particularly sensitive to small changes in food abundance (Medway and Wells, 1976). This interpretation probably holds for Blue-throated Bee-eaters (see Chapter 7). They may synchronize their breeding with increased foraging efficiency at the end of the long rains in March-April during the transitional period between the north-east and south-west monsoons.

The diet of Blue-throated Bee-eater nestlings consists mostly, although far from entirely, of dragonflies (266 of 732 identified food items, Bryant and Hails, MS), whereas the taxon eaten most frequently by provisioning adults is hymenoptera (21 of 72 identified food items, Bryant and Hails, MS). The highest feeding success both generally and of dragonflies was in sunny rather than cloudy conditions, although there may be additional, more subtle links with preceding weather conditions, e.g. cloud after a good feeding spell may depress feeding rates more than long-term overcast. These complex dependencies were not investigated, except for the finding that whenever observations were made during rain or immediately after a shower, no birds were feeding (see also Bryant and Hails, MS; and, for White-fronted Bee-eaters, Hegner and Emlen, 1987). For efficient foraging, Blue-throated Bee-eaters depend on sunny conditions, with little continuous rainfall. During nestling feeding in June the rains typical of the pre-breeding and early breeding season have eased so that the Bee-eaters do seem to exploit an overall advantageous pattern of rain for optimum feeding conditions for breeding.

In conclusion, the breeding season of the Blue-throated Bee-eater is probably timed to exploit the sunniest period of the year providing ideal conditions for feeding during the nestling phase, which immediately follows a rainy season, during which the population of insect food is probably built up.

Year-to-year synchrony of breeding

Many tropical birds may vary their breeding season from year to year, presumably according to the difference in availability of resources (Emlen and Wrege, 1991; Keats, 1985; Medway and Wells, 1976). Despite the year-to-year variations in climate reported in the Blue-throated Bee-eater study area, the Blue-throated Bee-eaters showed remarkable conservatism in breeding season (Chapter 5). For birds breeding in the temperate zone, early breeding is generally accepted as advantageous (e.g. Perrins, 1970), because reproductive success declines with season in many temperate species (Klomp, 1970). In the absence of strong seasonality and in a tropical environment, it may be more important to achieve synchrony of breeding at an intermediate date within the colony. Crick *et al* (1993) argue that even British single-brooded birds should be selected to breed when the optimum conditions have been reached and *not* before, and Brinkhof *et al* (1993) demonstrate experimentally that mid-season breeding increases fledging rate in Coots *Fulica atra.*

Two lines of evidence were used here to investigate whether it is advantageous for Bee-eaters to breed early or if mid-lay is a better strategy. Under the first hypothesis, the seasonal breeding success should be higher in general for early breeders. Early breeders, however, did not have higher numbers of fledglings (although they may nevertheless have had improved breeding success through fledging quality and an increased recruitment rate). Lessells and Krebs (1989) found this in European Bee-eaters, where nestlings of early breeding (and, incidentally, older) females returned to the colony more frequently, although fledging rates were the same for early and late breeders. This was explained as due to post-fledging care, which is a skilful job in Bee-eaters, so that older birds may have an advantage due to experience. In this study, the sample size of returning nestlings was small, partly because only a fraction of the nestlings were marked in those nestling seasons which were relevant for this investigation (cf Table 4.3). It is possible that capture caused disturbance to nestlings and caused them not to return to their natal colony, but this was not investigated. Those nestlings that did return were from broods with intermediate first-egg dates (Table 4.13), indicating that early breeding in Blue-throated Bee-eaters is not necessarily advantageous for breeding success in terms of recruitment, but since my data on recruitment was very sparse, this investigation remains inconclusive.

The second line of evidence comes from measuring the extent of synchrony itself. First egg dates were not significantly different between colony-years, indicating that the breeding season is adhered to from season to season and in different colonies, independent of variations in the environment (see above). In a later section (Chapter 5) I show that the year-to-year synchrony in breeding was probably achieved by year-to-year differences in the time-span between burrow initiation and burrow completion, which are complementary to the observed constancy of the laying date. Wrege and Emlen (1991) report an independence of local variation in climate also for White-fronted Bee-eaters, where the timing of breeding was not tied proximately to local environmental cues, although breeding seasons were adhered to. Instead, White-fronted Bee-eaters synchronized their breeding effort within their own colonies, but were out of phase with neighbouring colonies - so much so, that neighbouring colonies had different breeding seasons (one during the short and one during the long rainy season of Nakuru/Kenya) which produced a mosaic spacial effect of breeding seasons in the White-fronted Bee-eater population of Nakuru. The authors suspect that the extreme synchrony of breeding in each colony is a carry-over effect from a rigidly programmed molt in this species (Emlen and Wrege, 1991).

Thus, although the evidence from this study is inconclusive, it points towards a synchronous breeding season that is retained despite year-to-year variations in external cues, and no advantage in breeding success was found for early breeders (see also Table 4.10). This median-date synchrony corresponds to the hypothesis put forward by Crick *et al* (1993), stating that birds are selected to breed during optimum conditions (see also Chapter 5). Brinkhof *et al* (1993) found that the number of fledglings per brood was highest for birds breeding in the middle of the breeding season also for Coots, for example. In tropical House Wrens *Troglodytes aedon*, the breeding season is similarly timed so that food is most abundant during the most critical breeding stage, which in these birds is juvenile dispersal and molt (Young, 1994). For Blue-throated Bee-eaters, this finding thus further supports the notion that their breeding season is determined largely by conditions during nestling feeding, which is probably the most critical breeding stage of the Blue-throated Bee-eater.

Summary

I conclude that the effect of climate and weather on Blue-throated Bee-eaters is most likely to be indirect and that they are probably limited by food availability and foraging, like true tropical insectivores (e.g. Medway and Wells, 1976).

4.4.2 Migration

In the past, Blue-throated Bee-eaters in the densely forested Malay Peninsula used coastline and forest edge habitats (Medway and Wells, 1976), whereas nowadays most colonies are found on man-made pastures which might impose very different kinds of selection pressure. Even now, Blue-throated Bee-eaters sometimes (still?) breed in typical Bee-eater fashion in vertical river-banks (pers obs) which protect their nests from predation (Fry, 1984). It is possible that Blue-throated Bee-eaters can afford to nest on flat ground in man-made habitats because in such protected areas they are more sheltered. Predation was very low at less than 3 nests per number of nests monitored per colony, in all colonies. Although in small colonies this resulted in a higher overall predation rate, predation is probably not a serious threat to Blue-throated Bee-eaters any more.

The open-country population might itself be a new invader from the North, not part of the original forest-edge population (D.R. Wells, pers comm). Wintering Blue-throated Bee-eaters present near Kuala Lumpur belong to a different population (see Medway and Wells, 1976) and used very different foraging patterns during the winter months (pers obs during September and October, 1990). Recent changes in habitat may have increased competition with Blue-tailed Bee-eaters, which may impose migration on the Blue-throated Bee-eaters in Malaya. Blue-throated Bee-eaters are very similar to Blue-tailed Bee-eaters in size and, probably, in diet (Fry, 1984). For many birds in the equatorial Americas, seasonality of breeding is due to competition with overwintering migrants (Miller, 1963; in Medway and Wells, 1976). Although not generally applicable to birds in Malaya (Medway and Wells, 1976), this is nonetheless a possibility for the Blue-throated Bee-eater.

Waugh and Hails (1983) showed that similar birds with similar insect foods can form foraging guilds if their flight behaviour, morphology and prey choice between species is slightly different so that competitive exclusion of members of one species by members of another is avoided. It is possible that coexistence could not be achieved by the Blue-throated Bee-eaters when they found themselves in competition with the slightly larger, and therefore possibly dominant, Blue-tailed Bee-eater which may in turn dictate movement patterns of the Blue-throated Bee-eater migration.

4.4.3 Site and mate fidelity; philopatry

Although male and female breeders had similar return rates, these rates may be affected differently by other factors, such as previous breeding success. Despite an excess of first-year males, male and female European Bee-eater breeders are equally likely to return in future seasons (Lessells, 1990). If the partner from the previous season is present at the colony, there is every indication that the pair will attempt to breed together a second time. In Adélie Penguins *Pygoscelis adeliae*, pairs that stay together have higher reproductive success than those that have re-mated (e.g. Tenaza, 1971; see also Coulson, 1966). Bee-eaters are reported to usually pair for life (Fry, 1972; Lessells and Krebs, 1989), but many of the returning birds had to re-pair, perhaps because the survival rate is low and their mate had died. No divorce was reported (i.e. there was no case where both pair-members were present but attempted to breed with different partners), which may mean that both members of an unsuccessful pair do not return at all in the next season rather than divorcing the previous partner after an unsuccessful breeding attempt. Lessells and Krebs (1989; see also Lessells and Ovenden, 1989) report that 15-20% of European Bee-eater chicks return, more males than females, and chicks from the same brood are more likely to return together. In Blue-throated Bee-eaters, usually only 1-2 chicks survive, so the latter does not apply in this study. In White-fronted Bee-eaters, nestlings and previous breeders of both sexes usually return to their original colonies (Emlen and Wrege, 1988), but in European Bee-eaters males return closer to their natal sites than females (Lessells *et al*, 1993; see below). This pattern would explain the longer distance between the natal nest and the nest of its first breeding attempt of the only ringed and sexed female chick which returned to breed at the colony.

Colonies of White-fronted Bee-eaters commonly shift along the river bank where these Bee-eaters nest, between breeding seasons by an average of 1.3km (Hegner and Emlen, 1987). Red-throated Bee-eaters nest within 400m in successive seasons, and they sometimes re-nest in burrows of the previous years (Fry, 1972). In European Bee-eaters, male natal dispersal was 208m ±334(SD), female natal dispersal was 236m ±150, breeding males returned to within 130m ±223 and females to within 191m ±254 of their nests of the previous season (Lessells *et al,* 1993). In Blue-throated Bee-eaters, burrows are completely washed-in from year to year. Nearly all breeders that returned in successive breeding seasons in my study returned to the same micro-site within 10m of the previous nest. The same was also true for returning nestlings: those that did return, showed high allegiance to their natal site. Female Sparrowhawks *Accipiter nisus* increase their breeding success if they change nest-site after a nest failure (Newton, 1993). In Blue-throated Bee-eaters, however, site allegiance is very strong in successful breeders, and there is no evidence at all that failed breeders attempt to shift sites within a colony. My findings furthermore support the hypothesis that young birds do not, as was believed previously for some species, nest peripherally and gradually move to the centre of the colony in subsequent years (see Tenaza, 1971). Members of two populations of Guillemots *Uria aalge* for example returned to the same micro-site group, rather than re-assembling into denser groups which would be more successful (Birkhead, 1977). Tenaza (1971) reports the same for Adélie Penguins, which also returned to the same micro-site each year, even if it was located on the periphery of the colony where general breeding success was lower. My findings, that returning birds were very site specific and did not seem to shift between sites within the colony usually, is also found in other birds.

The effect of handling and marking

The only effect of interference I tested for was that of wing-tags on return rates. Wing-tags were amongst the most detrimental marking methods reported in a review by Calvo and Furness (1992). Wing-tags clearly reduced return rates in Blue-throated Bee-eaters either because they affected survival or because they discouraged birds from returning to breed. The effect of tags on foraging efficiency may have been particularly detrimental because Blue-throated Bee-eaters are aerial foragers and depend strongly on manoeuvrability in flight. Sightings made at one of the foraging areas indicated that tagged birds may return as non-breeding 'floaters' (see also Fry, 1984) without being seen at the breeding colony, however, so that the number of tagged birds that returned might be larger if such non-breeders could be counted. In a secondary investigation involving only a few birds, paint was not shown to affect return rates, a finding which is also reported by Best (1990). These markers are less long-lasting, and painted or taped feathers are shed in the post-breeding molt. It is possible that painting reduced return rates in Blue-throated Bee-eaters, but probably not as dramatically as wing-tags.

Wing-tags may have had other, indirectly damaging effects on birds such as causing changes in the behaviour. Many birds spent time preening their wings around the tags; although others showed no such response. Bright colours of wing tags, while useful for observation, may also make the birds more conspicuous to predators or change their attractiveness to mates or to conspecifics in general (e.g. Burley, 1988; see also Calvo and Furness, 1992).

Handling and other interference (e.g. early mistnetting, digging nests) may affect breeding singly or in combination, which may have caused desertions, especially early in the season (Calvo and Furness, 1992). This may also have biased the return rates of wing-tagged birds reported here, because more birds were wing-tagged early in the season. Some of those were never seen again and may have deserted in the same season as a result of early capture, rather than not returning because of the detrimental effect of the wing-tags.

4.4.4 Population differences in morphology

Gene-flow between Bee-eater colonies is rarely reported in the literature. Fry (1972) reports movement of birds between colonies of Red-throated Bee-eaters, but these colonies are close together and all movement was less than 1 km. Movement between the two study colonies of Blue-throated Bee-eaters would involve hundreds of kilometres, and there was no evidence for any such interchange. It is unknown for how long this may have been so. It is likely, that any differences in morphology between the two colonies is attributable either to different environmental conditions, to differences in the breeding structures of the two colonies (such as the mean age of breeders), or to genetic differences.

Birds from the two colonies were of different shape. PC2 and PC3, which are thought to contain variance due to shape, may contain 'noise' such as measurement error (Lougheed *et al*, 1991). There were, however, opposite but significant differences between the two colonies also in several of the size variables, which was interpreted as differences in overall body shape. Shape rather than measurement error is thus likely to be reflected in one or both of PC2 and PC3. Fry (1984) argues that Bee-eater morphology has evolved under social rather than classical selective pressure like predation, food or environment, and that races of Bee-eaters may vary widely in silhouette, particularly of the tail. Streamers greatly affect the appearance of the tail which is important for social signals in the Blue-throated Bee-eater. Birds in Nam Heng had subtly but significantly shorter and wider bills than birds in Sungei Buloh. Bill-shape may be related to specializations in prey (Fry, 1984) and could be correlated with potentially different prey choices in Sungei Buloh and Nam Heng. Wing shape and size in *Merops* correlates vaguely with the extent of flight acrobatics and migration performed by each species (Fry, 1984), so Nam Heng birds, which have longer wings, may spend more time flying during hunting or migration. The differences in body shape (and in streamer length) between colonies may be a sign of differentiating populations. Throat brightness and the extend of brown on the back were the only plumage characters I scored, but there may have been differences in the facial plumage that vary between individuals or populations, which went unnoticed. It seems therefore that there is some differentiation between Nam Heng and Sungei Buloh colonies, but the difference was not very marked. Since Sungei Buloh and Nam Heng are unlikely to have been separated for long enough for differential niche specializations to evolve, the differences in morphology between the two colonies are perhaps more likely to be part of a broader geographical trend through the Peninsula that could, for example, be explored via museum collections including material from the northern breeding range (e.g. South China).

4.4.5 The incidence of helping in Blue-throated Bee-eaters

At an estimated 5% on average, the incidence of helping was not as high in Blue-throated Bee-eaters as reported for other Meropidae, where between 30% and 50% of nests commonly have between 1 and 4 helpers (see Chapter 8, Table 8.3). It is possible that the incidence of helping was slightly higher, and that some helpers were not caught because many birds roosting in the burrow were not captured unless they left the burrow in the first two or three hours after dawn (see Chapter 2), or because helpers were less likely to use the burrows as roosts. Although there may have been more helpers at the colony than the estimated 5%, overall numbers were nevertheless low. The implications and reasons for this are discussed further in Chapter 8.

4.4.6 Summary and conclusions

Blue-throated Bee-eaters may live close to their food limit, as suggested for tropical birds and Malayan insectivores generally (Medway and Wells, 1976). The Blue-throated Bee-eaters in Malaya had a pronounced breeding season, the starting date of which did not vary between years. The birds take advantage of sunny weather beneficial for foraging, after a wet season when insect food populations are probably built up. As in other Bee-eaters, the breeding season is probably only loosely related to rain seasons and solar radiation (see Wrege and Emlen, 1991). Again akin to other Bee-eaters, it is possible that changes in weather between years rendered the food supply unpredictable for Blue-throated Bee-eaters, which is perhaps why first-egg-dates did not track year-to-year variations in weather. Other factors which may have influenced Bee-eater breeding numbers, return rates and breeding success are in particular interference disturbance (patagial wing-tags and golfing) and insect spraying.

There was no advantage in early breeding for fledging success (as there is for many temperate birds with pronounced breeding seasons; Perrins, 1970), and the few marked fledglings that were recruited to the breeding population were from broods of intermediate laying date. Synchronous breeding at intermediate dates may more important than early breeding for Blue-throated Bee-eaters; this is discussed further in Chapters 5 and 8. The Blue-throated Bee-eater in Malaya is the only locally breeding migrant (Medway and Wells, 1976). Migration may be a recently evolved behaviour, imposed by a recent (in evolutionary terms) shift in habitat and intensified competition with Blue-tailed Bee-eaters, a migrant species with very similar niche. It would be useful to compare the Malayan Blue-throated Bee-eater with other, sedentary Blue-throated Bee-eater populations. A recent shift in breeding habitat could also have reduced the predation risk for Blue-throated Bee-eater nests.

CHAPTER 5 - MATE CHOICE AND PAIR BEHAVIOUR

5.1 INTRODUCTION

In altricial bird species, the food brought by one parent alone often does not suffice to raise the young, so both parents help feed the brood (Wittenberg and Tilson, 1980). In these species, if one parent deserts, the breeding success of both parents suffers (reviewed e.g. by Davies, 1991). Lack (1968; in Davies, 1991) suggests that a monogamous mating system is predominant in 90% of bird species because it increases the reproductive output of *both* parents. If both members of a pair have similar interests in the survival of their young, they should cooperate during all stages of the breeding season: both act out of naturally selected 'selfishness' towards a common goal. Accordingly, either parent decreases its own reproductive success if it refuses to cooperate during provisioning or other breeding phases.

Selection pressure against desertion, and in favour of cooperation between pair members on breeding success, should be particularly strong in long-lived monogamous species with more or less obligate paternal help. This was demonstrated recently for Red-billed Gulls *Larus novaehollandiae scopulinus*, for which cooperation between pair members carries a particularly high benefit of breeding success (Mills, 1994). Cooperation between pair members should presumably be at its most pronounced, however, in species that benefit from the help of additional 'helpers-at-the-nest' (see Chapter 4). In those species, even the help of the male is often not sufficient to ensure that the nestlings can be fed at high enough frequencies. The assistance of auxiliary 'helpers' increases the number of nestlings that can be successfully raised to fledging for European, Red-throated and White-fronted Bee-eaters (Lessells, 1990; Dyer, 1983; Emlen and Wrege, 1991 respectively; see also review in Chapter 4). Accordingly, it is expected that in Bee-eaters the selection pressure for cooperation between pair members should be particularly strong, which makes them suitable for the study of pair cooperation and behaviour (see Chapter 1). In this chapter, the type and degree of association and interaction within pairs, the pair bond in general, behaviours of pair members, and the degree of their cooperation throughout the breeding season are described for Blue-throated Bee-eaters. Underlying this part of the study is the expectation that particular associations and behaviours will either enhance or depress reproductive success.

5.1.1 Pair association and mate guarding

Pair members may remain in physical, visual or audible contact for varying proportions of their time during the breeding cycle. The amount of contact maintained by pair members may be an indication either of the strength of the pair bond or of the extent to which they mate-guard (Lumpkin *et al*, 1982). Time spent together by pair members must therefore be interpreted within a context: pair members might simply associate because both dig or guard the nest; pairs may spend time together because they have a strong pair bond; males might be guarding their females against predation, competition for food by dominant flock members (Hogstad, 1992) or - most commonly - against being cuckolded (mate-guarding). Mate-guarding against cuckoldry is mostly observed during and just before laying, when the female is fertile. In birds, which unlike mammals commonly store sperm (Gomendio and Roldan, 1993), the fertile period may last up to 45 days before the first egg is laid until a little after the penultimate egg has been deposited in the nest (Birkhead and Møller, 1993; see also Birkhead, 1988). Lumpkin *et al* (1982) demonstrated that in Ring Doves *Streptopelia risoria* social contacts and proximity between pair members are mostly maintained by the male and occur mainly during the fertile pre-egg-laying period. Møller (1987 a) reported that males started associating with their female partners 1-3 weeks before the onset of laying, until during or after laying, for 47-94%, and mostly about 80%, of daylight hours at less than 5m. Similar findings are accumulating in the literature (e.g. for Great Tits *Parus major*, Bjoerkland and Westmann, 1986; Goshawks *Accipiter gentilis*, Møller, 1987b; Purple Martins *Progne subis*, Morton, 1987; Swallows, Møller, 1987 a; Sand Martins or Bank Swallows, Beecher and Beecher, 1987). White-fronted Bee-eater males mate-guard during the week before egg-laying (Hegner *et al*, 1982), which significantly reduces sexual harassment of females (Emlen and Wrege, 1986).

Two hypotheses, namely whether males are mate-guarding females or whether pair members cooperate with each-other in Blue-throated Bee-eaters, are investigated in this chapter using pair association patterns predicted under each hypothesis. While these are not necessarily mutually exclusive, which concept is prevalent may depend on the context and breeding stage. During pre-laying and laying, for example, male Blue-throated Bee-eaters may mate-guard, and the female may be cooperative or reluctant, depending on whether or not she judges him to be a high quality male (see Kempanaers, 1992). Several behaviours might be affected by the threat of infidelity of the partner. Firstly, since the male is expected to increase mate-guarding during the fertile period of the female, pair members should spend more time together during the pre-laying and laying season if the male is guarding, and secondly, males are expected to follow their partner disproportionately more often during that period than during other times. During laying and pre-laying, associative behaviour of pairs is therefore expected to differ from their behaviour at other times, unless laying coincides with cooperative nest-digging which could cancel-out the effect of mate-guarding. Alternatively, if pair cooperation is more important in shaping the pair behaviour and the female cooperates with the male throughout all periods of the breeding season including the pre-laying and laying period, no seasonal changes in association patterns are expected.

5.1.2 Synchrony of breeding

If all females in a population are fertile at the same time, the opportunities for polygyny are greatly reduced in species with obligatory paternal care, because each male can only help to raise one brood at any one time (Emlen and Oring, 1977). Synchrony of breeding may be a female strategy to impose monogamy on males, either to avoid being the subject of extra-pair male harassment, or to prevent their partner deserting the eggs and pairing with a second female (Lazarus, 1990; Emlen and Oring, 1977). The males then have to guard their own fertile females at the same time as other females are fertile, and mate-guarding usually takes precedence over seeking extra pair copulations (Birkhead and Møller, 1993; Birkhead and Fletcher, 1992). Synchrony of breeding within a colony thus encourages monogamy amongst males, counteracting the increased opportunity for intraspecific brood parasitism in colonially nesting birds (Davies 1991).

Breeding synchrony may be an adaptation to predation: the nests in a colony are vulnerable while the nestlings have not fledged, and by breeding synchronously, predators may be ‘swamped’ (predator saturation, reviewed e.g. by Endler, 1991). In Blue-throated Bee-eaters, stable but seasonal climatic conditions further encourages synchronous breeding because most members of a breeding colony should aim to raise their brood during optimum conditions (Chapter 4; also Perrins and Birkhead, 1982; Bryant, 1975).

In Blue-throated Bee-eaters, breeding synchrony may be achieved at one or more of three stages: arrival at the breeding grounds, digging and completion of burrows and laying. After synchronous arrival, relatively synchronized breeding behaviour during pair formation and digging would assure sufficient synchrony in laying and chick rearing. Alternatively, if synchrony is accomplished *after* arrival, the early arrivals could spend more time selecting a burrow by starting to dig several attempts before completing a burrow with a nest chamber, or they could dig a burrow and then wait for the later arrivals before starting to lay. Alternatively, synchrony within the colony is a less important incentive for burrow completion than the actual laying date.

Whether synchrony was achieved was established using estimates of the onset of laying (Chapter 4) as a criterion. The onset of laying was also used to make inferences about the timing of behaviour relative to breeding stage. If birds arrive at the breeding colony synchronously, digging and burrow completion are synchronous with respect to both season and first-egg-date of the pair. If synchrony is achieved by synchronous burrow completion, then the pattern of digging throughout the colony is asynchronous with respect to season and first-egg-date but burrow completion is synchronous. If synchrony is not achieved until the laying stage, burrow completion is also asynchronous with respect to season and first-egg-date. If egg-laying rather than breeding synchrony is the main incentive to complete the burrow, burrows are expected to be dug asynchronously with respect to season but completed with similar timing with respect to first-egg-date. In summary, these four hypotheses have different predictions on the relative timing of digging and burrow completion with respect to season and first-egg-dates which were investigated in this chapter.

5.1.3 Female choice and sexual selection

Intersexual selection by active female choice is now generally accepted as an important selective force on males in many mating systems. Females looking for a mate may use subtle secondary cues which signal the male's (a) social status (e.g. Brodsky *et al*, 1988; but see Alatalo, 1993), (b) condition, (c) resistance to parasites (Hamilton and Zuk, 1982) or (d) superior genetic fitness (e.g. von Schantz *et al*, 1989). Amongst birds, sexually selected traits of males often entail plumage coloration (e.g. Järvi *et al*, 1987), tail length (Andersson, 1982), ornament size (e.g. Brodsky, 1988) or body size: Bryant (1989) suggests that body size may be a criterion for female House Martins *Delichon urbica* to pair with larger, older males because these have overcome a survival handicap that 'being large' seems to carry in these birds. Sons of 'sexy' fathers would simply inherit the latter's secondary traits that make them similarly desirable as mates ('sexy sons' hypothesis; reviewed e.g by Harvey and Bradbury, 1991; Järvi *et al,* 1987). Alternatively, some females are interested in resources rather than male quality and seem to prefer a male which happens to occupy a territory of high quality (e.g. Alatalo, 1993), or who feeds her early in the breeding season during the egg production and laying phases ('allofeeding').

The selection pressure for sexual dimorphism is either provided by female choice (intersexual selection; Partridge and Halliday, 1984) or by sperm competition (intrasexual selection; Clutton-Brook *et al* 1977). Harvey and Bradbury (1991) argue that, given "no concurrent selection on females, the degree of sexual dimorphism in a species can be used as one measure of the magnitude of the intrasexual selection on male traits" (p.208). The theories on the evolution of secondary sexual characteristics (reviewed e.g. by Järvi *et al,* 1987) are confounded for several hypotheses. A male with conspicuous plumage may be (1) a better competitor, or he may be (2) preferred by females as partners because he advertises (a) lack of parasites (Hamilton and Zuk, 1982) or (b) that he has survived (i) in spite of being more conspicuous to predators (the 'handicap' principle; Maynard-Smith, 1986; Zahavi, 1975) or (ii) because he signals to predators that he is difficult to catch (the 'unprofitable prey' hypothesis; Götman, 1992; Baker and Parker, 1979). A healthy, successful male may be phenotypically better at helping to raise young (Petrie, 1983 b), or he might pass on his good health to his offspring (e.g. von Schantz *et al,* 1989). Partridge and Halliday (1984) point out that it is important to demonstrate heritability of sexually selected characters to establish whether these reflect genetic differences rather than phenotypic condition. Gustaffson (1986) and van Noordvijk *et al* (1980) demonstrated that generally over 50% of many body size measures was inherited in Great tits *Parus major* and Pied Flycatchers. Wing length had similar heritability (56-73%) in European Bee-eaters (Lessells and Ovenden, 1989). In some species, older males may have higher reproductive success because of their dominance over younger birds which gives them increased access to females (Post, 1992). In species where males vary in size, large males may prevent other males from mating and so enhance their own mating success (Hedrick and Teneles, 1989). Plumage variation may relate to individual recognition (Whitfield, 1988) or to dominance (Rohwer, 1975; also Holberton *et al*, 1989; Thompson and Moore, 1991). Conspicuously coloured males may be of higher social status: Järvi *et al* (1987) reported that older, darker male Pied Flycatchers were attacked less often by brown (younger) males than by other dark males. Plumage coloration may thus be involved in (1) social status signalling (Møller, 1987) or in (2) territory signalling (Slagsvold and Lifjeld, 1988), usually between members of the same sex (but see Wilson, 1992), and can relate to sexual behaviour and success (Møller, 1990). Hamilton and Zuk (1982; supported by Read, 1987; but not by Weatherhead *et al*, 1991) reported that across different species, striking displays and 'brightness' correlate positively with the incidence of blood infection by parasites, signalling possibly that within those species that have high parasite load, brightness signals resistance against parasites, and highly infected individuals consequently suffer reduced reproductive success (e.g. Mulvey and Aho, 1993). Weatherhead *et al* (1993) report, on the other hand, that ectoparasitic mite infection correlated positively not only with more striking plumage coloration (epaulet length) but also with higher testosterone levels, both of which are related to social dominance in Red-winged Blackbirds *Agelaius phoeniceus*.

Active female choice (e.g. Bensch and Hasselquist, 1992) of a male secondary character trait was first demonstrated unambiguously by Andersson (1982) in his classic manipulation experiments of tail length of male Long-tailed Widow-birds *Euplectes progue*, confirmed for Swallows by Møller (1988 a; see also Jennions, 1993; Andersson, 1992; Smith and Montgomery, 1991; review by Cherry, 1990). Komers and Dhindsa (1989) showed that female Magpies *Pica pica* preferred adult over first-year males and dominant over subordinate adults (see also Brodsky *et al*, 1988). Fitter male Pheasants *Phasianus colchicus* were actively selected by females on the basis of their spur length (von Schantz *et al*, 1989; but see Sullivan and Hillgarth, 1993). In monogamous systems, female choice should be reflected to some extent in pair formation. If only the early arrivals of both sexes have access to high quality partners and late arrivals have to pair with each other (e.g. Patokangas *et al*, 1992), this would lead to non-random mating of birds of similar quality (e.g. Petrie, pers comm). As often older birds are the more successful breeders (e.g. Port, 1992; Bryant, 1989), and age (or simply 'success') may be reflected in a larger size (Bryant, 1989) or by plumage colour (Järvi *et al*, 1987; see above), assortative mating (non-random mating between similar sized or coloured individuals) would occur (e.g. Olsson, 1993; but see Choudhury *et al*, 1992, for critique). Assortative mating is investigated for *M. viridis* in this chapter.

5.1.4 Mutual sexual selection

The idea that mating systems are driven by female choice is based on the following assumptions:

(1) single eggs are more costly to produce than single sperm (Trivers, 1972), or
(2) females have a more limited number of eggs per season than males have ejaculates, so that females are more selective when it comes to the quality of the male to fertilize her eggs. Alternatively,
(3) the female would at least have relatively more to lose if her brood does not succeed, because
(4) the male is able to compensate quality of offspring with quantity.

The first argument has been modified from 'difference in gamete *size* between males and females', to 'difference in potential rate of reproduction for males and females'. Accordingly, a male could still produce unlimited offspring, if only he could find enough fertile females to inseminate (Davies, 1991), whereas females have to make do with their limited number of eggs. Accordingly, Davies (1991) argues, that monogamous mating systems are predominant in altricial birds, where both parents care for the young, not so much because male parental care is needed (as originally suggested by Lack, 1968, in Davies, 1991) but because the opportunity for polygyny is limited, and if one partner can raise at least some young on their own, then which sex deserts in any one species probably depends on which sex has more opportunity to gain further mates (Davies, 1991). Some studies suggest that accordingly, female-female aggression may be important for maintaining monogamy because aggressiveness of the primary females reduces the opportunity for males to attract secondary females (e.g. Slagsvold, 1993). Females may resist non-committed males (Birkhead and Møller, 1992). Limitations on the number of offspring which a male can sire may thus indeed be determined by limited access to females. Males may be forced into monogamy and have less opportunity to compensate for lost nestlings by siring EPOs.

Evidence is emerging, however, firstly, that males may have limited reproductive resources just like females. They may incur a real cost of spermatogenesis (Partridge and Harvey, 1992; Dewsbury, 1982), for example, because both a high sperm count (i.e. a high number of sperm in the ejaculate) and the number of copulations are important for fertilization (Birkhead and Fletcher, 1992; Oring *et al*, 1992). The notion that females copulate repeatedly with the same male to 'deplete' his sperm reserves (Petrie, 1992) is based on the assumption that these can be depleted in the first place. Secondly, the mating system of some species suggests that perhaps there are relatively 'unlimited' reproductive resources also in females, for example in cases of sequential polyandry as in Spotted Sandpipers *Actitis macularia*, where several clutches are laid sequentially by more or less transient females, which are attended to by different males (Oring *et al*, 1993 and 1992). Thirdly, in most long-lived, monogamous birds, paternal help is needed to raise the nestlings, and the male cannot increase his reproductive output simply by substituting parental care with offspring 'quantity' (Mills, 1994). Hence, desertion is costly for such males and males should be selected to help feed their pair offspring (Mills, 1994).

Direct evidence for the importance of male parental care for the breeding success of both parents was provided for example by Henderson and Hart (1993) for Jackdaws *Corvus monedula*, and by Mills (1994) for Red-billed Gulls. In the latter, male provisioning greatly increased the breeding success of both partners in terms of the number of fledglings raised. Blue-throated Bee-eaters probably live very close to their food limit (see Chapter 4) and it is likely that nestling survival depends strongly on provisioning by both parents. In other Bee-eaters, nestling survival depends not only on the help of the male and female pair member alone, but their breeding success can be further enhanced by the help of auxiliary birds (see Chapter 4; also 5.1.1 above). Male Bee-eaters should therefore have particularly strong interest in feeding their pair offspring.

Since the main selective force that drives Bee-eater mating systems may not be female choice, alternative evidence presented in the literature has to be considered briefly. Female-female competition for male birds and mate choice by males occurs mostly in role-reversed species (Petrie, 1983 b) but is known also in monogamous birds where sexual selection may act less strongly on females than on males (Johnson, 1988). Although female-female aggression is often attributed to the defence of reserves in polygyny (e.g. Slagsvold, 1993; Slagsvold *et al*, 1992), Wagner (1992) showed conclusively for a monogamous species (Razorbills *Alca torda*) that females actually defend their 'pair bond'. This supports the idea that females compete for males. Female-female aggression is thus predicted from two hypotheses: not only could it reduce the opportunity for their male partners to engage in polygyny (Lifjeld, 1993), but instead it may be an expression of role reversal in mate guarding if males do not have unlimited reproductive resources.

If polygynous birds such as lekking species are more sexually dimorphic than non-lekking birds in general (Harvey and Bradbury, 1991), then species with mutual mate choice should perhaps be more monomorphic. Mutual mate choice was recently demonstrated by Jones and Hunter (1993) for Crested Auklets, where both sexes are ornamented. In this chapter, the rôle of the central tail streamers of the Blue-throated Bee-eater is investigated as an ornament in both sexes and as a dimorphic character in this chapter, as are body size, plumage coloration and plumage brightness.

5.1.5 Summary of aims

In this chapter, behavioural observations were used to investigate functional, and in particular also causal indications for mate choice and pair behaviour of Blue-throated Bee-eaters. For the study of mate choice, firstly pair formation and soliciting behaviour was examined for males and females to find out when pair formation occurred and whether female choice or mutual selection governed mate choice in Blue-throated Bee-eaters. Secondly, I aimed to identify some sexually dimorphic characters which may be subject to sexual selection, by looking at assortative mating and differential breeding success. I investigated the supporting behavioural evidence for two further hypotheses, (1) cooperation of pair members, and (2) conflict of interests between pair members. Cooperation between pair members is expected to be particularly high in Bee-eaters during all stages of the breeding season, not only in the form of parental care of the brood. It may be necessary, for example, to cooperate to dig a burrow quickly, so as to be able to start laying early or to breed during the peak breeding season. I looked at such behavioural adaptations throughout the breeding season.

5.2 METHODS

In this section, I introduce the methods relevant to the results obtained in this chapter in the attempt to answer the questions asked above. These methods include how birds were sexed in the field, observations of pair behaviour during different parts of the mating and breeding season, and measurements related to sexual dimorphism.

5.2.1 Sexing birds

Some researchers sex birds by laparotomy (e.g. Hegner and Emlen, 1987) or laproscopy (e.g. Richner, 1989). Because these methods appeared likely to cause injury to birds unless performed by an experienced researcher and, in any case, seemed rather distasteful, in this study birds were instead sexed by one or more of the following methods. During 1989 and 1990, I sexed several tagged birds by observation during mating or extensive soliciting behaviour. Furthermore, gravid females caught at the burrow between 1989 and 1991 during or just before laying were identified by palpating eggs in the abdomen. I also classed as females either (1) small birds (keel < 30mm) which were very heavy (≥40.0g), (2) birds which were much heavier than predicted from the regression of mass on keel for males (Fig. 5.1), or (3) birds for which mass varied by 7.0g or more between captures in the same season with no marked change in condition (a change in pectoral muscle score of less than 1; see Chapter 2). If two birds were caught at a known female's nest more than once, the partner was classed as male.

5.2.2 Behavioural observations of sexual interactions

A sexual interaction was defined as any interaction between two or more birds which involved one or more of the behaviours described in section 5.3.2 as sexual behaviours. For each observed sexual interaction, I noted which bird initiated the contact, the length of the interaction in minutes, whether it resulted in copulation, and if so, whether it was with or without cloacal contact (see Chapter 4). For sexual interactions involving marked birds, I checked whether it was possible that the interaction was with its partner or whether the other bird was definitely not the breeding partner in this season.

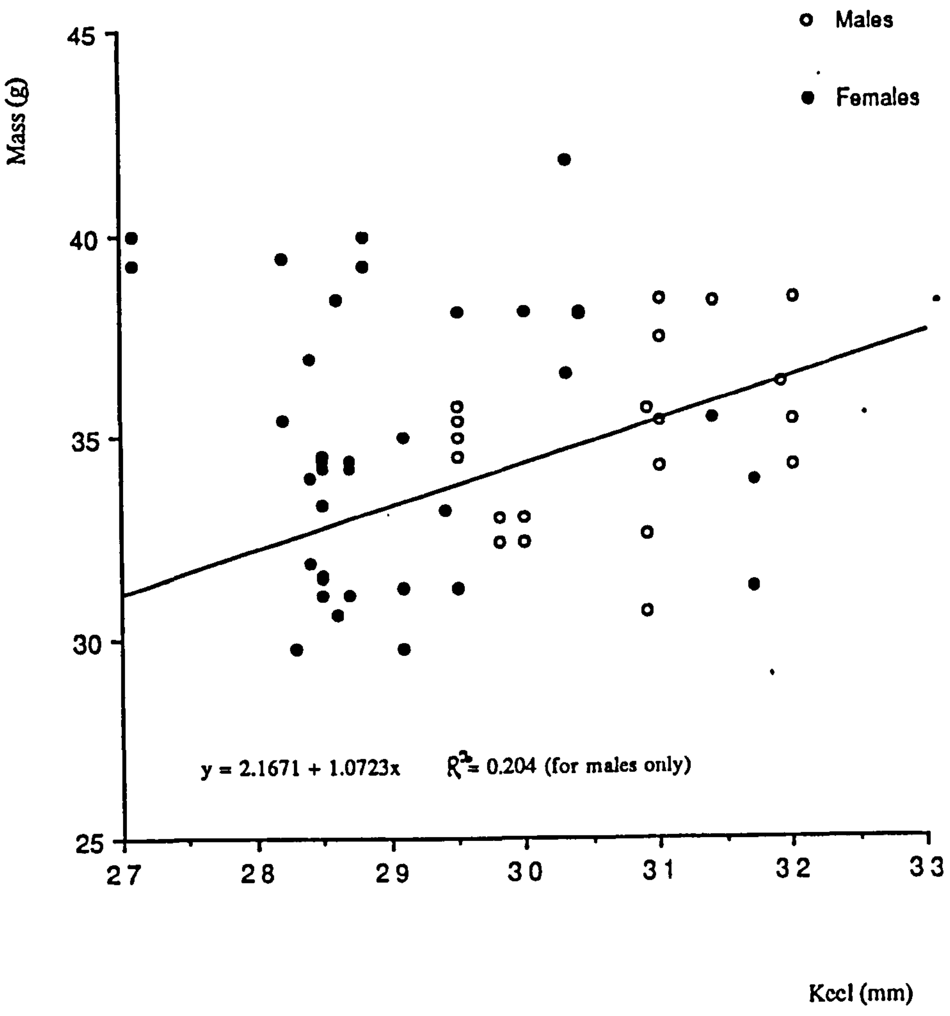


Figure 5.1: Body mass in relation to body size (keel length) for sexed birds. N= repeated measurements for 74 birds. Only males were used for the regression line of mass on keel length and its 99% confidence intervals. Breeding and gravid females were heavier than predicted from this regression, which is why body mass was excluded from the discriminant function analysis (see text). The variation in mass per size within 99% confidence intervals was about 8g for males, including different individuals of the same size as well as repeated measurements of the same individuals. The variation was higher for females if measurements were taken both during and outside laying.

5.2.3 Behavioural observations of association of pair members

Initiation of close associations was investigated using 16 marked and sexed pairs, for which 69 associations between pair members were observed with details on who joined or followed who (see query in Appendix 4). An association between birds is defined as any two birds being within one bird-length of each other (see Chapter 2).

The time spent together by pair members was investigated under continuous observations (see Chapter 2). The sub-colonies of 18 pairs (mostly the RH parts of SB, RH-mid and RH-end) were observed while both partners had readable tags. Continuous observations at a sub-colony lasted on average 95 minutes. For any one-minute observation of one partner, its mate was either present or not present at the sub-colony or had remained inside the nest for a long period (10-120 minutes during incubation; during provisioning and digging, birds can usually be seen with relative ease entering and leaving the nest). For each of a total of 2544 one-minute sightings, the type of association between the focal bird and its partner was recorded in 4 graded categories or association types from 3 to 0, as 'associated', i.e. within one bird-length of one another (association type = 3), 'both present at the sub-colony during the same minute but not associated' (association type = 2), 'both present at the sub-colony at least once during the observation period but not at the same time' (association type = 1) and 'partner not present at sub-colony at any time during the observation period' (association type = 0). Association type 3 was also referred to as 'physical contact', because if two birds were associates, they were able to communicate physically for example by bill-wrestling or sexual interaction. Birds at the same sub-colony (association type 2) were within each-others' vision and communicated by calls (purring, chirping; Chapter 2), so association type 2 was referred to as 'visual contact'. Birds that were both seen at the colony during the same observation period but not within the same minute were probably within audible distance of each-other and able to communicate, for instance, with the far-carrying 'long call'. Association type 1 was therefore sometimes referred to as 'audible contact'. When a bird was seen at a subcolony consistently without its partner, they were probably not within audible range, and the partner was hunting or loafing elsewhere. Association type 0 was therefore called 'no contact', except during incubation and the latter part of digging when the partner may be in the nest for a long period.

For part of the investigation, the day relative to the pair's onset of laying (dayx) was grouped into 5 seasonal blocks from early to late season: (1) 'day -30 or earlier', (2) 'day -29 to day -11', (3) 'day -10 to day 9', (4) 'day 10 to day 29' and (5) 'day 30 or later'. For the purpose of reference only, these periods correlated roughly with arrival (1), digging (2), pre-laying and laying (3), incubation (4) and provisioning (5). Period 3 (day -10 to day 10, pre-laying and laying) is of particular interest for mate-guarding, since females should be fertile at least during laying which at a maximum of 5 eggs laid every 2 days, lasts about 10 days. Seasonal blocks 1 and 2 ware sometimes referred to as 'before mating and laying', block 3 'during mating and laying' and 4 and 5 'after mating and laying'.

To investigate the change of pair association during the season more closely, I decided to use only sightings of pairs that were seen at the colony for most of the season. For 9 different pairs, observations were available for each of the phases of before, during and after mating and laying. The total number of observations for these 9 pairs was 1968. Four of these 9 pairs were observed during each of the 5 seasonal blocks (during 1-15 observation periods in each block).

The relative percentage of time spent in each association type was measured in the percentage of sightings in each observation period which can be assumed to be independent, since there was usually a gap of several hours between successive observation periods, during which the situation at a sub-colony will have had changed completely. Using percentages does not take account of the total number of observations or the length of observation periods. It is possible that short observation periods do not represent the seasonal pattern very accurately, but since any type of association can occur within short observation periods, no directional bias is expected. For χ^2 tests, independent Poisson sampling was assumed. Since I used repeated measurements of individuals, it is important to verify that at least the underlying distribution of the percentage of time spent together follows a Poisson distribution (Kramer and Schmidhamer, 1992): most observations were of birds alone (see Results), with successively fewer birds in closer association. This corresponds conceptionally to Poisson sampling.

5.2.4 Digging and nest guarding

Throughout the digging phase, 28 burrows were measured repeatedly (see Chapter 2). All burrows subsequently contained a brood, and they were all in SB; 18 in 1989 and 10 in 1990. The maximum measured length of any completed burrow was taken as its final length. Many burrows below 10cm were abandoned, but once burrow length had reached about 20cm, desertion was rarer. For its starting date, the latest record of having reached 20cm was used. Burrow 5-90 was washed in to < 20cm after reaching nearly 100cm in the early season, which is why I decided to use the most recent time a burrow reached 20cm length as an indication that it was 'active'.

Although digging observations were taken repeatedly from the same pairs at the same nests, the underlying random (Poisson) distribution should not be affected because firstly, *all* digging birds were usually recorded during any observation period and secondly, large numbers of repeated observations were taken from each nest.

Observations were carried out to establish whether the presence of the partner reduces the vigilance of the digging bird so that it can spend more time and concentrate more on the digging itself. These observations commenced as soon as the digging bird had started digging without disturbances. Records during which any irregularity occurred (e.g. if the birds were disturbed) were discarded. Vigilance of the digging bird was measured as the rate of looking up (defined as lifting of the head with the bill horizontal or above). Only those records were used where the partner of the digging bird was both present and absent during the same bout of digging, for either (a) more than 2 look-ups or (b) at least 1 minute each (bout length of digging in between looking up varied from 2 to 420 seconds (7 minutes)), i.e. the partner either arrived sometime after the digging had started or flew off before the digging bird finished. Observations were thus made in pairs, for the same digging bird with and without its partner, within 10 minutes to minimize the effect of changes in the environment.

5.2.5 Provisioning behaviour

Broods in which nestlings were estimated to have hatched within 1 day of each-other were classified as 'synchronous'. To investigate the provisioning pattern during the nestling period, provisioning rates were scored repeatedly throughout the nestling period for 9 synchronous broods. The total provisioning rate was calculated as the total number of visits divided by the total minutes of observations throughout the season. As the total rate per nestling, I used the total provisioning rate divided by the maximum number of chicks per brood. The mean rate per nestling was calculated as the average of all provisioning rates, per live nestling at the time, during the season in the brood.

Whenever possible, a note was made of the type and size of insect brought. The bird's bill was used as size reference, which is a method that indicated high repeatability when used by other workers (Bryant and Hails, MS; Hegner, 1982). The relative size of the insect brought was determined in one or more feeding observations in 124 observation periods. Small differences in length of prey items can represent a large difference in food value because different insect orders have different length-mass relationships (e.g. appendix 1 in Bryant and Hails, MS). The absolute size of each insect was determined from its relative size in the field, to allow different insect orders to be compared for size. For instance, a 'medium size Bee' was repeatedly scored as a 'large insect'; a 'medium size dragon-fly' as a 'small-to-medium insect'; a 'medium fly' as a 'small insect' and so-on. 'Absolute' sizes varied from 'very small' (1) to 'very large' (7).

I obtained brood size and chick size, mass and condition within 2 days of the provisioning observations. The degree of hatching asynchrony was tested with broods that had more than one nestling. Degree of hatching asynchrony was expressed as age-difference between eldest and youngest nestling. Chick condition was measured in two independent ways: firstly, in the field, by scoring the pectoral muscle thickness (0-5 in 0.5 steps; see Chapter 2; median = 3.0), and secondly by relative mass, calculated as chick mass divided by wing length (mean = 0.71, se = 0.017). Nestling satiation or 'hunger' was measured as the extent to which the abdomen protruded with insect food (Chapters 2 and 7). Extremely extended abdomen with very taut skin were called 'bulge' in the following account; all other shapes of abdomen were lumped.

To test the variation in insect size brought to broods compared to the degree of asynchrony in the brood, nests with at least 3 nestlings were selected, with a mean nestling age between 1 and 12 days. For each of 10 broods, the minimum and maximum absolute insect size seen brought to the brood within a 2 day period were noted and the different number of insect types. For each brood, between 2 and 15 observations were made. The difference between the age of the youngest and eldest nestling varied from 1 to 6 days. Insect size was 1 to 7.

5.2.6 Sexual dimorphism

For studying individual differences in size and plumage, mass was not used because it varied with condition and according to breeding stage and was therefore not a reliable measure of size. This was also found for female Savanna Sparrows *Passerculus sandwichensis* (Rising and Somers, 1989). In monomorphic species, where not all adults can be reliably sexed (see section 5.3.1), a small sample of sexed birds can be used for investigating sexually selected characters. On the other hand, a large sample of sexed birds may be needed to demonstrate real differences, since characters under sexual selection might be expected to differ only slightly between males and females in monomorphic species (see 5.1.5). The mean score for each size measure was higher for males, which were larger than females (as demonstrated by the discriminant function analysis; section 5.3.1 and Table 5.1). It is therefore possible to increase the sample size dramatically by assigning the larger pair member as male (termed 'male' or 'M' hereafter, with apostrophes) and the smaller as female (termed 'female' or 'F' in the following, including apostrophes), so that all pairs for which both adults were captured can be included in the analysis. For the investigation involving breeding dates and success, only the broods where both attending adults were measured were included, and the larger partner was treated separately from the smaller one, or the mean of both partner's measure was used. For 48 broods with measurements of both attending adults and laying date estimates, the general breeding success (GenSuc) was either: a failed clutch due to desertion or predation (GenSuc = 1); a brood with chicks which either did not fledge or with unknown outcomes (GenSuc = 2); 1 fledgling (GenSuc = 3); or 2 fledglings (GenSuc = 4). The number of fledglings produced was noted for 32 broods with chicks.

5.3 RESULTS

In this section I relate the findings of this study on the behaviour of mated pairs chronologically during the mating and breeding season. I begin with a discriminant function analysis which allowed me to sex a larger number of birds than were sexable from observations alone.

5.3.1 Discriminant Function Analysis to sex adults

Blue-throated Bee-eaters are monomorphic: most males and females cannot be readily distinguished in the field. The aim of conducting a discriminant function analysis is to be able to sex birds reliably with body size measurements (e.g. Hamer and Furness, 1991; Green and Theobald, 1989). The analysis was done on a set of birds of known sex for which biometric measurements were available. It involved, firstly, finding the best combination of biometric variables that sexes birds reliably. Secondly, I was interested in predicting the sex of new birds, for which only biometrics were available, with a high probability (say 95%). The analysis generates a function of the chosen variables, the value of which is the 'cut-off point' between males and females. Usually researchers split their sample of sexed birds in half and use the first half to calculate the discriminant function and the second half to test it (e.g. Hamer and Furness, 1991). This, however, reduces the sample size of birds on which the calculation of the function is based and hence makes it inherently less reliable. In view of the limited sample size I decided to use the complete sample of sexed birds to calculate the discriminant function.

Forty-three females and 31 males (N=74) were caught in SB and NH during 1989 to 1991 and sexed as described in the methods. Seven biometric size measures (see Chapter 2 and below) were available to be used in the analysis for all 74 birds. Body mass was excluded from this analysis because it varies with body condition and for females with breeding stage. I tested 7 biometric measurements for their usefulness in sexing. Only keel length (KEEL; ANOVA, F=21.98, $p < 0.001$), head and bill length (HB; F=9.24, $p<0.005$), bill length (BILL; F=4.19, $p<0.05$) and bill width (BW; F=6.11, $p<0.05$) were significantly different between males and females (Table 5.1). There was also an indication that wings and tails of males were longer (but neither significantly so). BW was the best single discriminator variable (Dimorphism Index (DI) = 5.9), followed by BILL, then wing length (WING), KEEL, HB and tail length (TAIL). Most measures seemed more variable between females than between males, in particular WING and TAIL, which I consider elsewhere (see section 5.9).

The frequency distributions of all 7 biometric variables were compared to normal distributions and, as expected for size measurements, none showed marked deviations from normality (see Chapter 2). The highest level of correct classifications was 82%, achieved by a combination of all variables rather than any sub-set (Table 5.2). The discriminant function (S) calculated for these (Fig. 5.2) was given as

$$S = 0.58\ \mathrm{KEEL} + 0.058\ \mathrm{WING} + 0.026\ \mathrm{BILL} + 1.49\ \mathrm{BW} + 0.13\ \mathrm{HB} - 0.12\ \mathrm{TAIL} - 30.21 \qquad (5.1)$$

Eighty-two percent accuracy is not precise enough to sex birds reliably. Since no hard-and-fast rules exist for the level at which to accept or to reject classifications as 'probably correct' (Green and Theobald, 1989), I chose $p < 0.05$ mis-classifications as the 'cut-off point'. Accordingly, birds are assigned correctly with $p > 0.95$ where

$S \geq 2.0$ (classified as males), and
$S \leq -1.7$ (classified as females).

Consequently, birds with values for S between -1.7 and 2.0 could not be sexed with 95% confidence. I therefore did not attempt to sex birds with values for S between -1.7 and 2.0. For these birds, the sex therefore remained unknown. Forty-four birds (18 females and 26 males) caught between 1989 and 1991 were sexed purely on the basis of their S values using the above equation (see database queries in Appendix 4.6 and 4.7).

Altogether, 118 birds were sexed in the field or by using the discriminant function described above. For all further analyses involving sexed birds, I added 128 birds caught by P.T. Green pre-1989, which were sexed as 'very heavy females' or birds with very variable mass, or their partners, but which I could not include in the discriminant function calculation because P.T. Green took slightly different biometric measurements (see also warning given by Hamer and

Table 5.1: Biometric measurements included in the discriminant function analysis.

DI = Dimorphism Index ('male % bigger than female')
= 100 * (Male mean - Female mean)/ Female mean
all measurements are in mm

Variable	Males		Females		p	DI(%)
	mean	SD	mean	SD		
KEEL	30.6	1.0	29.4	1.2	***	4.1
HB	58.2	2.2	56.6	2.2	**	2.8
WING	113.4	5.2	108.7	14.8	(NS)	4.3
TAIL	80.7	2.4	79.1	11.8	NS	2.0
BILL	28.5	1.6	27.2	3.0	*	4.8
BW	7.2	0.3	6.8	0.9	*	5.9
	(N = 31)		(N = 43)			(N=74)

Table 5.2: Discriminant Function Analyses using different combinations of biometric size variables and levels of correct classifications. The four combinations with the highest levels of classification are shown here.

Size variables	Eigenvalue	Correctly classified cases
KEEL, WING, BILL, BW, HB, TAIL	0.647	82.43%
KEEL, WING, BILL, BW, HB	0.550	79.73%
KEEL, WING, BW, HB	0.554	77.03%
KEEL, WING, BILL, BW	0.469	77.03%

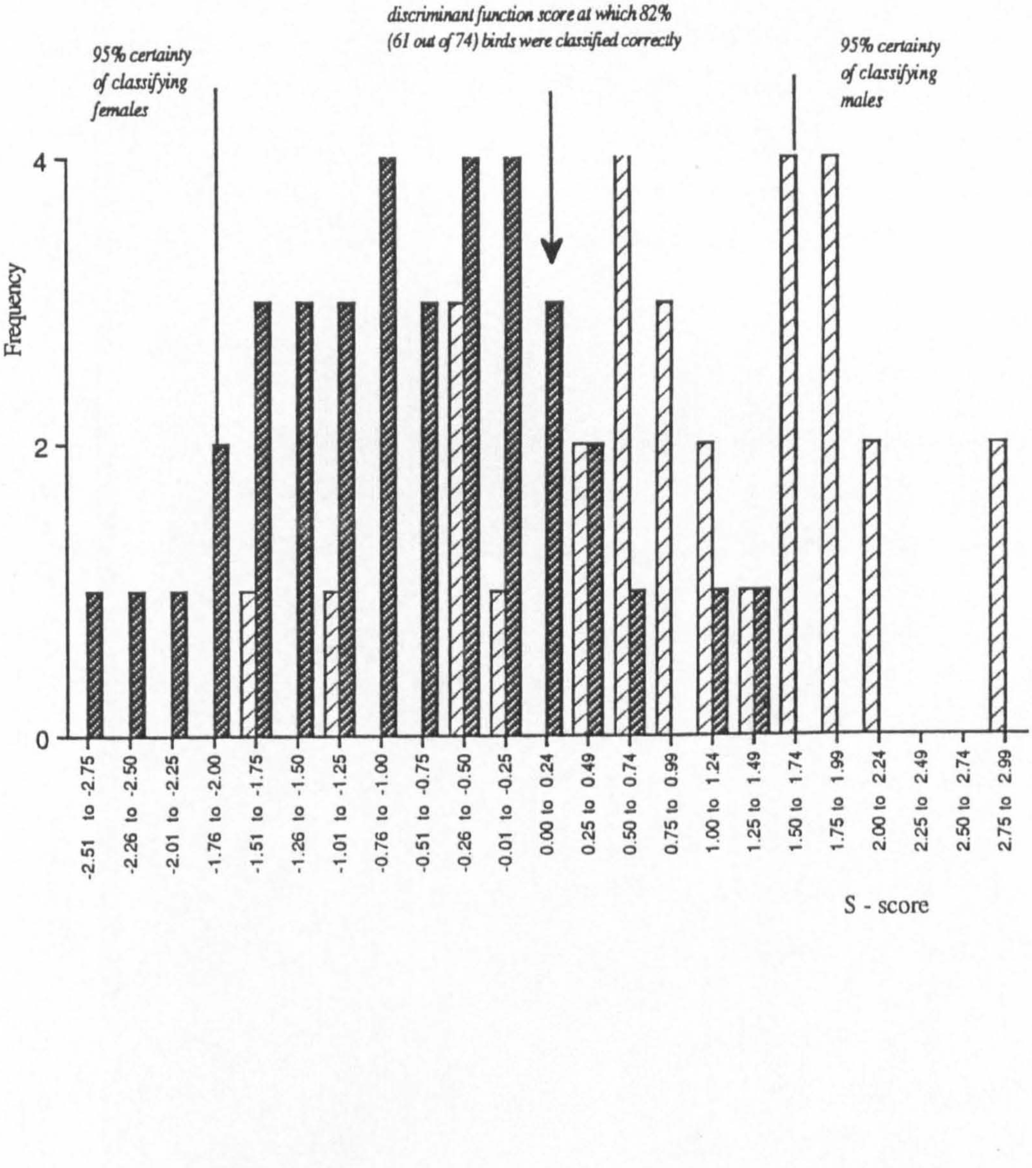


Figure 5.2: Distribution of the discriminant function S chosen to sex males (right) and females (left) with size variables (equation 5.1, see text). N = 74 sexed birds

Furness, 1991). Further analysis involving sexed birds was based on these 246 birds, unless otherwise stated. If birds had been sexed by their discriminant function scores alone, I did not include their partners in the sample of sexed birds, because this would have inflated the level of potential mis-classifications to above 5%. Hamer and Furness (1991) argue that the best results for sexing birds should be expected if discriminant function analysis was combined with within-pair comparisons between mates. I used the latter approach later, assigning the larger pair member of each pair as 'male', to increase the sample size for an exploration of morphological characters under sexual selection (see section 5.3.6 below).

5.3.2 Soliciting and copulation

Most observations of sexual behaviour were obtained by continuous observations at one or more sub-colonies (Chapter 2). Sexual interactions were only observed on perches, never on the ground or elsewhere. Sexual behaviour, sexual interaction and types of copulations are defined below in the description of behaviours. During 1989 and 1990, 32 sexual interactions were observed in each year, 64 in total.

Description of female sexual behaviour

At the beginning of the breeding season, most sexual interactions were female-solicited, and often began when the male arrived on the perch next to her, being greeted by the female with tail-flickering (see Chapter 4). The female solicited by 'ducking' flat against the perch in an almost horizontal position, apparently inviting copulation. She fluffed her feathers, especially those of the throat, with her bill pointing up (above horizontal) and away from the male who sat about 5-20 cm away on the perch (Fig. 5.3). In European Bee-eaters, the female utters a copulation call (Fry, 1984). This could not be confirmed for Blue-throated Bee-eaters, probably because I was too far away to hear. Although 'ducking' is mainly a female sexual behaviour, both sexes may fluff their feathers and 'duck', particularly at the beginning and during all stages of sexual display. A soliciting female may remain in the 'ducking' posture between about 5 sec and over 1 min, with changing intensity of the display.

Figure 5.3: Sexual behaviour prior to copulation, showing typical male and female postures. Drawn from photographs and observations (in the field)

Description of male sexual behaviour

Often males did not accept 'ducking' invitations by females. If responsive, the male would turn towards the female, side-step closer, and then sit as vertically elongated as possible by stretching himself, tail and wings pointing down and the bill pointing upwards (Fig. 5.3). This was similar to the erect perching behaviour of European Bee-eater males described by Fry (1984, p. 164 and his figure C on p. 165). Sometimes, the male Blue-throated Bee-eaters bowed rhythmically three or four times before mounting the female. Later in the season, sexual interactions were initiated by the male. Whenever a male initiated a sexual interaction, he invariably carried an insect in his bill ('allofeeding'). Apart from one case of a 'pair rape' (described below in section 'observations of extra-pair copulations'), all male-initiated copulations I observed involved the male offering an insect to the female who nearly always took it and ate it. The male usually mounted her swiftly, after no further courtship display, and such matings looked successful (i.e. with cloacal contact, see below).

During copulation, the male pressed his bill against the base of the female's bill or held onto her bill with his bill. Sometimes he shook *her* head quite vigorously while balancing to effect cloacal contact. Cloacal contact was assumed to be achieved when the male succeeded in folding his tail under the female's tail (C.M. Lessells, pers comm) and maintained this position for at least 1 second. After copulation, the male usually flew off and often came back to sit about 10 cm away from of the female, sometimes bowing a few times, before both preened or commenced hunting. From start to finish, a sexual interaction involving copulation lasted anything from a few seconds to about 30 seconds and occasionally several minutes. A 'sexual interaction', defined by the display of male or female sexual behaviour, may or may not culminate in copulation. Not all copulations were successful, but those that were involved apparent cloacal contact (see above) and, presumably, insemination.

Copulation success, duration and frequency

Of all 64 sexual interactions observed, 35 (55%) resulted in copulation; 19 (54% of copulations) were unsuccessful and 12 (34% of copulations; 19% of all sexual interactions) probably successful (for 4 copulations (12%), the success was not known). Most sexual interactions lasted for 2 minutes (= mode, Fig. 5.4; median = 3 minutes; Table 5.3), ranging from less than 1 to up to 16 minutes. The success of an interaction and its length were significantly correlated (Table 5.3), interactions with copulations lasting on average longer than interactions without copulations (median = 3 minutes; range 1-8 compared to median = 2 minutes; range 1-13; $p < 0.02$; Table 5.3; Fig. 5.4). Kruskal-Wallis nonparametric ANOVA tests showed no significant difference between the length of successful and unsuccessful copulations or between successful copulations and all other sexual interactions without cloacal contact (Table 5.3).

Timing of copulations

Sexual interactions were only observed early in the season. All but 4 sexual interactions observed were before the mean start of laying (13th May). Sexual interactions were roughly normally distributed around 30 days prior to the 13th of May (Fig. 5.5). Sexual interactions without cloacal contact occurred in general 30 days (SD ± 13 days) before the mean onset of laying, regardless of whether they included a copulation attempt or not ($t = 0.07$, $p > 0.90$, $N=48$). Successful copulations were observed on average on day -6 (SD +/- 16; see also Fig. 5.5). They were highly significantly closer to the mean onset of laying than both (1) copulations without cloacal contact and (2) interactions that ended without copulation ($t = 5.56$, $p < 0.001$, $N=60$).

Male and female solicited interactions

Significantly more interactions were initiated by the female (33, or 70%) than the male (13, or 26%; $\chi^2 = 10.08$, df = 1, $p < 0.001$; Table 5.4). In 2 (4%) cases, both partners started displaying sexual behaviour together. Five (38%) of all male-initiated interactions and 16 (46%) of all female-solicited interactions ended in copulation (Table 5.5). There was no significant difference between the number of male and female initiated interactions that ended in copulations ($\chi^2 = 0.082$, df = 1, $p > 0.70$; see also below). Two (40%) of male-solicited copulations and 6 (38%) of female-solicited matings were successful.

I conducted a two-way ANOVA of the day of the observation relative to the mean onset of laying (dayx) with the two main effects, success of interaction and the sex of the initiator. Male soliciting (mean 26th April ± 20 days SD) occurred on average 13 days *after* sexual interactions initiated by females (mean 13th April ± 15 days SD; $F = 8.10$, $df = 1$, $p < 0.01$; Fig. 5.6). Interactions initiated by the male were probably closer to the assumed fertile period of their female partners than female-initiated sexual interactions. Successful copulations were observed closer to the mean day0, regardless of who initiated the interaction (ANOVA, $F = 10.80$, $df = 2$, $p < 0.001$). Thus, over and above males initiating more interactions immediately before the mean day0 than females, successful copulations also occurred closer to the mean day0. Male initiated interactions tended to be more successful than female solicitations, but not significantly so (interaction of initiator sex and success: $F= 6.844$, $0.05 < p < 0.10$; compare with previous paragraph where a similar finding was reported). Males who successfully gain a copulation may be more experienced or persistent, but they did not solicit longer than unsuccessful males: the two successful male-initiated copulations were quite short at 2 and 3 minutes (Table 5.5). Successful females, on the other hand, solicited far longer than unsuccessful females (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 4.27$, $p < 0.05$, $N=33$) and than all other females combined ($\chi^2 = 4.60$, $p < 0.05$, $N=58$).

Observations of extra-pair copulations (EPCs)

Only one observed male-initiated mating was not solicited by courtship feeding: a forced pair mating after a female-solicited extra-pair copulation: O6B and her partner S9O had already been observed copulating several times, when on one occasion I witnessed O6B soliciting to an unmarked bird. After a long bout of pre-copulatory sexual behaviour, an apparently successful copulation followed. A few seconds after the other male had flown off, S9O landed next to O6B, and bowed vigorously. He mounted her shortly afterwards, without any sexual behaviour by O6B. Of all 64 sexual interactions observed, all but one could have been between partners (PIs). Five interactions were PIs of 3 breeding pairs. A further 5 interactions were probably between partners, but the birds did not stay on to breed and thus pairing could not be confirmed by captures or observations at the same nest. The confirmed EPC, on 22nd April 1989, occurred 19 days before the estimated onset of laying of the pair, probably before the fertile period of the female.

Table 5.3: The difference of length (in minutes) of sexual interactions of different success (type). N= Number of interactions observed

Types of interactions	δ median	Kruskal-Wallis 1-way ANOVA χ^2	p	N
No copulation vs unsuccessful copulation vs successful copulation	1; 0	6.40	0.041	56
no copulation vs unsuccessful copulation	1	2.94	0.086	45
unsuccessful copulation vs successful copulation	0	0.70	0.401	27
no copulation vs copulation (unsuccessful plus successful)	1	5.80	0.016	56
all unsuccessful interactions vs successful copulations	1	3.57	0.059	56

Table 5.4: Success (copulation or no copulation) of male and female solicited sexual interactions. Percentages are different from those in the text because 2 sexual interactions, which were initiated jointly by the male and female, are not included here.

	no copulation	copulation	total
Male-solicited	8	5	13 (28.3%)
Female-solicited	17	16	33 (71.7%)
Total	25 (54.3%)	21 (45.7%)	46 (100%)

Table 5.5: Median length (minutes) and non-parametric statistical summary of successful ('success'; with copulation attempt) and unsuccessful ('unsuccess'; without copulation attempt) sexual interaction initiated by males and females

Length(min)	median	mode	min	max	N
Unsuccess male initiated	3	1	1	13	11
Success male initiated	2.5	2	2	3	2
Unsuccess female initiated	2	2	1	8	27
Success female initiated	4.5	5	2	8	6

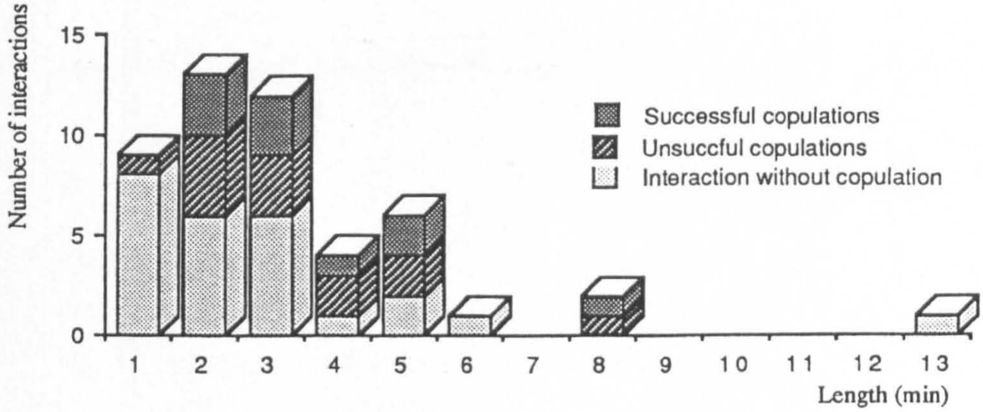


Figure 5.4: The length of sexual interactions and their success

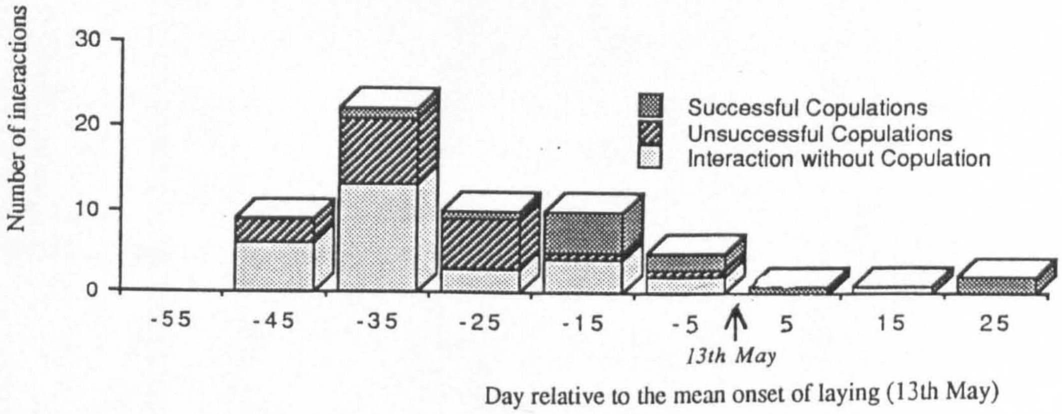


Figure 5.5: Frequencies of sexual interactions of different success during the season.

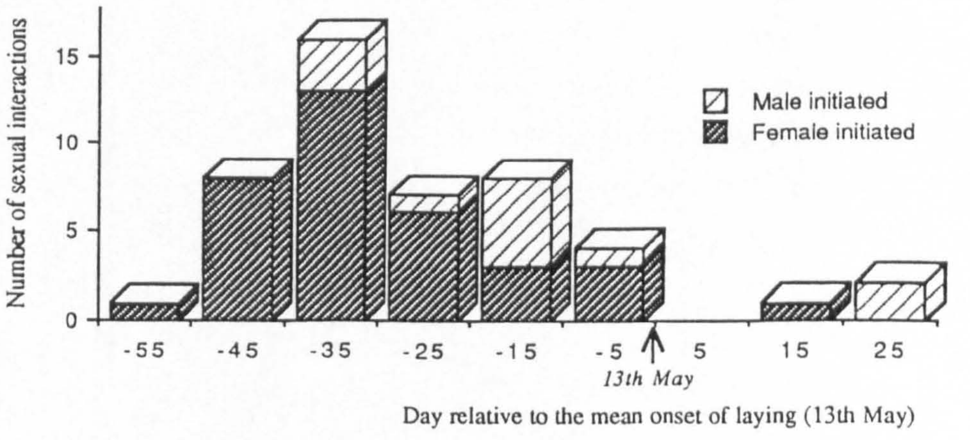


Figure 5.6: Frequencies of male and female initiated sexual interactions during the season.

5.3.3 The Pair Bond: Associations and Interactions of pair members

According to the hypotheses formulated in the introduction, pair association and cooperation is expected to be inconsistent during the breeding season. These parameters should differ during the presumed fertile period of the female prior to and during laying, if females are mate-guarded during or near their fertile period in case they engage in EPCs. In the following I investigate if such a change in pair associative behaviour occurred during the breeding season.

Initiating close associations

Most of observed associations occurred between late March and early May (Fig. 5.7), just after arrival (the earliest time for which pair formation might have been observed) and during digging and the main mating season (see previous section). In 37 out of 69 cases (54%), the female joined or followed the male, and in 32 observations (46%), the male joined or followed the female; there was no significant difference between the number of males and females initiating an association with their partner ($\chi^2 = 0.362$, df = 1, $p > 0.5$).

The overall timing of male and female initiated associations did not differ ($\chi^2 = 0.031$, $p > 0.8$). The pattern of female initiated associations did not follow that of female soliciting, however: females did not initiate more associations early in the season. Prior to 20 days before the general onset of laying (13th of May), for example, males joined or followed their partners 21 times and females 20 times (Fig. 5.7). Around the general onset of laying, presumably the fertile period of many females, the proportion of males joining or following might be expected to increase because of mate-guarding. Between day -20 and day 20, however, more females (13) than males (6) initiated associations (although the difference was not significant; $\chi^2 = 2.579$, $p = 0.108$). This was not significantly different either from the earlier or later associations ($\chi^2 = 0.080$, $p > 0.7$; Table 5.6).

If the pair associations observed were mainly due to male mate-guarding, there should have been a peak in male-initiated associations during the fertile period of the female, which was assumed to be just prior and during laying, from about day -10 to day 10 of the breeding

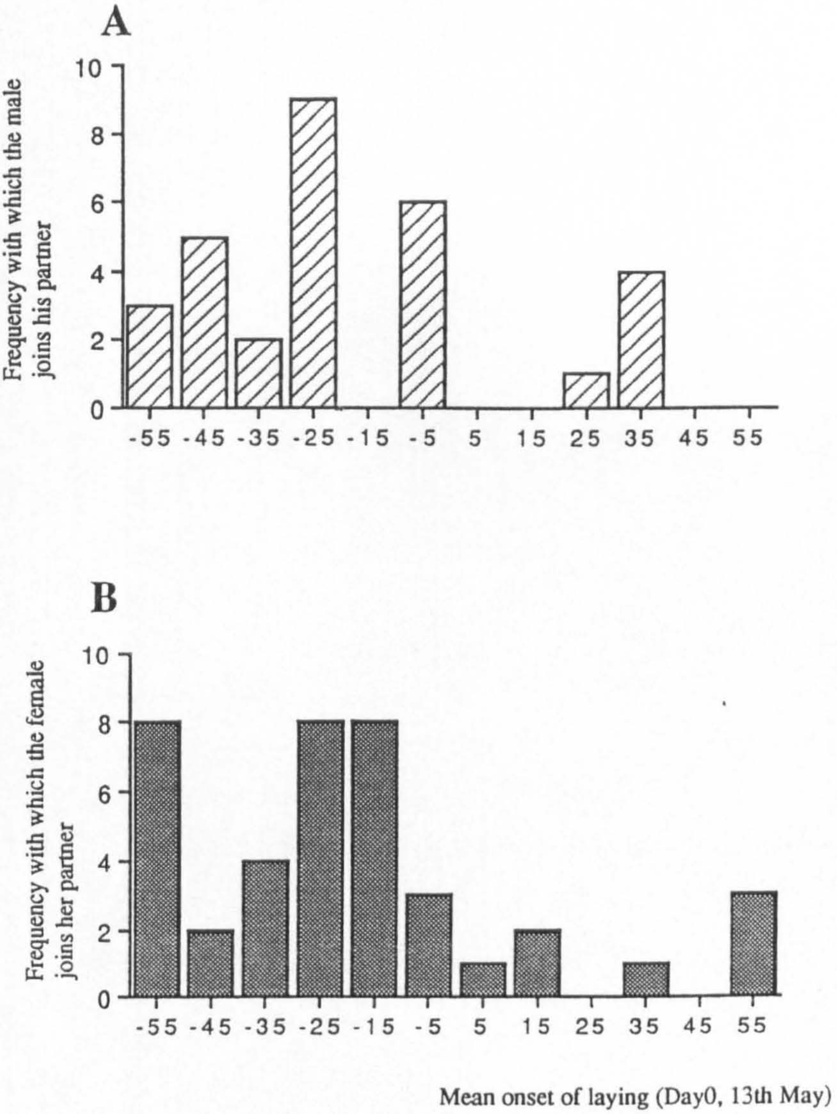


Figure 5.7: Frequency with which males (A) and females (B) join their partner (initiate pair contact) relative to the estimated mean laying period.

Table 5.6: sex of any bird joining its partner near the general onset of laying (day -20 to day 20) compared to early/late in the season.

	Male joins or follows	Female joins or follows	Total
Before day -20 or after day 20	26	24	50 (73%)
Near Day0 (day -20 to day 20)	6	13	19 (27%)
Total	32 (46%)	37 (54%)	69 (100%)

cycle. Although most associations occurred well before or around the general Day0, the 13th of May, this date is probably not representative for the onset of laying of all pairs watched. Most observations were from the SB colony, whereas most of the data for the general Day0 calculation were collected in NH91, where Day0 tended to be about 9 days earlier than at SB, but not significantly so (see Chapter 4). For 11 observations, the onset of laying of the female herself was estimated (see Chapter 4). Apparently, more pair associations were centred around the estimated onset of laying of each female herself (day -10 to day 0, midpoint -5; Fig. 5.8). The number of observations, however, for birds with known Day0 was too small to test if the male is mate-guarding the female during her own onset of laying. This means that although it seems that there were more associations during the assumed fertile period of the female, I could not show if this was due to increased mate-guarding indicated by the male following the female. Since at least half of the associations included above were of partners joining each-other at the burrow to dig, it is furthermore possible that the context of most observations was vigilance (see section 5.3.4 below) and not mate-guarding.

Time spent together and distance between pair members

Observations ranged from day -64 to day 77 of each pair's own onset of laying. Most observations were around day 17 (= mean; SD = 26) with a roughly normal distribution. Most observations overall were of association type 1 ('audible contact', N=992, Fig. 5.9). Early in the season (relative to their own laying), both partners visited the colony on their own, and not within the same observation period (association type 0, 'no contact'). Few observations were available during that time, probably partly because birds did not start coming to the colony regularly until later. Association types 2 and 3 (visual and physical contact) both peaked during the period between day -10 and day 10 relative to onset of laying. During this time, the most frequent association type observed was visual contact, of pairs both being at the same sub-colony together. Physical association was also observed most frequently during the mating and laying period (day -10 to day 10), indicating that birds preferred to stay in visual contact, but in general, the birds spent very little time next to each-other. Change-overs in incubation were probably recorded in observations of type 1. Provisioning (from day 30) was again marked by 'shift changes' between partners, either within the observation period (association type 1) or outside it (type 0). Some birds probably hunted at the colony together

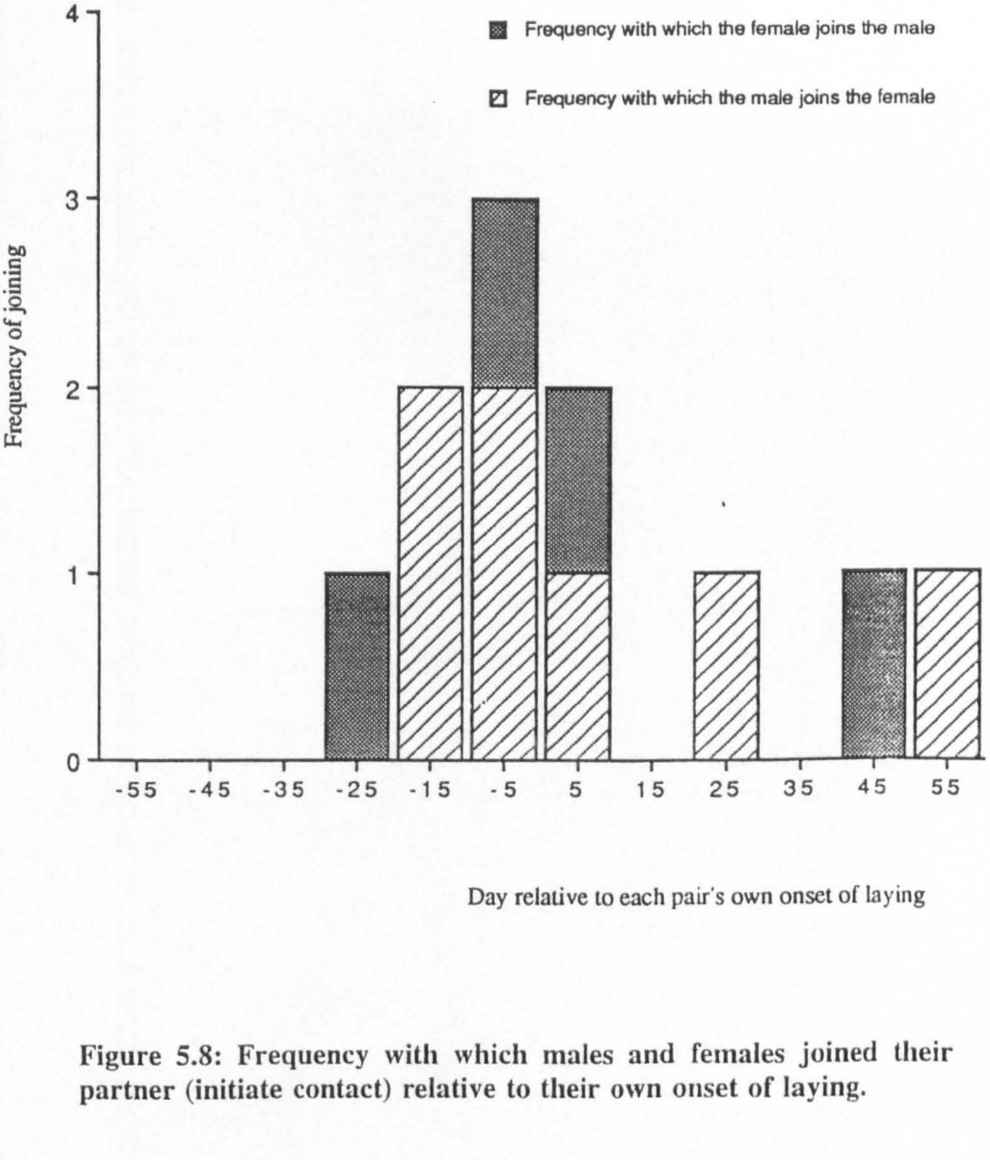


Figure 5.8: Frequency with which males and females joined their partner (initiate contact) relative to their own onset of laying.

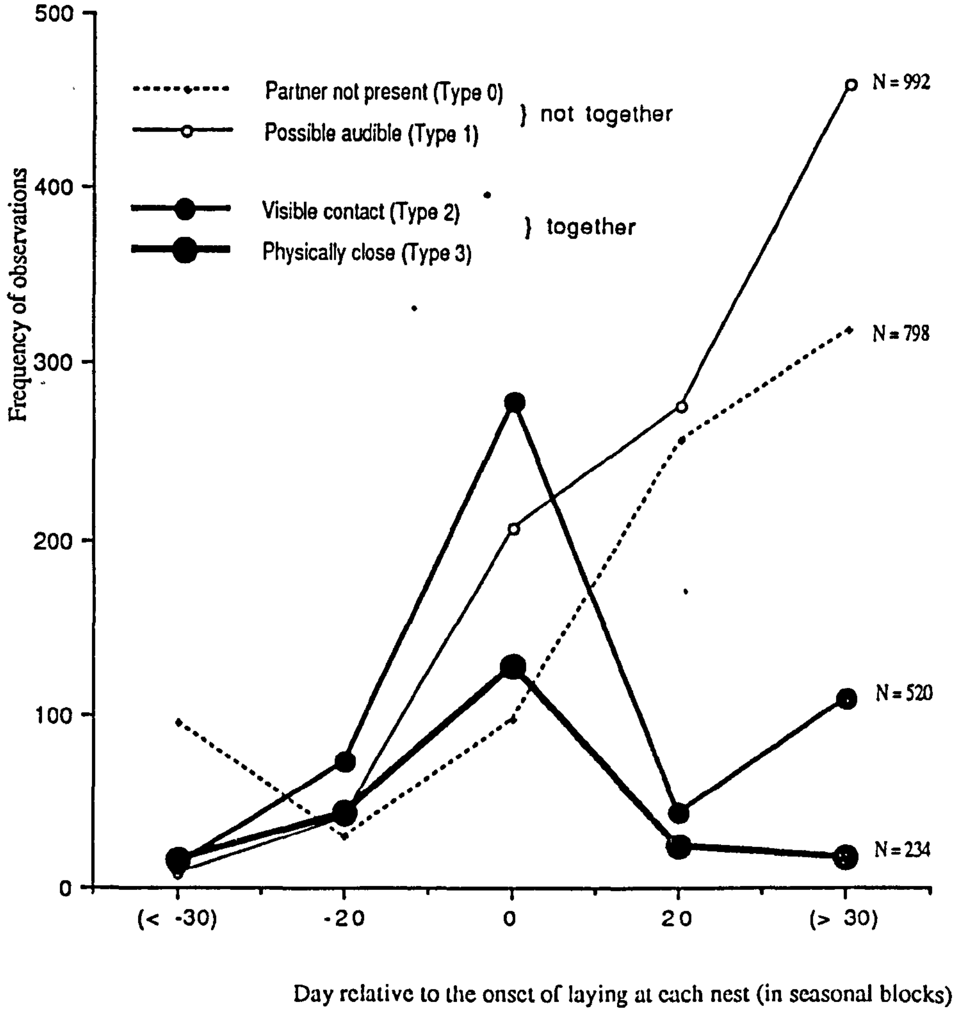


Figure 5.9: Frequency of observed association types during the season by seasonal blocks (see text). Type 0-1 = not together, type 2-3 = together, in visual or physical contact (see text). N = 2544 sightings.

(type 2). Overall, association types 0 and 1 had a very similar pattern of changes in frequencies during the seasons and were distinct from association types 2 and 3 which in turn follow a similar pattern to each other.

The percentage of time spent in each association type differed significantly between seasonal blocks (association type 0: $\chi^2 = 17.24$, $p < 0.002$; type 1: $\chi^2 = 9.73$, $p < 0.05$; type 2; $\chi^2 = 22.92$, $p < 0.0001$; type 3: $\chi^2 = 19.34$, $p < 0.001$; Fig. 5.10). The birds spent most of their time at the colony without their partner (association type 0), especially early in the season (day -64 to day -30), where over 80% of a bird's time at the colony was spent, on average, without the partner being at the colony or obviously nearby (Fig. 5.10). The second and third seasonal phase looked distinct from the other seasons and similar to each other. From day -29 to day 9, pairs associated more closely (type 2 and 3). Again, most of their time (more than 50%) was spent with the partner not in visual contact. This may be because the partner was inside the nest digging (second phase) or laying (third phase). During incubation and provisioning (period 4 and 5), there were a lot of change-overs (type 1) and very little physical contact (type 3).

Most of the close associations were during the second phase. Birds typically dug together (see section 5.3.4 below). To investigate pair association while the birds were *not* digging during the second phase, all the observations made at nests were excluded from the following analyses for the second seasonal phase. I showed previously that the frequencies of association types 0 and 1 on one hand, and types 2 and 3 on the other, co-varied with each-other (Fig. 5.8). Association types 2 and 3, where the birds were either in visual contact or physically associated, are henceforth termed 'together' and compared in the following to association types 0 and 1, where the birds are 'not together'. The highest percentage of time spent together was still during the digging stage, but this was now 38.0% (Fig. 5.11) rather than 42.4% as previously, when observations at the nest had been included (Fig. 5.10). The percent of time together did not differ significantly between seasonal periods 2 and 3 ($\chi^2 = 0.06$, $p > 0.80$), but was significantly lower in the other seasonal periods: significant differences in percent time spent together were between periods 1 and 2 ($\chi^2 = 11.01$, $p < 0.001$) and between periods 3 and 4 ($\chi^2 = 14.52$, $p < 0.0001$). I found no difference in time spent together between periods 4 and 5 ($\chi^2 = 0.46$, $p > 0.4$). In summary, the birds spent

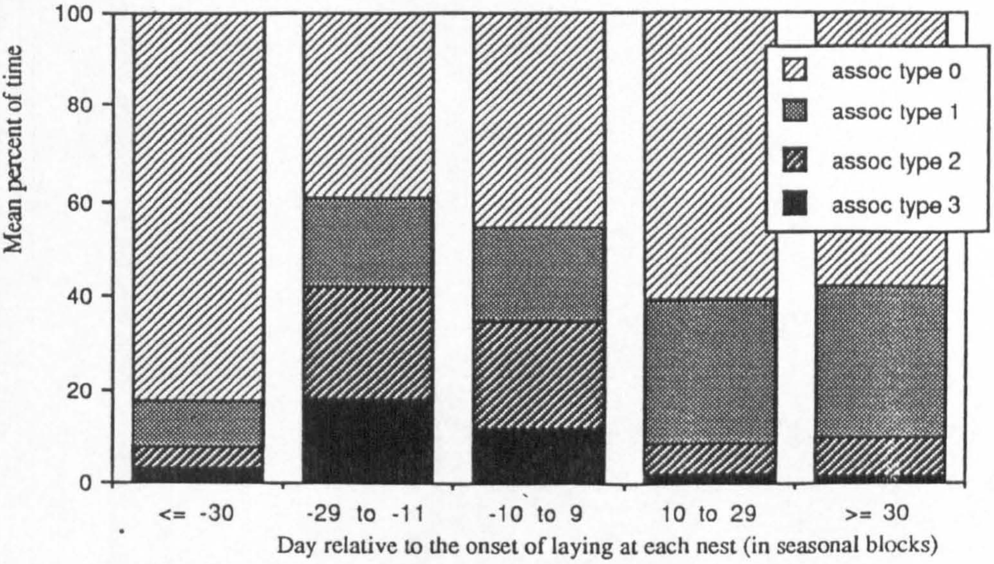


Figure 5.10: The mean percent of time during any one observation period spent in each association type (0-3, see text).

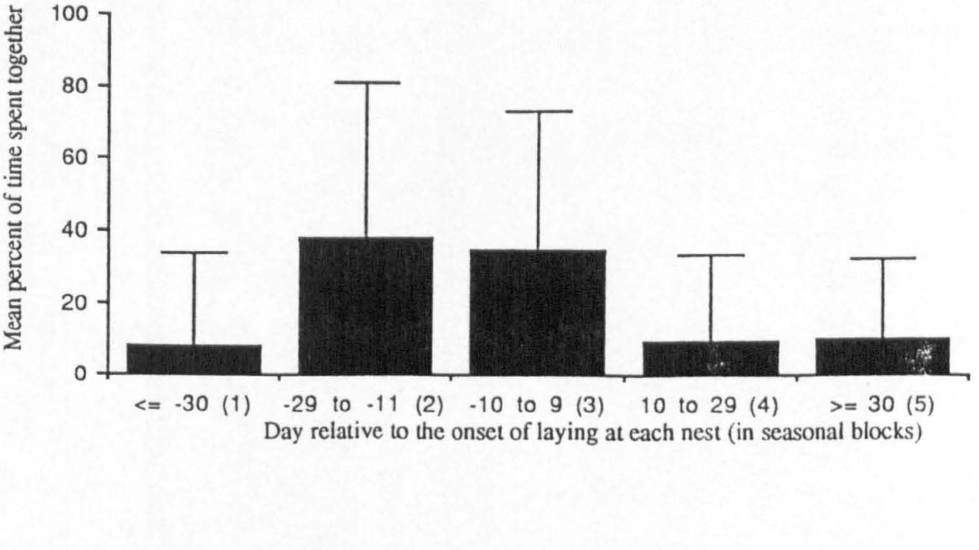


Figure 5.11: Percent of time spent together (association types 2-3) excluding observations of digging, in seasonal blocks relative to each pair's onset of laying (see text for details). (Means and SD)

nearly half of their time together during the period between day -30 and day 10 relative to their estimated onset of laying, which was significantly more than during the remaining season when they spent on average around 10% of their time at the colony in visual or physical contact. The proportion of time spent together and pair-association changes during the season, however, varied tremendously between pairs. This is illustrated with observations of 4 pairs for which observations were available for each seasonal phase. The observations show that the total amount and relative timing of associating at the colony varied considerably between pairs (Fig. 5.12 a-d). The pair from nest 18 in particular was never observed together until the provisioning phase, while the other 3 pairs spent very little time together late in the season.

In summary, pair members were most often seen alone at the colony. When they were in visual or physical contact, it was mostly during their own pre-laying and laying periods. This pattern was consistent both for observed frequencies of associations and for percentages of times spent in different association types. Pairs moved around separately after arrival, and upon pairing spent nearly half of their time at the colony together at least in visual contact until the start of incubation and provisioning of the brood (day 10 onwards). Both these they typically did in shifts: one bird was seen around without the other at any one time, but often both were seen during the same observation period. At the beginning of the season until mating and laying commenced, pairs seemed to spend little time at the colony, but there was a change in association type within this period: more time was spent in visual and in physical contact later, which probably was a reflection of pair formation. For mate-guarding on the other hand, the significant increase in type 3 and 4 in the 2nd and 3rd period was most relevant, which rose to just under 40% of their time, even when digging birds were excluded.

It is possible that the observed behavioural patterns were not, in fact, reflections of the behaviour of single pairs, but that, due to non-random observations, different pairs may have contributed to observations of different periods within the breeding season. To provide a qualitative test of the assumption that behavioural observations were representative of the behaviour of pairs throughout the season, all sightings for 5 pairs which bred at the same sub-colony in the same year (RH-mid and RH-end, Sungei Buloh, 1989) are compared below.

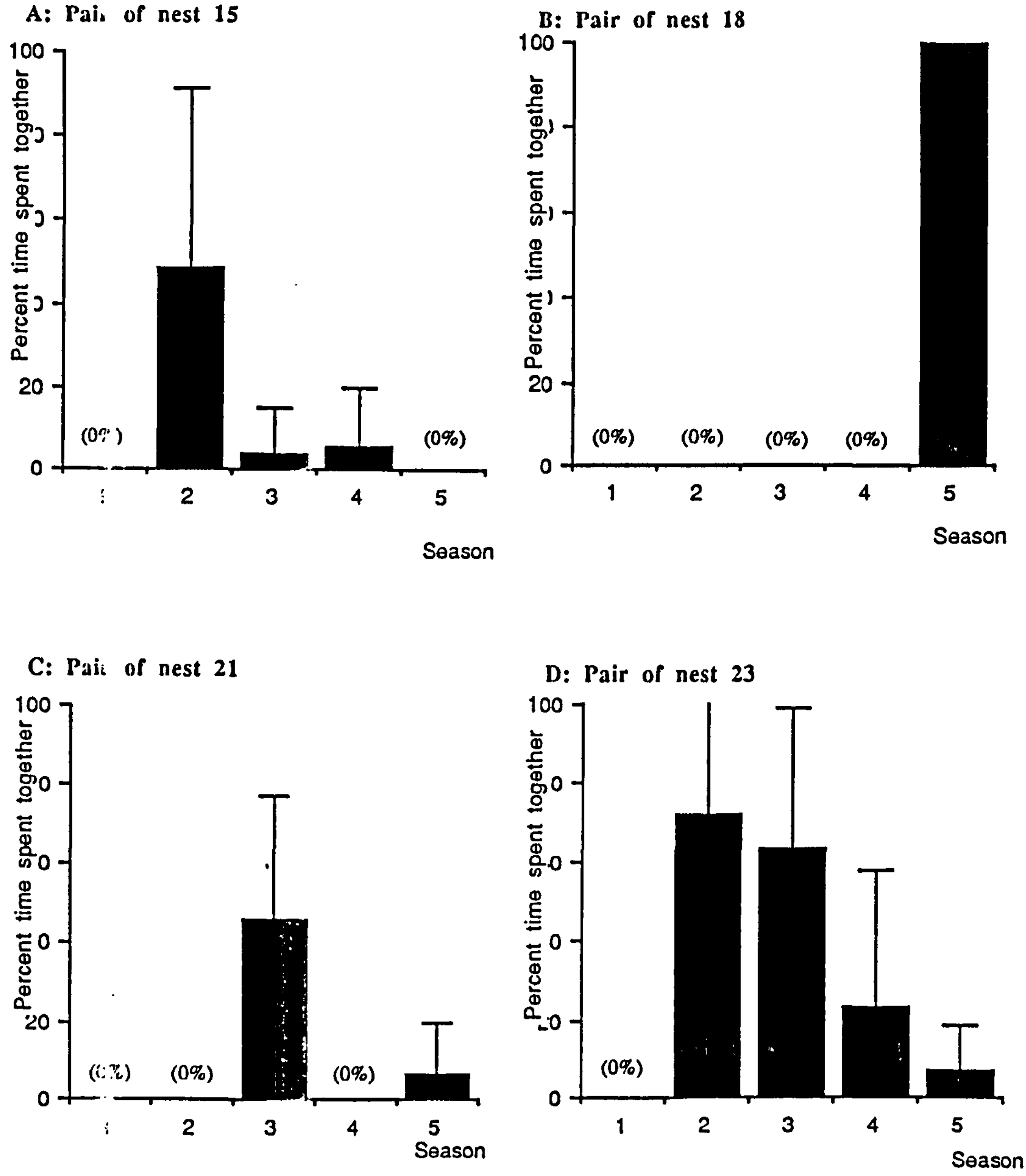


Figure 5.12: Percent time spent together (association types 2-3) of four pairs in Sungei Buloh 1989, in the 5 seasonal blocks (see text for definitions) relative to their own onset of laying (see text for details). Sample sizes: for 5 seasonal blocks, pair at nest 15, N = 15,11,13,7,1; pair at nest 18, N = 1,1,1,1,1; pair at nest 21, N = 1,2,10,4,5; pair at nest 23, N = 5,9,10,13,12.

Colony use and associative behaviour throughout the season for 5 pairs

For each observation period, I listed the number of sightings for each pair, and whether or not partners were seen together (Table 5.7). Since they all bred at the same sub-colony in the same year, each pair-member should have been seen, if present, during any one observation period. Often, however, some or most of the 10 birds were *not* seen at their sub-colony, and if they were, then it was at very different frequencies during different observation periods (Table 5.7). There were nevertheless some general similarities in colony use and association between pairs. During the early part of the season, few sightings were made, and pair members were seen mostly on their own. Mostly, these birds visited the colony once or twice per observation period, but occasionally a bird spent long spells sitting on a perch at the colony (indicated by many sightings during one observation period, e.g. SVB). It seems that during this time after arrival, most birds had not yet paired. They usually started digging soon after both partners had been seen at the colony. Early pairing may be important for early breeding: S1O was amongst the first birds arriving at the colony, for example, but became a late breeder because it did not start laying until after its partner, AXY was seen at the colony for the first time. During the second half of April (and, for the late breeders S1O and AXY at 41-89, in June), the pair members were often seen together and sightings included some matings, but not near the estimated onset of laying. Some agonistic interactions with-extra pair birds were observed during this period. During incubation and provisioning, pair members spent less time together. In general, therefore, the behaviours of this sample of birds were in agreement with the main trends reported previously, and the observed differences in behaviours are not likely to be a bias introduced by observation schedules.

Table 5.7: The number of one-minute observations and typical behaviours observed at 5 nests at RH-mid and RH-end in SB89 for which both adults arrived tagged or which were tagged early in the season (except birds at 9-89, which were tagged shortly before laying). Association of pair members is noted as well as the estimated onset of laying (Day0).

Dates in different seasonal blocks (see section 5.3.3) are separated by double lines

Typical behaviours seen: D = digs, S = sits on perch, PC = pair copulation(s), EPC = extra-pair copulation, A = agonistic interactions with extra-pair members, P = 'prospects' on ground, I=incubates, F=feeds brood

Numbers of one-minute sightings of either pair member
(1 = obs type 0 and 1, 2 = both pair members present)

Date of observation date N Dayx Season	33O,4OO 9-89	O6B, S9O 20-89	SVB, V6R 2-89	MXO, T9R 29-89	S1O, AXY 41-89
28/3 1 -46	-				
30/3 3 -44	-				2 (1) S1O S
31/3 4 -43	-		16 (1) SVB S	2 (1) T9R S	
01/4 2 -42	-	6 (1) S9O S			
04/4 3 -39	-				
05/4 5 -38 1	- (D)		26 (1) SVB S		
06/4 2 -37	-		4 (1) SVB S		
08/4 4 -35	-	2 (1) S9O S		2 (1) T9R S	
10/4 2 -33	-	1 (1) S9O S			
11/4 3 -32	- (D)	1 (1) S9O S	7 (1) SVB S	3 (1) T9R S	
13/4 3 -30	-	1 (1) S9O S		7 (2) PC	
17/4 5 -26	- (D)		9 (1) SVB S	9 (1,2) S	
18/4 1 -25	-		1 (1) SVB S		
19/4 1 -24	-		4 (1) SVB S	3 (1) D	
22/4 3 -21	-	4 (1,2) EPC PC A		4 (1) D	
24/4 3 -19	-	2 (2) PC			
25/4 2 -18 2	-		1 (2) SVB S	4 (1,2) S	
26/4 3 -17	-		3 (1) SVB S	6 (1) S	
27/4 3 -16	(tagged)				
28/4 5 -15	(deserted	31 (2) S P			
29/4 2 -14	for a				
30/4 3 -13	while?)	5 (1,2) P A	9 (1,2) P S	2 (1) S	
01/5 1 -12		26 (1,2) P D		10 (2) D	
03/5 5 -10		16 (1,2) S P	1 (1) SVB S	26 (1,2) S	
04/5 3 - 9		54 (1,2) S P		17 (1,2) S	
06/5 3 - 7		35 (1,2) S D	10 (1,2) S		
08/5 3 - 5	21 (1,2) A (Day0)	57 (1,2) S D	12 (1,2) S		

Table 5.7 - cont

Date	N	Dayx	Season	33O, 40O 9-89	O6B, S9O 20-89	SVB, V6R 2-89	MXO, T9R 29-89	S1O, AXY 41-89
09/5	2	-4	3	4 (1) S		17 (1,2) S	2 (1) S	
11/5	2	-2		15 (1,2) S		2 (1) S		
12/5	2	-1		8 (1,2) S	(Day0)	3 (1) S		
18/5	3	6		1 (1) S	16 (1,2) S	3 (1) S (Day0)	(Day0)	2 (1) AXY S
23/5	5	11		5 (1) S		18 (1) S A	84 (2) S A F(♀)	27 (1,2) S
25/5	3	13		31 (1) I	50 (1,2) I	28 (1,2) I	89 (1,2) S I F(♀)	41 (1,2) S
27/5	2	15		5 (1) I	10 (1) I		33 (2) I F(♀)	
29/5	4	17		4 (1) I	39 (1,2) I	21 (1,2) I	47 (1,2) I S	
31/5	1	19		5 (1) I	35 (1) S	7 (1) F	16 (1) I	35 (1,2) S (Day0)
01/6	2	20	4	3 (1) I	2 (1) I		13 (1) S	
02/6	2	21		7 (1) S	1 (1) S			45 (1,2) PC A F(♀)
03/6	2	22		2 (1) F	2 (1) I		10 (1,2) S	14 (1,2) S
06/6	1	25			6 (1) I	2 (1) F	5 (1) S I?	34 (1,(2)) S
07/6	2	26						
10/6	2	29						
12/6	1	31		4 (1) F	24 (1,2) F	14 (1) F	11 (1) S	14 (1) I? S
14/6	1	33					5 (1) S	
15/6	4	34		5 (1) F	25 (1,(2)) F	15 (1) F	8 (1) S	6 (1) I? S
20/6	1	39			1 (1) F			1 (1) S
22/6	1	41						
01/7	2	50		52 (1) F	6 (1) F			16 (1) I F
02/7	2	51	5	9 (1) A4G (helper!) F	66 (1,2) F		4 (1) S	
04/7	1	53			7 (1) F		(MXO dead)	2 (1) F
05/7	3	54			65 (1) F	4 (1) S	5 F	13 (1,2) F
07/7	3	56					1 F	7 (1) F
13/7	1	62			35 (1) F		2 F	
14/7	1	63			28 (1) F		3 F	4 (1) S
17/7	2	66						
19/7	1	68						
02/8	1	82						

5.3.4 Digging, nest guarding and breeding synchrony

Digging with respect to season and laying dates

Burrow length was plotted against season days for 18 nests in SB89 and 10 nests in SB90 (Fig. 5.13 a and b). In 1989, burrow length increased as the season progressed (Fig. 5.13 a). Most nests were completed by day -20 (24th April, 1989). Using the overall regression equation (length = 129 + 2.40 dayx; N=245 length measurements), the mean date of digging onset (where length = 0) was day -54 (20th March, 1989). Digging rates, however, were not uniform between burrows. Some burrows were neglected until shortly before the main bout of digging, whereas others increased in length more steadily. In 1990, the burrow length also increased with season (length = 123 + 1.78 dayx; N=128; Fig. 5.13 b), with an onset of digging of day -64 (10th March, 1990), 10 days earlier than in 1989. The 6 early burrows of 1990 were started earlier than those of 1989. The burrows of 1990 did not increase in length linearly. A synchronized phase of excavation over a short period of time (2-5 days) immediately prior to completion was typical for the earlier nests in both years. Early burrows were completed around the 24th April in both years at SB, despite the earlier onset of digging in 1990, with a short bout of digging which coincided in date almost exactly in 1989 and 1990.

Burrows were completed 35 to 4 days before day0, usually by 12 days prior to the first egg (Fig. 5.14). The synchronized effort of burrow completion with respect to the season was seemingly not repeated with respect to onset of laying. This was confirmed by direct observations of marked digging pairs at 13 burrows with known onset of laying (Fig. 5.15). Although most of the digging was observed in the earlier days (day -30 to day -20), there was no preferred period prior to laying during which the digging effort was concentrated. Some pairs were seen digging their burrows as early as 50 days before laying. Notable was the number of days birds were seen digging *after* their eggs had been laid. This was confirmed by the *reductions* of burrow length observed in Figures 5.13 and 5.14: if burrows were left unattended, rain washed the soft sand into the burrow very quickly, and shallow burrows could vanish completely after a monsoon shower. The birds seemed to maintain a low level of digging of their burrows throughout the nesting period.

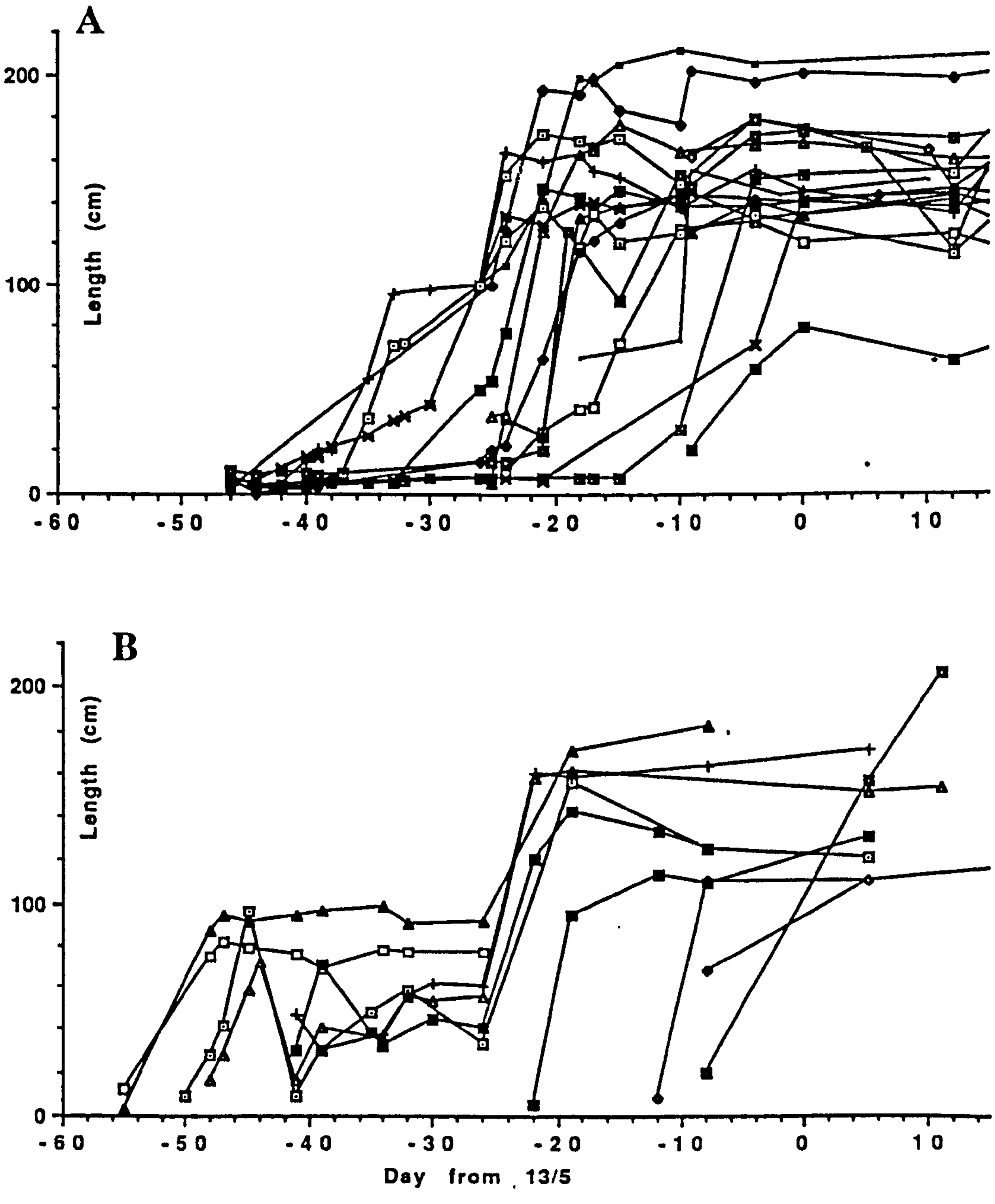


Figure 5.13: Length of completed burrows throughout the digging phase to show the pattern of digging with respect to season. A: 18 burrows in Sungei Buloh, 1989. B: 10 burrows in Sungei Buloh, 1990

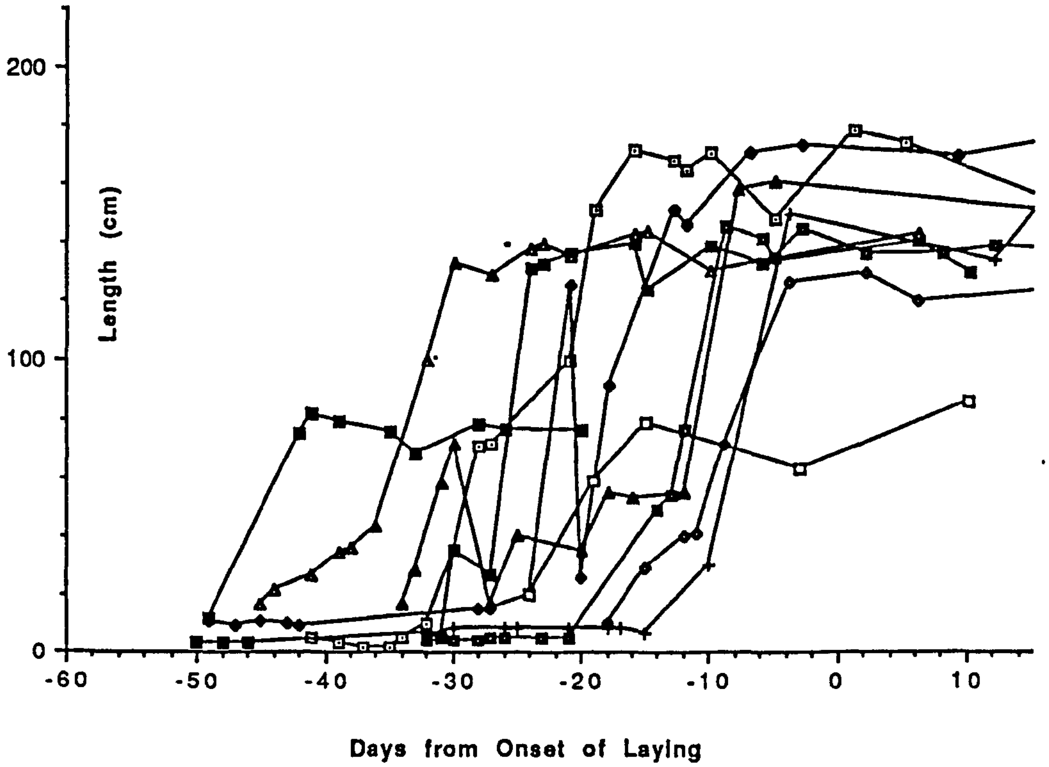


Figure 5.14: Length of burrows with resepect to the first egg date (onset of laying) in each burrow.

Preferred time of day for digging

All sightings of digging birds were used to evaluate whether digging occurred at particular times of the day, such as during the cooler periods or after feeding. The 574 sightings of digging birds were normally distributed around a mean of 13:12hrs ±6 minutes (Fig. 5.16), the hottest part of the day. There was a slow build-up in the number of sightings of digging birds between 09:00 and 11:15hrs, presumably reflecting birds coming to dig after their first hunting period early in the morning. There was less digging again around noon, and another peak at 13:00-13:30hrs, decreasing to a low level until about 19:00hrs.

Nest guarding

Nest guarding by sitting at the burrow entrance either alone, in pairs or occasionally in groups of up to 3, was commonly observed throughout the pre-breeding season. For 16 complete scans that included birds sitting at a nest, the proportion of sightings of birds sitting at a nest during pre-laying and laying was 8 - 86% (mean = 32.8%, SD = 0.21). This was probably an under-estimate of the total period that was spent nest guarding, since nests can probably also be guarded from a perch, and birds were observed to displace intruders at their burrows by 'sallying' from their perches.

Digging time and length of burrow

Fig. 5.17 shows a general decline in burrow length with the date when it was started, which indicates that birds digging late nested in shorter burrows, but the regression was not significant ($R^2 = 0.14$, $F = 2.58$, $p > 0.10$, $N = 16$ burrows, pooled from 1989 and 1990 in SB). Late diggers may also have tended to breed later, as shown in Fig. 5.18, but again the relationship between the relative onsets of digging and laying was not significant ($R^2 = 0.20$, $F = 3.05$, $p > 0.10$, $N = 14$ burrows for which day0 was available). To establish whether shorter burrows were dug by later *digging* rather than later *laying* birds, a stepwise multiple regression was performed on the maximum length reached by each burrow, with both the onset of digging (day last recorded as having reached 20cm) and the onset of laying as independent variables. The onset of laying was entered at $p < 0.11$ ($R^2 = 0.21$, $F = 3.17$), but

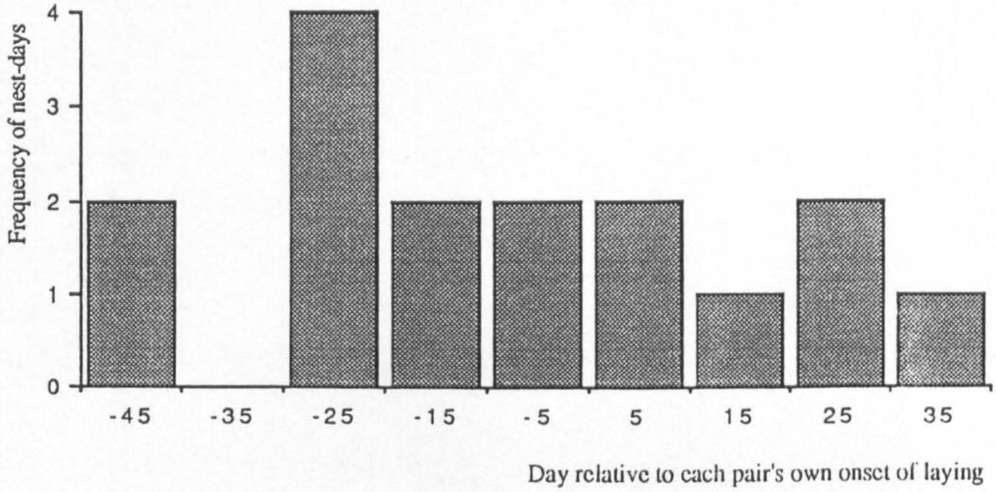


Figure 5.15: The number of days on which the marked resident pair was seen digging at its burrow, relative to its onset of laying.

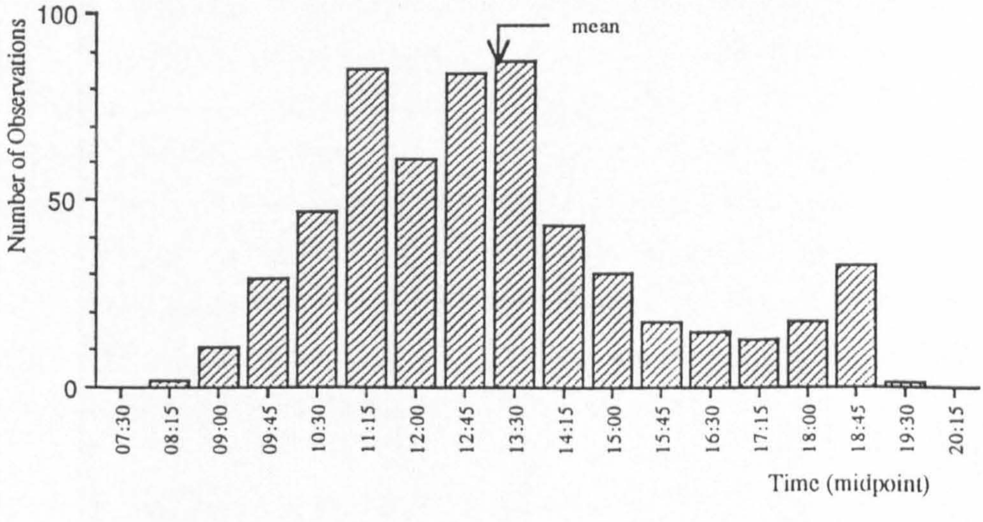


Figure 5.16: The number of independent one-minute observations of digging birds throughout the day. (Mean time for digging is 13^{12} ± 6 minutes se)

the digging onset had not been entered until $p < 0.50$, indicating that final burrow length may have been related to laying date (Fig. 5.19) but not to onset of digging independently of onset of laying. This indicates that later breeders may have tended to nest in shorter burrows which may be a cost incurred for these birds. This trend could not be confirmed, however, for a larger sample of all burrows for which only the final length (and not the digging history) plus onset of laying were known (N=54; 23 from SB in 1989 and 1990, 31 from NH in 1991). Since no significant difference in the mean onset of laying was recorded between SB and NH or between different years (Chapter 4), data were pooled. Final burrow length did not then depend on relative day0 in a linear regression analysis ($R^2 = 0.03$, $F = 0.76$, $p > 0.4$).

Birds which arrived and dug later than the synchronous earlier pairs may therefore have tried to avoid late breeding by compensating with shorter burrows, and birds that started digging late nevertheless started laying around the same time as the earlier diggers, rather than delay breeding.

Effect of early digging

Late breeders may have arrived later, paired later or not found a burrow location as early as other birds. If birds do not find the right substrate immediately, they may have to have several attempts to test the soil before completing a burrow and settling in to breed. They could compensate by arriving early, or they may end up breeding late. If there is a cost incurred from digging, pairs that have had more attempts may have fewer resources for raising their brood and thus be less successful in their season's breeding effort. If those birds that dug more burrows were less experienced, they may also have been less experienced at raising a brood, so that an apparent less-than-average breeding success for birds that have more digging attempts could be a confounded effect due to inexperience. This makes it difficult to establish effects of early digging on breeding success.

I watched 23 marked pairs in SB and NH during the digging phase in 1989 to 1991. The first day relative to 13th May on which a known pair was seen to dig (FD13/5) correlated highly with the total number of different nests which a member of the pair was seen digging at least once (TOTNESTS; median = 1, range = 1-5): the later birds started to dig a burrow, the fewer

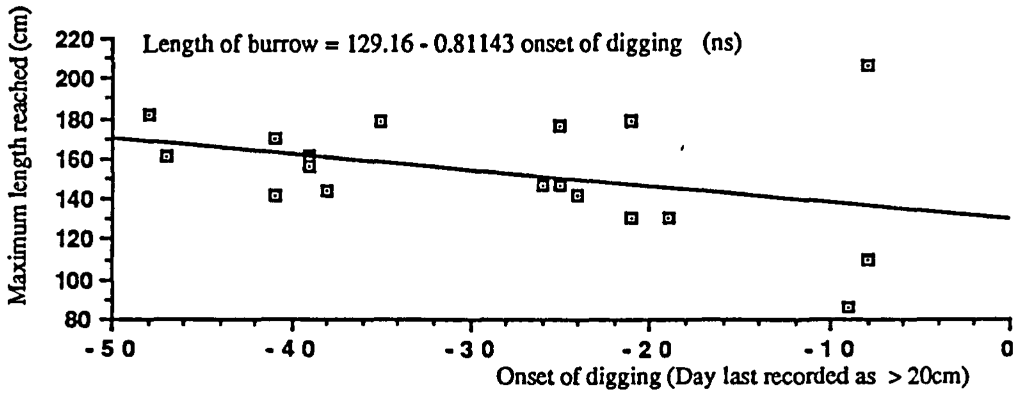


Figure 5.17: Final burrow length (as the maximum recorded) compared to the day in the season (relative to 13th May) when the burrow was started (> 20cm)

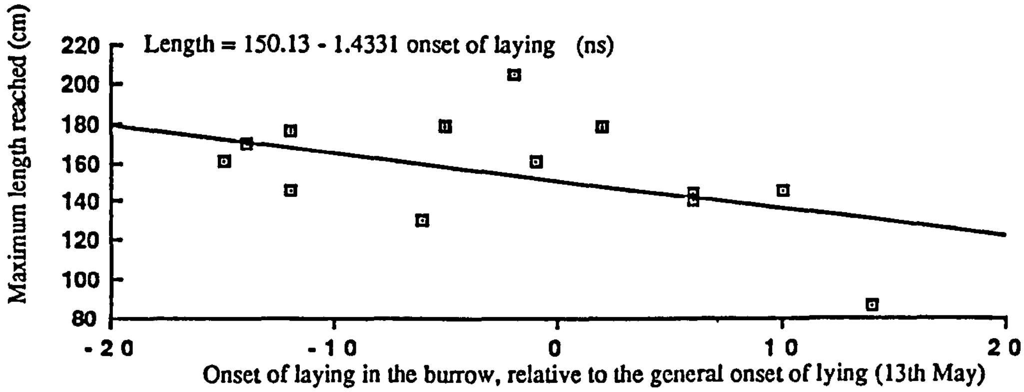


Figure 5.18: Final burrow length with respect to the relative onset of laying in each nest.

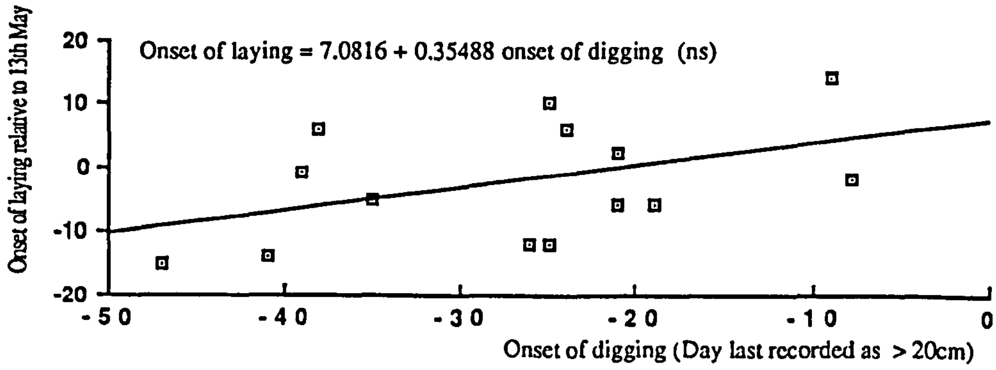


Figure 5.19: Do early breeders start digging earlier? The relative onset of laying in relation to the onset of digging.

attempts they made (Table 5.8 a; TOTNESTS correlation with first digging day). There were 4 pairs which were not seen digging before June. These probably did not dig an original burrow at all but used a burrow dug by another pair, and the digging observed was maintenance after completion. Each of these pairs was observed to dig only at one burrow on one day. The number of different nests at which any member of the pair was seen digging on 2 different days or more (NO2D; median = 0, range = 0-2), which focused on burrows at which the pair was digging more consistently, correlated better with the first day seen digging ($r=-0.62$, $p<0.001$; Table 5.8 a). The pair's relative onset of laying was not related to the number of burrows the pair was seen to dig at, for 11 pairs for which an onset of laying was estimated (correlations day0 relative to 13th May with TOTNESTS and with NO2D, Table 5.8 b). It seems therefore, that an early start of digging allowed a pair to attempt to dig more burrows without incurring the cost of breeding later.

For each of the 23 pairs observed during their digging phase, the breeding success in that season (SUCC) was either 'no brood' (0) for 3 pairs, 'eggs but no chicks' (1) for 9 pairs, 'chicks, perhaps fledged' (2) for 7 pairs, and 'definitely fledged 1 or more chicks' (3) for 4 pairs. Table 5.8 a shows that success may have increased with the number of nests dug more consistently (correlation of NO2D with SUCC), and was not related to the total number of attempts observed (TOTNESTS). Eight pairs which were not seen digging any nest for more than one day failed with eggs. The 3 pairs digging at 2 nests each for more than one day all had chicks, some of which fledged (SUCC 2 or 3). No evidence was thus found for the hypothesis that attempting to dig several burrows reduces seasonal breeding success. It seemed on the contrary that pairs which dug more than one burrow on more than one day were less likely to fail as breeders. The onset of digging (FD13/5) correlated negatively with success (Table 5.8 a), but the 4 pairs which were known to have fledged chicks all started digging on intermediate dates with respect to season, neither early nor late. Two of the 4 pairs which were observed only in maintenance digging (and marked as very late starters) deserted their clutches, the other two raised chicks and may have had fledglings. Success was thus not invariably dependent on an early start of digging (see also section above).

Table 5.8: Spearman Rank Correlation Coefficients (r) of breeding success with timing of digging and of breeding and with numbers of burrows attempted, showing that success (SUCC) correlates with early arrival (FD13/5), and that early arrivals attempt to dig more burrows (TOTNESTS and NO2D).

FD13/5 = first day a member of the pair was observed digging related to 13th May; SUCC = season's breeding success (0= no brood, 1 = eggs, no chicks, 2 = chicks, 3 = fledged at least 1 chick); TOTNESTS = total number of burrows a member of the pair seen to dig at; NO2D = number of burrows a member of the pair was seen digging at on 2 or more days; DAY013/5 = onset of laying of the pair as calculated in 5.3, relative to 13th May in the same year (mean onset of laying). Significance levels are given as ns, *, ** and *** (see Chapter 2).

A: The number of different burrows attempted relative to the onset of digging and breeding success (N = 23 pairs)

	FD13/5 (r (p))	SUCC (r (p))	TOTNESTS (r (p))
SUCC	-0.36 (0.047) *		
TOTNESTS	-0.55 (0.003) **	0.07 (0.384) ns	
NO2D	-0.62 (0.001) **	0.34 (0.054) (ns)	0.50 (0.008) **

B: Number of burrows attempted and first egg day (N = 11 pairs)

	TOTNESTS (r (p))	NO2D (r (p))
NO2D	0.59 (0.028) *	
DAY013/5	0.23 (0.244) ns	0.15 (0.326) ns

Digging in pairs and pair formation during digging

Of all sightings of birds digging during 1989 to 1991 at SB and NH at 60 different burrows, 215 (37%) were of birds digging without an associate (partner within one bird length) and 359 (63%) were of birds digging with one or more associates, which was significantly more than expected if birds dug equally frequently alone and in pairs ($\chi^2 = 36.13$, df = 1, $p < 0.001$). This may still have included an underestimate of the relative frequency of digging in pairs, since birds without an associate may have had a partner 'purring' somewhere nearby, which was difficult to assess. The sightings of all digging birds were roughly normally distributed around the mean of dayx = -18 (i.e. 18 days before the mean first egg date 13th May; se = 1.1). Birds dug in pairs or groups (mean = 21 days before 13th May, se = 1.2) more often than alone (mean = 14 days prior to 13th May, se = 2.0) earlier in the season (Student's t = 3.10, $p < 0.01$). Most birds started digging in pairs, but the maintenance digging late in the season was mostly done by a bird on its own.

In general, therefore, pairs seemed to have been established before the birds started digging. Some birds that were paired, however, may never have dug together: 63O was seen digging alone in 9 sightings, and its partner M6G was not seen digging at all, nor did it guard the burrow while 63O dug. They were not seen to associate at all during the breeding season. Two pairs that had re-mated from previous seasons probably dug together early in the season (33O and 40O at 9-89 and AMB and T3R at 5-90; Fig. 5.20 a and b). Two untagged birds dug early at 9-89, which were probably 33O and 40O before they were tagged (see also Table 5.7 for the activities of this pair). Both pairs started digging early and started laying before the mean onset of laying. The burrow 5-90 was typical of Sungei Buloh in 1990, where pairs excavated early but stopped until close to the onset of laying (see above). It is possible that different burrows were dug at different times during the season and the resident pair which dug each burrow may have had typically high or low levels of pair-digging. Indeed, when the variation associated with 'burrow' was accounted for, a seasonal difference in pair-digging was not significant any more: an ANOVA of dayx with sightings at 11 burrows (for which at least 10 digging observations on 2 or more different days were available, N = 321 sightings all together), with incident of pair-digging ('yes' or 'no') and 'burrow' as main effects, showed that different burrows were dug at different stages in the

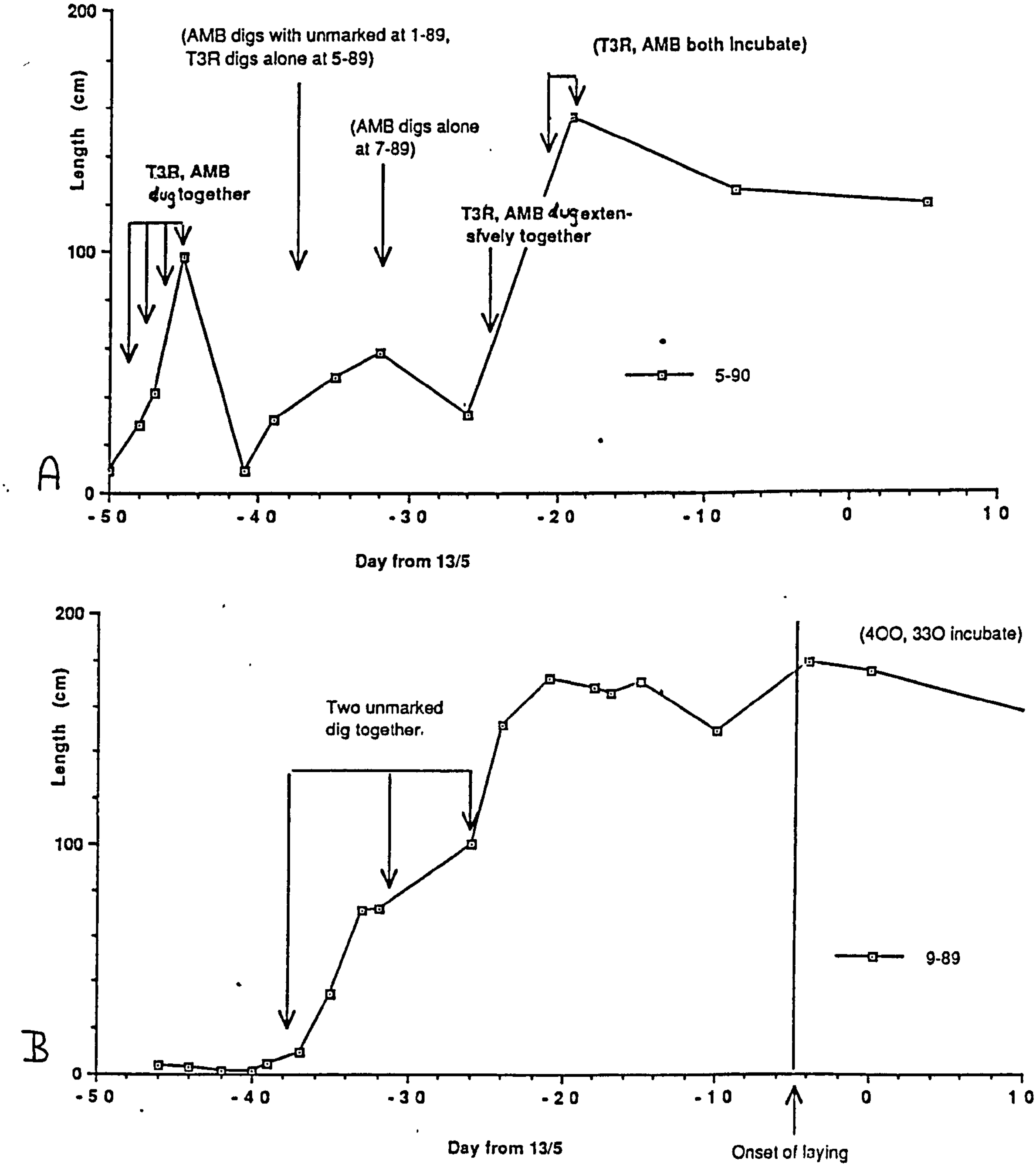


Figure 5.20: The increase in length of the burrows of two pairs which re-mated with the partner from the previous season, including observations made at these burrows or of the birds during the digging phase.

season (main effect burrow on dayx, $F = 189.28$, $p < 0.001$), while there was no relationship between incidence of pair-digging and burrow (interaction term, $F=0.73$, $p > 0.60$) and pair-digging only had a tendency to decrease with season (main effect association on dayx, $F = 3.57$, $p = 0.060$). The trend was the same as in the previous analysis: earlier digging birds tended to be more likely to dig in pairs or groups (mean dayx = -31, N=223 observations), and later birds were more likely to dig alone (mean dayx = -26, N=98).

It seems therefore, that because burrow excavation is nearly always done in pairs, birds have to wait when digging their burrow until they are paired, and those pairs which form early have the advantage of being able to start excavating early. Furthermore, late breeders may not have been able to share burrow excavation.

Distribution of labour during digging

If the female is preparing to lay, she may be more immediately motivated to finish the burrow, or she may be too gravid to dig much without damaging a partly formed egg shell. The male on the other hand may be mate-guarding during this stage, so that he is reluctant to dig alone. To investigate whether birds of one sex dug consistently more than birds of the other, I initially examined whether in general more females dug than males, using all sightings of digging sexed birds. Out of 94 such observations, 49 were of females and 45 of males, which was not significantly different from equality ($\chi^2 = 0.17$, df=1, $p < 0.70$). These observations came from 11 different birds, 8 females and 3 males, but the number of females seen to dig is again not significantly higher ($\chi^2 = 2.27$, df=1, $p > 0.10$). Secondly, I evaluated whether males were more likely than females to dig with their partner (if they are mate-guarding). Of males, 40%-100% of the sightings of digging (mean = 74.02, N = 3 males) were with an associate. For females, the percentage of associated digging was 0%-100% (mean = 56.93, N = 8 females). Overall, sightings by males and females were equally likely to be with an associate (χ^2 on sightings = 1.28, df=1, $p > 0.20$). Thus there was no conclusive evidence for differential division of labour between males and females during burrow excavation.

Digging in pairs and vigilance of the digging bird

Blue-throated Bee-eaters usually dug in pairs (see above). One partner dug while the other pair member kept watch nearby, either at the entry of the burrow or from a nearby perch. Often the vigilant bird vocalized softly throughout ('cooes' or 'purrs'; see Chapter 4 for description). Sometimes, especially at the beginning of digging, both partners would sit perched, one or both 'purring' or 'sharp-cooeing', sometimes very loud and strongly pronounced (almost producing a different type of call from those described in Chapter 4), and flying to the ground and back up to the perch, before one of them descended and started to dig almost hesitantly. When one bird was digging, the watching partner would 'alarm-call' if a potential predator (e.g. a golfing party) approached. If the digging bird can consequently decrease its look-up rate, digging in pairs has the benefit of shared vigilance. There are various possible contexts of vigilance, such as watching out for predators or for potential competitors. Alternatively, the birds may dig in twos for other reasons, for example because the male is mate-guarding, or because two birds can deter an intruder and defend their nest more effectively than one.

I made 42 paired observations of digging bouts of the same bird digging both with and without the partner present during 1989. Such pairs of observations were made within 10 minutes. The digging bird significantly reduced its look-up rate by more than half, from 8.128 per minute (se = 1.151) to 3.373 per minute when the partner was watching (se = 1.156; paired student's t-test of $\log_{10}$ of rates of look-up per minute; $t = 6.21$, one-tailed $p < 0.0005$). This indicates that shared vigilance was indeed important during burrow excavation.

Cost of digging

Costs associated with burrow excavation might be connected to condition (mass loss) or abrasion of feathers. Adults abraded their crown feathers to a varying degree, probably depending on their digging effort. The extent of their crown abrasion may thus reflect how much digging they have done. A correlation of condition and feather abrasion during digging would indicate if extra effort during digging carries a cost. The crown abrasions of 81 birds caught between day -30 and day 20 (cf 13 May) were scored on a 0-4 scale (increment 1.0) and compared to their condition (thickness of pectoral muscle, scored on a 0-5 scale, increment 0.5, see chapter 2). Head abrasion may have correlated negatively with condition (Spearman $r = -0.13$, $0.02 > p > 0.10$). Condition correlated strongly with season ($r = -0.653$, $p < 0.001$), but since crown abrasion did not ($r = -0.005$, $p > 0.40$), the observed trend was probably not confounded by season. Crown abrasion stayed the same during the season probably because most birds were caught while roosting in their burrows which necessarily was after excavation. Digging may thus carry a cost of reduced body condition, and birds of better condition did not seem to dig more. Digging may be a very expensive activity over a short term during a time when energy is needed for reproduction. It would conserve energy to usurp a burrow, at risk of not securing one at all, or ending up with the rejected (and therefore second-rate) burrow of another pair. I do not have consistent data on this, but there was anecdotal evidence for successful take-overs of burrows in this study (pers obs).

5.3.5 Provisioning and parental care

In this section provisioning rates and patterns were investigated. Adults were observed provisioning food to 53 broods during 218 periods of continuous observations during 1989 to 1991. Provisioning rates were not normally distributed but peaked at a median of 2 per hour (range = 1 to 18 times). Brood sizes ranged from 1 to 4 nestlings (median = 2). The degree of synchrony in a brood ranged from 0 to 7 days (median = 1 day).

Provisioning rates for different brood sizes and at different nests

The mean feeding rate per nest was positively related to the mean brood size per nest (Kruskal- Wallis 1-way ANOVA, $\chi^2 = 11.85$, $p < 0.01$; N= 53 broods). Feeding rates per brood ranged from 1.0 to 60.0 feeds per hour (median = 1.9). Per live chick in the brood at the time of feeding observations, this divided into a median of 1.0 feeds per hour per chick (0.3 to 30.0). The provisioning rate per nestling varied significantly between nests (Kruskal-Wallis 1-way ANOVA; $\chi^2 = 72.39$, $p < 0.02$, N = 218 rates at 53 broods). In the following analyses, I therefore controlled for nest and for brood size.

Provisioning, nestling age and brood mass

For the 9 synchronous broods (with hatch spread ≤ 1 day, see methods), mean provisioning rate per nestling varied considerably between broods (Fig. 5.21). In a series of ANOVAs on $\log_{10}$-transformed provisioning rates (provisioning rates were skewed, see above), I controlled for the effect of nest (main factor) and entered first brood age and then brood mass as covariates. The provisioning rate both of the whole brood and per chick (i.e. independent of brood size) increased significantly with brood age ($F = 5.34$, $p < 0.03$; and $F = 6.41$, $p < 0.02$; $N=47$ observation periods at 9 nests; Fig. 5.21). Brood provisioning rates also increased with brood mass after controlling for the effect of nest as above ($F = 6.63$, $p < 0.02$), but the rate of provisioning *per chick* was not related to brood mass ($F = 0.24$, $p > 0.60$). Although adults were frequently observed to avoid handing over food items to nestlings which were about to fledge (see also Fry, 1972), there was no drop in the provisioning rate per nestling at any particular brood age. Any such drop might have been obscured either if nestlings about to fledge had younger siblings still in the nest which were being fed at higher rates, or if nestlings fledged at different ages (see Chapter 7).

The mean size of insects fed to the brood increased with the mean age of the brood (Spearman Rank Correlation coefficient $r = 0.245$, $p < 0.01$, $N = 108$ periods of observation) at 51 nests for which the mean chick age was known.

Time of day and feeding rates

Observations were carried out between 7.15 and 19.15 local time (MST), that is, during the full range of daylight hours. Provisioning frequencies were compared for broods and observation periods during which at least one visit was made to the brood. Only broods for which provisioning observations were made during at least two different observation periods were included in the following analyses ($N = 20$ broods). The $\log_{10}$-transformed feeding rate per nestling was tested in an ANOVA against nest (main factor) and time of day (covariate), but neither nest nor time of day differed significantly at different provisioning rates ($F = 1.28$, $p < 0.20$ for nest, $F = 0.073$, $p < 0.80$ for onset time of observation period, $N = 186$ observation periods). Nestling provisioning rate did not therefore increase or decrease linearly with time of day. Provisioning rates peaked near noon, however, with smaller peaks during mid-morning and late afternoon (Fig. 5.22). When I tested the peak time of high feeding rates (as a main effect) against the remaining times while controlling for differences in broods (also as main effect) and season (day, as covariate), the greatest difference in feeding rates was obtained when observations starting between 10.00 and 13.00 were grouped against the rest ($F = 8.86$, $p < 0.01$).

Provisioning bouts

For individual birds, the interval between two visits to the nest varied from less than 1 minute to over one hour (Fig. 5.23). The birds may alter provisioning and other activities (such as self-feeding, maintenance or 'loafing') opportunistically on an overall random basis, or they may feed at high rates in bouts, whenever conditions and resources allow this. To test whether intervals between visits were random or whether provisioning occurred in bouts, the data were fitted to a Log Survival Curve (e.g. Slater and Lester, 1982). A Log Survival Curve is a plot of each interval between successive visits per bird against the $\log_{10}$ of the number of intervals which are longer. If visits occur randomly, the model fits a straight line. A change in slope at an inflection point suggests non-random pattern of bout interval length, with short and frequent intervals to its left, and intervals longer and less frequent than within a bout to its right. The point of inflection can be estimated by eye (Martin and Bateson, 1988). Two or more points of inflection, or a more gradual slope suggest that the behaviour occurs in more than one type of bout or in a more complex pattern (Berdoy, 1993). Feeding visits with the shortest intervals between them fitted the random model up to intervals of about 10 minutes between visits, when a slight change of slope occurred (Fig. 5.24). This indicates that there may have been a distinct type of bout, with intervals of 10 minutes or less between feeds ('provisioning bout'). There is a second point of inflection, at about 20-minute intervals, concurrent with a gradual levelling of the slope until an interval length of about 35 minutes when it steepens again to resume approximately random frequency for longer intervals. This shows that medium intervals were more frequent than expected from the random model. It is possible that some of the birds provisioned in bouts of frequent visits and other birds typically provisioned at intermediate frequencies, i.e. the two points of inflection represent two different provisioning strategies by different birds. Since the data were pooled from

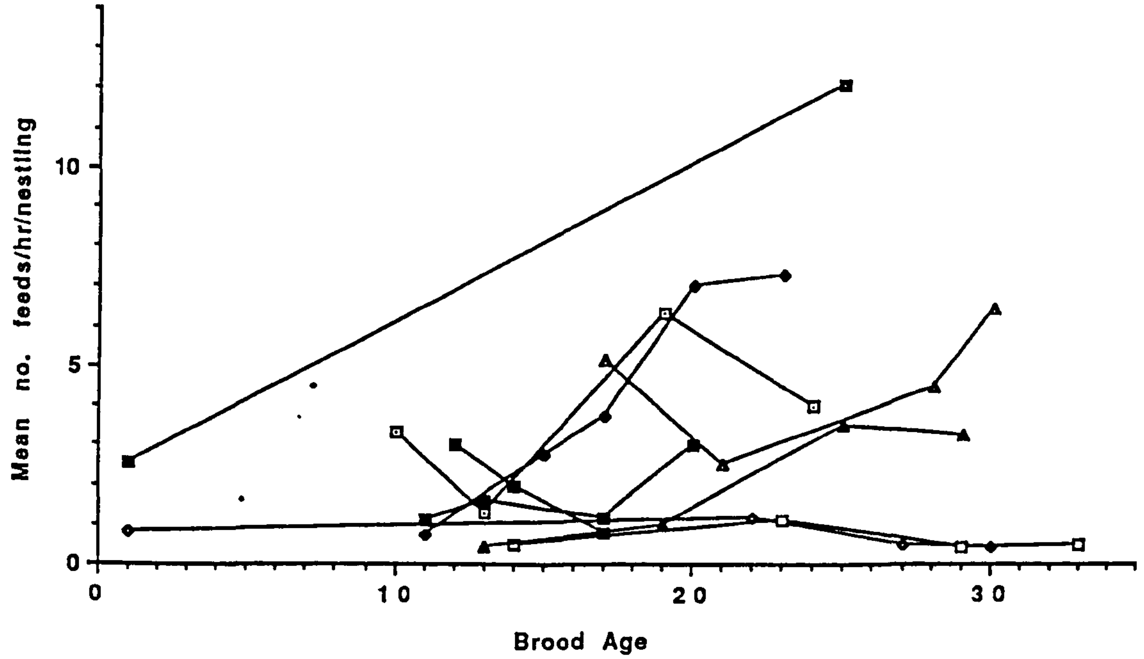


Figure 5.21: Provisioning rates (feeds per nest) per nestling during the nestling phase (brood age) for 9 synchronous broods. Lines join same nests.

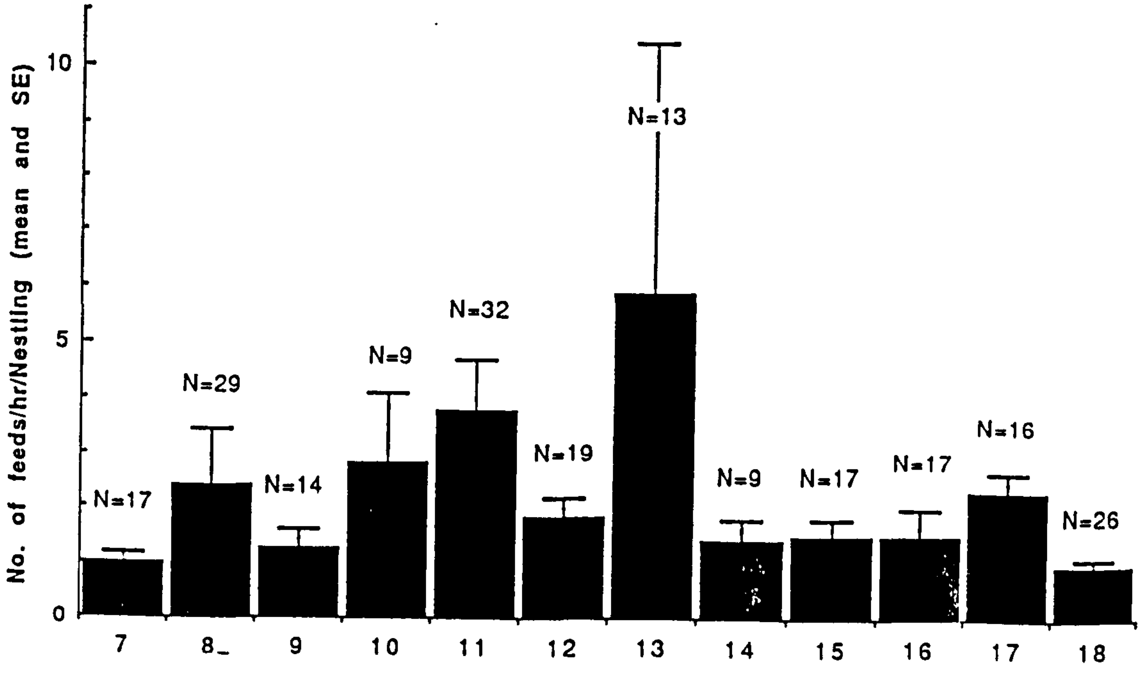


Figure 5.22: Provisioning rate per nestling throughout the day (see text)

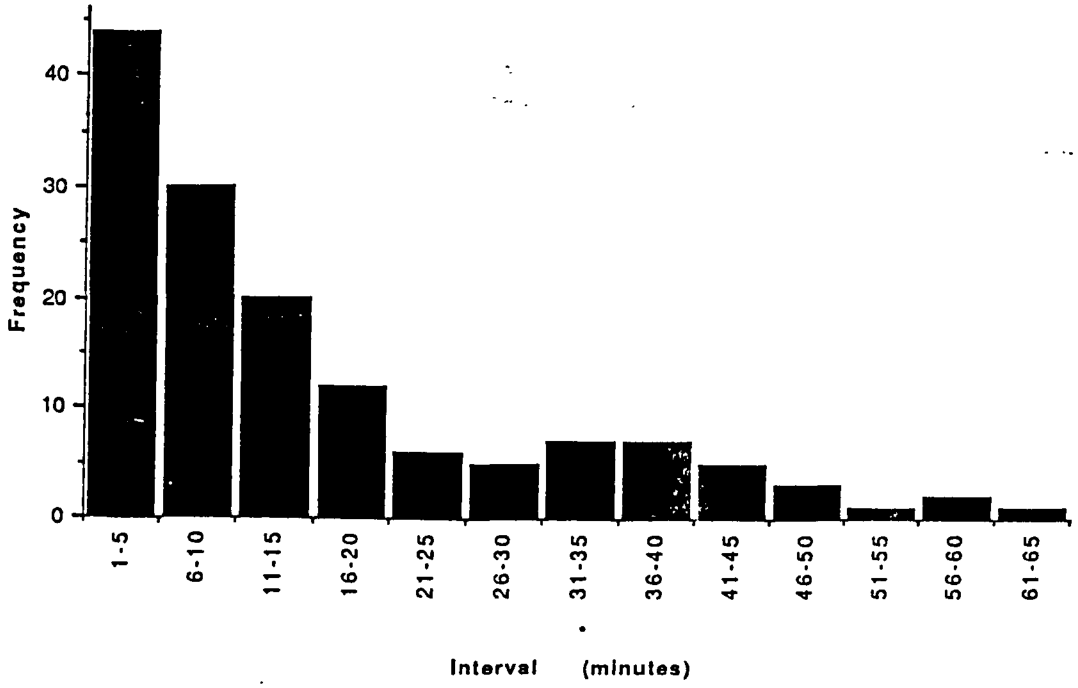


Figure 5.23: Frequencies of observations of intervals between feeds at nests, pooled for all marked birds.

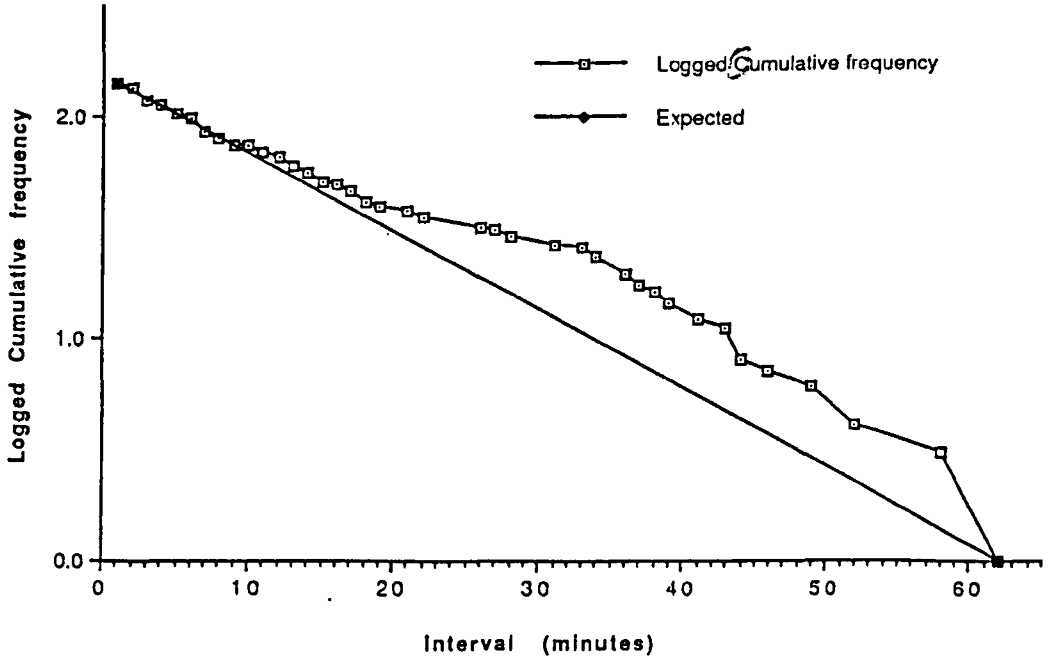


Figure 5.24: Log Survival Curve (see text) of the interval between feeds for marked individuals (as Figure 5.23).

repeated observations of several marked birds, each bird may alternatively have adopted a mixed strategy of feeding either in bouts or at a more constant, intermediate frequency, perhaps depending on prey availability or distance hunted. In Fig. 5.25 a-c I have plotted Log Survival Curves of feeding frequencies of each parent at the 3 nests with the most consistent data. S2G (nest 28-89) and 63O (nest 30-89) both only fed at intermediate frequencies, whereas the other 4 birds had bouts of visits in quick succession (see arrows to show points of inflection). The overall frequency of visits was lower for S2G and 63O than for their respective partners who were provisioning in bouts. It therefore seems that, rather than each bird adopting different patterns of provisioning visits opportunistically, some birds consistently had short intervals between visits (interspersed with longer breaks), whereas other birds fed at a more constant rate every half hour or so. Furthermore, this provisioning pattern strategy was not consistent between partners, since each of the two members of two of the three pairs adopted different strategies.

The two birds which provisioned at low-frequency intervals carried larger insects on average (mean absolute insect size fed by S2G and 63O = 4.2 ± 1.6 SD, N = 29 visits) than their partners (mean absolute insect size fed by 44O and M6G = 3.9 ± 1.4 SD, N = 57 visits), but this difference was not significant (Mann-Whitney U test, $U = 726.5$, $Z = -0.962$, $p > 0.30$).

Sequence of provisioning by pair members

For each of the pairs feeding the three broods above, a first-order Markov analysis was performed on the sequence of visits of pair members (Martin and Bateson, 1986). This tests whether nest visits of pair members are dependent on each-other, i.e. whether visits by either pair member depend on which partner had visited last, or whether both pair members visit randomly with respect to the partner's visits. The sequence of feeding visits of both pair members is entered into a transition matrix (as in Table 5.9). Two tests can be applied to each visit-sequence transition matrix: feeding visits are either dependent on or independent of overall feeding frequencies. Table 5.9 shows transition matrices for feeding visit sequences of 3 pairs.

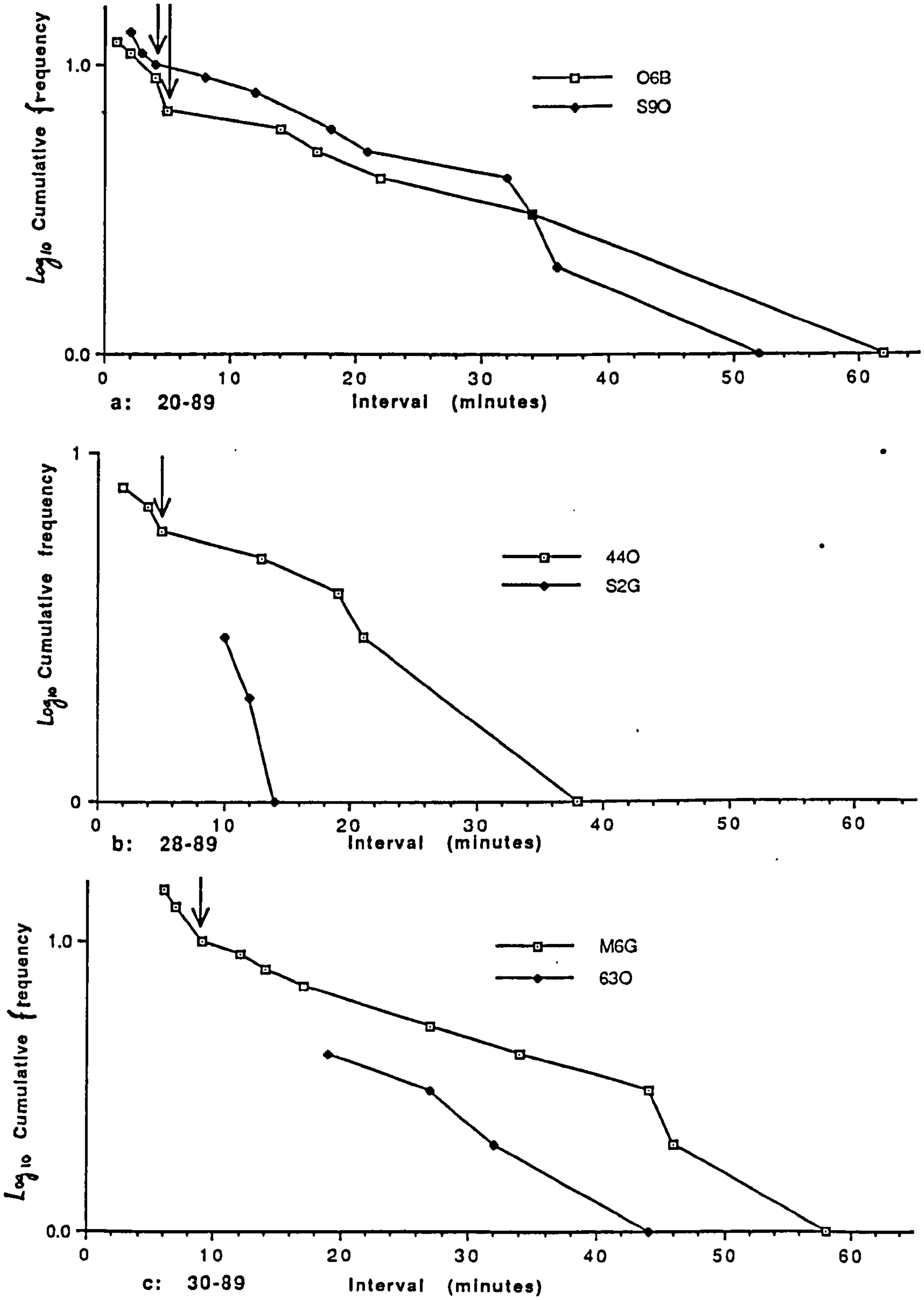


Figure 5.25: Log Survival Curve (see text) for the intervals between feeds for each adult provisioning at one of 3 nests at SB. Arrows: inflection points, indicating bout length

Table 5.9 A-C: Transition matrices for analyzing the sequence of successful provisioning visits of the two pair members at each of three nests. Each visit in a sequence of visits within several observation periods is categorized into one of four classes: the visit is by Bird1 and follows (1) a visit by Bird1, or follows (2) a visit by Bird2, or it is a visit by Bird2 and follows (3) a visit by Bird1, or (4) by Bird2. Equal numbers in all four categories mean that the pair members visit the nest independent of who visited last.

Rows: first visit,
columns: second visit.

A: Nest 20-89

	O6B	S9O	
O6B	5	5	10
S9O	6	11	17
	11	16	27

n frequency: $\chi^2 = 3.70$, $p > 0.20$
test independent of frequency (random): $\chi^2 = 1.16$, $p > 0.30$

B: Nest 28-89

	44O	S2G	
44O	7	12	19
S2G	11	5	15
	18	16	34

test dependent on frequency: $\chi^2 = 3.51$, $p > 0.20$
test independent of frequency (random): $\chi^2 = 6.32$, $0.05 < p < 0.10$

C: Nest 30-89

	63O	M6G	
63O	0	8	8
M6G	7	12	19
	7	20	27

test dependent on frequency: $\chi^2 = 14.87$, $p < 0.01$
test independent of frequency (random): $\chi^2 = 3.76$, $p > 0.20$

At nest 20-89, S9O may have provisioned at slightly higher frequencies (Fig. 5.25 a), which is reflected in most visits of S9O following visits of itself (Table 5.9 a). This increase, however, was not significant (first test, dependent on frequency; $\chi^2 = 3.70$, $p > 0.20$), and so the pair had an overall random sequence of visits (second test, independent of frequency, not different from random; $\chi^2 = 1.16$, $p > 0.30$). For the pair at nest 28-89, most scores fell into the bottom left and top right cells (tendency to differ from random, $\chi^2 = 6.32$, $0.05 < p < 0.10$; Fig. 5.25 b; Table 5.9 b): the pair tended to feed the brood in alternating visits. The notion that 44O perhaps provisioned at a lower level proved to be non-significant ($\chi^2 = 3.51$ $p > 0.20$). In the previous section, I showed that at nest 30-89, 63O fed at intermediate intervals whereas M6G visited in bouts and more frequently (Fig. 5.25 c). This was again reflected in the sequence analysis: The difference in feeding frequency was highly significant (Table 5.9 c; $\chi^2 = 14.87$, $p < 0.01$). The provisioning sequence however was nevertheless random ($\chi^2 = 3.76$, $p > 0.20$).

In summary, although one pair tended to provision in alternating visits, and another pair provisioned at different frequencies, there was no consistent pattern either of alternating visiting by pair members ('regular' visits, significantly different from random) or of 'shifts' of bouts by each pair member ('clumped' visits, also significantly different from random).

Feeding frequency and nestling condition, hunger and hierarchy

For the 9 synchronously hatched broods (including broods with only 1 nestling; see above), two measures of chick condition (Chapter 2) were used in an ANOVA as a covariate, while controlling for the difference between broods as before. Condition improved with $\log_{10}$ of brood provisioning rate (pectoral thickness: $F = 6.81$, $p < 0.02$; relative mass: $F = 6.53$, $p < 0.02$). If all 53 broods for which provisioning observations had been made were used to test the mean condition of each nestling against the mean brood feeding rate, for each chick in the hierarchy (1-4) separately, then for both of the elder 2 nestlings, the mean condition was not affected by mean provisioning rate (Linear Regression Analyses of the $\log_{10}$ transformation; R^2 = between 0.0001 and 0.020, p between 0.30 and 1.0). For the 3rd and 4th nestling pooled, pectoral muscle thickness did not increase with feeding rate to the brood either ($R^2 = 0.027$, $p > 0.50$), but relative chick mass (mass per wing length) showed a tendency to improve with increased provisioning rate ($R^2 = 0.21$, $p < 0.08$). In summary, chick condition improved with increasing brood provisioning rate in synchronous broods, but a high provisioning rate may have been more important for runts than for high ranking nestlings in general.

The tendency to have an abdominal 'bulge' (mean nestling hunger) was not related to the mean provisioning rates within 2 days of each nestling capture, for any of nestlings 1 to 4 separately or for high ranking nestlings 1-2 compared to low-ranking chicks 3-4 (Kruskal-Wallis ANOVAS; χ^2 between 0.011 and 2.400, p all < 1.00 and > 0.10).

The total brood provisioning rate (total number of feeding visits divided by the total hours of observation) did not change with the degree of synchrony, neither per brood (Kruskal-Wallis 1-way ANOVA; $\chi^2 = 10.55$, df = 6, $p > 0.10$) nor per nestling ($\chi^2 = 8.82$, df = 6, $p > 0.10$). This was true even though the age difference between youngest and eldest is necessarily larger in large broods, so that synchronous broods were bigger (Spearman Rank Correlation coefficient = 0.60, $p < 0.001$, N = 41 broods) and were therefore fed more frequently (see above). Asynchronous broods with a difference in age of 3 days or more between eldest and youngest nestlings were more likely to have a wounded runt at any stage than synchronous broods ($\chi^2 = 5.09$, df=1, $p < 0.03$, N=34 broods with more than one nestling). Broods with wounded runts got more feeds per hour than broods with no wounded nestling (Kruskal-Wallis 1-way ANOVA of total feeds per total duration at each nest, $\chi^2 = 8.60$, $p < 0.005$), but this effect disappeared when the rate was divided by the number of nestlings ($\chi^2 = 1.60$, $p < 0.30$).

Food size and hatching asynchrony

Insect sizes brought to broods ranged from 'very small' (1) to 'very large' (7) Table 5.10 shows correlations between insect sizes and brood ages. For each brood, the range of different insect sizes brought ot the brood was highly correlated with the age differences between nestlings in the brood. The size of the largest insect brought correlated with the age difference in the brood, but the size of the smallest insect did not, probably because broods with a larger age gap between nestlings also had higher mean age. Both the minimum and the maximum

Table 5.10: **Spearman Rank Correlation Coefficients r (and significance p) for insect types and sizes in relation to brood ages and age differences (N = 10 broods; for insect type N = 8). Age difference = degree of asynchrony.**

	Mean Brood Age	Age difference	Min Insect Size	Max Insect Size	Insect Size Diff.	No. of Insect Types
Age difference	0.562 (0.045)					
Min Insect Size	0.557 (0.047)	0.314 (0.189)				
Max Insect size	0.552 (0.049)	0.725 (0.009)	0.767 (0.005)			
Insect Size difference	0.204 (0.286)	0.789 (0.003)	0.161 (0.329)	0.731 (0.008)		
No. of Insect Types	0.346 (0.201)	0.444 (0.135)	-0.252 (0.274)	0.163 (0.350)	0.491 (0.109)	
No. of Observations	0.189 (0.300)	0.382 (0.138)	-0.541 (0.053)	-0.170 (0.319)	0.299 (0.201)	0.827 (0.006)

absolute sizes of insects brought correlated with the mean chick age (Table 5.10). Therefore, parents of asynchronous broods can clearly bring insects of different, and presumably appropriate sizes, to their broods.

5.3.6 Sexual dimorphism

The possible rôle in mate choice of plumage brightness, streamer length and size variables was investigated by examining them for individual variation, variation with respect to laying date, assortative mating and differences between the sexes.

Individual variation in size and plumage characters

For 7 size and 4 plumage variables, means were calculated for each of 279 birds (over 1-12 different captures per bird during 1989 to 1991; mean = 1.8 captures per bird ± 1.7 SD). Of the size variables, the greatest variation between individuals was in BILL and streamer length (SD compared to mean; Table 5.11 a). Streamers not only varied in absolute length between individuals but abraded during the season. Since most birds were caught with their streamers already abraded to varying degree, the sample of birds for which the original length was known was small, and streamer length was therefore examined separately in the following. Of the plumage characters, brightness of the throat was the most variable trait between individuals (Table 5.11 b).

Size variables: Principal Component Analysis

The 7 size variables (means for each bird, as above) were used in different combinations in a series of Principal Component Analyses (PCAs; Table 5.12). The first Principal Component (PC1) in birds usually contains the variation due to size (Rising and Somers, 1989). The PC1 of size variables that explains most of the variation (70.6%) between individuals was a combination of wing and keel length (Table 5.12). Since for interpretation PCs have to be 'translated' into their component variables, this PC was used in the following analyses alongside the size variables.

Table 5.11: Variation of (A) size and (B) plumage score variables between individual birds (total N = 293). For each individual, a mean score was used. The birds are not separated according to sex. Size variables are length (in mm) unless otherwise stated.

A

Variable	Mean	SD	Range	N (no. of birds)
keel	29.89	1.32	25.85 - 34.50	279
wing	112.0	3.0	104.0 - 122.5	273
head+bill	56.41	2.71	47.50 - 63.30	263
bill	27.10	5.23	24.80 - 32.90	273
bill-width	7.19	0.34	5.80 - 8.40	266
tail	79.7	2.7	73.0 - 91.0	273
streamers (maximum measured)	113.5	17.8	81.0 - 172.0	276

B

Variable	Mean	SD	Range	N
Brightness of throat ('Bright')	2.8	1.1	1 - 6	229
Mite infestation ('Mites')	1.1	1.5	0 - 5	186
Brown on nape ('Brown')	2.8	0.7	1 - 4	252
Green on nape ('Green')	0.9	1.0	0 - 5	269
Head abrasion ('head')	1.7	0.9	0 - 4	140

Table 5.12: Principal Component Analyses (PCAs) using means for individual birds, of all biometric variables measured consistently, to find the combination of measurements that represents body size most accurately, i.e. that explains most variance between individuals in the first principal component (PC1). Ordered by descending Eigenvalue.
(All measures are of length unless stated otherwise; all measurements are in mm)

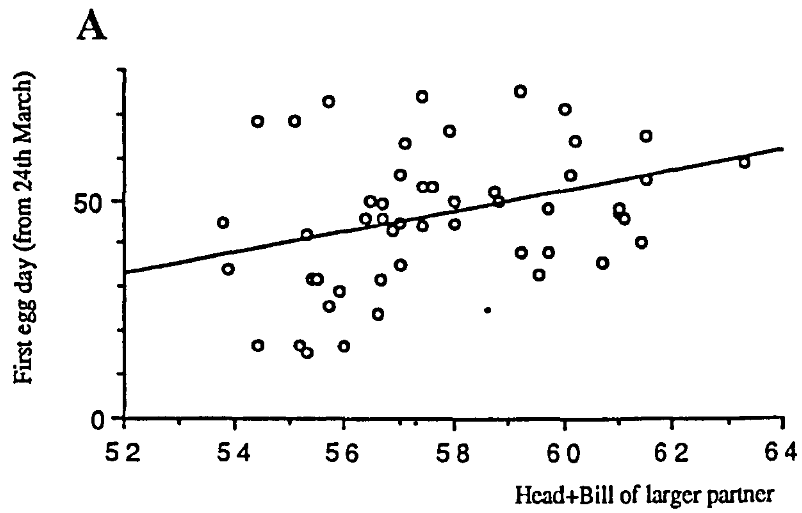
Variables included in the PCA	Eigenvalue of PC1	% variance explained by PC1
wing, keel	1.412	70.6
wing, head+bill	1.256	62.8
wing, bill-width	1.244	62.2
head + bill, bill	1.186	59.3
keel, wing, head+bill	1.753	58.4
bill-width, tail	1.162	58.1
wing, bill	1.140	57.0
bill, tail	1.124	56.2
bill-width, bill	1.092	54.6
keel, wing, bill	1.495	49.8
wing, head+bill, bill	1.392	46.4
keel, wing, head+bill, bill	1.841	46.0
wing, head+bill, bill-width	1.446	48.2
keel, wing, bill-width, bill	1.777	44.4
keel, wing, bill-width, tail	1.767	44.2
head+bill, bill-wdth, bill	1.298	43.3
keel, wing, head+bill, bill, bill-width	2.065	41.3
head+bill, bill, tail	1.199	40.0
head+bill, bill-width, tail	1.172	39.1
wing, head+bill, bill-width, tail	1.522	38.1
wing, head+bill, bill, tail	1.499	37.5
keel,wing,head+bill,bill,bill-width,tail	2.113	35.4

Variation of plumage and size with laying date and breeding success

The general breeding success of a pair (failed, with chicks or with 1-2 fledgling: GenSuc, see methods) did not vary linearly with its laying date estimate (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 1.628$, $p > 0.80$, N=48 broods with known breeding success). The number of fledglings (NoFle, see methods) similarly did not depend on laying date (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 0.470$, $p > 0.70$). Larger (or smaller) birds did not generally lay earlier (Table 5.13), except for pairs where the larger pair member had a shorter head and bill (HB) or the pair member with the shorter tail had a significantly shorter tail (Fig. 5.26 a and b). Only two out of the 21 (<10%) regressions in Table 5.13 were significant, which could have arisen by chance. Body size and laying date was therefore not consistently related in a linear manner. (No parabolic relationship was distinguished by eye, which might occur if size is correlated with mid-lay which was advantageous; see Chapter 4). The onset of laying did also not correlate with most of the plumage characters, except the extent of brown on the nape; particularly the more brown on the nape (BROWN) of the less brown bird, the earlier the pair bred (Table 5.14). Of all the size and plumage variables, only the average wing length of both partners and the size-PC of the smaller partner ('female') had an inverse relationship with NoFle (Fig. 5.27) but none with GenSucc (Table 5.14). Again, only very few of the ANOVAs (2 out of 40 = 5%) were significant, a result that is likely to have occurred by chance. No significant relationships were shown if size or plumage variables were compared to the breeding success of either pair member (Table 5.15). Consistent or strong relationships between size and success could thus not be demonstrated.

Environmental effects on throat brightness

Throat brightness did not correlate with the extent of mite infestation (Spearman rank correlation coefficient = 0.017, $p > 0.40$). Non-infested birds did not have less bright or brighter plumage on the throat than all infested birds (Kruskal-Wallis ANOVA, $\chi^2 = 1.50$, $p > 0.20$) or than a few heavily infested birds (score 4 or 5; $\chi^2 = 0.143$, $p > 0.70$). Throats did, however, become duller as the season progressed (Spearman Correlation Coefficient of BRIGHT with day relative to 13th May = -0.313, $p < 0.010$), indicating that throat brightness was not so much affected by ectoparasites as by feather abrasion during digging and breeding.



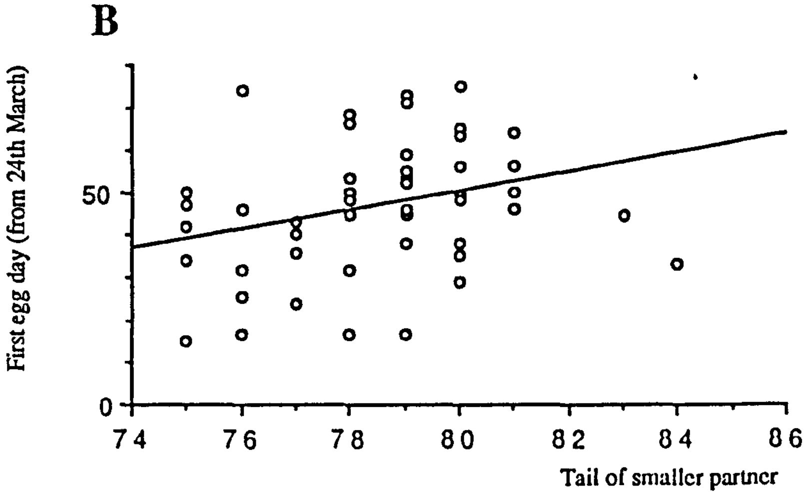


Figure 5.26: The two significant correlations of measures of body size of each pair member with the pair's timing of breeding, which were head and bill length of the larger partner and tail length of the smaller partner respectively (see text).

Table 5.13: Regressions of size and plumage variables of the larger (‘M’) and the smaller (‘F’) pair member and the average of both pair members on the date of the onset of laying (from 24th of March). N = 52 broods

Variable	’M’			’F’			Both		
	Slope	R^2,	p	Slope	R^2,	p	Slope	R^2,	p
PC1[a]	-0.002	0.001	0.815	0.006	0.024	0.271	0.002	0.004	0.653
wing	-0.003	0.000	0.925	0.008	0.004	0.654	0.003	0.000	0.886
keel	-0.003	0.004	0.660	0.008	0.017	0.360	0.002	0.002	0.717
head+bill	0.037	0.077	0.047 *	0.012	0.008	0.527	0.025	0.051	0.109
bill	-0.009	0.010	0.485	-0.018	0.063	0.074	-0.013	0.033	0.194
bill-width	-0.003	0.039	0.163	-0.003	0.025	0.266	-0.003	0.040	0.154
tail	0.003	0.000	0.877	0.035	0.083	0.038 *	0.019	0.030	0.216

[a] the score of PC1 (first principal component of wing + keel) is not meaningful

Table 5.14: **Kruskal-Wallis one-way ANOVAs of the onset of laying with plumage characters.** As with size, the pair members with the higher score for the character were grouped together.

Variable	partner (higher score)			partner (lower score)			Both Partners		
	Med	χ^2	p	Med	χ^2	p	Med	χ^2	p
Brightness of throat (‘Bright’)	3.0	1.232	0.942	2.0	6.048	0.109	2.9	1.635	0.802
Brown on nape (‘Brown’)	3.0	6.591	0.086	3.0	9.710	0.008 **	3.0	9.992	0.007 **
Green on nape (‘Green’)	1.0	5.465	0.243	0.0	0.069	0.966	0.9	0.475	0.789

Table 5.15: Kruskal-Wallis one-way ANOVAs (χ^2 and p) of size and plumage variables with brood success of the partner with the higher score ('M') and the partner with the lower score ('F') and the average of both pair members (Both).

Variable	'M' Med[a]	χ^2	p	'F' Med	χ^2	p	Both Med	χ^2	p
PC1[b]		1.448	0.485[c]		8.544	0.014 *		4.859	0.088
		1.654	0.799[d]		6.417	0.170		4.261	0.372
wing	113.0	5.715	0.057	110.3	5.294	0.071	112.0	6.008	0.050 *
		5.588	0.232		5.644	0.227		5.333	0.255
keel	30.8	0.423	0.809	29.0	3.826	0.148	29.8	1.949	0.377
		1.763	0.779		5.318	0.256		2.224	0.695
head+bill	57.3	1.356	0.508	55.0	0.212	0.899	56.2	0.769	0.681
		3.618	0.460		7.495	0.112		5.070	0.280
bill	29.3	3.802	0.149	28.0	0.687	0.710	28.7	1.119	0.571
		5.648	0.227		3.668	0.453		1.954	0.744
bill-width	7.4	1.787	0.409	7.0	4.683	0.096	7.2	4.476	0.107
		2.494	0.646		0.632	0.959		1.075	0.898
tail	81.0	1.585	0.453	79.0	0.256	0.880	79.6	0.134	0.935
		2.989	0.560		3.693	0.449		3.621	0.460
'Bright'	3	0.686	0.710	2	4.687	0.096	2.9	3.136	0.209
		2.222	0.695		4.881	0.300		2.816	0.589
'Brown'	3	1.564	0.457	3	1.054	0.590	3.0	0.126	0.939
		5.550	0.235		3.271	0.514		3.827	0.430
'Green'	1	1.191	0.551	0	1.328	0.515	0.9	1.211	0.546
		0.877	0.928		3.548	0.471		1.143	0.887

[a] Med = median

[b] the score of PC1 (first principal component of wing + keel) is not meaningful

[c] top line (NoFle) fledging success (0-2 fledglings) of nests with hatched chicks,

[d] bottom line (GenSucc): general success (eggs but no chicks, chicks but not fledged or not known to fledge, 1 fledgling, 2 fledglings)

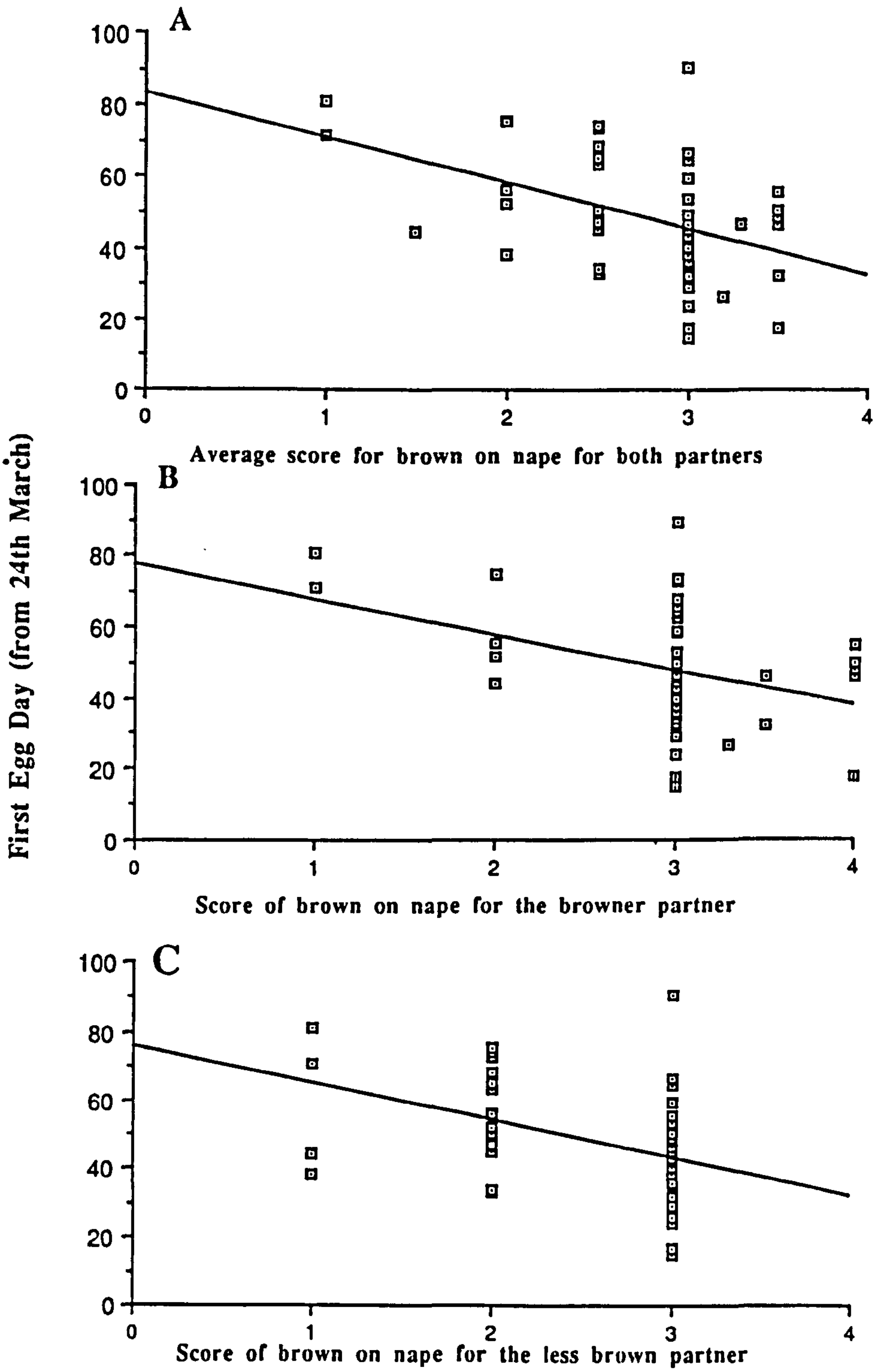


Figure 5.27: The onset of laying of birds with different extent of brown on their nape (BROWN). A: BROWN was measured as the average of both partners, B: the Browner partner and C: the less brown partner. For all three measures, higher scores of BROWN was correlated with earlier breeding (see text for statistics)

Assortative mating

For each brood for which both adults had been captured and measured, the mean values for each pair member (see above) of all biometric and plumage variables, including the PC1 of wing and keel length (see above), were correlated between pair members, mostly with high significances except for keel length and PC1 (Table 5.16).

Sexual dimorphism of streamer length

At the beginning of the breeding season, both males and females had long streamers which abraded during the breeding season (Pearson Correlation Coefficient of streamer length and day relative to 13th May = -0.465, $p < 0.000$, N = 112 different sexed birds). Of all sexed birds, 56 females and 32 males were caught while their streamers were still intact. Males did not have significantly longer streamers than females (Fig. 5.28; Student's t-test, $t = 1.30$, $p > 0.20$), but the variation in streamer lengths of males was significantly higher than streamer length variation between females, while the streamers were still intact (SD males = 15.8, SD females = 6.6; $F = 5.80$, $p < 0.000$; Fig. 5.28) but not when tails were abraded (SD males = 16.8, SD females = 15.7; $F = 1.14$, $p > 0.60$). This means that streamer length may be more variable amongst males than females. Overall streamer length, including abraded streamers, was probably higher in males ($t = 1.90$, $p = 0.059$; Fig. 5.28).

The difference between intact streamer length and abraded streamer length was larger in females. While both males and females abraded their streamers during the digging phase, females tended to do so more than males (Fig. 5.28).

Sexual dimorphism of plumage characters

Males tended to have brighter throats than females (Median test $\chi^2 = 2.923$, $p = 0.087$) although both sexes were similarly, albeit rarely, infested by mites (median = 0; Median test $\chi^2 = 0.408$, $p > 0.50$), as expected (see above). Males had fewer green feathers on the head (Median test χ^2 of 'Green' = 14.574, $p < 0.0009$) and their brown nape tended to extend further down their backs than in females (Median test χ^2 of 'Brown' = 2.88, $p = 0.090$).

Table 5.16: Plumage scores and size variables correlations between pair members. All size measurements, including the PC1, were normally distributed and were used in parametric correlations, whereas the plumage scores were used for (non-parametric) Spearman-rank correlations.

Variable	mean	sd	N (pairs)	corre-lation[a]	coef-ficient	p	
brightness of throat (1-6)	2.8	1.1	84	S	0.511	0.000	***
brown on nape (1-4)	2.8	0.7	89	S	0.564	0.000	***
green on nape (0-5)	0.9	1.0	93	S	0.429	0.000	***
keel	29.87	1.33	97	P	0.173	0.045	*
wing	112.0	3.02	93	P	0.359	0.000	***
head+bill	56.37	2.72	93	P	0.343	0.000	***
bill	27.09	5.20	93	P	0.760	0.000	***
bill-width	7.18	0.34	92	P	0.438	0.000	***
tail	79.6	2.7	93	P	0.566	0.000	***
PC1[b]			92	P	0.238	0.011	*

[a] S = Spearman Rank correlation; P = Pearson's correlation

[b] the score of PC1 (first principal component of wing + keel) is not meaningful

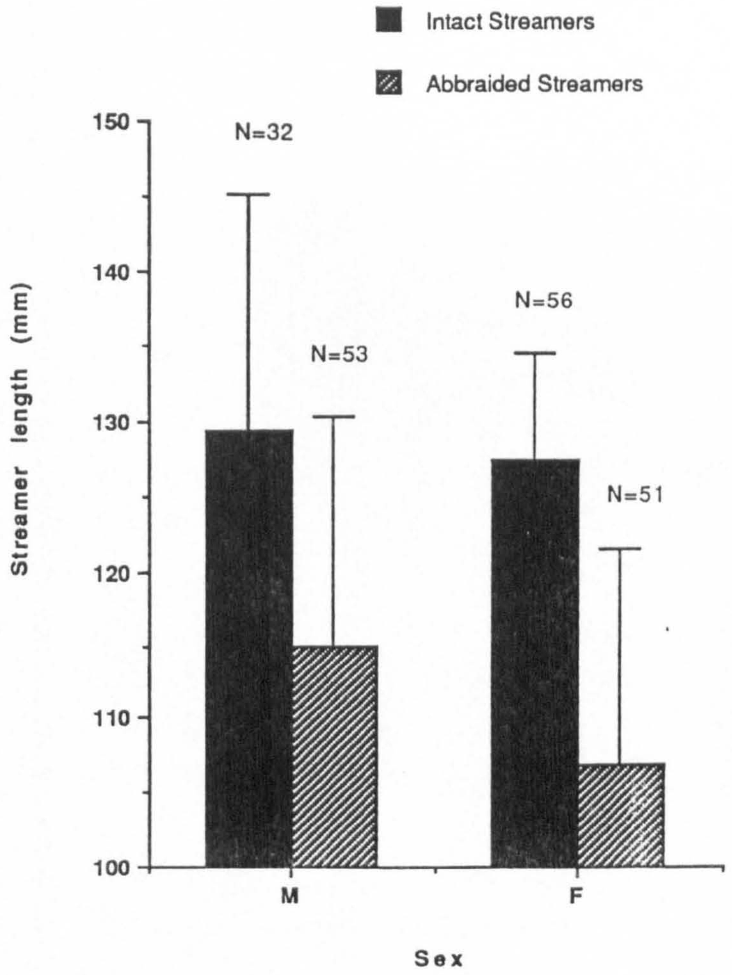


Figure 5.28: Streamer length for males and females (means and sd) during the early (pre-laying) season and after digging (see text). The length of intact streamers were not significantly different between males and females, but variation in intact streamer length was higher for males (see text for statistics and additional tests)

5.4 DISCUSSION

5.4.1 The functions of copulations

The traditionally assumed function of copulation is fertilization. Bird eggs are usually fertilized within 24 hours of being laid (review e.g. by Birkhead and Møller, 1992). Nearly all sexual interactions observed in this study, however, occurred well before the mean laying date in the colony. It is possible that most of the sexual interactions observed were of early breeders, which started laying before the general breeding season, so that the main sexual activities observed would be close to the actual onset of laying of these birds. Some female birds are able to store sperm which can fertilize their eggs for at least 16 to 18 days (Birkhead, 1992; Oring *et al*, 1992). Most observed copulations were female initiated. Female initiated sexual interactions occurred even earlier than male initiated interactions, while I observed no change in male soliciting frequency throughout the mating season (but it is possible that males used a more subtle soliciting posture early in the season which I missed, whereas later in the season they invariably allo-fed the female prior to any copulation). If female *M. viridis* store sperm, early copulations could lead to fertilizations later in the season. This is particularly relevant if early-arriving males are of high genotypic quality (see below) but not willing to pair with poorer quality females. These females may attempt to 'sneak' sperm carrying 'good genes' early in the season to fertilize her eggs later.

Copulations and sexual behaviour in Blue-throated Bee-eaters may have functions other than fertilization. This may be a reason why most of the sexual encounters and interactions observed were unsuccessful. Alternative functions of sexual behaviour, together with corresponding predictions for soliciting behaviour, timing and success of sexual interactions, are summarized in Table 5.17.

In cooperative species, the breeding female may solicit to prospective 'helpers' (Emlen, 1982 a) which, in some species, may have a share in paternity (e.g. Rabenold *et al*, 1990; this is not the case, however, in European Bee-eaters; see Jones *et al*, 1991). The White-fronted Bee-eaters studied by Emlen (1982 a) are not migrants, however, like Blue-throated Bee-eaters which probably have to establish pair-bonds after arrival at the breeding colony. In Blue-

Table 5.17: Hypotheses of the function of copulations and predictions on timing of soliciting and success of sexual interactions (adapted from Sheldon, 1993).

Proposed function of copulation	Predictions for Female soliciting	Predictions for Male behaviour	Predictions on copulation success	Likely to apply to *M. viridis*
Fertilization	during fertile period	solicits during fertile period	yes	yes
EPC from 'better' male	during fertile period	no prediction	no prediction	not tested
Mate acquisition (pair formation)	early (before fertile period)	no prediction	no	yes
Mate acquisition (future season)	throughout season or late	no prediction	no	not tested
Helper acquisition	throughout season	accepts and copulates	yes	not tested
Mate-assurance of paternity	early and during fertile period	accepts and copulates	yes	not tested
'Swamping' EPCs	accepts	forces or solicits	no prediction	yes

throated Bee-eaters, therefore, the many early, female initiated interactions were more likely to have been in the context of pair formation and of female choice of partner. Female Spotted Sandpipers are known to engage in extra-pair copulations to acquire a future mate (Colwell and Oring, 1989; see Chapter 6). In many species, males and females do not arrive synchronously, and the more successful breeders arrive earlier (e.g. Bryant, 1989; see also below). In Kestrels *Falco tinnunculus*, early-arriving males arrived before most females but late-arriving males arrived much later than early females so that females have to choose quickly amongst the early males (Patokangas *et al*, 1992). If birds arrive loosely paired and establish the pair bond during the pre-laying phase (see Introduction), early-arriving females may try to establish a pair bond with an early-arriving male, by copulating with him during the stage of pair formation. This may be before their fertile period and would correspond with the observed pattern of copulations, where females initiated most early sexual interactions, and, furthermore, successful copulations were significantly closer to the general onset of laying (i.e. unsuccessful interactions were earlier). These are indications that the earlier interactions, which end less often in cloacal contact and are more often initiated by the female, are most relevant to pair formation, pair bond establishment or securing of future partners. If females actively chose early arriving, 'good' males by soliciting to them, then it would make particular sense that so many female solicitations were observed very early in the season.

Successful copulations were closer to the onset of laying than unsuccessful sexual interactions and thus perhaps more relevant for fertilization. These may have been pair copulations, since pair matings peak during the fertile period in most birds. Females of several mainly monogamous species actively solicit EPCs if this is to her benefit (Birkhead and Møller, 1992), in which case female solicited EPCs would also be expected to peak during her fertile period. These successful copulations in the fertile period of the Blue-throated Bee-eaters, however, tended to be initiated more often by males, who are either more concerned with maintaining an established pair bond by initiating more matings later-on or may copulate at higher rates so as to out-compete sperm from other males either by numbers (Birkhead *et al*, 1988; Oring *et al*, 1992) or by increasing his chances for 'last sperm precedence' in fertilizing each of her eggs (see Chapter 6). Therefore, these later, male initiated copulations were probably pair matings. Females who solicited a successful sexual interaction, solicited for longer than 'unsuccessful' females and than males in general. If they actively and persistently persuade males to inseminate them, perhaps this may persuade the male that he is likely to have fathered her nestlings later and increase the likelihood of his providing paternal care later. This could not be investigated, because too few marked birds were observed copulating.

To summarize, three proposed functions of copulations were supported by this study for Blue-throated Bee-eaters, dependent on circumstances. These were: fertilization, pair formation and 'swamping' EPCs (Table 5.17).

5.4.2 The evolution of soliciting behaviour

Soliciting behaviour for females and males and their significance and possible origin are discussed in this section.

Ducking was the signal used by the female Blue-throated Bee-eaters to indicate consent to copulation (see also Fry, 1984 for other bee-eater species). It is perhaps derived from the juvenile begging posture: I have seen behaviour of begging post-fledging juveniles similar to ducking. If ducking originated in begging behaviour by the female to be fed, then perhaps the reason why males flew off, regularly terminating sexual interactions without copulation, was that females ducked also without signalling fertility as well in some other way. (It is possible that males fly off to persuade the female to fly off too so that her fertile status (with egg) can be judged (see Alves, 1993). Similarly, female 'soliciting' could rather be seen as female 'begging'. Some successful copulations were solicited with ducking behaviour by the female alone, however, without courtship feeding. If female-solicited copulations outside her fertile period are related to pair formation and pair bond (see above), a male who is solicited by a female, may indicate his consent to the bond by accepting or rejecting a copulation. Males may reject females on the basis of their condition, for example, as being low-quality (see Bortolotti and Iko, 1992).

Allo-feeding of the female by the male precedes matings in several Bee-eater species (White-fronted, Fothergill, 1988; Red-throated, and European, Fry, 1984), where it is often called courtship-feeding. In Blue-throated Bee-eaters, the male initiated all sexual interaction with allo-feeding, except when forcing the female (see Chapter 6 for the description of a pair-'rape'). Allo-feeding is not necessarily followed by sexual behaviour, however, during laying and incubation ('incubation-feeding'). This may have been the original function of allo-feeding. Fry (1984) reports observations by Krebs on European Bee-eater males providing the laying female with nearly all of her dietary needs by feeding her frequently at the nest, with mostly large food items. Male paternal care is in some species extended to the protection of the female herself, e.g. from dominant flock members (Hogstad, 1992), or by allowing her access to his territory (Wolf and Stiles, 1970), which both improves her chances of survival and thus, indirectly, his reproductive success (Hogstad, 1992; Hannon and Martin, 1992; Wolf and Stiles, 1970). Male allo-feeding of the female has similar effects, and in both cases the male may be able to breed earlier because of the female's improved condition (Hogstad, 1992), by bringing the hatching date forward during incubation (Nilsson and Smith, 1988) or by making the difference between success and failure. In Red-billed Gulls, pairs where the male allo-feeds the female divorce less often between seasons and have a higher probability of breeding in the next season (Mills, 1994). In this species, attentiveness of the male and allo-feeding is a successful strategy in terms of his breeding success.

To summarize, female ducking is a soliciting behaviour which my have originated in food begging. Allo-feeding of the female by the male precedes male-initiated copulations and might improve breeding success of a pair.

5.4.3 Mate guarding and pair association

Pair members of Blue-throated Bee-eaters spent most of their time at the colony (60%) alone. Mate-guarding House Martins follow the female on up to 70% of flights (Riley *et al*, in press); the female was guarded by the male in 75% nest visits and 91% of foraging trips in Starlings *Sturnus vulgaris* during egg laying (Power *et al*, 1981); similarly high levels are quoted for other mate-guarding birds (see e.g. Møller, 1987 a and c). Even during the egg-laying phase, male Blue-throated Bee-eaters did not spend most of their time within sight of their female partners and females had ample opportunity to engage in extra-pair copulations even during their assumed fertile period.

The proportion of time spent together was nevertheless significantly higher during laying and in the period prior to laying than after arrival and during incubation and provisioning. This was so even when the time spent digging or sitting at the nest was excluded, which is important because pairs dig in pairs probably for reasons related to vigilance (see results in 5.3 and below). Both close physical associations and visual contact are more frequent during and before laying, which is consistent with predictions from the mate guarding hypothesis: during her fertile period, the guarding pair member can remain vigilant to his partner's activities while still being able to engage in other activities himself. On the other hand, the birds may spend time together at the colony to watch and guard the nest from a perch near the nest rather than to mate-guard. This explanation, however, cannot account for the increase in close association (within one bird-length of each-other) of pair members during this period, which is more likely to occur in the context of pair bond or mate-guarding. There was no overall difference in the frequency with which males or females joined or followed their partner, and there was no clear seasonal pattern. The evidence from pairs with known onset of laying is anecdotal but does suggest that the male follows the female mostly between day -30 and day 10 (5 out of 7 observations), whereas there is no such pattern in females (2 out of 4 observations). Again, the evidence is ambiguous as to whether mate-guarding does occur in the Blue-throated Bee-eater, but suggests that if so, it is the male who guards the female during her presumed fertile period.

There are several explanations why mate-guarding in Blue-throated Bee-eaters is not very pronounced. Time spent at the colony, for example, may not be representative of the birds' overall behaviour. The observations in this study, however, were all made at the colony, which may not be relevant if most PCs and EPCs occur at the feeding grounds. The pre-laying period is spent nearly exclusively at the feeding territory in White-fronted Bee-eaters (Emlen and Wrege, 1986). It is also possible that male Blue-throated Bee-eaters consort with the female at the feeding ground, and EPC attempts are prevented there. They are also likely to spend time hunting and loafing at the feeding grounds, and perhaps most copulations take place there, as in Tree Swallows *Iridoprocne bicolor*, where EPCs occur at the feeding or roosting sites, not the nest site (Dunn *et al*, 1994). Perhaps behaviour at the colony was atypical, for example because the birds are careful not to attract predators to their nests, or due to disturbance. Those birds that did use the colony regularly behaved normally, i.e.

hunted, preened, basked or descended to the lawn, and did not spend extended periods on perches, as birds do during disturbances at the colony. They also used conspicuous perches and vocalized often and loudly, which did not suggest that they were behaving inconspicuously. It is thus more likely that those birds which may have been disturbed shifted their main activities away from the colony, and that birds remaining did not behave atypically.

It is possible that Blue-throated Bee-eater males cannot mate-guard efficiently, because time spent together with the female may be lost to time spent in other activities, like foraging or digging, so that post-EPC copulations may be less costly to breeding males than mate-guarding. This should be true particularly if competition for food forces the Bee-eaters to feed apart, because finding food is more important than avoiding EPCs. In falconiformes, males provision the brooding females, and mate-guarding may be a reason why male Kestrels take small prey items back to the nest more readily than expected from prey abundances (Korpimaeki *et al*, 1994). Male Blue-throated Bee-eaters may be restricted in mate-guarding if females refuse to join them for hunting. While the male is incubating, the laying and still fertile female is on her own, and the male is dependent on her cooperation in avoiding EPCs (see below), unless he delays incubation to avoid being cuckolded, as reported for male Starlings (Power *et al*, 1981). Male Blue-throated Bee-eaters might therefore be constrained in their mate-guarding activity.

In their recent comparative review, Møller and Birkhead (1993) conclude that mate-guarding is the best paternity guard, and that alternative strategies, high-frequency copulations (see Chapter 8) are adopted mainly by males who cannot mate-guard. If the female can use stored sperm to fertilize her eggs, the assumption that her fertile period is directly prior to egg-laying may not be valid, and copulation rates rather than mate-guarding would minimize EPCs (Oring *et al*, 1992). Furthermore, in species where female cooperation is needed for copulations to be successful, as in Red-billed Gulls for example, female cooperation is presumably also needed to resist EPC attempts (see Mills, 1994). Males cuckolded in such a way can do little to prevent it (Oring *et al*, 1993), so this may be the reason why male Blue-throated Bee-eaters did not seem to guard their female partners very closely (see also Chapter 8).

Paired Blue-throated Bee-eaters cooperate with each-other at all stages of the breeding cycle. Both pair members are involved in brood-care, in which they take turns, so that they spend little time together, apart from digging; during laying, the male allo-feeds the female, and they take turns to incubate. It is possible that this high level of cooperation also extends to the fertile period and that female Blue-throated Bee-eaters choose not to engage very frequently in extra-pair copulations. In this section, I have discussed the evidence that mate-guarding occurs in Blue-throated Bee-eaters. Female choice in paternity and extra-pair offspring are discussed further in Chapter 8.

5.4.4 Pair formation and synchronization of breeding during excavation

It is not known if breeding pairs of Blue-throated Bee-eaters stay together during the winter or if the birds pair-up prior to migrating to, or after arrival at, the breeding grounds. Red-throated Bee-eaters form new pairs and re-establish old pair bonds at the beginning of the season, prior to and during excavation (Fry, 1972). Since return rates of Blue-throated Bee-eaters were low (see Chapter 4), few birds re-mated with a previous partner, so that most pairs were newly formed. The members of all of the pairs for which detailed observations were reported arrived at the colony singly and visited the colony alone, not yet mated. Pair formation probably occurred normally after arrival.

The optimal timing of breeding is adaptive (Perrins and Birkhead, 1983; Perrins, 1970; see Chapter 4 for a detailed discussion). In Chapter 4 I showed that breeding in the middle of the breeding season may be advantageous for fledgling success in Blue-throated Bee-eaters. Although I found quite a wide spread of laying dates, and late birds were still laying while the first broods were fledging, most pairs laid synchronously, close to the mean onset of laying, supporting the notion that the optimal time for breeding is in the mid-season. It is possible, however, that the advantage in mid-season breeding lies in synchrony of breeding within each colony rather than mid-season breeding *per se*. Breeding synchrony may, for example, enforce monogamy onto males (Emlen and Oring, 1977) and reduce the risk of suffering forced EPCs for paired females (Birkhead and Biggins, 1987). Three hypotheses for the timing of breeding and their predictions on the relative timing of digging and laying are considered. If mid-season breeding is advantageous, then it is likely that the same breeding season should be adhered to each year - probably following the overall seasonal distribution of insect food or 'weather window', as discussed in the previous chapter. Laying-dates should then be synchronous not only regardless of arrival and digging times, but also across years. There was no significant difference between the mean onset of laying between colony-years; indeed synchrony across years was adhered to in Sungei Buloh from 1989 to 1990, despite the fact that the earlier burrows of 1990 were started much earlier than burrows in 1989 but they were completed at the same time as the burrows in 1989 (Fig. 5.13). Across years, there was thus a staggered onset of digging, but completion of the burrows was synchronous from 1989 to 1990. Furthermore, burrows were completed synchronously with respect to season (Fig. 5.13) but not with respect to each pair's first egg dates (Fig. 5.14). This shows not only that seasonal synchrony of breeding was adhered to across years, but that it was achieved during digging by delaying the completion of the burrow.

Since early-arriving Blue-throated Bee-eaters do not necessarily get to lay earlier, they may benefit instead from having more time to choose the right burrow site. Evidence for this notion is (1) that the number of burrows attempted was higher for pairs which started digging earlier, (2) pairs who dug more than one burrow before laying were more likely to fledge their brood, and (3) digging late carried the possible cost of breeding in shallower burrows. This suggests that laying (and the fertile period of the female) does not coincide with nest burrowing, which is also shown in Fig. 5.14: all burrows were completed at least 10 days before the estimated onset of laying, and mostly much earlier than that. European Bee-eaters dig their burrows 2 weeks before laying and then depart (C.M. Lessells, pers comm). The relative timing of digging and laying is important for mate-guarding in the Blue-throated Bee-eater. If digging coincided with laying, it would facilitate mate-guarding for males, because a pre-laying female would have a strong interest in completing the burrow and be easier to guard, and because digging in pairs is preferred by and advantageous for Blue-throated Bee-eaters (see results in 5.3). This is discussed in more detail below.

During the digging period, pairs have to cooperate. The digging bird could reduce its look-up rate by more than half if digging while a partner is watching nearby (see results). It is thus advantageous for Blue-throated Bee-eaters to dig in pairs. The function of association during digging might be related to vigilance for predators or competitors (see e.g. Pulliam, 1973, for review); it would also allow both partners to rest between digging bouts without flying to safety, which is costly. The latter is supported by the observation that birds do indeed nearly always take turns when they dig in pairs. Because birds should start digging early (see above), but pairs probably form on arrival (see above), they have to wait for the digging of their nest until they have found a partner to dig with. This notion predicts firstly, that pair formation should commence as early as possible, and secondly, that digging should commence soon after pair formation. Pairs that had stayed together from the previous season should furthermore start digging early, but this could not be confirmed with observations of two pairs that re-paired from the previous season. One pair started to excavate early and at several burrows, but the other pair probably did not. The second notion was supported, however, by the detailed observations of several pairs which all started to prospect and dig soon after the first time they were both seen at the colony. During digging, both pair members used vocalizations which may have had as their context encouragement of the partner to dig (Chapter 4), and which may be needed for cooperation to develop between pair members at this stage.

5.4.5 Pair cooperation during provisioning and provisioning patterns

There was no evidence from three nests looked at, that pair members consistently cooperated during provisioning and either always worked in 'shifts' of bouts or always alternated their visits. The pattern of provisioning varied greatly between birds. One of the 3 pairs *did* visit alternatingly, so it is possible that different pairs adopt different strategies. Alternatively, pairs may change their pattern of visiting sequence according to circumstance, which is likely since provisioning rates were adjusted to brood age (but not to nestling hunger) and the size of individual food items brought to the nest changed with chick age. Prey availability may have been important in shaping provisioning rate or pattern. Pair members followed the same general pattern of activity and took turns in provisioning the brood, which is suggested by the pattern of association, with no physical or visual, but probably with vocal contact between pair-members (Fig. 5.11).

Different intervals between the visits of pair members suggests that pair members used different foraging patches away from the colony. Most birds provisioned consistently in bouts with intervals of less than 10 minutes between visits, interspersed by periods during which they do not provision at the nest. During a bout, provisioning may be at a maximum rate, alternating with periods of rest, maintenance or self-feeding, or they may be unsuccessful in hunting, or hunting very far from the colony. Two distinct patterns of provisioning were observed: in high-frequency bouts with short intervals as above, and at low frequencies with intervals of mostly intermediate length. Two of six birds provisioned consistently at low frequency rather than in bouts. It is possible that these provisioned with a different strategy. If they hunted consistently on territories or sites which were further away from the colony, then they may have had to catch mostly large insects for the nestlings, to make the trips worthwhile (Central Place Foraging; Ward and Zahavi, 1973; see also Emlen, 1982, for White-fronted Bee-eaters). Central Place Foraging could not be shown for Blue-throated Bee-eaters, although the mean size of insects fed by the two birds with the second strategy might have been slightly higher. Alternatively, birds may have fed at low frequencies because they were less successful in hunting prey worth bringing back to the colony for example, such as young birds may be (Curio, 1982), or because they had to engage in more self-feeding to improve their own body condition.

The provisioning rate to the whole brood and per nestling (controlling for brood size) did not vary with the degree of asynchrony in the brood. Hatching asynchrony thus did not seem to reduce the work load on the parents, at least not in terms of number of visits. The range of prey sizes brought to the brood, however, was larger for synchronous broods, and it is possible that this represents a reduction in search time or effort for the parents (Margrath, 1990).

5.4.6 Sexual dimorphism in Blue-throated Bee-eaters

Blue-throated Bee-eaters are monomorphic and sexual dimorphism is expected to be subtle. Males were on average larger than females (section 5.2) and tended to have brighter throats and browner crowns and napes, which had fewer green feathers and tended to extend further down their backs. If larger males were more attractive to females, they should pair assortatively and lay earlier, but there was no such indication. The extent of brown of both birds was related to the first egg date and may have been important for breeding success in both sexes. The extent of brown on the nape could therefore be a social status signal (cf Rohwer, 1975) and may increase with age as does the black plumage coloration of Pied Flycatchers, where usually older, dominant males are darker (Slagsvold and Lifjeld, 1988). If the extent of brown on nape is related to age or status also in the Blue-throated Bee-eater, then the erectly sitting posture prior to copulation helps to exaggerate their brown nape and may help to signal male quality.

I could not demonstrate active mate choice, but assortative mating was highly significant for plumage and size characters. Barnacle geese who pair for life, choose partners which are familiar to them regardless of morphological traits (Choudhury and Black, 1994), which the authors interpret as choice for complementary mates which are adapted to the same local habitat. European Bee-eaters mated assortative with respect to age (Lessells and Krebs, 1989): in 80% of pairs, partners were either both juveniles or both older. Assortative mating with respect to age was also found for European Bee-eaters by Lessells and Krebs (1989; see also Reid, 1988) who could not test if this was from active choice in newly formed pairs or because pairs stayed together. A non-random mating pattern in established pairs may be a reflection of intra-sexual selection, availability of mates or similar use of habitat (Choudhury *et al*, 1992). Highly assortative mating could further be an indication for mutual selection. Alternatively, females may choose males, but only good or early females get to choose the best males (Patokangas *et al*, 1992). If size is being sexually selected, then birds might not be able to use keel length as a reliable predictor of body size on which to accept a partner, despite the fact that keel and wing lengths were the main contributors to PC1, the 'size Principal Component'. This could be why keel length (and the Principal Component of keel and wing length) was least correlated between pair members of Blue-throated Bee-eaters.

Assortative throat brightness between pair members may have been an artifact of the timing of pair captures, since the birds get duller as the season progresses. The extent of brown, which varied with laying date for both partners, could be a character under mutual sexual selection (cf Jones and Hunter, 1993). Alternatively, it may reflect aggressiveness as well as dominance and is subject to non-random mating because of compatibility for instance, as in the Arctic Skua *Stercorarius parasiticus* (O'Donald, 1983).

Streamer length may be related to sexual selection. Intersexual selection on traits like tail length or shape by active female choice can only be distinguished from other selective forces by careful experiment. While this was outside the interest of the present study, such research has been conducted recently (reviewed e.g. by Jennions, 1993; Harvey and Bradbury, 1991; Cherry, 1990). Some studies found that females preferred males with experimentally elongated tails (Andersson, 1992; Smith and Montgommery, 1991; Møller, 1989 and 1988; Anderson, 1982), but in some species, tail length influences factors like territorial ownership and is affected more likely by intrasexual selection and not by female choice (e.g. Savalli, 1994; see also Cherry, 1990). Intact streamers in Blue-throated Bee-eaters were more variable amongst males early in the season, but not when they were abraded. This is consistent with predictions for intersexually selected ornaments: females may choose males on the basis of streamer length early in the season while they are still intact, during pair formation. Later, during digging, when pairs had been formed, the streamers of both sexes became abraded and did not have higher variation amongst males than amongst females any more. Streamer length may be significant as a signal only for mate choice during the early breeding season. The same is true for throat brightness which may also be significant for mate choice. Streamers and throat feathers abrade during the season, so these plumage characters could only be useful as a signal during the early season. In Italian Sparrow *Passer italiae*, for instance, the bright breeding plumage - but not the 'status badge' - abrades during the winter and is replaced during the molt prior to the breeding season (Bogliani and Brangi, 1990). Other research suggests that males with longer streamers may be more likely to break them (Smith and Montgomery, 1991), and females may chose males on their ability to keep streamers intact over a long time (Barnard; in Cherry, 1990) or on streamer symmetry (Møller, 1993; see also reviews by Brookes and Pomiankowsky, 1994, and by Liggett *et al*, 1993).

5.4.7 Conclusions

Females apparently choose males early in the breeding season by offering copulations which are not necessarily related to fertilizations of her eggs. Males seem to have a more passive role in mate choice, and accept or reject solicitations. Male-initiated sexual interactions occur more while the established pair bond is maintained. The male then assures his paternity with low-level mate-guarding and by soliciting matings, both during the presumed fertile period of his partner. The level of mate-guarding at the colony was comparatively low, the reasons for which are discussed (see also Chapter 8).

The evidence on pair behaviour and mate choice from this study, although often not conclusive, points towards Blue-throated Bee-eater pairs cooperating at all stages of the breeding cycle. They dig in pairs which is less risky with regard to predators or competitors. During laying, the male allo-feeds the female, and they take turns to incubate eggs. Both pair members are involved in brood-care, in which they take turns, so that they spend little time together once the pair-bond is established, which I interpret as a sign of cooperation.

Sexually dimorphic traits were body size and streamer length. Streamer length may be related to sexual selection similar to tail length or ornamentation in males of sexually dimorphic birds. The main trait correlated with breeding success was the extent of brown on nape, which may be a social signal related to a combination of age, dominance and social status especially for males but also for females. Throat-brightness was not correlated overall with breeding success, but there was a population difference between Nam Heng and Sungei Buloh: there were no very bright-throated birds at Nam Heng (Chapter 4).

CHAPTER 6 - MIXED REPRODUCTIVE STRATEGIES AND DNA FINGERPRINTING

6.1 INTRODUCTION

Intraspecific brood parasitism (IBP) has sometimes been used in the literature as synonymous with intraspecific *nest* parasitism (INP), but in this study, INP stands for egg 'dumping' by a female of the same species, whereas IBP is the general term used for all forms of intraspecific parasitism as the result of which one or more members of a brood are raised by adults which are not both genetic parents. This includes (1) INP by non-relatives, (2) INP by a female that was fertilized by the pair male ('quasi' parasitism) and (3) extra-pair fertilization (EPF) where the pair-male is cuckolded by an extra-pair male who fertilizes the pair-female. IBP constitutes a set of reproductive strategies which may be adopted by individuals as an alternative, or additional, to the main mating system, such as monogamy. These mixed reproductive strategies are introduced below.

6.1.1 Male strategies to maximize fertilizations

In an apparently monogamous mating system, each male can have two roles - as a pair member and as an extra-pair male. Looking for opportunities to father extra-pair offspring may carry the risk of being cuckolded in colonies which breed synchronously, if it interferes with the ability of a male to guard his own paternity. Because of the high cost assumed to be involved for the male in being cuckolded, mate guarding (see Chapter 5) is predicted to take priority over seeking EPCs (Birkhead and Fletcher, 1992; Birkhead and Møller, 1992; Birkhead *et al*, 1989; Brodsky, 1988), and in some species males seem to confine their pursuit of EPCs to periods before and after their own female's fertile period (Riley *et al*, in press; Hasselquist and Bensch, 1991; Westneat *et al*, 1990).

Competition between males may result in the adoption of several behavioural strategies to ensure successful fertilization of the female(s). Firstly, in many species, males guard their female partners during her fertile period against extra-pair males seeking copulations (see Chapter 5). Secondly, whether or not a copulation results in a successful fertilization may depend on the timing of copulation in relation to egg-laying (Birkhead *et al*, 1987). Each egg is fertilized most probably about 1h after the previous egg has been laid (e.g. Cheng *et al*, 1983). The last mating before egg-laying, or a mating during the 'insemination window' - between the laying of one egg and the fertilization of the nest, has the highest probability of fertilizing each egg ('last sperm precedence', e.g. Birkhead and Møller, 1992). One EPC at the 'right' time can thus be successful, which has been demonstrated by Birkhead *et al* (1988) for Zebra finches *Taeniopygia guttata*, and Cheng *et al* (1983), for Mallards *Anas platyrhynchos*. Thus, if an EPC is immediately followed by a pair mating, it is less likely to lead to fertilization (Birkhead *et al*, 1988). Thirdly, insemination by an extra-pair male (or the 'beta' male in polyandrous systems) can be 'swamped' by a high rate of pair copulation (Hunter *et al*, 1992; Davies, 1983). Usually, most copulations (both within-pair and EPC) occur at the time of highest fertilization probability (see review by Birkhead and Møller, 1992; Cheng *et al*, 1983). Accordingly, after his mate has been involved in an EPC, a male might increase his own copulation rate (Møller, 1987 a; Birkhead *et al*, 1987) and may even force a PC (Birkhead *et al*, 1990).

If a male cannot prevent his female participating in EPCs, he can adjust the level of parental care he provides later. Polygynous male Dunnocks give paternal help according to their share of copulation (Davies *et al*, 1992; Birkhead *et al*, 1987; see also Møller, 1991 b - criticised by Wright, 1992), and Birkhead and Møller (1992) report a general negative relationship between paternal care and the rate of extra-pair paternity in birds. Cuckolded monogamous males, however, often do not give less paternal care in raising subsequent offspring (Lifjeld *et al*, 1993; Birkhead and Møller, 1992; Jamieson and Craig, 1987). If paternity is zero, because the male has had no access to the female (as in some male removal experiments), and if a replacement male is present to take up the slack, then the original male may not feed the nestlings at all (Davies *et al*, 1992; Burke *et al*, 1989). A replacement male, on the other hand, may commit infanticide if the chicks of his mate were not fathered by him (Whittingham *et al*, 1993; see also Robertson and Stutchbury, 1988). The only evidence for males assessing their share of paternity comes from Dunnocks *Prunella modularis* (Davies *et al*, 1992; Burke *et al*, 1989), and there is no unequivocal evidence for adjustment of paternal care in cases of shared paternity. This may be because although males apparently gauge their share in paternity by assessing their share of copulations during their female's fertile period, they probably cannot distinguish offspring they did father, from those they did not (e.g. Burke *et al*, 1989). They would lose more by not feeding their own offspring than they would lose by providing less parental care.

6.1.2 Female interests and EPCs

Fertilizations by an extra-pair male (EPFs) can be disadvantageous also for the pair-female. Forced EPFs may incur a direct cost to female survival or reduce female choice (Birkhead and Møller, 1992; Birkhead and Biggins, 1987). For example in waterfowl, forced EPCs may cause injury (Morton *et al*, 1990; Crook *et al*, 1987; Birkhead and Biggins, 1987; Emlen and Wrege, 1986; Butler, 1982), or the female may be chased (Jones, 1986), and even killed, in extreme cases of multi-male EPC attempts (reviewed by Birkhead and Møller, 1992). A current view, however, is that in most species females control the occurrence and timing of copulations (Birkhead and Møller, 1993 b), and they will avoid attempted EPCs (e.g. Bjoerklund and Westman, 1983) by ignoring courtship, by moving away, by reacting aggressively to EPC attempts (Bjoerklund *et al*, 1992), or by adopting specific behaviours such as 'wing fluttering' (Butler, 1982).

Males may deceive females that they are still unmated and able to help raise the young, as in the Pied Flycatchers. In this species, males fertilize, but do not provide parental care for secondary and tertiary females in different territories (Alatalo *et al*, 1982 and 1986; but see Stenmark *et al*, 1988, and Temrin *et al*, 1989, who argue that secondary mates are the best of a bad option for these females). In Tengmalm's Owl *Aegolius funereus*, however, secondary females are often helped because primary nests are often predated and bigamous males can then reallocate their provisioning to their secondary nests (Sonerud, 1992).

EPCs can be adaptive for females (e.g. Wagner, 1991). In House Sparrows *Passer domesticus*, EPCs may be used as an insurance against male infertility (Wetton and Parkin, 1991). A female soliciting a mating from a male of higher quality than her consort would increase the fitness of her offspring if they inherit the father's superior traits ('genetic quality' hypothesis; e.g. Kempenaers *et al*, 1992). Females actively select attractive 'high quality' males for EPCs in Blue-tits (Kempenaers *et al*, 1992). In Black-capped Chickadees *Parus atricapillus*, where individuals know each other's social status, females seek EPCs from males of a higher rank than their partner, whereas the female partners of high-ranking males are faithful (Smith, 1988; see also Lifjeld *et al*, 1993). Alternatively, females may solicit matings from a second male to entice him into helping to raise her brood (Gjershang *et al*, 1989; Lewin, 1989 b), part of which may or may not be sired by him (Burke *et al*, 1989) or to establish a social bond with a future partner (Colwell and Oring, 1989).

In many altricial birds, male parental care is important and females try to ensure that their male partners stay to feed the brood. If males are likely to reduce parental help if they suspect or observe the female to be involved in EPCs, it pays females to use strategies to convince the male that he is the only possible father of the offspring. Females may thus have an interest in copulating at high levels with their pair male to ensure paternal help is subsequently forthcoming (Birkhead and Møller, 1992). Wagner (1992) argues that female Razorbills mate-guard their pair-males, and in polygynous mating systems females are often aggressive towards each-other and may even destroy the clutches of other females to monopolize their partner's paternal help, as in House Sparrows (Veiga, 1990).

Although the conclusions from previous chapters suggest that Blue-throated Bee-eaters behave essentially according to a monogamous mating system, mixed reproductive strategies may include extra-pair copulations, evidence for which is presented in this chapter

6.1.3 Intraspecific nest parasitism

In his review of intraspecific nest parasitism, Yom-Tov (1988) lists 53 species for which egg dumping has been reported. INP occurs mostly in species with precocial young (Rohwer and Freeman, 1989), such as ducks and other waterfowl. With the advent of DNA fingerprinting, however, evidence for INP in altricial birds is accumulating fast, mostly for colonial species (Petrie and Møller, 1991; Rohwer and Freeman, 1989). Direct observations of egg dumping are rare (Yom-Tov, 1988), and Horn and Rubenstein (1984) conclude that more such observations are needed to determine whether egg dumping really is an evolutionary strategy or just accidental.

Studies such as that by Brown and Brown (1988; see also references therein) on colonial Cliff Swallows not only provide evidence of the regular occurrence of INP in altricial birds (but see Smyth *et al*, 1993), but also investigate mechanisms by which it may have become a successful evolutionary strategy. Egg 'dumping' can have evolved into a successful strategy only if 'dumped' chicks have had a chance to survive in the host's nest. For this it is important to consider the constraints on nest parasites and their strategies to overcome these.

For the host in altricial species, the costs of feeding a parasitic nestling are high (Rohwer and Freeman, 1989), particularly if the host can only bring up a limited number of nestlings and is raising a parasitic one instead of one of its own (Payne, 1977). Blue-throated Bee-eaters usually raise 1-2 nestlings from 3-4 eggs (Bryant and Tatner, 1992) in any one season, experiencing high brood reduction, presumably particularly in 'bad years' when there is too little food to raise the young. Consequently the selection pressure on such a host to avoid being the victims of nest parasitism is very high. Several mechanisms of host defence have evolved as a consequence. Hosts commonly guard their nests during laying (Møller, 1987 f); House Martins forcibly exclude potential intruders, and perhaps as a result, there is no evidence of INP in this species (Riley *et al*, in press). Birds often expel eggs appearing in the nest before the onset of their own laying (e.g. Pinxten *et al*, 1991 b), and even delay laying or desert the nest (Briskie and Sealy, 1987) if parasitic eggs appear in their nest repeatedly (C.M. Lessells, pers comm).

Even if a parasitic egg has been accepted by the host, it may not hatch and survive the incubation and nestling phases to fledge. If an egg appears in the nest too long after the host female has stopped laying, it is unlikely to hatch (Pinxten *et al*, 1991 a). The nest parasite must therefore lay its egg within a time 'window' relative to the host stage: ideally the parasitic egg should be 'dumped' *after* the onset of laying of the host female, so as not to be expelled, but *before* or near the time that she finishes laying, if it is to hatch and be fed as one of the host's own nestlings. Hosts are usually poor at recognizing their own offspring when they are young, as observed for interspecific cuckoo- hosts who accept chicks which grossly mismatch their own nestlings in appearance (Lotem, 1993). Once a 'dumped' egg has hatched, the illegitimate nestling is therefore more likely to be brought up as a true genetic offspring.

Nest parasites have evolved strategies to counter host defences against INP. Cliff Swallows actively transfer eggs between nests (Brown and Brown, 1988 b), which was also recorded for Northern Flickers *Colaptes auratus* by Blomme (1974), for Swallows by Møller (1987 f), and for other species (see references in Brown and Brown, 1988 b). Eggs that were marked in some nests appeared in other nests well after incubation had started, and they hatched at the same time as the rest of the host's clutch, indicating that they must have been partly incubated elsewhere (Brown and Brown, 1988 b; Davies, 1988). White-fronted Bee-eaters 'dump' preferentially into nests at the right breeding stage, i.e. during laying, so that the 'dumped' eggs hatch at the same time as the host eggs (Emlen and Wrege, 1986; see also Hamilton and Orians, 1965). In Starlings, eggs are 'dumped' later in the day than the usual early morning laying period, to avoid the hosts in the nest, and parasitic females lay eggs very quickly thus avoiding detection by the host (see review by Davies, 1988). The female may remove one or more of the host's eggs when dumping her own (Pinxten *et al*, 1991 a; Lombardo *et al*, 1989; Brown and Brown, 1988 b; Davies, 1988; Emlen and Wrege, 1986). Emlen and Wrege (1986) observed that parasitic female White-fronted Bee-eaters typically surveyed prospective host nests and tested host defences prior to parasitising them.

6.1.4 Coloniality and intraspecific brood parasitism

Blue-throated Bee-eaters usually nest in colonies. Colonial nestling provides an opportunity for all forms of IBP: if many birds breed together more or less synchronously, fertile females and active nests are available at high concentration and are a predictable resource for potential intraspecific brood parasites (Morton *et al*, 1990; Birkhead *et al*, 1987; Møller, 1987f). The probability of becoming a victim of conspecific 'egg dumping' (intraspecific nest parasitism, INP) may be greater in colonies (Rohwer and Freeman, 1989; Shields *et al*, 1988), for instance because prospective egg 'dumpers' are less conspicuous (Hamilton and Orians, 1965). Similarly, in species where the mating system is essentially monogamous, the proportion of individuals involved in extra-pair copulations (EPCs) is about ten times higher if they are colonial (Birkhead and Møller, 1992). IBP can significantly increase the breeding success of particular individuals, such as older males who may father more offspring through extra pair fertilizations (EPFs). For example Morton *et al* (1990) suspect that in Purple Martins, coloniality may have evolved because older males have induced younger birds to breed in nearby nest cavities to increased their own opportunity to cuckold these younger males.

EP males are often breeders at the same colony. In White-fronted Bee-eaters for instance, pair-males mate-guard their females at the colony and also seek EPCs there (Emlen and Wrege 1986). Females may avoid EPFs by synchronous breeding, which tends to impose monogamy on the males of the colony (Westneat *et al*, 1990; Birkhead and Biggins, 1987) because it affects the operational sex ratio, i.e. the number of females potentially available for fertilization to each male (Birkhead and Møller, 1992; Emlen and Oring, 1977).

6.1.5 Genetic evidence of IBP: DNA fingerprinting

An investigation of the mating system requires genetic evidence for extra pair parentage, to assess the true reproductive success of individuals. Originally, evidence for mixed mating strategies and IBP came from heritable variation of such morphological characters as plumage (Lank *et al*, 1989; Birkhead *et al*, 1988) and tarsus length (Gephardt-Henrich and Nager, 1991; Norris and Blakey, 1989; Møller, 1987 b; Alatalo *et al*, 1984), and later from electrophoretic evidence (Petter *et al*, 1990; Price *et al*, 1989; Sherman and Morton, 1988; Brown and Brown, 1988; Mumme *et al*, 1987; Wrege and Emlen, 1987; Westneat, 1987). Electrophoretic isozyme patterns can be influenced by age or the treatment of the gel, however, so that the outcome for the same individual can be different (Romagnam *et al*, 1989). Furthermore, this method can only eliminate, but not positively confirm, parentage and thus may give an underestimate of IBP (Westneat, 1990 and 1987). Evans (1988) could confirm incidences of INP with biochemical means only in exceptional circumstances, namely where the genotype of the extra-pair parent was very rare. Brown and Brown (1988) suspect that their estimate of 6% of nests being parasitized in the Cliff Swallows is likely to be an underestimate because they missed out most of the eggs that were laid directly into a different nest (rather than transferred after laying). They conclude that DNA fingerprinting was needed to assess parentage of nestlings more precisely (see also Birkhead and Møller, 1992; Westneat, 1990; Davies, 1988; Quinn *et al*, 1987). DNA fingerprints are somatically stable and they do not vary for each individual according to age or other influences (Jeffreys, 1985 b). If used with caution, DNA fingerprinting gives reliable evidence of relatedness between nestlings and their alleged parents.

DNA fingerprinting makes use of regions in the DNA which are highly variable. These 'minisatellites' of probably non-coding, selectively neutral DNA are inherited down the germ line following the same principle as highly variable phenotypic characters; except that here, the polymorphism considered is in the fragment lengths of the DNA after restriction. Each fragment is made of different numbers of repeats of a small 'core sequence' (10-30 base-pairs (bp) in size). Jeffreys *et al* (1985 a and b) reported the isolation and use of a 'probe' which was called 'multi-locus', because of it binds indiscriminantly to the similar core sequences of many different minisatellites. The following steps outline the principles of the use of this multi-locus probe to generate genetic 'fingerprints': take any tissue, blood or semen sample containing an individual's DNA (although some tissues yield better results than others), isolate the DNA and cut it into fragments with restriction enzymes. Electrophoresis on an agarose gel will separate DNA fragments by length, as they travel at different rates on the gel and so align in different 'bands'. The DNA is transferred and fixed onto a membrane ('Southern Blotting'). This is then washed with the probe which will hybridize only with fragments of the minisatellite DNA. The probe is radioactively labelled so that the positions of the hybridized fragments (bands), can be visualized on a photographic film (autoradiograph). Each individual's allele for each minisatellite will have slightly different positions, producing a unique 'fingerprint' for each individual. Depending on the number of minisatellite loci screened (i.e. depending on the probe used) and the polymorphism at each of these loci, the fingerprint of an individual, a human for example, is likely to be unique amongst $4x10^{-30}$ non-relatives (Jeffreys, 1987). Apart from genetically identical twins, screening many such minisatellites together thus gives a unique 'fingerprint' for each individual person, plant or animal.

DNA fingerprinting is used in paternity studies. Since minisatellite fragments are inherited in a Mendelian fashion (Wetton and Parkin, 1991), roughly half of an offspring's bands are expected to match with the fingerprint of each of the genetic parents. Band sharing between an offspring and both parents should be complete, i.e. mismatches of nestling bands should occur only occasionally due to mutations. An unexpectedly high level of nestling bands that do not have a match from either putative parent indicates that the nestling is not the genetic offspring of one or both putative parents. If band sharing of such a nestling is high with one parent, but low with the other, it is probably either an extra pair offspring (EPO) and has a different father, or it has a different mother who 'dumped' the egg into the nest of the father ('quasi' parasitism). If a nestling with mismatching bands shares few or no bands with either putative parent, it is probably a 'dumped' chick. It is thus possible with DNA fingerprinting to distinguish between dumped, EPO and 'quasi' parasitized offspring (e.g. Pinxten *et al*, 1993; Birkhead *et al*, 1990; Westneat, 1990; Brookfield, 1989; Wells, 1988; Quinn *et al*, 1987).

Two methods have been commonly used to estimate relatedness of nestlings and putative parents with band sharing analysis. If large families are available, a linkage (segregation) analysis of the bands can be used to determine the proportion of scorable bands which are linked or allelic (i.e. not inherited independently). From this proportion, the probability of bands shared by related and unrelated individuals can be calculated (Birkhead *et al*, 1990). Alternatively, it is possible to estimate the base level of variation between unrelated individuals and the distribution of its frequencies, and to separate this from the frequency distribution of band sharing between fully related individuals, in which case it is not necessary to do a segregation analysis (Hunter *et al*, 1992; Westneat, 1990). Barret and Pemberton (1992) argue that linkage is only a problem amongst inbred populations or when there are too few scorable bands. If the 'base level' of band sharing between non-relatives is distinct from that of close relatives, then non-relatives can be distinguished from full relatives quite easily, and even second-order relatives can sometimes be classified (Jones *et al*, 1991). In general, however, multi-locus DNA fingerprinting does not lend itself to discrimination between first-, second- or third-degree relatives (Lewin, 1989 a; Lynch, 1988).

Exclusion of parentage by band mismatching and assignment of parentage by band sharing may be expressed as models of relatedness between a nestling and its putative parents as follows. Nestling is:

1. fully related to both adults: the nestling has no unexplained bands;
2. fully related to the female, not to male (EPO): half of nestling bands are unexplained;

3. fully related to the male, not to the female ('quasi' parasitism): again, half of nestling bands are unexplained;
4. not related to either putative parent (INP by non-relative): all nestling bands are unexplained.

6.1.6 Summary of aims

In this chapter, I document mixed reproductive strategies in Blue-throated Bee-eaters. Firstly, I investigate the extent of IBP and the level of the alternative strategies EPF, INP and 'quasi' parasitism, using DNA fingerprinting. Secondly, I examine host defence behaviour against INP by experimentally dumping eggs into nests of Blue-throated Bee-eaters at various stages during and after laying. To assist readability, the two aspects investigated are reported separately, and consequently each have their own methods and results sections.

6.2 Intraspecific Brood Parasitism examined by DNA fingerprinting

6.2.1 Methods

Blood collection

Avian blood has nucleated erythrocytes, so DNA for avian fingerprints is normally readily extracted in sufficient quantities from whole blood. Accordingly, blood samples were taken with a 1mm diameter capillary tube (about 50 µl volume) from an incision made either into a blood vessel in the leg or the wing of the live bird and directly transferred into either dry ice (before storing at -70°C) in 1989, Los Alamos Buffer (in 1990; Appendix 6) or absolute ethanol (in 1991). In those instances where the bird was recaptured one or two days after having been bled, the incision had healed completely. In a few cases, moribund 4th or 5th hatched nestlings which were about to die were killed with a cut across the neck and the blood collected with capillary tubes. For each bird I tried to collect at least 2-4 capillary tubes of blood. Nestlings which had recently died in the nest were dissected in the field and their lungs, heart or liver stored in absolute ethanol (1991 only).

Each sample carried a unique 'tube number', the date, the ring number (and chick number) written twice, the nest-id (nest number and year) and, for some adults, the wing tag (as a 4th 'fail-safe' check). In 1989, the capillary tubes were stored in labelled non-opening screw-top containers, or (when this laboratory equipment ran out) in pencil-lead cases which closed equally safely and had a protected label. In 1990 and 1991, Eppendorf tubess were labelled directly with markerpen in the field. In 1991, each sample was individually wrapped later with cellophane and a sticky label attached and marked with pencil. In about 20 samples of 1991, where surplus ethanol washed off too much of the label, so that these samples had to be discarded. Any label could be double-checked, as the tube numbers and amount of blood taken for each individual was recorded with the individual's capture data for that date.

The blood samples for each family were stored together, separate from other samples, in small plastic bags, or in separate containers, making an accidental mixing of individuals across families unlikely, except possibly for families run on the same gel. When transferring the information for DNA extraction, *all* of the information on the tubes was transferred into the laboratory record book and each sample was then given a unique processing number (e.g. E1 to E12 or G1 to G12) which was also noted. Inconsistencies can be revealed through double checking at this stage as well. In my laboratory, the only error that occurred of which we are aware was one case of loading the same individual twice into two different lanes on the gel. For non-Bee-eater samples, Carole Campbell (CC; pers comm) reported one case where two repeat blood samples from the same nestling had been labelled as coming from two different sibs. Such errors are easily dealt with and have no effect on the interpretation of results.

DNA extraction

Washing

About 60µl of whole blood was removed with a sterile spatula or pipette from its storage medium and added to 1ml of 1 x SET buffer (0.15M NaCl, 0.05M Tris, 1mM EDTA, pH 8.0, sterile) to 'wash': After gentle mixing on a turntable (15 rpm), the blood was precipitated by a centrifuge pulse (top speed, at 14000 rpm, for about 20 seconds), the first wash of SET carefully poured or pipetted off, exchanged for a second 1 ml of 1 x SET, mixed on the turntable for 30 minutes, pulsed down and the SET poured off as before. The washed blood was re-suspended in 400µl of 1 x SET. If the blood was clotted (mostly blood stored in ethanol), a sterile spatula was used to homogenize the blood. Organs stored in ethanol were placed into a mortar with liquid nitrogen and ground to powder. About 100µg was added to 400µl SET and DNA extraction commenced as for blood samples.

Lysis and removal of protein

To the 60µl whole blood (or 100µg ground tissue) in 400 µl SET buffer was added, 10µl of 25% weight per volume (w/v) sodium dodecyl sulphate (SDS) and 15µl of proteinase K (10mgml^{-1} at -20°C) and the samples left overnight in a waterbath at 55°C. If the blood had not dissolved completely at this stage, the sample was mixed by occasionally shaking or flicking the tube during the first few hours.

The samples were washed 2-3 times in phenol which binds the protein and other impurities. The phenol was made up from 50ml solid phenol, 75ml 1M Tris (60.55g Tris base, about 21ml concentrated HCl to get pH 8.0) and about 0.1% 8-hydroxyquinoline to pH 8.0, shaken and left to separate into an aqueous layer on top and the organic phenol at the bottom. About 150µl of TE (10mM Tris, 1mM EDTA, pH 8.0) were added. After adding 500µl of phenol to each sample, they were mixed on the turntable for 30 minutes, centrifuged for 10 minutes at 14,000 rpm and the aqueous layer containing the DNA pipetted into fresh Eppendorf tubes using partly cut-off, sterile pipette tips. Here it is important not to transfer any interface but to take up as much of the DNA solution as possible. If the sample volume fell below 300µl, more TE was added. This phenol extraction was repeated once or twice, until the samples were clear and no protein was left at the interface. Then two phenol/ chloroform/ isoamyl alcohol (24:23:1 v/v) extractions followed (same volume was added, but centrifuging only for 5 minutes), finishing with one extraction in pure chloroform to remove all traces of phenol from the DNA.

Precipitation of DNA and storage

After transferring the DNA (top layer as before) from the chloroform (spun into the bottom layer) into a fresh Eppendorf, twice the volume of absolute ethanol, stored at -20°C, was added (plus, for samples of blood stored originally in ethanol, 10% v/v of 3M sodium acetate), the mixture left on the turntable for about 10 minutes, deepfrozen overnight and centrifuged for 10 minutes after which a pellet of pure DNA had formed at the bottom. This pellet was opaque to white and was retained when the ethanol was poured or pipetted off. Now 750µl of ethanol (70%, at -20°C) was added, mixed on the turntable for 10 minutes and poured or pipetted off. The pellet was dried of excess alcohol by warming the open Eppendorf beneath a lamp for up to half a day. The pellet was suspended in 150µl TE (less if the pellet was particularly tiny), placed into a waterbath (55°C) overnight and stored at 4°C.

DNA restriction

Blood collection and much of the DNA extraction was done by the author. All of the further steps were carried out by Carole Campbell in the local laboratory with methodology used by

Roy Carter at the Department of Genetics, Queen Medical Centre, Nottingham (Carter, 1989; Carter *et al*, 1989). The fingerprint of a trial family was prepared by Helen Riley in the Nottingham laboratory (see Riley, 1992). The DNA yield varied greatly between samples and was determined by fluorometer assay as far as possible. For the trial family, AluI was used; although for all other fingerprints, HaeIII was used. Both seemed suitable for the Bee-eater fingerprints, giving a sufficient number of bands. Ten units of enzyme were incubated with about 20µl DNA in TE overnight at 37°C with 4mM spermidine trichloride to facilitate the binding reaction. A small 'mini-gel' was used to assess whether the restriction had been completed: 2µl of the solution was stained with 0.5gml^{-1} ethidium bromide and electrophoresed in a 10cm agarose gel (see below) at 80V for one hour. The pattern of the stained DNA smear was visually assessed under UV light. The restriction reaction was stopped and dyed with 6 µg per 40 µl 2 x bromophenol blue ('loading buffer' 0.04M EDTA, 4% ficoll, 0.05% BPB, 0.05% xylene cyanol w/v).

Electrophoresis

Agarose gels were made by dissolving 0.8% w/v LE agarose into 350ml 1 x TAE buffer (1 x TAE, 0.04M Tris Acetate, 1mM EDTA, pH 8.0) by microwave, cooling it to 55°C and pouring it into a 22x20cm gel mould with 16 8x2mm loading wells. The gel was then placed into an electrophoresis tank with 2.5l of 1 x TAE buffer. Samples of 6µg of DNA with stain were pipetted into the central loading wells and molecular weight markers consisting of bacteriophage λ DNA digested with HindIII, were loaded into the outermost wells, all near the cathode of the gel. DNA is negatively charged and migrates towards the anode. The samples were left to equilibrate for 10 minutes before commencing electrophoresis at 30V for 40hrs. This time and voltage gave the best resolution for Blue-throated Bee-eater DNA (alternatively 40V could have been applied for 30hrs) without losing too many of the smaller fragments from the gel.

Southern Blotting

To prepare the DNA for transfer onto zetaprobe GT filter, the gel was soaked first in 0.2M hydrochloric acid for 20 minutes to break up the larger DNA fragment for transfer, followed by a 35 minute soak in 0.5M NaOH, 1.5M NaCl to separate the double-stranded DNA into single strands. The gel was neutralized by immersion in 3M NaCl, 0.5M Tris, pH 8.0 for 45 minutes.

For blotting onto the zetaprobe filter, the gel was turned upside down onto a wick, placing the filter membrane on top of the gel, i.e. on its original underside. The gel was immersed in 20 x SSC (3M NaCl, 0.3M sodium citrate). On top of the gel was placed a stack of paper towels weighed down with a glass plate. The solution was drawn through the filter by the absorbent filter paper, carrying the DNA strands which are deposited onto the filter membrane. Gels were left to blot overnight, the filters were rinsed in 2 x SSC and then first air-dried for 30 minutes followed by a bake at 80°C for 2 hours between 3MM paper for fixing.

Preparation of the probe and probing

The DNA fixed on the filter originates from the complete genome. Only the tandem repeats of hypervariable DNA of non-coding minisatellites are of interest here, and the probe recognizes only the core sequence of these tandem repeats but not DNA of other origin. The core sequence of the tandem repeats of all satellites are similar (but not identical), so that under the right conditions of low stringency the probe will bind DNA from satellites of many different loci. We used the human probe DNA 33.6 or 33.15 (Jeffrey *et al*, 1985 a and b), which is available commercially already inserted into plasmid DNA pSPT19 (see Carter, 1989; Carter *et al*, 1989). Probes of RNA have proved to provide clearer fingerprints than DNA probes (Carter *et al*, 1989) and a RNA probe was therefore used here. This was produced by making a stock from a drop of streaked out bacteria, pelleting the cells, isolating the DNA similar to above, re-suspending and then radioactively labelling with P^{32} during the transcription reaction into RNA. Nucleotides, one type of which contained the radioactive label, were added to the probe RNA together with SP6 of T7 RNA polymerase. When a geiger counter indicated 80% incorporation, the transcription reaction was stopped by adding cold TE.

The filters were pre-hybridized with blocking agents to avoid non-specific binding of the probe. The filters were immersed in 1 x SSC, 1% SDS, 1% blotto (1% 'Marvel' powdered milk, 0.02% sodium azide w/v) in a container in a shaking waterbath at 65°C for 8 hours. To this, 200µl of the solution containing the RNA probe was added and left overnight. Then the filters were washed 4 times in 1 x SSC, 0.1% SDS for about 30 minutes each.

Autoradiograph: the fingerprint

The filters were wrapped in cellophane and placed next to a pre-flashed Fuji RX X-Ray film with one intensifying screen into a cassette. The X-ray film was left to absorb the beta-radiation from the filter for between 6 hrs and 14 days at -70°C (faster) or for 3-5 days at room temperature (slower), depending on the amount of radioactivity on the filter.

Scoring the fingerprint

An example of a fingerprint of 3 families is given in Fig. 6.1. The marker-lanes have bands of known fragment sizes that range from 2.0 to 23.1 kb. The autoradiograph was 'scored' with the help of illumination from a 'light-box' to find the relative positions of successive bands and whether they are shared or unique. Scoring started at the largest fragments and stopped when the bands became too blurred and overlapped. In this study, bands below 2.5kb were not scored. Occasionally bands of different intensity overlapped in position. In these cases only the band of stronger intensity was scored, since the less intense band could be hidden by the stronger band.

Band sharing coefficient (BSC)

For each pair of individuals, A and B, scored on the same fingerprint, the number of bands shared by A and B (N_{AB}) was divided by the total number of bands for each individual, N_A and N_B, to give a band sharing coefficient (BSC) between 0.000 and 1.000:

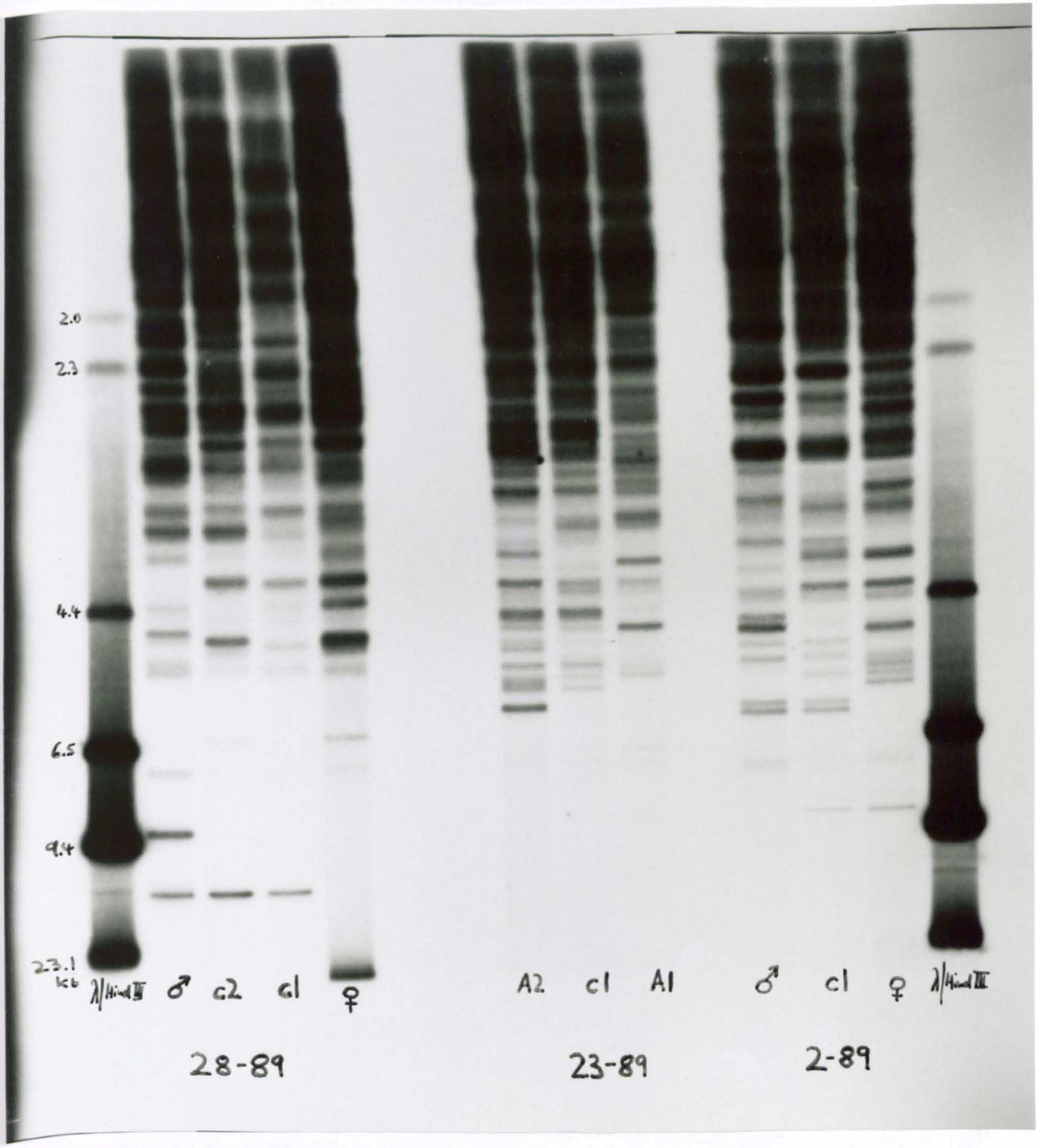


Figure 6.1: Fingerprints of three families with no Intraspecific brood Parasitism (IBP). The putative parents are on the outside, the nestlings in the middle lanes; each family is printed together to fasciliate scoring. C=chick, nn-89 = brood number and year.

$$BSC=\frac{2N_{AB}}{N_A \times N_B} \qquad (6.1)$$

The BSC, which was called 'x' by Jeffreys *et al* (1989 a), was also used for example by Wetton *et al,* (1987).

6.2.2 Results

Variability of fingerprints of unrelated birds

Ten individuals of mostly unknown sex were randomly chosen from each of the two colonies (3 each from SB89 and SB90 and 4 from NH91) and run together on a gel. The proportion of bands shared was scored and calculated for all two-by-two combinations of individuals from the two different colonies. Since there was evidence for no dispersal between Sungei Buloh and Nam Heng, it was assumed that the birds in one colony are not related to birds from the other. This level of band sharing between individuals from different colonies (SB and NH) can therefore be used to estimate a base level of band sharing between individuals, which is *not* due to inherited fragments.

The average band sharing coefficient for unrelated birds from different colonies is 0.165 (Fig. 6.2 a). If each band had represented a rare, independently inherited allele, we would expect zero band sharing between unrelated birds. The higher observed base level of band sharing might be explained by inbreeding. This is not likely, however, because the two colonies are about 400 km apart. Secondly, some bands might be linked, or, thirdly, the area of genome investigated is less than 100% variable amongst non-relatives. Fourthly, it is also possible that some bands have not migrated sufficiently and cannot be distinguished from each other, so that different bands were incorrectly scored as identical. This is particularly likely for smaller fragments.

The range of band sharing between birds from different colonies is 0.043 to 0.302. Standard deviations were computed for the arcsine transformation of the proportion of bands shared,

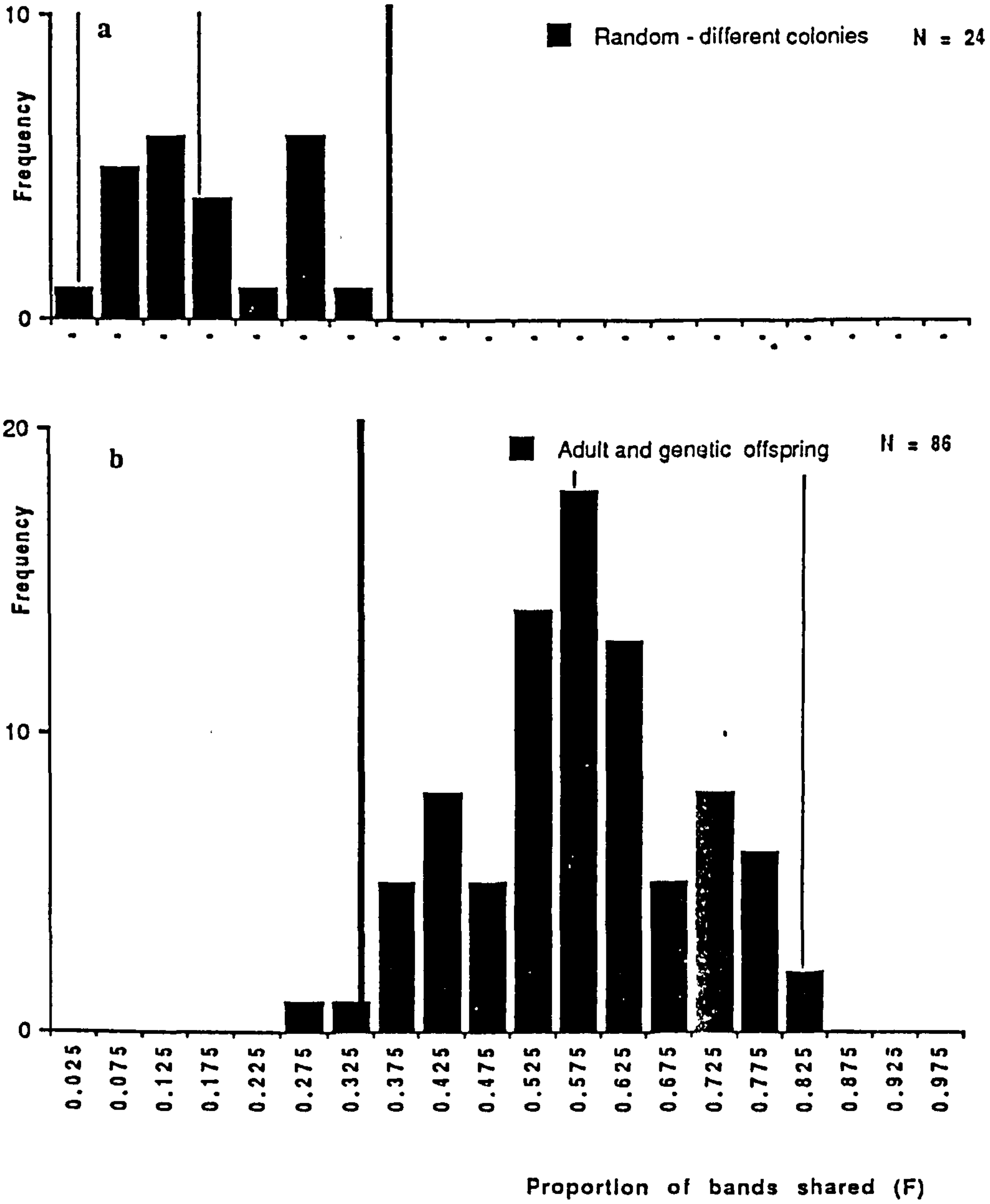


Figure 6.2: Distribution of the band sharing coeficient BSC for unrelated (a) and fully related (b) birds. Including 95% confidence intervals: the upper confidence limit for unrelated birds (BSC=0.362) overlaps slightly with the lower limit for relatives (BSC=0.348).

and confidence intervals re-transformed to original percentages (which is why they are asymmetrical). The 95% confidence interval for the proportion of bands shared by any two unrelated birds is 0.035 to 0.362. If two birds of unknown relatedness share more bands, they cannot be assumed to be unrelated; if they share 0.362 or fewer bands, they are unrelated in all but 5% of cases.

Band sharing between first degree relatives

Nestlings were fingerprinted alongside their putative parents. Only those families with more than 10 distinct bands per individual were used. In total, 63 nestlings were scored from 36 nests between 1989 and 1991, at NH and SB. For 43 chicks, all bands were derived from either parent, with 0 or 1 band unexplained (allowing for 1 mutation, which is conservative; see below). These are therefore assumed to be the full, genetic offspring of the pair (first degree relatives of each putative parent, for which the coefficient of relatedness $r = 0.5$), and can be used to calculate band sharing coefficients between full relatives. The mean band sharing coefficient between a nestling and a true genetic parent was 0.571 ranging from 0.290 to 0.800 (Fig. 6.2 b). The 95% confidence interval of band sharing between any genetic parent and its offspring was 0.348 to 0.834. The confidence intervals of related and unrelated birds overlapped slightly. Therefore, two birds of unknown relatedness with F between 0.348 and 0.362 could not be assigned, but those with band sharing of more than 0.362 were in all probability first degree relatives.

Relatedness within the colony

Colony-years in general

The ten random adults from the 'between-colony' fingerprints were from three different colony-years, SB89 (3 birds), SB90 (3) and NH91 (4). These were also scored amongst each-other (3 plus 3 plus 6 pairwise comparisons respectively). An additional 8 pairwise comparisons came from unpaired adults of families of the same colony-year which were printed on the same gel. In Fig. 6.3 b, the distribution of the band sharing coefficient F within colony-years is shown, with a slightly lower mean than for birds from different colonies (Fig.

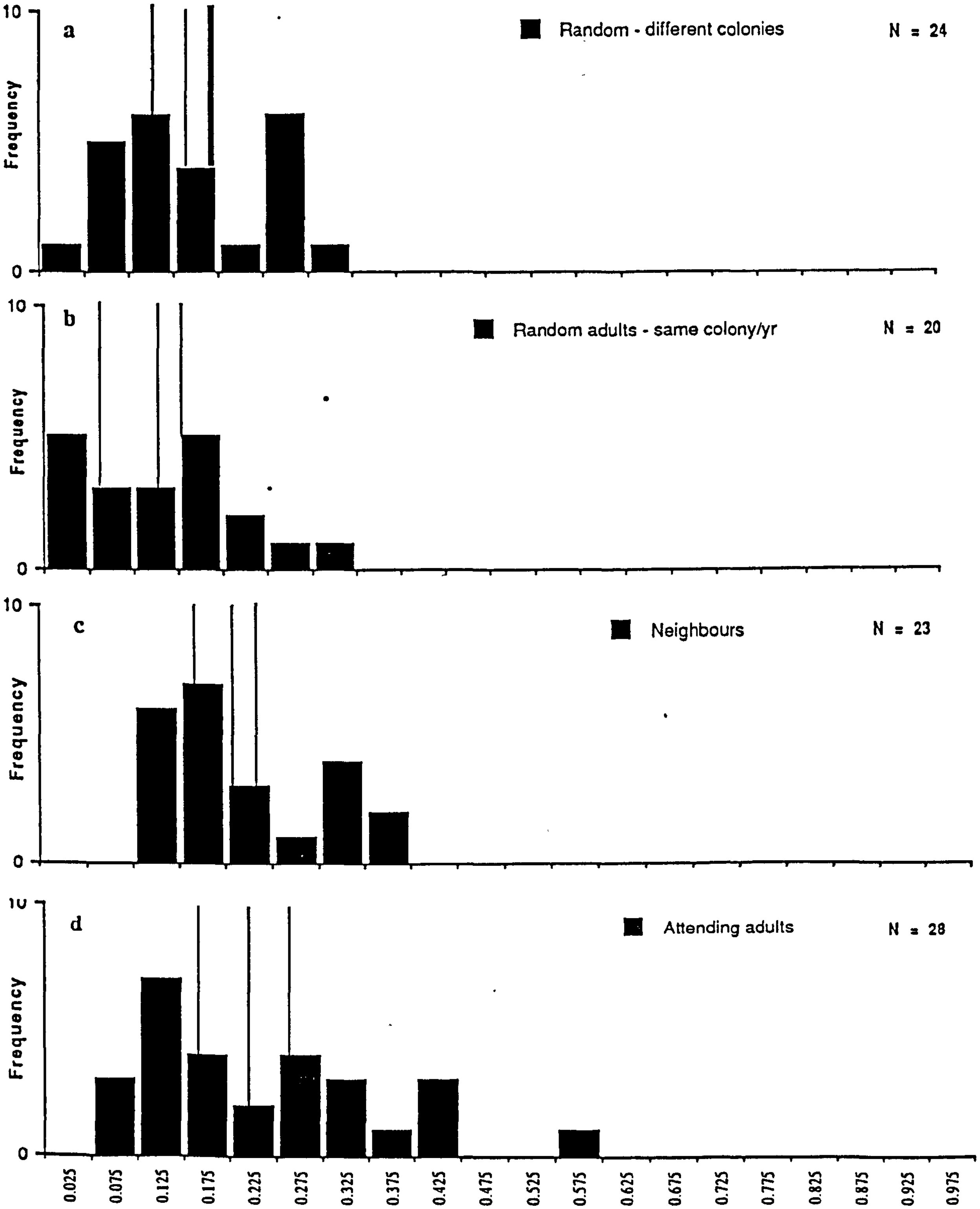


Figure 6.3: Distribution of the band sharing coefficient BSC amongst non-relatives (a), birds from the same colony (b), birds within the same sub-colony (c) and pair members (d). Including the mean (middle line) and 95% confidence intervals of the mean)

6.3 a) but with largely overlapping 95% confidence intervals of the mean. An ANOVA of the transformed band sharing coefficients revealed no significant difference between colony-years ($F = 3.611$, $0.05 < p < 0.10$).

Relatedness of neighbours

To test if related birds nest close together, adults from two groups of neighbouring nests in the NH colony were DNA fingerprinted on the same gel. The nests in each neighbour group were particularly close but discrete from other clumps or the main colony (Fig. 6.4). Even if related birds did nest close together, only one partner would have been related to the extended family, so that at most only half of the birds were expected to share more bands than unrelated birds. Bands were compared pairwise, each bird with each of the other birds in the neighbour group. Although slightly higher in the mean band sharing level, band sharing between neighbour was not significantly different from that of unrelated birds at different colonies (ANOVA on transformed data, $F= 3.371$, $df=1$, $0.05 < p < 0.10$; Fig. 6.3 a and c). This was possibly because DNA was not available for birds from all nests within the same group, or from both partners at each nest, and my sample could by chance have included mostly birds that were not related, i.e. partners of the related birds. Compared to random adults within a colony year, however, neighbours were found to share more bands (ANOVA on transformed data, $F=10.221$, $df=1$, $p < 0.005$). Most neighbours shared about BSC = 0.175 bands (within the 95% confidence limits for unrelated birds), but a second peak appeared around 0.325 (Fig. 6.3 c), which was well out of the 95% confidence limits for the mean of unrelated birds. This would have been expected if only one pair member had been nesting close to its relatives. In the second neighbour group (nest 115- to 117-91), one bird from nest 117 shared a smaller number of bands (band sharing coefficient BSC = 0.103) with a bird from each of two neighbouring nests, but the birds from 115 and 116 shared several bands (BSC = 0.364) and were probably related.

Pairs of attending adults

The mean BSC for pairs of attending adults caught at the same nest was 0.232 (N=28 pairs, excluding those with adults that had less than 10 scorable bands), ranging from 0.065 to 0.552

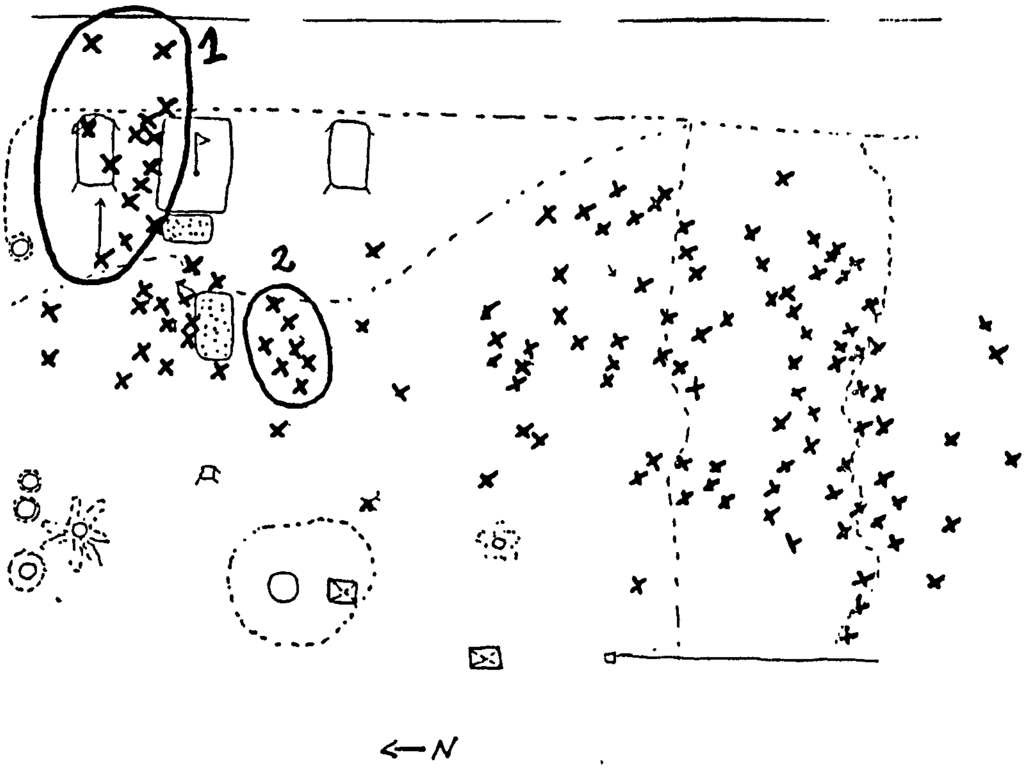


Figure 6.4: The main colony of NH91 with neighbour groups 1 and 2 to indicate spacing between nests and general density. Scale = 1:200, or 0.5cm = 1m. X = nest.

(see Fig. 6.3 d). The 95% confident limits for the mean was from 0.171 to 0.265. This was significantly higher than for unrelated birds (F = 4.639, df=1, $p < 0.05$).

Relatives sometimes shared burrows with a breeding pair, and on one morning, three birds were caught at the same nest and fingerprinted. T4G was classified as a gravid female (above 40g), and 29W was classed independently by his size as a male. T4G and 29W shared BSC = 0.333 bands. The two were caught with a third, slightly smaller bird (94O), with which T4R shared BSC = 0.571 bands but with 29W only 0.286. It seems therefore that 94O was a first-order relative of the female pair member. This finding could not be confirmed by observation or comparison of fingerprints to nestlings produced in that nest, however, because the birds were not caught or observed again and did not breed in the same burrow. To test if the mean BSC for attending adults was inflated by cases which might have been relatives rather than members of a breeding pair, I looked at the number of mis-matches in their alleged offspring. Apart from one exception, all adults caught at the same nest with BSCs which fell within the confidence interval of full relatives (BSC of above 0.362) had at least one nestling with less than 2 unexplained bands (classed as legitimate offspring, see 6.2.2.4), however, which means that these pairs were indeed mated pairs and not a parent and its relative. The high band sharing between pair members was therefore more likely to have been due to breeding pairs being related than because relatives which share burrows were mistaken for the breeding pair. Inbreeding could be a result of Bee-eater dispersal, if relatives nest close together (see above) and share the same social group.

Mixed reproductive strategies

Nestlings with mis-matches

The principal criterion for identification of an illegitimate offspring is the number of mis-matching bands. Any nestling band that could not be traced to either of the resident pair of adults (mis-match) must either have been a mutation or have originated from the true genetic parents. Fig. 6.5 is a frequency plot of the number of mis-matches for all nestlings. The frequency distribution of mis-matches due to mutations should follow a Poisson distribution, whereas the distribution is expected to depart from Poisson if mis-matches due to genetic differences are included. The distribution clearly followed a Poisson distribution when up to 3 mis-matches were considered ($p > 0.20$) but departed from Poisson significantly when nestlings with 5 bands were included ($p < 0.005$), nestlings with up to 4 mis-matches were intermediate, and nearly differed significantly from a Poisson distribution ($p < 0.070$; Table 6.1). According to this criterion, up to 3 mis-matching bands in a nestling were mutations, whereas 5 mis-matches or more indicated an illegitimate offspring. Mismatches alone, however, provided inconclusive evidence for cases of 4 mis-matches.

To classify nestlings with 4 mis-matches, a second criterion was used to determine whether they were legitimate offspring. For this, the BSC of the nestlings with both their putative parents was used (Fig. 6.6). Out of 50 nestlings with 0-3 mis-matching bands, 48 fell within the 95% confidence limits of the BSC for full relatives for both parents. Two out of the 50 nestlings with 0-3 mis-matches (4%) were just outside the lower confidence limit for relatives for one parent (marked with subscript 1 and 2 on Fig. 6.6), which was within the 5% of BSCs expected to fall outside the 95% confident limits by chance.

If nestlings with 4 mis-matches were fully legitimate, their BSCs with either parent would not be expected to fall outwith the 99% confidence limit of BSCs for relatives, the lower limit of which was calculated as 0.289, by chance. Following this concept, both of the chicks (Chick 4 in nest 156-91 and Chick 5 in nest 101-91), were unrelated to at least one of their putative parents (Table 6.2; subscript 4 and 5 in Fig. 6.6). In line with the second criterion therefore, it is concluded that the nestlings with 4 mis-matches should be considered as illegitimate. Out of 61 nestlings from 35 broods, 11 nestlings (18%) from 8 broods (23%) were therefore not the legitimate offspring of one or both of their putative parents.

The 11 nestlings classified as illegitimate were assigned to their putative parents using BSCs (Table 6.2). Of the 11 illegitimate chicks, 4 (36%) shared less bands than the lower confidence limit for relatives (BSC = 0.348) with both putative parents, and were therefore classed as unrelated to their putative parents (see Table 6.2 and bottom left panel in Fig. 6.6). Six of the 11 chicks (56%) shared more than BSC = 0.362 bands with one of the adults and less than 0.348 of bands with the other (Table 6.2), so that most probably one adult was the parent and the other was not (see top left panel in Fig. 6.6). Of the putative parents of these

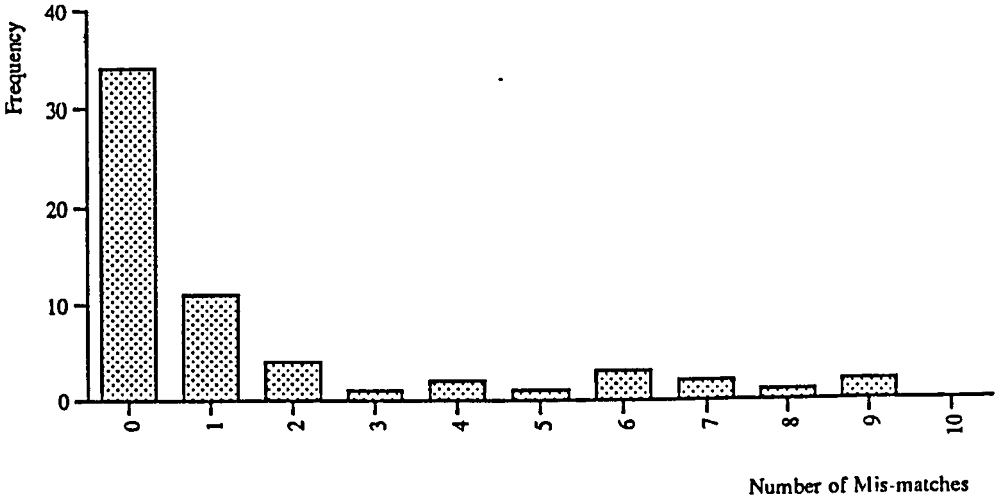


Figure 6.5: Observed frequency distribution of band mis-matches of nestlings with putative parents

Table 6.1: First criterion of allocating illegitimate offspring: observed frequency distribution of band mis-matches of nestlings with their putative parents as compared to expected frequencies under Poisson distribution. Zero to 2, 0-3, 0-4, 0-5 and 0-6 mis-matches were included progressively to find the exact cut-off point which changed the distribution from Poisson to non-random. The tails of the expected frequencies were pooled so that no expected frequency was below 1.0 (Cochran, 1954, in Zar, 1984). Because some expected frequencies were less than 5, however, χ^2 was calculated with Yates' Correction. Degrees of freedom (df) were calculated as number of categories of expected frequencies - 2 (Zar, 1984); comparison of categories 0-1 mis-matches were therefore not possible. Frequency distributions with up to 3 mis-matches did not differ significantly from a Poisson distribution, but when 5 mis-matches were considered, the observed distribution changed clearly from Poisson to non-random (differed significantly from Poisson). This indicated that up to 3 mismatches were expected by chance due to mutations, but more than 5 indicated an illegitimate offspring. Four mis-matching nestling bands were intermediate, and these nestlings had to be classified with a second criterion (see text)

Number of mismatches	Observed* frequencies	Expected** frequencies (0-2)	(0-3)	(0-4)	(0-5)	(0-6)
0	34	33.50	32.23	29.23	27.39	21.74
1	11	12.99	14.18	16.86	18.08	20.37
2	4	2.52	3.58	4.86	5.97	9.73
3	1			1.05	1.56	3.91
4	2					
5	1					
6	3					
χ^2 (with Yates' correction)		0.858	1.241	5.034	11.909	13.896
df		1	1	2	2	2
p		>0.300	>0.200	<0.070	<0.005	0.001

* see Figure 6.5 for distribution

** expected frequencies were calculated as in Zar, 1984.

Table 6.2: Band sharing coefficients (BSC) and number of mis-matching bands for nestlings with more than 2 mis-matches.

Nest	Nestling number	number of mis-matches	BSC		Related to		Model[a]
			with F	with M	F (A1)	M (A2)	
30-89	3	7	0.240	0.167	No	No	D
192-91	1	9	0.235 <->[b]	0.270	No	No	D
156-91	4	4	0.345 <->	0.143	No	No	D
101-91	1	9	0.216 <->	0.242	No	No	D
25-89	1	7	0.270	0.438	No	Yes	R_M
20-89	1	6	0.000	0.364	No	Yes*	R_M
29-89	1	6	0.214	0.500	No	Yes	R_M
29-89	2	8	0.121	0.606	No	Yes	R_M
101-91	5	4	0.176 <->	0.400	No	Yes	R_{A1}
11-91	1	6	0.242 <->	0.571	No	Yes	R_{A1}
156-91	1	5	0.381 <->	0.537	Yes*	Yes	R_{A1}

[a] : Models: R = offspring of both putative parents, R_M or R_{A1} = Related fully only to the male or to one adults (A1), D = 'dumped': unrelated to either putative parent

[b] <->: attending adults are unsexed, so that BSC-values are interchangeable.

* : very close to upper 95% confident limit of non-relatives = 0.362. This nestling was most probably related only to one of its putative parents (see text).

6 chicks (two were nestlings of the same brood, 29-89, see Table 6.2), 2 pairs could not be sexed with at least 95% confidence (see Chapter 5) so that for the 2 corresponding nestlings I could not establish whether the extra-pair parent was the male or the female (in Fig. 6.6, these 2 nestlings were grouped together with the other 4 nestlings with sexed putative parents). All 4 nestlings with sexed putative parents had band sharing levels that identified them as fully related to the putative father but not the putative mother. One nestling (9%) of the 11 illegitimate fell outside the 95% confident intervals of BSCs for non-relatives with both putative parents (see subscript 3 on Fig. 6.6; chick 1 of brood 156-91, Table 6.2). It is conceivable that a single chick could have had BSCs outside the confidence limits for non-relatives by chance, although it was not strictly within the 5% expected. Since the BSC with one of the putative parents was nearly within the 95% confidence limit for relatives, this nestling was most likely the true offspring of one putative parent (unsexed) with a different partner.

Level of illegitimate offspring

Comparisons with chick-capture records showed that one of the nestlings classified as 'dumped' had wandered from another nest into nest 192-91 probably just after the true chick 1 of the brood had fledged (no blood sample was available for the assumed fledged chick 1 of 192-91). Nestlings were occasionally observed to leave their nest prior to fledging, presumably because their parents deserted. Where observed, such pre-fledging nestlings were mobbed by breeding adults and starved eventually.

The putative parents of brood 11-91 were both caught at a different nest together earlier in the season, but only the adult identified as the genetic parent was later caught at 11-91 (the two were unrelated, BSC = 0.243) and probably changed partners to produce the brood of 11-91; although no second bird was captured at 11-91 to confirm its true parentage.

Excluding these two nestlings, 9 illegitimate nestlings out of 59 (15%) were confirmed. Of these, 3 (5%) were not related to either putative parent, 4-6 (7-10%) to only the putative father but not mother and 0-2 (0-3%) to the putative mother but not father. Note that there was no confirmed case where the nestling was related only to the putative mother.

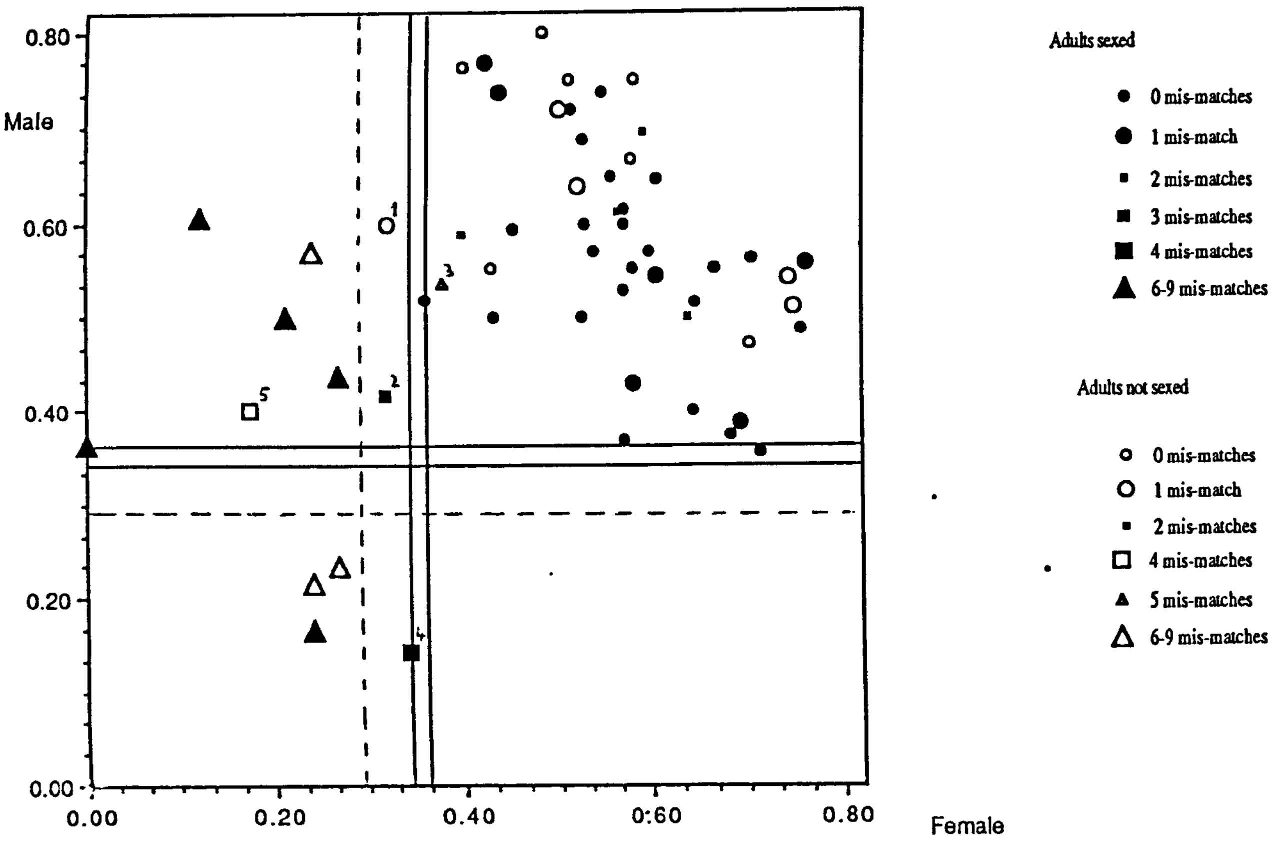


Figure 6.6: Band sharing coefficients (BSC) of all nestlings with both putative parents. Each point represents one nestling. A BSC of above 0.348 is expected between relatives (lower limit of 95% confidence interval, see text), wheras non-relatives share less than 0.362 bands (upper 95% confidemce limit). The 95% confidence intervals of non-relatives and full relatives overlap. The upper right-hand panel contains nestlings with few or no mis-matches and share many bands with both parents. These are the genetic offspring of both putative parents. The bottom left panel contains 'dumped' nestlings related to neither parent, nestlings in the bottom right corner are related fully to the female but not the male (EPO), and the top left corner represents 'quasi' parasitism. BSC between nestlings and putative parents which were not sexed (marked with open symbols) were assigned arbitrarily to males and females and could equally have been the other way around, so that some of these nestlings might have been placed in the bottom right corner, indicating an EPO. The lower limit of the 99% confidence interval of BSC for relatives was included with a dashed line (see text). Notes ^{1} - ^{5} are explained in the text.

Interpretation of the DNA-fingerprint results

Behavioural observations at nests with illegitimate nestlings

In order to interpret each type of illegitimate offspring correctly in terms of mixed reproductive strategies, behavioural observations were made at nests with illegitimate nestlings, which are summarized below (see Table 6.2 for brood numbers). These results demonstrate mostly the difficulty of interpreting results from fingerprints when behavioural observations are incomplete. Even if the birds were observed with relative consistency, behavioural observations of IBP may be absent.

Nests with nestlings illegitimate for the female

Only one nest with 'quasi' parasitism was at a sub-colony where behavioural observations were carried out regularly. The pair members at 29-89 both arrived early with wingtags intact, within two weeks of each-other. Their behaviour was typical for a cooperative pair (see Chapter 5): an early copulation was initiated by the female, they dug the burrow of nest 29-89 together, copulated during laying and the male fed the female during laying and incubation. Both incubated the clutch but the female was found dead in the net one morning after the chicks hatched, with the lowest score of condition for an adult during this study (see Chapter 2). The male raised two chicks until fledging age on his own. The only indication of visits by other birds around the onset of laying was by S6R, a non-breeder, about a week before the calculated onset of laying, and a brief displacement of another male by the pair male on the wire, in the presence of the pair female, during laying. The pair members spent a lot of time within sight of each-other during the early season, when the male was probably mate-guarding, and there was quite a lot of cooperation between the pair members, all of which are quite typical for monogamous pairs (Chapter 5). There was no behavioural indication of 'quasi' parasitism. This might still be expected perhaps if there is female-female competition so that 'quasi'-parasitic females 'dump sneakily'. Furthermore, behavioural observations were inevitably not continuous. In this section, I discuss a fingerprint of 29-89 with all available associates of the breeding pair and extra-pair birds seen at the nest (Fig. 6.7).

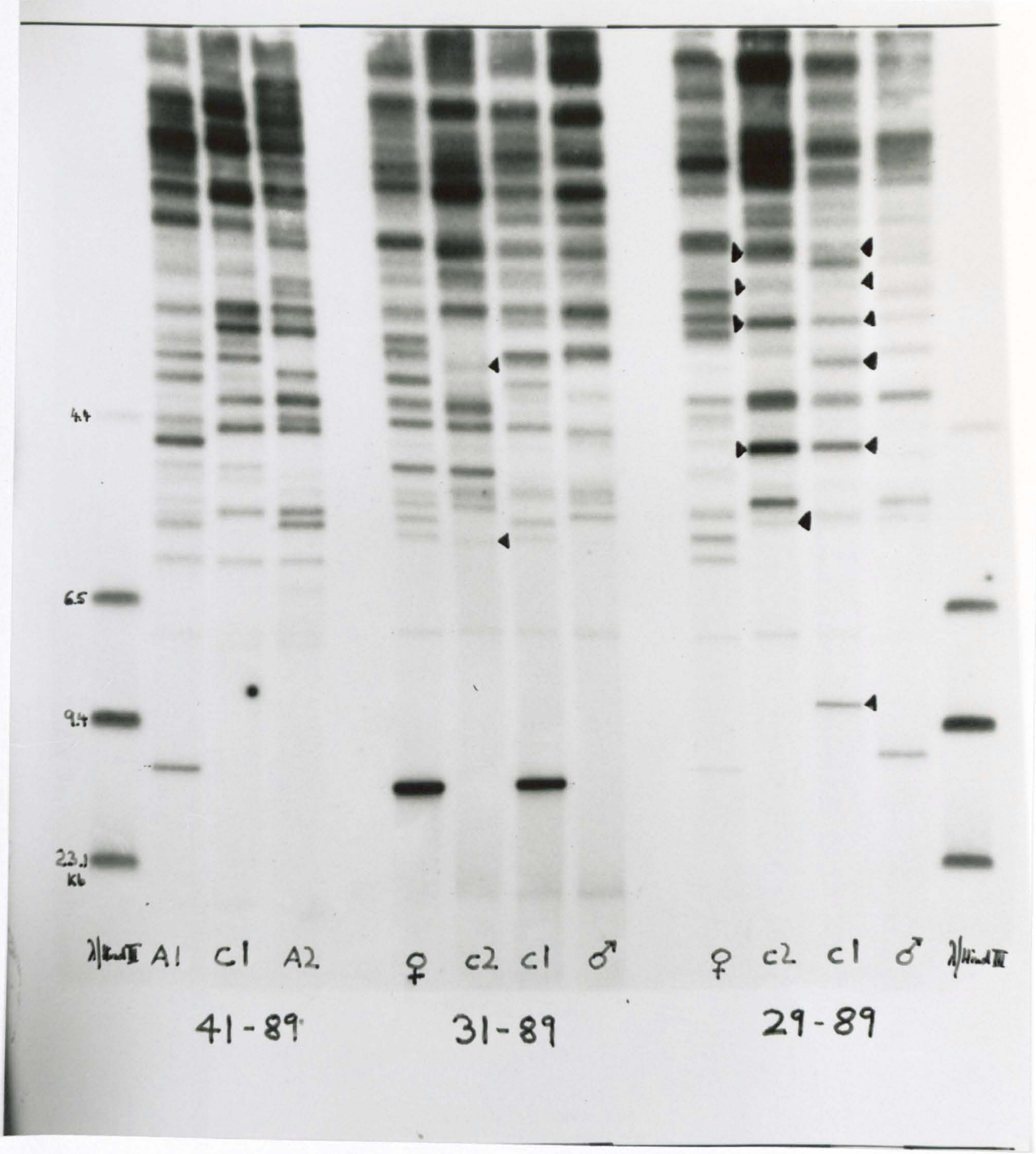


Figure 6.7: fingerprints of three families, with varying degree of mismatching of nestling bands. Mismatches are marked with solid triangles. Chick 2 (C2) of brood 31-91 is probably related: it shares bands with the male and the female, and the two mismatching bands are probably mutations; the two chicks of 29-89 are not related to the pair female. They share some of the extra bands but may have different mothers. Both nestlings share several bands with the pair male. (The band sharing is clearer on a 'light box'.) These are the most clear cases of apparent 'Quasi' parasitism occuring in a pair which cooperated throughout the early season before the pair female diedduring nestling feeding, probably from exhaustion.

Nests 25-89 and 30-89 were not located at the main colony in SB, so that observations of these pairs were haphazard. The female at 25-89 (AMO), a tagged return from previous seasons, was re-captured in the early provisioning phase together with an unrelated bird (66O; BSC=0.065) which probably deserted subsequently. AMO shared few bands with the chick but was seen twice to feed the brood. The male may have had another partner who laid her eggs, fertilized by him, into AMO's burrow. Although both birds had an orange tag which should both be equally conspicuous and easy to read, it is possible that AMO used a more conspicuous perch when visiting the colony. On the day calculated as the onset of laying, an unsexed breeder visited the burrow briefly but was not seen to enter. The female was not tagged until provisioning, so there were no reliable pair cooperation data during incubation. Both parents provisioned the offspring, but most observations were of the female.

Mate guarding in pairs with possible EPPs

For the two unsexed pairs which had nestlings with mis-matches, observations during the pre-laying and laying period were not available. Both pairs were first tagged in the provisioning phase.

INP by relatives

The most common type of illegitimate offspring was where the nestling is not related to the pair-female, which is commonly interpreted as 'quasi' parasitism (e.g. Birkhead *et al*, 1990). Since I have no behavioural evidence for 'quasi parasitism', however, alternative explanations should be considered. If quasi-parasitism was not the correct model, then an alternative explanation may have been that eggs were 'dumped' by close relatives of the male. These relatives may have nested nearby and may even have been allowed access to the nest.

Do males share more bands with each-other than females amongst neighbours?

To investigate whether males were more likely to have relatives in the colony than females, the proportion of bands shared was calculated for pairs ('dyads') of sexed adults first for birds from the same colony and year (but not the same nest) and then for birds in the same neighbour group (section 6.2.3). Band sharing in male-male dyads was compared to the band sharing in female-female dyads. Of the adults of SB89 which were printed and scored on the same gel either as putative parents of different families, or as associates or visitors to the nest (brood 29-89, see below), only four males and five females were sexed; all fingerprints of other colony-years and the within-colony random sample of adults (section 6.2.3) did not have sufficient numbers of sexed adults amongst them. Four male-male BSCs (0.516, 0.341, 0.143 and 0.121) were not significantly different from six female-female BSCs (0.400, 0.375, 0.148, 0.133, 0.125 and 0.000; Wilcoxon matched-pairs signed-rank test, $Z = -0.426$, $p > 0.60$). Of the neighbour groups, three of each males and females were sexed in group 1, sharing BSC = 0.339, 0.304 and 0.286 bands between males and BSC = 0.208, 0.182 and 0.154 bands between females. This was significantly different ($Z = -1.964$, $p < 0.05$). Males therefore did share more bands amongst each-other than did females in clusters of neighbouring nests within the colony but not across the whole colony. Although the samples were very small and from two different colonies, and may therefore not reflect a true relationship, these findings indicated firstly that males were more likely than females to have close relatives amongst neighbours in the colony and therefore that it was more likely that relatives of males rather than females 'dumped' eggs. Secondly, this raised the idea that neighbours 'dump' eggs in each-other's nests.

The identity of the genetic parents of the parasitized nestlings

Because identical bands migrate at different speeds on different gels, it is not possible to score bands across different fingerprints with multi-locus-probe fingerprinting, and to establish a 'library' or database of a large number of individuals within a colony, which could yield the true parents of nestlings with unexplained bands. For two broods with IBP, behavioral observations (interactions or associations and sightings of potential extra-pair females at the nest) were used to try to find the true parents of these nestlings and, if blood samples and sufficient DNA were available, these adults were fingerprinted with the family that they had associated with, on a second fingerprint. Incidentally, none of these visitors or associates was seen to feed the nestlings.

Brood 29-89

Behavioural evidence established that MXO and T3R were a breeding pair (see above). Both nestlings (C1 and C2) in brood 29-89 had more than 2 mis-matching bands (Fig. 6.7) and shared very few bands with the putative mother F-29 (MXO) but were classified as fully related to the putative father M-29 (T3R; see Table 6.3). No regular helper was observed, but both adults associated with other birds, and the burrow was inspected by other adults on occasion (which were often attacked and displaced by the resident pair). The family was reprinted with a haphazard sample of visitors to the nest and associates of adults. DNA fingerprints indicated none of the visitors and associates as the true mother of C1 or C2 (Table 6.4 a).

Brood 192-91

Chick 2 (C2) had only 1 mis-match and was probably their legitimate offspring. For chick 1 (C1), 9 bands were inherited from neither of the attending adults, and band sharing with both adults was as for non relatives. C1 and C2 were also not, or only distantly, related. These values were confirmed by ringing records which showed that the chick had probably entered the burrow from another brood (see above). It is still useful to attempt to find genetic parents who may have 'dumped' this nestling, if only to show that the original interpretation is likely to be correct. In Table 6.4 b, all BSC above the upper 95% confidence limit (0.362) for non-relatives are highlighted in bold typescript and are discussed here. Chick 2 (C2) was fully related to both attending adults, but also to two other adults, CBC and RPC, which themselves shared more bands with each-other than unrelated birds. Chick 1 (C1) had no close relative amongst any of the other birds fingerprinted, including its putative parents. Although the pair RPC and RBY paid a swift visit to 192-91 on day 8, when RPC entered the burrow for about 1 minute while RBY sat looking around outside (section 6.3.2), C1 was apparently not 'dumped' by this pair. RBY and RPC may in fact have 'dumped' an egg during their visit, but I inspected the nest too late to bleed later nestlings, none of which survived. Ringing records confirmed that C1 was not the genetic offspring of the adults attending 192-91: the fingerprinted chick was not the offspring of CBC, which had one ringed fledgling from its nest 211-91, whereas C1 appeared in nest 192-91 unringed, after the real first chick (ringed,

Table 6.3: The relatedness of nestlings and their putative parents in 35 broods. R = offspring of both putative parents, R_M = Related fully only to the male, R_F = related fully only to the female, R_{A1} = related to only one of the parents which were not sexed, D = 'dumped': unrelated to either putative parent.

a: Nam Heng, 1991

Nest	Nestling 1	Nestling 2	Nestling 3	Nestling 4	Nestling 5
192-91	D*	R			
222-91	R	R	R		
221-91	R	R			
108-91	R		R		
107-91	R		R		
144-91	R				
143-91	R	R			
140-91		R			
156-91	R_{A1}	R		D	
233-91	R	R			
170-91	R				
171-91	R	R			
100-91		R			
224-91	R				
231-91	R	R		R	
211-91	R				
202-91	R				
101-91	D				R_{A1}
145-91	R				

*: probably appeared from a different brood after the original first chick had fledged

b: Sungei Buloh, 1989

Nest	Nestling 1	Nestling 2	Nestling 3	Nestling 4	Nestling 5
28-89	R	R			
23-89	R				
2-89	R				
43-89	R	R			
30-89	R	R	D		
25-89	R_M				
20-89	R_M	R			
9-89	R	R			
35-89			R		
41-89	R				
31-89	R	R			
29-89	R_M	R_M			

Table 6.3 c: Sungei Buloh, 1990

Nest	Nestling 1	Nestling 2	Nestling 3	Nestling 4	Nestling 5
17-90	R	R	R		
21-90	R	R			
37-90	R	R			

d: Sungei Buloh, 1991

Nest	Nestling 1	Nestling 2	Nestling 3	Nestling 4	Nestling 5
11-91	R_{A1}**				

**: probably the result of a change of partner (see text)

Table 6.4 a: Band sharing (BSC) between the family at nest 29-89 and some associates and nest visitors, on the same fingerprint

	M-41	**F-31**	**F-29**	**C2-29**	**C1-29**	**M-29**	**F-20**	**M-2**
F-31	0.108							
F-29	0.467	0.000						
C2-29	0.205	0.333	0.118					
C1-29	0.000	0.077	0.207	0.357				
M-29	0.121	0.167	0.296	0.307	0.364			
F-20	0.111	0.148	0.133	0.207	0.000	0.077		
M-2	0.341	0.063	0.171	0.000	0.067	0.143	0.064	
F-2	0.195	0.125	0.400	0.235	0.267	0.143	0.000	0.056

b: Band sharing (BSC) between family at nest 192-91 and some associates and nest visitors on the same fingerprint (BSCs above 0.362 are highlighted in bold, see text).

	CBC	**A1-192**	**C2-192**	**C1-192**	**A2-192**	**RBY**
A1-192	0.333					
C2-192	**0.400**	**0.638**				
C1-192	0.333	0.235	0.255			
A2-192	0.178	0.054	**0.520**	0.270		
RBY	0.324	0.256	0.333	0.138	0.313	
RPC	**0.421**	**0.400**	**0.372**	0.133	0.121	0.148

and slightly older and larger) had hatched. The blood sample of the real C1 of 192-91 had been lost (see methods). No nest was apparently missing a nestling around the time that the new chick appeared in 192-91. Thus, the genetic parentage of C1 could not be established.

Hatching hierarchy and IBP

Three out of 9 (33%) nestlings lower down in the hierarchy (nestling 3 to 5) were illegitimate, compared to 6 out of 50 (12%) for Chick 1 and 2 combined (Table 6.5). If illegitimate nestlings were concentrated on only some broods in such a way that broods either had either offspring with no unexplained bands or only illegitimate nestlings, then the legitimacy of high-ranking and low-ranking nestlings of the same brood would not be independent of each-other so that a χ^2 test would be inappropriate. Out of 5 nests with an illegitimate nestling and with 2 and 3 fingerprinted nestlings, 3 had more than 1 parasitized nestling (see Table 6.3). Although most broods did not have illegitimate nestlings (15 out of 20 broods with 2 or more fingerprinted nestlings, or 75%) and 2 broods (10%) had only illegitimate nestlings, there were 3 broods (15%) with both fully related nestlings and illegitimate nestlings. Since no broods with both illegitimate and legitimate offspring would be expected if illegitimate nestlings were clumped with respect to brood, this is unlikely to have been the case.

The difference between the proportion of illegitimate nestlings was not significantly different in lower-ranking nestlings (χ^2 with Yates Correction = 2.153, $0.20 > p > 0.10$), which probably constitutes a 'Type II error', because for sample sizes in the scope of this study, the χ^2 and G statistical tests do not possess the power to detect a real difference of the magnitude shown. If this difference between 12% and 33% parasitized nestlings was in fact real, it would have taken about 100 nestlings in each of the hierarchy-groups to have an 80% chance of demonstrating this with 95% confidence (Graves, 1991). Therefore, it is possible that illegitimate nestlings were more common lower down in the hierarchy, but the difference would be too subtle to be detected with the available sample sizes.

Colony size and IBP

SB89, SB90 and SB91 were small colonies compared to NH91, with an estimated 10-30 breeding pairs in the main colony at SB as opposed to about 100 in NH. Families from SB89 were therefore pooled (N = 27 nestlings in 16 broods; Table 6.3 b-d) and compared to the families at NH91 (32 nestlings in 18 broods; Table 6.3 a). There was no difference in the degree of IBP between the two colony sizes ($\chi^2 = 0.151$, $p > 0.40$; Table 6.6), but there were more illegitimate offspring in the smaller colony SB (5) than in the larger NH (4).

Table 7.1: Hatch Day Difference (HDD) to the first hatched nestling The first-hatched nestling has a HDD of 0; a HDD of -2 means that hatching day was estimated as being 2 days before the first chick hatched.

	Med HDD	Range	χ^2	p	N
Nestling 1	0.0	(0.0 - 0.0)			73
Nestling 2	1.0	(-2.0 - 7.0)	60.43	< 0.0001	63
Nestling 3	2.5	(-2.0 - 5.0)	26.68	< 0.0001	36
Nestling 4	3.5	(1.0 - 9.0)	0.86	ns	10

Table 7.2: Temperature of eggs at different laying stages
Note: this includes clutches which were subsequently deserted

clutch size (=laying stage)	Median Clutch Temp.	χ^2 between clutches of successive size	p	χ^2 between 'before' and 'after' each egg	p	N
1	cool			1 vs 2-6:		18
		1.18	ns	1.70	ns	
2	lukewarm			1+2 vs 3-6:		39
		0.07	ns	0.04	ns	
3	lukewarm			1-3 vs 4-6:		79
		0.07	ns	0.19	ns	
4	lukewarm					57

6.3 Egg 'dumping' experiment and observations

6.3.1 The 'Egg Dumping' Experiment

Methods

For the 'Egg dumping' experiment, an artificial egg (within the natural size, shape and mass range of the eggs of *M. viridis*) was placed into the nest chamber after digging into it from the 'back'. Artificial eggs were marked using a black permanent marker pen with the nest number. If an egg was expelled, it was re-'dumped' into the same nest. Altogether 76 eggs were dumped into 49 different nestchambers. If nests were inspected before the resident pair had started laying their eggs, an egg was placed into the centre of the finished nestchamber. If the chamber already contained eggs or chicks when it was first dug up, the artificial egg was placed together with the clutch or chicks. All nests were visited every 1-4 days to see whether the artificial egg had been expelled or dug into the chamber floor, and to re-dump an egg if the previous one was missing. Desertions were clearly distinguished from acceptances because nests were monitored until either a brood was raised or no bird had entered the burrow for 3 weeks or more.

Results

'Dumped' eggs are expelled before the onset of laying

At 11 empty nest-chambers (i.e. without eggs) into which eggs were 'dumped' experimentally, the pair deserted. Sometimes the nest was taken over later in the season by different adults. Desertions may or may not have happened as a result of the experiment (Briskey and Sealey, 1987), but nevertheless, these nests were not included in the following analysis.

Altogether, 27 eggs were expelled before the next check (Table 6.7). Without exception, all of the eggs which were expelled had been 'dumped' into a previously empty chamber (but not all of the eggs 'dumped' into an empty chamber were expelled, see below). None of the artificial eggs 'dumped' after the first egg had been laid was removed. In 10 cases, however, between 1 and 4 eggs had been laid presumably after the 'dumped' egg had been expelled following my visit. It remains possible, however, that one or more of these eggs was laid *before* expelling the artificial egg. These ambiguous cases are therefore not included in the statistical analysis (using the numbers in brackets in Table 6.7). In 5 cases, the egg was not expelled before the first egg was laid (Table 6.7). One had been dug into the soil completely, and would not have been incubated. Digging eggs into the soil is thus an alternative to expelling them. In two nests, the 'dumped' egg was expelled only after my *second* visit several days later. Either the birds had deserted and the burrow was repossessed, or the birds did not use the burrow again before my next visit. Only 2 out of 5 pairs consistently left the dumped egg in their burrow before starting to lay (Table 6.8). Either the artificial eggs were accepted as 'eggs' by these pairs, or these birds could have ended up raising a brood of which the eldest and most likely chick to survive is not their own. If only the first incidence of experimental egg 'dumping' per nest was used (otherwise data are not independent), eggs were more likely to be expelled before laying ($\chi^2 = 28.15$, $p < 0.001$).

What happened to expelled eggs?

Of 27 marked eggs that were 'dumped' into empty nest chambers, 12 were found again outside on the lawn later, either near the burrow (less than 1m, 4 eggs), or several metres away from the nest, either in the flight direction from the nest (5 eggs), or beneath a favourite perch of the pair using the burrow (3 eggs). Real Bee-eater eggs were also often found near burrows and under perches. Some of them were broken, but most natural eggs found outside burrows were intact. Only 4 out of 12 experimentally 'dumped' eggs were found very near to the nest. They could have been rolled out of the burrow. Since most of the expelled eggs were found either in the flight line or beneath the perch of the pair that would have expelled it, it is likely that the birds grab hold of the egg (with the bill ?) and carry it out of the chamber rather than kicking the egg out with their feet.

6.3.2 Observations of egg 'dumping'

Casual observations were collected at nests where both members of the breeding pair were tagged and with known onset of laying. These were 'screened' in the database for birds other

Table 6.7: Fate of artificial eggs experimentally dumped into nests at different stages

	Stage dumped:							
	No. of eggs							No. of chicks
	0	1	2	3	4	5	6	1-3
expelled	27 (11)							
not expelled	5 (2)	6 (3)	5 (3)	10 (5)	3 (2)	2 (2)	1 (1)	6 (5)

N = 65 eggs dumped into 38 different nests
(N) = 34 eggs included in the analysis.

Table 6.8: Fate of artificial eggs (repeatedly) dumped at individual nests throughout the breeding cycle

expelled before *and* after first egg[a]	0
expelled before but not after first egg	9
expelled after but not before first egg	0
expelled neither before nor after first egg[b]	1

N = 10 nests in which eggs were expelled and re-'dumped' repeatedly

[a]: eggs were replaced when expelled, see methods

[b]: two nests could not be classed in any one category were not included: in one the dumped egg was expelled before the onset of laying, except for a period of 1-2 days. Possibly the birds did not visit the nest in between checks. The second nest expelled the artificial egg once, then laid their clutch without expelling the re-dumped egg.

than the breeding pair at burrows just before and during laying for possible parasitic behaviour. The only clear evidence of birds other than the breeding pair entering a burrow during or just before laying was of brood 192-91 (see above). RPC and RBY were first caught at 162-91, a completed burrow with nest chamber which they deserted without laying eggs. On the day before entering 192-91, they were observed digging 214-91.

Activities by birds who were themselves near the onset of laying were returned from the database and examined. Only for one pair was there observational evidence that they may have looked for a burrow to 'dump' eggs: the male S9O of 20-89 was seen sitting at 9-89 and at 28-89 on 18th May, 1989. The onset of laying was estimated for these birds as 13th May. On 18th May, both pair members were observed sitting on perches in their sub-colony, however, but not at their own burrow.

6.3.3 Do parasitic birds remove host eggs?

The mean clutch size of the nests in which there was a 'dumped' nestling classified by DNA fingerprinting was 5.5 (4 and 7 eggs, N=2), which is larger than the mean clutch size of mostly non-parasitized broods. The other 2 parasitized nests had 3 nestlings each, but the eggs could not be accounted for. It is therefore not possible to comment on the likelihood of parasites removing eggs prior to 'dumping'. Eggs were, however, regularly found on the surface of the lawn. They may have been host eggs removed by the egg 'dumpers', or 'dumped' eggs removed by hosts. No direct observations were made of birds expelling eggs from burrows. Anti- egg 'dumping' behaviour by hosts is investigated in the following section.

6.4 DISCUSSION

In 59 nestlings of 35 broods, there were no unequivocal incidences of EP paternity. Two chicks with mis-matches had putative parents which were not sexed and might have been EPO. Where putative parents could be sexed (in 4 out of 6 cases where one putative parent was classed as extra-pair), it was the male that was more closely related to the EP nestling. This may be because of 'quasi' parasitism, where the male mates with more than one female who lay eggs into the clutch in his nest. If males have more relatives amongst neighbouring breeders, as in European Bee-eaters (Lessells *et al*, 1993) and if relatives dump eggs on each-other in Blue-throated Bee-eaters - perhaps if their own breeding has been interrupted, as has been reported for White-throated Bee-eaters (Emlen and Wrege, 1986), cases of apparent quasi parasitism could alternatively have been INP by close relatives of the pair male. Without consistent observations of behaviour and genealogical histories, the interpretation of fingerprints is not straight-forward. Below, I consider possible interpretations of the results reported in this chapter; implications for mixed reproductive strategies in Blue-throated Bee-eaters are considered in Chapter 8.

6.4.1 Validity of fingerprints of Blue-throated Bee-eaters

In this study, average band sharing between unrelated adults was 0.165, comparable to the 0.2-0.3 in most bird studies (Lewin, 1989 a); this includes other Bee-eater species, e.g. 0.193 for European Bee-eaters (Jones *et al*, 1991). Rather than comparing birds from different colonies (populations), most studies compare individuals from one population amongst which there may be some relatives. The band sharing levels used for unrelated birds in this study were therefore more representative than in most studies involving DNA fingerprinting.

6.4.2 Extra Pair Copulations and EPO

In colonial species, EPO are often particularly common (e.g. Morton *et al*, 1990; Birkhead *et al*, 1987), which raises the question of why is there no evidence for EPO in Blue-throated Bee-eaters. Firstly, if more IBP-derived nestlings were to be found lower in the nestling hierarchy, these would fall prey to brood reduction in most years and were also infrequently sampled because of this high mortality rate. EPO lower in the hierarchy may have been missed because of sampling problems. Males slacken their mate-guarding towards the end of the fertile period in some species (reviewed by Birkhead and Møller, 1992; see also Riley *et al*, in press). It is therefore possible, if EPCs would consequently be more common later in the laying sequence, that EPO were more common in later-hatched nestlings. The full implications of IBP in later-hatched nestlings for reproductive strategies are discussed after the next chapter in which brood reduction is investigated in detail.

It is possible, moreover, that EPO were not identified because the cuckolded males could not be sexed, if they were smaller than average. In 2 cases, the nestlings may in fact have been EPO, and the putative parents were not sexable. One reason for this was that the male was smaller than the size specified by the 95% interval for males. These males were thus smaller than the average male, which may be a reflection of quality, status or competitive ability (Partridge and Halliday, 1984; Harvey and Bradbury, 1991). Furthermore, changes of partners, or 'rapid mate switching' (e.g. Birkhead *et al*, 1990), would produce the same fingerprint interpretation as EPCs (e.g. for brood 11-91).

6.4.3 Evidence for intraspecific nest parasitism

One-third of the offspring with mismatches did not share bands with either putative parent at the level indicating full relatives. It is possible that samples were mixed up, which can reportedly be a source of error in fingerprinting (Romagnano *et al*, 1989; Birkhead *et al*, 1990). My samples were labelled with four overlapping identifications and replicates of the ringnumber (see methods), and several samples were available for most birds so that if in doubt, DNA could be re-extracted. Brood 156-91, for example, was re-printed several times from different extractions. Carole Campbell and I were aware of no sample mix-ups in the history of the local laboratory despite continuously and carefully double-checking all samples with records. Lastly, several of the EPO shared more bands with the putative mother or father than was reported as typical for unrelated birds. Not only is that an indication for consistent use of the correct blood samples, but the question arises whether some EPO were dumped by relatives (of the male mostly, see below). I conclude that it is unlikely that the mismatches of nestlings with putative parents were the result of human error and argue that the young were actually unrelated or second- or lower-degree related to their putative parents. This notion was furthermore supported by the case of one chick which was interpreted as 'dumped' from the fingerprinting results, while ringing records revealed that the chick had in fact strayed from another brood. Straying nestlings were not observed very commonly, but nestlings may leave the nest before they can fly if the home nest was predated or the last nestling was deserted by the parents after the first chick(s) have fledged.

Apparent INP would also be reported if more than one female laid claim to a burrow (Birkhead *et al,* 1990). Romagnano *et al* (1989) point out that it is important to inspect nests regularly for field evidence of INP. If more eggs than one female can lay (usually one per 2 days for Blue-throated Bee-eaters, Bryant and Tatner, 1992) appear in a nest, one of those new eggs is likely to be dumped (Bryant and Tatner, 1992; Yom-Tov, 1988). I tried to visit nests every day during laying, but most nests that were visited frequently during laying were either deserted, or seemingly birds stopped laying for several days. It was therefore impossible to be sure about 'dumped' eggs from nest inspections in this study. Where data were available, clutch sizes were high in nests with 'dumped' chicks.

Birds other than the resident pair recorded as entering the burrow during or before laying at only one nest (section 6.3.2), but the fingerprint showed that neither of these birds was in fact the parents of the two nestlings which were later found in the burrow. One of the intruders was probably a relative of one of the parents (see Table 6.4 b).

The results of the egg 'dumping' experiment suggested that, as expected, eggs 'dumped' before the initiation of the clutch of the resident female are invariably expelled. This anti-nest parasitism behaviour may itself be evidence for INP. The observed expulsion behaviour, however, is also expected for birds that 'steal' each-others burrows: it is possible that birds 'clear out' their burrow prior to laying. Take-overs of burrows dug by another pair were commonly observed. There is probably competition for specific burrows, and I found whole clutches expelled in both years. Evans (1988) suggests that in Starlings, more than one female may lay claim to the same nest box, which can then lead to INP in starlings. Once the female starts laying, she cannot distinguish her own from parasitic eggs. This is probably why male Starlings stop expelling eggs close to their own females' onset of laying (Pinxten *et al,* 1991 b). Moskens (1992) discovered that, unless the mimicry is good, birds may reject conspecifics' eggs placed in their clutches on the basis of dissimilarities to their own eggs. In his study species, Chaffinches *Fringilla coelebes* and Bramblings *F. montifringilla*, eggs of different females of the same species are very dissimilar, while each female lays similar eggs. In Blue-throated Bee-eaters, egg sizes and shapes vary widely within clutches (Fig. 6.8). It is therefore unlikely that Blue-throated Bee-eaters can distinguish between their own and 'dumped' eggs.

I saw no active egg transfers during this study, but eggs were marked only in the last season (1989). Usually each burrow was visited by only two birds, the male and female of the 'resident' pair. Any additional birds are either 'helpers', or they are intruders which are chased away vigorously. Helping female White-fronted Bee-eaters sometimes 'dump' eggs on their hosts (Emlen and Wrege, 1986). Other prospective 'dumpers' may escape routine recordings, because they enter and leave nests quickly and quietly (Davies, 1988). I conclude that the Blue-throated Bee-eaters must carry at least some of the dumped eggs out, probably in their bill, and drop them either in flight or from the perch. Egg 'carrying' behaviour has been reported for Cliff Swallows (Brown and Brown, 1988), Northern Flickers by Blomme (1974) and recently for female and male Starlings (Pixten *et al*, 1991b), but few studies have concentrated on observing expelling behaviour.

6.4.4 'Quasi' parasitism or IBP by relatives?

At least 4 (and perhaps 6) nestlings were classed as legitimate offspring of the putative father but not the mother. These may have been cases of 'quasi' parasitism, where an extra-pair female had 'dumped' an egg which was fertilized by the pair-male into his nest. Consistent observations at a nest with 'quasi' parasitism did not, however, show that the pair male consorted with a secondary partner, and there was no other observational evidence for EP females being consorted by breeding males.

At two nests with illegitimate chicks, the cuckolded female provisioned at least as hard as the male. Thus, if the cuckolded female partner feeds the offspring regardless, 'quasi' parasitism would be doubly costly for her. Not only does she lose the chance to raise her own offspring,

Figure 6.8: Two eggs from the same clutch. These 2 eggs differed more in size and shape than eggs from different clutches in general.

but she also spends energy raising offspring which are not her own - unless this cost is reduced because illegitimate nestlings, which necessarily occur lower-down in the nestling hierarchy, are nearly always eliminated from the brood by brood reduction (see Chapters 7 and 8).

In the absence of behavioural observations in support of 'quasi' parasitism, alternative explanations must be considered. It is possible that some of the putative parents were sexed wrongly (see Chapter 5 and above, 6.4.2). Furthermore, a relative or otherwise associated bird could have been mistaken for one of the parents (Romagnano *et al*, 1989). In one nest, blood taken from three birds spending the night together there, revealed that the third bird was probably a first-order relative of one of the pair members (possibly the female; section 6.2.3), so there is evidence from DNA-fingerprints that relatives do share burrows. If one of the adults caught as 'putative parents' is in reality a helper or simply a relative allowed to roost in the burrow overnight, then chicks with mis-matches and intermediate band sharing levels may be second- or third-degree relatives of one or both adults caught ($0 < r < 0.5$).

If an intermediate BSC means intermediate relatedness, some of the apparent cases of 'quasi' parasitism could be explained with egg 'dumping' by related birds. In White-fronted Bee-eaters, Emlen and Wrege (1986) observed helpers and other members of the clan (daughters of one or both members of the breeding pair) 'dumping' an egg into their nest. Other birds allowed access to the nest included the breeding partner of the previous year. INP between relatives is apparently quite common in ducks for example, where daughters and mothers parasitize each-other and kin selection plays a major part in the evolution of INP (Andersson, 1984).

When examining the evidence for this notion in Blue-throated Bee-eaters, we first look at its philopatry and dispersal. I showed that, while birds at any one colony-year in general (selected at random) shared no more bands than unrelated birds from different colonies, individuals from neighbouring nests shared significantly more bands than birds within colony-years selected at random. Male neighbours were related more closely than female neighbours. It is not clear which sex is more likely to be philopatric, but in altricial species it tends to be the male that returns to its birth-place (Rohwer and Freeman, 1989; Andersson, 1984).

Lessells *et al* (1993) demonstrate very clearly that in European Bee-eaters, females disperse further than males. Philopatry and return rates in Blue-throated Bee-eaters were discussed elsewhere (Chapter 4). The finding, firstly, that relatives nest closely together and, secondly, that nestlings which have more than 3 mis-matching bands with their putative parents may nevertheless not be completely unrelated to them, may indicate that in Blue-throated Bee-eaters, relatives nest close together and lay eggs into each others' nests or take over their mates. In territorial species, where paternity for EPOs could be assigned, often the true fathers of extra-pair chicks are males from neighbouring territories (e.g. Westneat, 1990). Similarly, Møller (1987f) reports that eggs in Swallow colonies are 'dumped' by neighbours. In White-fronted Bee-eaters, colonies consist of clans of relatives (Emlen 1990). Lessells *et al* (1993) demonstrate clearly that brothers of European Bee-eaters nest closely together, because of a benefit of helping, and that relatedness amongst neighbours is not just an artifact of distance of dispersal. 'Egg dumping' by related neighbours may be the valid alternative interpretation of the cases of apparent 'quasi' parasitism observed. Egg 'dumping' by related birds, should be less costly for the attending pair-male than INP by non-relatives, which could explain why this type of intraspecific brood parasitism was seemingly more common than INP by non-relatives in the Blue-throated Bee-eaters.

To reconcile egg 'dumping' by relatives with levels of band sharing and band mismatching, intermediate levels of band sharing have to be assigned to intermediate levels of relatedness. Because of high level of 'background noise' due to band sharing between unrelated birds, intermediate relatedness can often not be determined by fingerprints (Lewin, 1989 a; Lynch, 1988). This has nevertheless been successfully undertaken in two studies, by Birkhead *et al* (1990) and Jones *et al* (1991). Birkhead *et al* (1990) used segregation analysis (which I could not do here) to estimate expected BSC for second-degree relatives, while Jones *et al* (1991) had ringing records of second-order relatives for which they calculated BSCs. To assign nestlings to these additional models with band mis-matches and Band Sharing Coefficients of their fingerprints, band sharing levels between known second or third degree relatives were used to 'calibrate' the coefficient of relatedness r for intermediate values (0.125 to 0.25). The long-term ringing data needed for such a calibration, however, were not available in this study. The only second degree relatives were siblings that shared only one parent. This was found in 3 broods which had both an EPP or 'quasi'-parasitized nestling, and either a fully related chick or a 'dumped' nestling (nestling 1 in brood 20-89 and nestling 4 in brood 156-91 were intermediate and did therefore not qualify). Bearing in mind that of course the classification of these nestlings themselves may be erroneous if they could be assigned to the additional models of relatedness and BSC, it is nevertheless of interest to consider if half sibs share intermediate levels of bands. In a plot of BSC and relatedness, BSC values for 3 out of 4 half-sibs, including the mean of the 4 half-sibs, were within the 95% confidence interval for non-related individuals (Fig. 6.7). It was therefore not possible to assign band sharing levels to more distant relatives, and I could not distinguish clearly between intermediate models and the four traditional models. There is thus no available means to differentiate further than between first-degree relatedness and non-relatedness, and it is not possible to assign particular (intermediate) levels of band sharing to second- or third-order relatives. Nevertheless, models of IBP by relatives should be considered in this context. Additional models of relatedness between nestlings and attending adults are listed in Table 6.9. A nestling is second-order related (r = 0.25) to both putative parents if an egg is 'dumped' for example by a daughter of both attending adults or to one of the putative parents if 'dumped' by the son's partner or the daughter of only one of the pair, either the pair male or the pair female, who is the grand-parent (r = 0.25) of the nestling. Second-order relatives 'dumping' eggs on a breeding pair cause third-order (r=0.125) relationships between members of the breeding pair and the resulting nestling.

6.4.5 Influence of colony size on IBP

It has been predicted that in large colonies, the incidence of IBP will be higher than in smaller colonies (e.g. Birkhead *et al*, 1987; Birkhead and Møller, 1992), but in Blue-throated Bee-eaters, the indication was in the opposite direction (only 2 colonies compared). IBP was more frequent in the medium-to-large size colony in Sungei Buloh during 1989 (about 40 pairs) than in the large Nam Heng colony in 1991 (100 pairs or more, see Chapter 4). Møller (1987f) and Brown and Brown (1988), however, found that only very small colonies of Swallows and Cliff Swallows (1-4 and 10 pairs) compared to medium or large colonies (17-32 and 10-1000 pairs) had significantly less IBP. No IBP was reported for the smaller colony at Sungei Buloh in 1990 (less than 30 pairs), and only one family was fingerprinted from SB91, so that SB89 was the largest of the colonies in this area in any of the 3 study years and

Table 6.9: **Models of relatedness between nestlings and putative parents**

True father	r (Pair Male, Nestling)	**Nestling Model**	r (Pair Female, Nestling)	**True Mother**
Pair	0.5	**R**	0.5	Pair
EP	0.0	$\mathbf{R_F}$	0.5	Pair
Pair	0.5	$\mathbf{R_M}$	0.0	EP
EP	0.0	**D**	0.0	EP
INP by relatives of pair members				
Son of both	0.25	$\mathbf{D_R}$	0.25	Non-relative
Non-relative	0.25	$\mathbf{D_R}$	0.0	Daughter of both
2nd order rel to both	0.125	$\mathbf{D_R}$	0.125	Non-relative
Non-relative	0.125	$\mathbf{D_R}$	0.125	2nd order rel to both
Son of mother	0.0	$\mathbf{D_R}$	0.25	Non-relative
Non-relative	0.0	$\mathbf{D_R}$	0.25	Daughter of mother
Son of father	0.25	$\mathbf{D_R}$	0.0	Non-relative
Non-relative	0.25	$\mathbf{D_R}$	0.0	Daughter of father
2nd order rel to mother	0.0	$\mathbf{D_{(R)}}$	0.125	Non-relative
Non-relative	0.0	$\mathbf{D_{(R)}}$	0.125	2nd order rel to mother
2nd order rel to father	0.0	$\mathbf{D_{(R)}}$	0.125	Non-relative
Non-relative	0.0	$\mathbf{D_{(R)}}$	0.125	2nd order rel to father
Pairing between first-order relatives				
Pair	0.75	$\mathbf{R_I}$	0.75	Pair
Pairing between second-order relatives				
Pair	0.625	$\mathbf{R_{(I)}}$	0.625	Pair

R = related, D = dumped, M = male, F = female, I = inbred, () = partly probably had a larger proportion of nests with IBP than in 1990. In that case, the original prediction would hold true for Sungei Buloh. The difference in IBP incidence between Sungei Buloh and Nam Heng could be due to other causes, i.e. there may have been more opportunity for IBP at Sungei Buloh that at Nam Heng for reasons other than colony size, such as spacing and density of breeding birds.

6.4.6 Conclusions

Nine nestlings of 59 (15%) had more than 3 bands in their DNA fingerprints not derived from their putative parents. Three (5% of all nestlings) were either 'dumped' by non-relatives or have strayed from a deserted nest; 4 nestlings were most likely the result of 'quasi' parasitism, although there were no behavioural records in support of this interpretation; no definite case of extra-pair paternity was established, but the parents of 2 nestlings related to only one putative parent were not sexable. While other alternative interpretations are offered, it is argued that these could have hatched from eggs 'dumped' by relatives particularly of the male pair member. The main implications of these results are: the frequency of IBP of Blue-throated Bee-eaters did not differ in general from that described for avian colonies (see 6.1; also Birkhead and Møller, 1992 for EPO). 'Quasi' parasitism probably exists, even if on a low level, EPO may be rare or absent. This is discussed further in Chapter 8.

The power of DNA fingerprinting decays with genetic distance (Lewin, 1989 a; Lynch, 1988). This should be particularly so in the present study, where the 95% confidence limits of band sharing levels between first-degree relatives overlap with those of band sharing between non-relatives. DNA fingerprinting with multi-locus probes can therefore not distinguish clearly between the different interpretations of band matching and mis-matching in *M. viridis*. If more blood samples from the Bee-eater study colonies had been available, the identity of some true parents may have been found by re-printing them together with the family (cf Westneat, 1990). I re-printed families for which blood samples for other birds observed at the nest or associating with putative parents were available, but did not identify the parents of any mis-matched offspring. To identify parents of extra-pair offspring using multi-locus probes, it is necessary to run DNA samples from all prospective parents on the same gel as the chicks. Triggs *et al* (1991) used cut-out standard size photocopies of fingerprints to compare individuals from different gels, but this is not generally considered as reliable (see e.g. Westneat, 1990), and it was felt that comparisons should not be done across gels for fingerprints of Blue-throated Bee-eaters. The identity of nest parasites could be tested in future research with DNA profiling using single-locus probes (e.g. Burke, 1989). This method is more powerful but requires the isolation of species-specific probes, which was outside the scope of the present study.

In order to distinguish degrees of relatedness, large numbers of scorable bands are needed. For the correct interpretation of DNA fingerprints, they must furthermore be supplemented with behavioural observations (e.g. Birkhead *et al*, 1990; Lewin, 1989; Romagnano *et al*, 1989; Wrege and Emlen, 1987) and long-term ringing data (e.g. Jones *et al*, 1992), since first-order relatives and non-relatives cannot be distinguished from second- and third-order relatives without ringing records to calibrate the band sharing coefficient with the coefficient of relatedness. Despite extensive observations of nesting Blue-throated Bee-eaters, no observational evidence of IBP was obtained for any of the fingerprinted families. In the present study, band sharing coefficients of related birds furthermore overlapped with those of presumably unrelated birds.

CHAPTER 7 - BROOD REDUCTION AND SIBLICIDE

7.1 INTRODUCTION

In this chapter, I investigate nestling growth and the proximate and ultimate causes of nestling mortality. I first investigate incubation onset in Blue-throated Bee-eaters, before evaluating the evidence gathered on the 'brood reduction hypothesis' and its predictions, and if nestling mortality is obligate or facultative in Blue-throated Bee-eaters. Thirdly, I aim to illuminate mechanisms by which nestling mortality is mediated and the roles of food and siblicide in controlling it.

7.1.1 Hatching asynchrony as a means of brood reduction

Lack (1954) suggests that some birds start incubating before the clutch is complete, so that the chicks do not all hatch on the same day. This gives the first hatchlings a 'head-start' and establishes a size hierarchy amongst the nestlings in the brood. Since the younger, last-hatched chicks often die as a result of food shortage, hatching asynchrony is seen as an adaptation to adjust brood size to temporal fluctuations in food supply (Lack, 1954; Ricklefs, 1965). This notion is referred to as the '*brood reduction hypothesis*'. Blue-throated Bee-eaters consistently lay more eggs than they fledge: Bryant and Hails (1983) report that more than half of the clutch perish as nestlings; invariably the youngest nestlings dying of starvation (Bryant and Tatner, 1990). Lack (1954) notes that hatching asynchrony occurs 'particularly in species which lay their eggs at 2-day intervals' (p40), which applies to European Bee-eaters (Lessells and Avery, 1989), and, indeed, to Blue-throated Bee-eaters (Bryant and Tatner, 1990). Hatching asynchrony is particularly marked in Bee-eaters (Lessells and Avery, 1989; Bryant and Tatner, 1990).

There are several functional explanations as to why clutches hatch asynchronously and greatly exceed brood size at fledging. The '*insurance hypothesis*' was originally proposed for raptors by Stinson (1979), who suggests that even though by default only one chick is reared to fledging, two eggs are laid in these species to insure against hatch failure or defective first-hatching chicks (see also Forbes, 1993; Godfray and Harper, 1990; Magrath, 1990; Bryant and

Tatner, 1990; Sutherland, 1989). It may be advantageous to start incubation immediately so as to reduce the nestling period, at least for the first hatchlings, either because of predation risks (*'nest failure hypothesis'* Clark and Wilson, 1981; see also Hussel, 1985) or to avoid deteriorating feeding conditions at the end of the season (*'hurry-up hypothesis'*; both reviewed by Magrath, 1990). An early onset of incubation, resulting in asynchronous hatching could also occur simply because the end of ovulation and the start of incubation are controlled by the same hormone (Mead and Morton, 1985), so that synchrony could not evolve unless its selective advantage outweighed the costs of separate hormones (*'hormonal hypothesis'*, Mead and Morton, 1985).

These hypotheses do not consider sibling size hierarchy as an adaptive feature, but as a by-product of selective pressure on incubation schedule or clutch size. Parents might, however, benefit directly from a spread in chick size in their brood, because it might, for example, enable them to forage on prey items of a wider range of sizes (Forbes and Ankney, 1987; Bryant 1978), or reduce the total amount of food brought to the nest per day (*'peak-demand reduction hypothesis'*; Hussell, 1972; Bryant, 1978). An established nestling size hierarchy could reduce the energy expended by nestlings in competition (*'sibling-rivalry reduction hypothesis'*, originally proposed by Hahn, 1981). Reduced energy expenditure in asynchronous broods was demonstrated by Bryant and Tatner (1990) for White-bellied Swiftlets *Collocalia esculenta*. Godfrey and Harper (1990) conclude from a model they propose of the evolution of sibling aggression, that siblicide is less likely to occur in asynchronous broods because of reduced competition between nestlings in broods of different size nestlings. Bryant and Tatner (1990) suggest that if in Blue-throated Bee-eaters hatching asynchrony reduces sibling competition in accordance with the 'sibling-rivalry reduction hypothesis', energy expenditure should be lower for nestlings in asynchronous broods. The trend they observed, however, of increased nestling energy expenditure in asynchronous broods, was opposite to that predicted by the sibling rivalry hypothesis for hatching asynchrony in Blue-throated Bee-eaters.

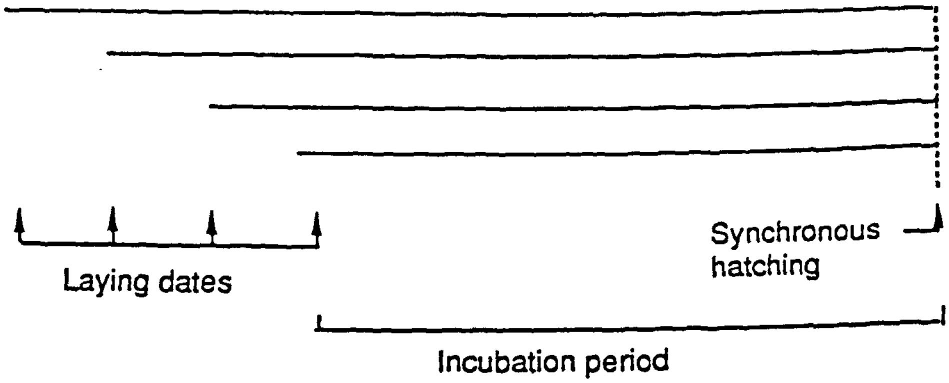
The brood reduction hypothesis predicts that under improved food conditions, elder siblings are satiated and parents can allocate more food to the runts which may then recover, partly or wholly, to survive and fledge (Lack, 1954). My aims here are to investigate the *mechanisms* by which nestlings die, in order to throw some light on the adaptive significance of the nestling size hierarchy, in particular with respect to the brood reduction hypothesis and the rôle of food in siblicide. First I describe hatching spread and the period and schedule of incubation. This is followed by evidence for food constraint from nestling energy requirements, feeding rates and nestling growth patterns. I manipulated the food supply to top-ranking nestlings by supplementary feeding. Lastly, the mechanisms of food allocation between nestlings are investigated with observations and experiments on nestling behaviour in response to adult food calls before and after receiving supplementary food. The issues considered are whether elder nestlings beg more, whether they are more successful at positioning themselves favourably at the burrow entrance or at preventing their younger siblings from doing so, or whether chicks directly attack each-other.

7.1.2 Incubation and hatching asynchrony

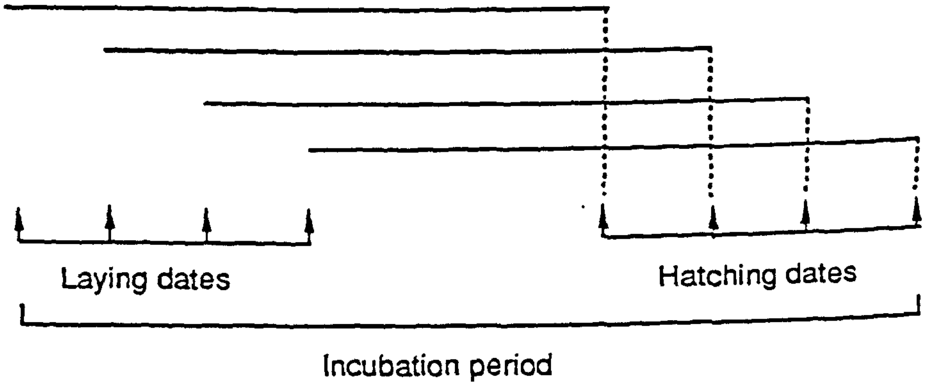
The incubation period is generally defined as the period between clutch completion and the hatching of the last nestling (Drent, 1975), assuming that full incubation behaviour commences when the last egg is laid. Fig. 7.1 a is a model of the expected hatching spread under this assumption, for birds that lay four eggs in regular 2-day intervals, hatching 4 nestlings. In temperate birds, in the total absence of incubation, the eggs remain below a minimum temperature needed for embryonic development (which is 25-27°C, White and Kinney, 1974; tolerance temperature span = 16-36°C according to Webb, 1987, depending on species and duration). This causes a developmental delay for the first few eggs of the clutch, which results in synchronous hatching for the clutch. The burrows of Blue-throated Bee-eaters have a temperature of 29°C (D.M. Bryant, pers comm) which might allow some embryonic development to occur even in the absence of incubation, and large clutches may further buffer heat loss (see Chapter 4; Afik and Ward, 1989). Therefore any developmental delay of first-laid eggs prior to the onset of incubation will be less pronounced.

Altricial bird species, however, typically hatch asynchronously (Lessells and Avery, 1989). Blue-throated Bee-eaters usually lay one egg every two days (Bryant and Tatner, 1990). If incubation starts immediately after the first egg is laid, we expect a difference in hatching roughly similar to that of laying as illustrated in Fig. 7.1 b. Both of the models above assume that the rate of embryo development does not depend on the position of the egg in the laying

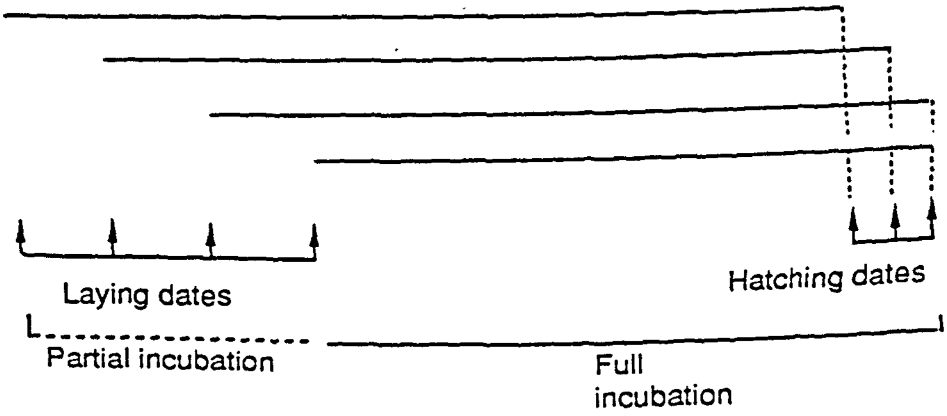
(Figure 7.1)


Laying dates
Synchronous hatching
Incubation period

A


Laying dates
Hatching dates
Incubation period

B


Laying dates
Hatching dates
Partial incubation
Full incubation

C

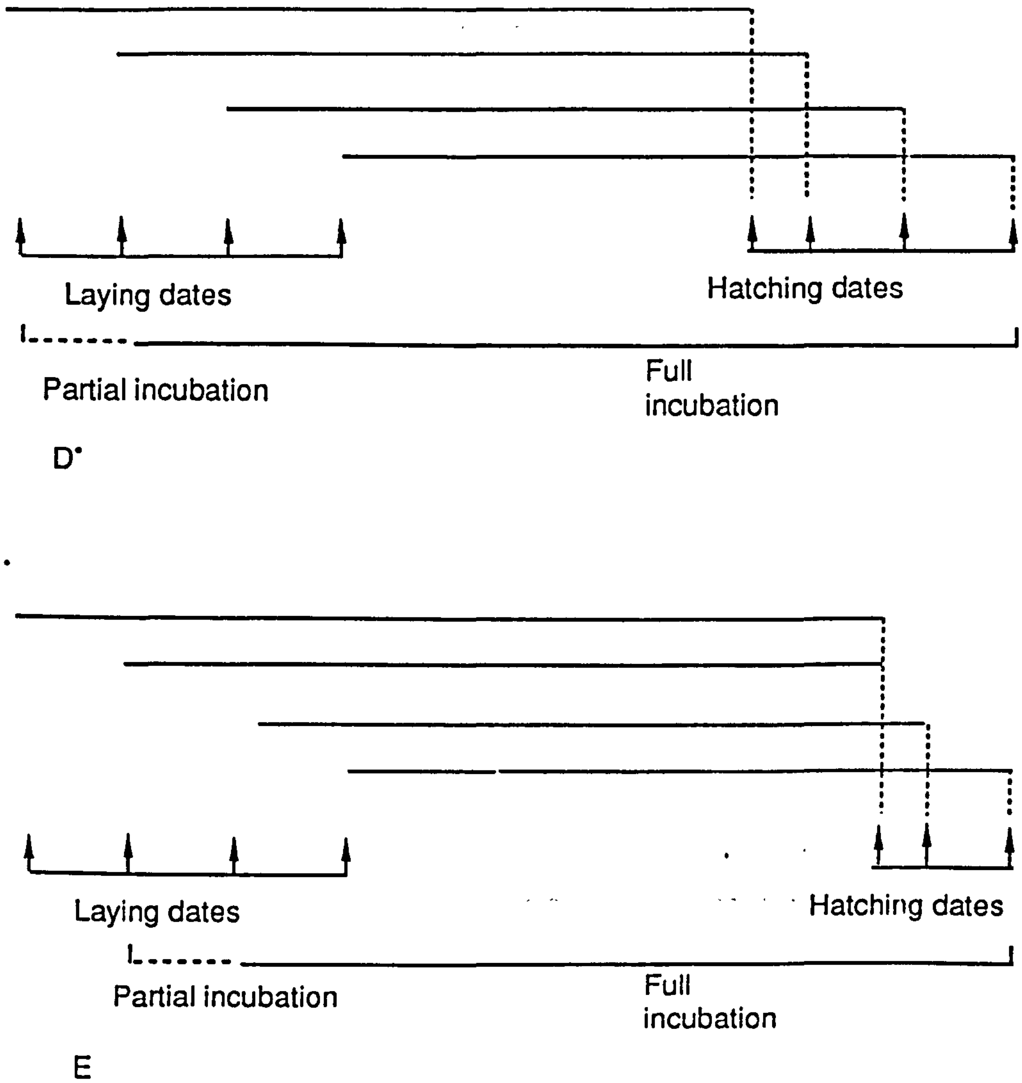


Figure 7.1: Models of the hatching spread for clutches of 4 eggs which were laid in 2-day intervals, as dictated by different onsets of incubation during laying. Each line represents an egg through time during the egg period, from laying (left side) to hatching (right side). (A): if full incubation begins after the last egg was laid, all eggs hatch on the same day (= synchronous hatching). (B): if full incubation starts immediately after the first egg was laid, the hatching spread is the same as the laying interval (= asynchronous hatching). (C): partial incubation starting immediately after the first egg was laid and continuing during laying advances each egg by part of the difference in egg age, reducing the hatching spread. (D) and (E): a gradual increase in incubation, from part incubation during early laying to full incubation after later eggs were laid, advances the first one or two eggs which hatch closer together, while hatching dates of the younger nestlings are spread out further. All models assume regular laying intervals (every two days), regular incubation throughout the egg period *after* laying, and that incubation is independent of laying sequence, egg position or size.

sequence and that eggs hatch in the order of laying. Although this is generally a reasonable assumption (e.g Lessells and Avery, 1989), it may not always hold (Drent, 1975) if, for instance, egg size or quality change with laying sequence (O'Connor, 1979).

Many species start part-incubating before clutch completion, with full incubation commencing after the last egg has been laid (Drent, 1975). Female White-crowned Sparrows *Zonotrichia leucophrys oriantha*, for example, attend to the nest during the daytime after the first egg is laid but do not incubate at night until the penultimate egg (Mead and Morton, 1985). Lessells and Avery (1989) found that nest attendance of European Bee-eaters increased during the laying period, but hatch dates indicated that actual incubation was less gradual, with a marked increase just before the second-last egg was laid. A direct method of detecting the onset of incubation is by measuring clutch temperatures during and after laying. Unless warmed by an adult, the eggs should assume the temperature of the surrounding burrow; warm eggs must be partly or fully incubated, and any consistent change in egg temperature during the laying period from 'more often cold' to 'more often warm' would indicate an increased incubation effort. Depending on the onset of partial and full incubation, several mixed models predict a varying degree of synchrony in the elder nestlings compared to the later hatched chicks (example in Fig. 7.1 c-e). By observing hatching dates and with the supporting evidence of egg temperature data, it should be possible to determine which incubation strategy was used.

Mead and Morton (1985) argue that, at least in species where only the female incubates, hatching asynchrony may be a direct result of hormonal control of incubation onset rather than imply a selective advantage over synchronous broods (see 7.1.1). Hormone release, which is necessary for the brood patch to form, is probably influenced by external stimuli. These might be provided by the mate (Drent, 1975), in which case incubation behaviour would be expected to be established gradually during laying rather than to switch suddenly towards incubation either at the onset of laying or after clutch completion, as in the two models discussed above (Fig. 7.1 a and b).

The incubation period and timing of onset of incubation have not been described previously for Blue-throated Bee-eaters. My aim here is to estimate the time between laying and hatching (named 'hatching time' hence forth) for Blue-throated Bee-eater eggs at different positions in the hatching sequence, in order to calculate the onset of laying for broods with chicks of known age, and to discuss the implications of the pattern of incubation during laying for hatching asynchrony.

7.1.3 Food constraint

An important assumption for brood reduction is that there is not enough food for all chicks to survive the nestling period. The energy needs of chicks for relatively unrestricted growth were compared to the food available to nestlings as observed in feeding rates. For Blue-throated Bee-eater nestlings, metabolic energy requirements of chicks are known for the complete nestling period (Bryant and Hails, 1983). Bryant and Bryant (1988) provide the relevant data to convert these into the corresponding wet insect mass needed.

7.1.4 Nestling growth and mortality: resource tracking and threshold model

Starving nestlings may slow growth until conditions improve (Emlen *et al*, 1991). In species whose food supply for the nestling period is unpredictable at the laying stage and which therefore can not adjust their clutch size to the likely number of nestlings that can be raised, the brood reduction hypothesis explains how brood size can later be adjusted during the nestling period at minimum extra cost (Ricklefs, 1969; Lack, 1954). This, however, is part of a parental strategy which does not necessarily comply with the interests of all nestlings - in particular the potential victims of brood reduction (O'Connor, 1978). Selection pressure may favour resilience of runts against brood reduction by retarding growth, which supports the '*resource tracking hypothesis*'. This postulates that the size hierarchy in Blue-throated Bee-eaters may serve under adverse conditions to temporarily allocate the majority of resources to the eldest chicks, rather than eliminating the youngest nestling. Once resources recover, the youngest nestlings may still survive but perhaps take more time to fledge (Bryant and Tatner, 1990; Temme and Charnov, 1987).

Adaptations like retarding growth might help nestlings to survive periods of food shortages which has been investigated by Emlen *et al* (1991), using the appearance of nestling White-fronted Bee-eaters but not their body size measures, mass or condition. I used body size measurements to describe and compare growth patterns between nestlings of different rank in the nestling size hierarchy, to establish whether there was any evidence for growth retardation at any stage. The growth of bee-eater chicks is known to depend on hatch sequence (Bryant and Tatner, 1990; Emlen *et al*, 1991).

Ricklefs (1969) argues that starvation should increase with nestling age, because older nestlings need more energy for maintenance. This kind of brood reduction would be inefficient, since much investment would be wasted on older nestlings that perish late in the nestling period. The brood reduction hypothesis predicts instead that if the food supply is unlikely to support the whole brood, those nestlings that are likely to perish should do so as quickly as possible. Strategies for early brood reduction would therefore be favourable, because this would be an advantage in terms of total brood success (e.g. Sutherland, 1989). Magrath (1989) shows that hatching asynchrony can be such an adaptation for early brood reduction: asynchronous broods are more successful in times of food shortage because the runt dies more quickly. Another such adaptation is siblicide (see next section). Assuming that runts can fledge when there is sufficient food, there should be a threshold level of food supply brought to the brood, below which the runt should die as quickly as possible, and above which it should to survive. The threshold is the amount of food needed for all nestlings to fledge. The more efficient the response to this threshold, the fewer resources are wasted. Such a threshold exists, for example, in the Blue-footed Booby *Sula nebouxii*, where siblicide seems to be triggered at a 20-25% mass deficiency of the top-ranking nestling (Drummond *et al*, 1986). I refer to this as the '*threshold hypothesis*'.

Supplementary feeding and induced recovery experiments

Blue-throated Bee-eaters rarely fledge their median brood size of 3. If in conditions of food constraint, additional food is made available to nestlings, facultative runt mortality and resource tracking would be indicated by faster growth, improved condition or fledging of later-hatched nestlings. Under the resource tracking hypothesis, the recovery of a supplementary fed chick that would otherwise be likely die would therefore be expected. Experimental supplementary feeding of older chicks, on the other hand, allows investigation of the mechanisms by which runts recover: as the elder nestlings get satiated, they become less aggressive, which allows the parents to re-direct food to runts (Lack, 1954). Alternatively, runts may suffer fewer attacks so that their condition improves, even if no extra food is allocated to them which improves their ability to withstand attacks (Mock *et al*, 1987). If runt mortality is obligate, then satiated elder chick(s) should continue to bully the younger one(s) even if they are satiated; an increase in food supply should in fact increase the efficiency of the attacks because elder siblings are better-fed, and speed up the demise of runts. Thirdly, it is possible that parents may respond to supplementary feeding by bringing less food to the brood instead, so that nestling mortality does not change with additional food given to the top-ranking nestlings.

7.1.5 The rôle of siblicide

Evidence for aggressive competition between siblings has been accumulating recently from many altricial, non-passerine bird species (e.g. v Noordwijk, 1988; Mock *et al*, 1987). Asynchronous hatching may give the first-hatched nestling a competitive advantage (Godfrey and Harper, 1990; Dickins and Clark, 1987). In American White Pelican *Pelecanus prythrorhychnos* broods, for example, only the second-hatched chicks suffered bruises, not the first-hatched chicks (Evans and MacMahon, 1987). Second and third-hatched Brown Pelicans *Pelecanus occidentalis* nestlings suffer similar victimization, and such later-hatched chicks were subordinate in 8 nests out of 10 (Pinson and Drummond, 1993).

Whether siblicide is obligate or facultative depends on the ultimate role of food supply in controlling brood size (Mock *et al*, 1987). Forbes and Ydenberg (1992) propose models of siblicide which show that obligate siblicide could evolve even if in most years enough food is available for all nestlings, because the cost of allowing runts to survive is very high in bad years. Since the elder chick should eliminate pending competition, they argue, it is irrelevant whether food is abundant or not at the time when siblicide occurs. Aggression and siblicide should then also be independent of proximate food supply, nestling condition or hunger. If, on the other hand, siblicide is facultative and depends proximately on food supply, aggression will be inversely related to food supply and mediated by nestling hunger or condition (*'food amount hypothesis'*, Mock *et al*, 1987). Evidence for this hypothesis was presented first by Drummond *et al* (1986) for the Blue-footed Booby, where survival of the second-hatched chick depends on the condition of its first-hatched nestling. Drummond and Chavelas (1989) confirmed for the same species, that when food ingestion was experimentally reduced, aggression increased but decreased again when food became less limited. The latter suggests that Blue-footed Booby nestlings follow the 'resource tracking hypothesis'.

From his work on herons and egrets, Mock (1985) proposes further that sibling competition by siblicide should be expected in species where food items are small enough to be monopolizable by single chicks and are fed to individual nestlings (*'prey size hypothesis'*, see also Pinson and Drummond, 1993). Mock (1985) argues that siblicide assumes that nestlings should be able to 'constitute a potentially lethal threat to one-another' (p.340), such as would be provided by weaponry. Bee-eaters are single-loading aerial hunters who nearly always feed single insects to single chicks, which means that sibling competition should be expected. Sibling rivalry and siblicide was studied in Blue-throated Bee-eaters by Bryant and Tatner (1990) who report that nestling Blue-throated Bee-eaters have a hook pointing downwards from the upper mandible (Fig. 7.2). Nestlings loose this hook before fledging during the time of their highest energy demand, a seemingly unique feature amongst birds (Bryant and Tatner, 1990). Runts have peck wounds, which make them more likely to die (62% of chicks with > 2 wounds die, 6% of runts with ≤ 2 wounds). The number of wounds depends on the condition of the immediate elder chick (Bryant and Tatner, 1990). All this points towards siblicide facilitating the high nestling mortality reported for Blue-throated Bee-eaters by Bryant and Tatner (1990). In this study, I aim to investigate whether this siblicide follows the obligate or facultative predictions, i.e. whether food plays a proximate rôle in sibling aggression. I study this by experiment describe competitive nestling behaviour, categorize it, and assess if it is mediated by hunger, condition or other nestling characters.

7.1.6 Mechanism of nestling competition and siblicide

If Blue-throated Bee-eaters follow the resource tracking hypothesis, then if food becomes less limited after a period of food shortage, siblicide behaviour should cease and runts can recover. Experimentally satiated bigger chicks should give way to the runts to be fed by the parents and some recovery should be observed under this hypothesis. If siblicide is obligatory, no such recovery would be expected. Food allocation within the brood may be controlled by the

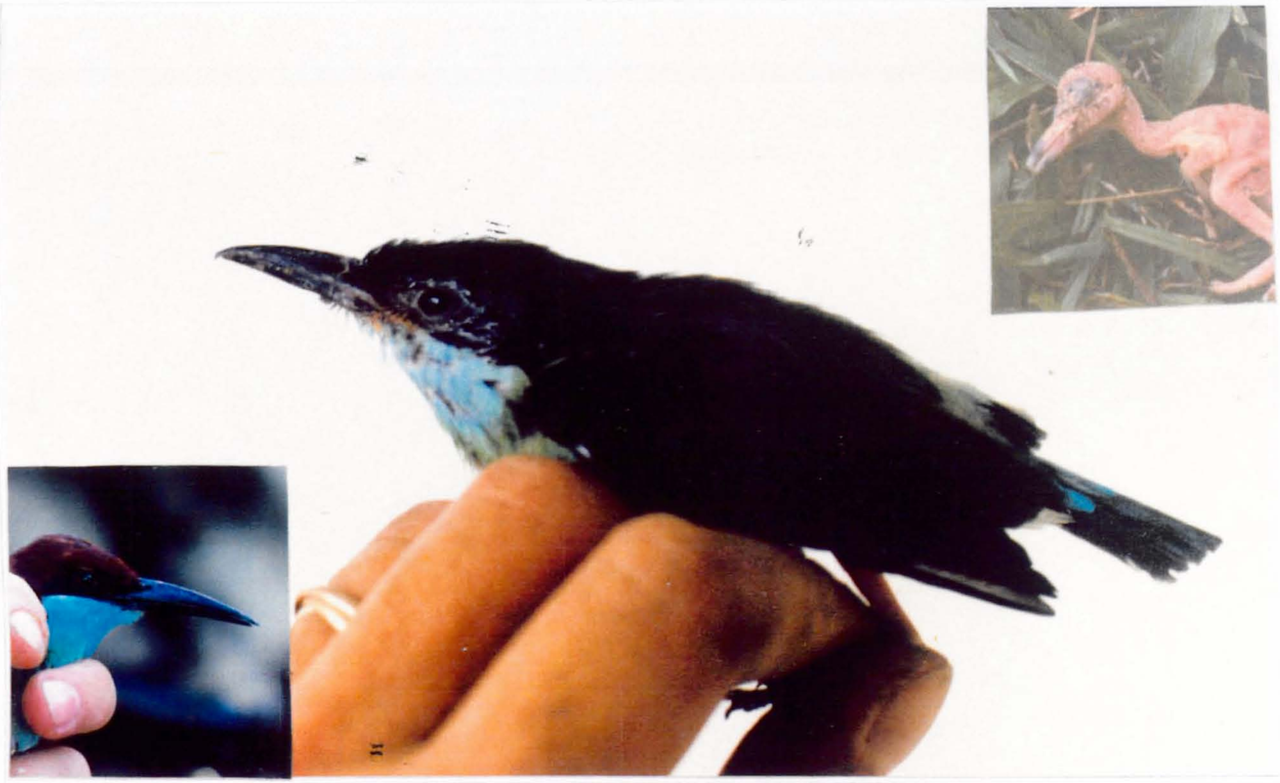


Figure 7.2: The mandibular hook: nestlings have a sharp hook pointing downwards from the upper mandible, over the slightly shorter lower manible (main picture). At hatching, the lower mandible is slightly longer or the same length as the upper mandible, and the hook is still soft (top right inset: a dead chick one or two days after hatching). At fledging, the hook is blunt and completely absent in adult (right bottom inset).

adults or the nestlings. There is little evidence in the literature that the adults choose which particular nestling to feed (McRae *et al*, 1993). As this would involve individual recognition of nestlings, it is even more likely in hole-nesting species such as bee-eaters that the control over how food is allocated to nestlings within a brood lies with the nestlings themselves. Nestlings may compete either (1) indirectly, for example by begging (Drummond and Chavelas, 1989) or by assuming a favourable position in the nest (McRae *et al*, 1993; Greig-Smith, 1985), or (2) directly by displacing each-other from good positions for feeding (McRae *et al*, 1993) or intimidating each-other during or outside adult feeding visits (Mock, 1985), or (3) with siblicidal behaviour such as pecks (Drummond and Chavelas, 1989) or attacks which weaken the losers and hasten the demise of runts. My aim here was to test these three hypotheses concerning the mechanism of brood reduction, by experiment and by direct observations of nestling behaviour in an artificial burrow in reaction to the calls of an adult arriving at its nest with food.

Nestling behaviour in an artificial nest

I first describe the behaviour of Blue-throated Bee-eater nestlings quantitatively. I have separated the behaviour into quantifiable aspects, paying particular attention to the aggressive behaviour of chicks towards each-other and to any other activities that might be involved in competition. I recorded nestling age and rank in the size hierarchy which might affect the behaviour of the chicks and give clues about how brood reduction is facilitated through competitive behaviour. I observed if chicks peck, push or run in response to the simulation of an adult arriving at the nest entrance; each behaviour supporting one of the three hypotheses above. Their response could be mediated either by 'hunger' (gut fullness, i.e. the limiting factor is how much food can be processed by the chick at one time) or by body condition (i.e. a well-fed chick in terms of condition is less aggressive or less eager to get to the food). The difference in response to the arriving 'adult' between chicks was therefore also tested before and after supplementary feeding.

7.1.7 The hook experiment

The mandibular hook of nestling Blue-throated Bee-eaters described by Bryant and Tatner (1990) may have two functions on which its role in nestling competition depends: to attack siblings or to grab hold of food. In the 'hook experiment' I tested if hooks speed up chick mortality or act in another way (e.g. on runt condition) to 'economize' the process of brood reduction. For this, I abraded the hooks of high ranking chicks in experimental broods and investigated the incidence of brood reduction and siblicide through monitoring wounds, growth rates and runt mortality. If the mandibular hook is a weapon to aid siblicide (Bryant and Tatner, 1990), and if siblicide is an adaptation for more efficient brood reduction, then runts in experimental broods should perish later, and total brood productivity in terms of number or quality of fledglings should be reduced (cf Magrath, 1989).

7.1.8 Summary of aims

In this chapter, I aim firstly to describe nestling growth and establish the evidence for nestling mortality in Blue-throated Bee-eaters. I investigate the incidence of mortality (whether it is a common occurrence) and if nestlings are likely to be under food constraint. As the age of most nestlings was not known, I first had to age nestlings indirectly. I compared different size measurements for their usefulness in nestling age estimates.

Secondly, some proximate factors of nestling mortality are investigated to establish ultimate factors, namely whether nestling mortality is adaptive according to the brood reduction hypothesis. The mechanisms investigated include in particular the roles of sibling aggression and food supply as predicted by the brood reduction hypothesis and resource tracking.

7.2 METHODS

7.2.1 Incubation and hatching

During 1989 to 1991, 47 nests were inspected regularly, starting from before or during laying. Of these, 25 had eggs. On a total of 196 visits, egg temperature was measured as: 1 = 'cool' (below about 27°C), 2 = 'lukewarm' (about 28-29°C) or 3 = 'warm' (above about 29°C). This included clutches that were subsequently deserted, but data for clutches that were not warm or lukewarm during at least some visits were discarded. Clutches with lukewarm or warm eggs were assumed to be incubated at least partly. In order to determine incubation period in this way, nests must be inspected prior to laying and visited at least once a day until clutch completion. The birds are sensitive to disturbance especially during and before laying, and a large number of pairs deserted those nests that were frequently monitored before laying (see Chapter 2). It is likely furthermore, that adults neglect eggs after being repeatedly disturbed in the nest during monitoring. The disturbance caused by frequent monitoring during laying and incubation would thus introduce bias. I therefore visited each nest only once every 2 or 3 days, and estimated laying dates of eggs laid in the intervals.

Hatching time, the time it took for each egg to hatch, was estimated from hatching and hatching dates. Hatching dates were either directly observed in the field or estimated from nestling age (section 7.2.3 below). For each egg, I estimated the longest and shortest possible hatching time in days. The longest possible hatching time (LPHT) was calculated as the hatch date minus the last date the nest was observed as empty, which is the earliest day an egg could have been laid; the shortest possible hatching time (SPHT) equals the hatch date minus the date of inspection when the last egg was first found in the nest. For example, if visit A was made on day 1 and an egg had appeared before the next visit on day 4, and the hatching date was estimated to be day 28, then LPHT was 27 days (day 28 - day 1) and SPHT was 24 days (day 28 - day 4). In broods for which I had information of individual laying dates, I assigned eggs in sequence to hatched nestlings. Most broods did not hatch more than 4 nestlings, so that I have excluded 5th nestlings or pooled them with 4th hatched chicks for reasons of sample size. Hatching intervals were recorded as hatch day difference (HDD), in relation to the eldest chick, for which accordingly HDD = 0. Hatching spread is the HDD between the first and last hatched nestling.

7.2.2 Nestling energy requirements

Relative size of insects was measured for all insect types that were identified in feeding observations (Appendix 2), on a scale of 1-7 (1 = very small, 2 = small, 3 = small-medium 4 = medium, 5 = medium-large, 6 = large, 7 = very large). A combination of insect length and width relative to the bill length of provisioning adults was used as insect size (see Chapter 5).

Insect wet mass (IWM) was calculated from 6 samples of freshly frozen Grasshoppers Acrididae commercially raised, consisting of between 7 and 22 grasshoppers each, which were fed to nestlings as part of the supplementary feeding experiment (section 7.3.5). Grasshopper 'feed mass' was estimated by weighing the nestling before and after feeding and subtracting the first value from the second. Wet mass was also available for large Isoptera alates (medium insect, size = 4; Appendix 2; N = 6 samples of between 4 and 14 alates) caught near the colony and also fed to the nestlings in the supplementary feeding experiment. One sample of 28 medium Isoptera alates (small insects, size = 2) was administered.

7.2.3 Nestling growth and age

I increased inspection of nests with hatching eggs from every 2-3 days (pre-laying and laying) to daily inspections throughout 1989 to 1991. This allows chicks to be aged accurately to the nearest day, because hatchlings from the day of the previous visit could be distinguished from those of the same day because day-old chicks have longer wings than freshly hatched chicks (Bryant and Tatner, 1990) and the latter have a reddish 'complexion'. Freshly hatched chicks furthermore have abdomens replete with yolk, whereas in day-old chicks the abdomen is only about two-thirds filled. I aged 78 chicks this way. Chicks were re-measured every 2-3 days, until death or fledging (the maximum was 22 times). These data were used to describe growth patterns and to find the best size measurements or combination of size measurements to age nestlings which were not aged at hatching because their nests were first visited after they hatched. Chicks were numbered according to their place in the hatch sequence (Chickno or Rank). I used the observed hatch sequence when ranking chicks, except in a few broods in which the eldest chick died in its first week, in which case I moved their younger siblings up in the hierarchy. The first-hatched nestling (chick 1) usually survived, the second-eldest (chick 2) survived sometimes, and chicks that hatched third or later (chick 3 to 5) almost never survived. I therefore classed chicks 3 to 5 together as 'runts' (note: different classifications are used in sections 7.2.5, 7.2.6 and 7.2.7).

Nestling size was measured as wing length, bill length (from nostril), head & bill length, keel length (mean of two measurements at each capture), and body mass (all in mm, apart from mass which is in g; for descriptions see Chapter 2). Keel length cannot be measured reliably for chicks younger than about one week because their bones are still very soft. Keel length is therefore included here only for completeness. I measured mostly young, small chicks, but for each age the values were distributed normally (see Chapter 2). I therefore used parametric statistics throughout this chapter.

7.2.4 Nestling mortality

Predated and deserted broods, although rare, were excluded from the analysis of nestling mortality. The maximum nestling age of pre-fledglings in the nest during this study was 40 days; there was no record of a 39 day old nestling, but 2 chicks were still in the nest at 38 days. Allowing for an over-estimated outlier, the nestling period was set at 38 days for the analysis here. The first half of the nestling period lasted until age 19, and the second half started at day 20.

I used three measures of condition: Cond1 which is the relative thickness of the pectoral muscle (see Chapter 2 for detailed description); Cond2 which was calculated as observed mass minus expected mass from the growth curve for chicks of the same age and place in the hierarchy, divided by this expected mass; and Cond3 like Cond2 but the expected mass was taken from the growth curve of the top-ranking nestling (chick 1).

7.2.5 Experiments

I conducted 4 experiments. Three involved giving nestlings additional food (supplementary feeding experiment, induced recovery and observations in an artificial nest) and one removing the mandibular hook.

Supplementary feeding experiment

Of 8 experimental and control pairs of broods, 4 had two chicks, 2 pairs of broods had 3 and 2 had 4 nestlings at the start of the experiment. To satisfy the assumptions of independent sampling, only one chick was used per brood in any statistical comparisons. Controls are assumed to be under constraint, so the experiment was conducted in NH91, a dense colony where success was usually limited to 1 or 2 chicks (see Chapter 4). Bee-eater broods were probably under food constraint in general, see section 7.3.2. Broods were first inspected within the first two weeks after the first chick hatched. Only broods of two or more nestlings were used in the experiment. Broods were arbitrarily assigned to either the control or the experimental group, and pairs of broods were matched for (1) number of chicks at the start of the experiment and (2) date of first chick hatching (within 2 weeks of each-other).

In experimental broods, *all chicks except runts were fed* to see if hunger and condition of the top-ranking nestlings affect mortality patterns of runts. Broods in the control sample were handled but none of the chicks was provisioned. Runts were defined as follows: Chick 2 in broods of 2 or chick 3 (and 4) in broods of more than 2 chicks. In one brood of 3, the youngest nestling died on the day after the onset of the experiment and the second nestling was assigned the position of runt.

Chicks were fed or handled usually once a day (occasionally twice a day when I could not give the required amount on one visit) with insect food (live meal-worms, live-frozen, weighed grasshoppers and crickets, both provided by local pet-shops, or live alates of various large ant species collected locally). Each chick was given an amount corresponding to roughly 20% of its daily energy requirement (DME) as calculated in section 7.3.1, i.e. according to age between 0.7 and 2.5g (or about 10% of its own mass; see results, Table 7.3). Feeding usually commenced immediately after the brood was assigned to the experiment and until either all the runt had perished or until about day 20 when nestling mass decreases prior to fledging (section 7.3.3). Condition was measured as observed mass minus expected mass from the growth curve for chicks at the same place in the hierarchy, divided by the expected mass (Cond2, see section 7.2.4).

Induced recovery experiment

Some runts were expected to perish within the next 24 hours of inspection, as judged from a decline of condition (a score of 1 or less for Cond1), an empty abdomen and untypically lethargic behaviour (i.e. not perched on their legs; pers obs). Such runts were supplementary fed twice a day. This was intended only as an indicative study with no expectation of quantitative results. Nestlings were therefore included in the induced recovery experiment on opportunistic basis.

Nestling behaviour in the artificial nest

Bee-eater chicks were transferred temporarily to an artificial nest for the duration of observations. The artificial nest consisted of a plastic nest chamber, a see-through container of roughly the size and shape of a Bee-eater nest chamber, with a sandy floor, embedded into sand in a large plastic wash-up bowl (Fig. 7.3). The nest chamber was closed except for a tube attached to one end, 5 cm in diameter and 50 cm long, to mimic a burrow. Although some light came through this tunnel, the nest was kept in near complete darkness by a large photographic cloth. I watched the chicks in this artificial nest through a tight-fitting hole in the cloth and with the help of a dim red torch in the bowl. Trials involved true siblings from broods taken from nests. Chicks were left at the back end of the darkened chamber for a few minutes before each trial to allow them to settle down. Usually 2 siblings and sometimes whole broods were tried together. On any one day, 2-4 trials per brood were made in succession, lasting for a total duration of 15 to 45 minutes which the chicks spent in the artificial nest. First of all, I established how best to mimic an adult arriving at or entering the burrow by blocking the light coming in through the tube, making scraping sounds at the tube end etc. A tape-recording of the calls of an adult arriving with food, which had been recorded

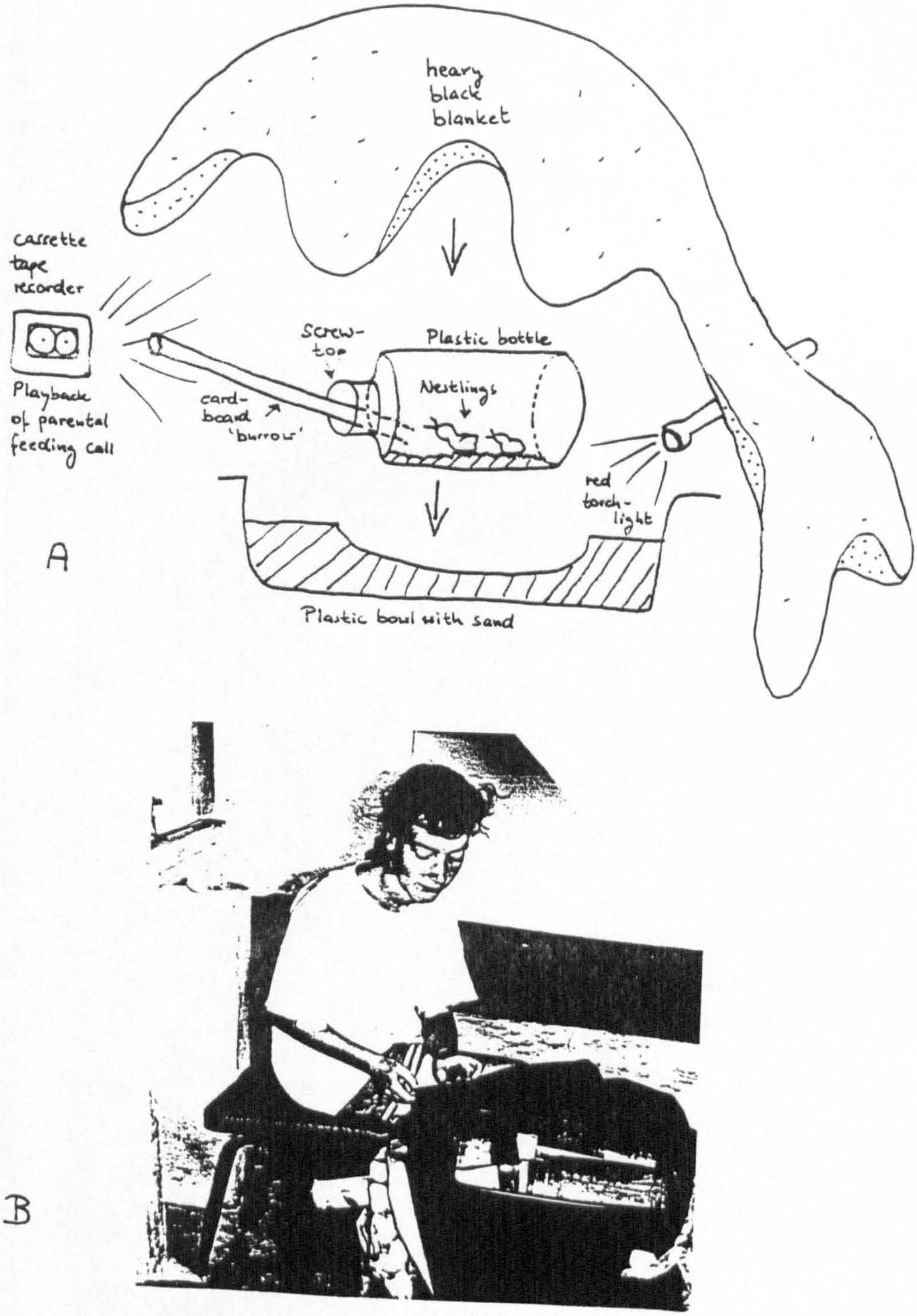


Figure 7.3: The artificial nest. A: diagram, B: photograph. During observations, the 'nest' consist of a plastic bottle which was covered completely by the blanket (apart from one end of the cardboard 'burrow'). The observer put her head through a close-fitting hole in the blanket. The brood was thus in near-darkness, with very little light coming in through the carboard 'burrow'. For observations, a dim red torch was used.

at a nest, played on a small tape recorder just outside the tube elicited the strongest response from the chicks in preliminary trials. The call of an adult arriving at the nest with food is very distinctive (see Chapter 4 for description), and most chicks repeatedly showed a marked response to it. Each trial lasted for 2-3 minutes of play-back, containing about 7-10 bouts of adult food calls. Secondly, nestling behaviour in the nest was described and divided into different activities (see results). Thirdly, observational trials were made before and after supplementary feeding. During each trial, the behaviour of each of the chicks was scored per activity to quantify nestling behaviour (see results).

For each chick, I noted condition or Cond1 (pectoral muscle thickness, see Chapter 2), whether the abdomen was replete (to allow some indication of 'hunger'; see also Chapters 2 and 5), if eyes were open, closed or opening and its place in the size hierarchy (chickno). Rank = 1 for the eldest chick in trials with 2 chicks or the eldest two chicks in trials with 3 or 4 chicks, and rank = 2 for the runt (which was chick 2 in a trial with 2 chicks, or chicks 3 (and 4) in trial with 3 (or 4) chicks). For each chick, the nest from which it comes was recorded together with the time and date of the trial, and the trial number for the particular nest and day.

The hook experiment

To see if wounding and mortality pattern of runts was directly affected by the mandibular hook of their elder siblings, an experiment was conducted abrading mandibular hooks. Broods which were first inspected within a week of the first chick hatching were arbitrarily assigned to either the control or experimental sample. Pairs of experimental and control nests were matched only when they had the same number of hatchlings, and if their hatching dates were close to each-other (usually within a few days, always within the same month). Seven pairs of experimental and control broods were thus matched; two more un-matched 'pairs' of control and experimental nests were included in unpaired analyses. In experimental broods, the mandibular hooks of all chicks except the smallest runt were filed-off carefully before it became sharp with a commercial nail-file. The filing was repeated every few days while the hook was growing. In control nests, hooks of all nestlings were left intact, but the nestlings were handled every 2 days.

7.3 RESULTS

In this section I report the results relevant to nestling mortality and siblicide. These include incubation period and incubation during laying, the discrepancy between average nestling energy requirements and observed feeding rates, nestling growth and mortality, ageing of nestlings and the results obtained from the 4 experiments.

7.3.1 Incubation and hatching

The results obtained from data collected during laying and incubation include hatching spread, incubation period, incubation during laying, some laying intervals and egg temperatures.

Hatching synchrony and spread

The Hatch Day Difference (HDD) within broods was significantly different between each of the first three nestlings (Table 7.1). Hatching intervals between subsequent nestlings increased from 1 day (between chick 1 and 2) to 1.5 days (between chick 2 and 3). Chick 4 did not hatch significantly later than chick 3, probably because of the large variation in HDD with respect to the 3rd-hatched chick, ranging between 1 and 9 days. In all subsequent analysis, I pooled hatching times for 3rd and 4th-hatched chicks because their hatch days did not differ significantly.

Incubation period

Out of 48 aged nestlings for which I assigned a longest or shortest possible hatching time (LPHT and SPHT), the 14 used in this analysis had either (1) a LPHT of 20 days or less (i.e. their hatching time must have been only 20 days or less), (2) a SPHT of at least 23 days (i.e. their hatching time was 23 days or longer) or (3) an estimate of within 5 days of the observed period between laying and hatching. The mean SPHT was 24 days (range = 19-26), and the mean LPHT was 21 days (range = 13-28; no nestling could possibly hatch only 13 days after the egg was laid, this was probably an extreme under-estimate because of bias in hatch day estimates. The next-highest LPHT was 17 days which is more realistic and was therefore used instead of 13 days). The two values overlapped because they were derived from different nestlings. The average incubation period was therefore around 22.5 days; the observed range was 13 to 26 days, i.e. from the smallest value of the LPHT to the highest value of the SPHT. The mean incubation period for the first-hatched nestling was 24 days (range 23-25; N=6), compared with 23 days (range 20-26) for the second chick (N=3) and 20 days (range 17-23) for runts (N=5).

Egg temperature and hatching success

Hatching success (chicks hatched per total eggs laid; mean = 0.74, see chapter 4) correlated with the temperature of the clutch (Spearman Rank Correlation coefficient $r = 0.175$, $p < 0.05$, N=113 visits to broods for which hatching success was known). The median hatching success for warm clutches was 1.00 (N=18), for lukewarm clutches 0.65 (N=48) and for cold clutches 0.00 (N=47; range for each temperature = 0.00 -1.00). Egg temperature therefore seems to be a reflection of incubation constancy and was used in the following section to investigate incubation pattern.

Incubation during laying

For 196 inspections of 25 clutches during and after laying, the clutch was cool 43.4%, lukewarm 42.4% and warm 14.2% of visits. All clutches with single eggs which were not subsequently deserted were lukewarm when inspected, indicating that they were being incubated. Unless these clutches were all complete clutches of a single egg, this shows that partial incubation commenced after the first egg had been laid. The temperature of a clutch during inspection did not increase with the number of eggs present in a clutch in general (Median = 3 eggs, Spearman Rank Correlation coeff. $r= -0.092$, $p>0.1$) and thus showed no clear increase with laying stage. Neither did the temperature increase on average with each successive egg (Table 7.2, first column of χ^2), or at any particular laying stage after any one egg had been laid (Table 7.2, second column of χ^2). Clutch temperature may have increased slightly with the time of day between 07:00 and 18:00 ($r= 0.108$, $p = 0.065$), but the time of day and number of eggs in the clutch did not correlate ($r= 0.066$, $p>0.1$). There was therefore no evidence for an increase in incubation during the laying phase, such as would be expected if incubation switched from part to full incubation at any particular laying stage. After clutch completion, i.e. generally in clutches of 3 or 4 eggs, the median clutch temperature was still only lukewarm. If full incubation is indicated by 'warm' egg temperatures, then eggs were rarely fully incubated throughout the incubation period.

Laying intervals

The model of hatching intervals based on incubation onsets assumes that the birds lay an egg every 2 days (see Fig. 7.1) as reported for Blue-throated Bee-eaters by Bryant and Tatner (1990). In this study, I could confirm a clear one-egg-per-two-day pattern only in one out of the 19 broods for which some data on laying sequence were available. In 4 broods, the laying interval was longer than predicted; in 3 of these broods this was due to the last egg which appeared 1, 3 and 9 days later than expected. In two broods, a last egg appeared in the clutch more than 20 days after the penultimate egg. The data for laying intervals of a further 12 broods were inconclusive.

7.3.2 Nestling energy requirements

Whether nestlings are under food constraint can be shown by calculating their daily metabolized energy in terms of wet insect mass and comparing it to average insect mass delivered by the parents. The daily energy requirement for a chick in terms of insect wet mass (IWM) depends on its daily metabolized energy (DME):

$$\begin{matrix}\textit{DME as IWM}\\ \textit{per day}\end{matrix} = \frac{\textit{DME}}{\textit{energy density}} \; \frac{\textit{dry mass content}(\%)}{\textit{assimilation efficiency}} \tag{7.1}$$

The DME for Blue-throated Bee-eaters chicks was calculated by Bryant and Hails (1983; their raw data are listed in Table 7.3 below). The dry mass content of insects = 32% (average for flies, dragonflies and grasshoppers; Bryant and Bryant, 1986). In those 32% dry mass, the average energy density = 24 J/mg (Bryant and Bryant, 1986); i.e. 3.125g of wet insects contain 24kJ. The assimilation efficiency for insect food of Blue-throated Bee-eater nestlings

Table 7.3 a: **Chick energy requirements** Chick mass for a chick at given age was taken from the raw data of this study, means per day, of all aged chicks (see section 7.3.3), for nestlings with the least likelihood of retarded growth (Chick 1). Daily metabolized energy DME for a chick in kJ/day was taken from Bryant and Hails (1983; Bryant, pers comm). This was translated into IWM (insect wet mass; such as grasshoppers) by using Equation (7.1) to calculate DME as IWM. Thus, a newly hatched nestling needs to be fed the equivalent of 3.65g or 57.4% of its body mass in fresh insects such as grasshoppers every day, to meet its daily metabolized energy demands.

Age (days) (0 = hatch day)	Mass Chick 1 (g)	DME (kJ /day)	DME as insect wet mass IWM (g)	DME - IWM mass as % chick mass
0	6.36	16	3.65	57.4
1	6.68	17	3.88	58.1
2	7.07	22	5.03	71.1
3	9.56	25	5.71	59.7
4	10.94	31	7.08	64.7
5	11.17	35	8.00	71.6
6	13.23	39	8.91	67.7
7	13.99	41	9.37	67.0
8	23.60	44	10.05	42.6
9	23.25	46	10.51	45.2
10	22.73	49	11.19	49.2
11-18	29.58	54	12.34	41.7
19-29	30.61	49	11.19	36.6

Table 7.3 b: **Feeding rates per chick compared with mean brood age, for 9 nests during 70 observation periods.** Results of an ANOVA controlling for nest are included.

Mean nestling age	1-10 days	11-18 days	> 18 days	Total
Mean feeding rate per nestling	0.36	0.40	0.67	0.49
N (observation periods)	11	34	26	71

F (age) = 14.804, df = 2, $p < 0.001$
F (nest) = 5.098, df = 8, $p < 0.001$
F (nest x age) = 1.677, df = 9, $p > 0.10$

is 0.57 (Bryant and Bryant, 1988). For nestlings between 11 and 18 days old, DME = 54kJ/day (Bryant and Hails, 1983). DME therefore corresponds to 12.3g of fresh insects (equation 7.2; Table 7.3 a):

$$\frac{54kJ}{24kJ}\ \frac{3.125g}{0.57} = 12.3g \tag{7.2}$$

As a general indication of how much of the DME of growing nestlings each chick receives on average, provisioning rates and insect sizes were used to calculate an estimate of IWM provisioned on average per nestling, which could then be compared directly to the DME as IWM calculated above. Because of their different food values, prey items were sized differently for different insect orders on a scale of sizes between 1 and 7 (see methods in Chapter 5). Insect masses for 3 sizes were established: an insect of size 1 (medium Isoptera alate) weighed 0.050g on average, of size 3 (large Isoptera alate) 0.088g (0.067 - 0.100g) and size 4 (medium-size grasshopper) 0.133g (range = 0.128 - 0.143).

Feeding rates varied significantly between different pairs and with brood age (for 9 different broods, N = 70 periods of observations, Table 7.3 b; see also Chapter 5). The mean size of insects was 3.7 (SD = 1.36; range = 1-7), corresponding to 0.133g per insect. For all feeding rate observations, including those where prey was not identified and sized, the median feeding rate was 1.9 (range = 0 - 60; N = 128 observation periods at 53 nests, see methods in Chapter 5). Birds were seen to provision between 07:20 and 19:20hrs approximately, i.e. during about 12 hours per day. The average IWM brought to a nestling per day was therefore

$$1.9\ \frac{feeds}{hr} * 0.133g * 12hrs = 3.03g\ \frac{fresh\ insect}{per\ chick,\ day} \tag{7.3}$$

This would meet nearly the daily requirement of a newly hatched chick, but only about one-quarter of the average DME requirement of a nestling between 11 and 18 days old (Table 7.3 a), and it is therefore likely that there was severe food constraint on most nestlings. This average, however, was probably an under-estimate, for which there are several possible reasons. There were large differences both in feeding rates and in prey sizes (ranging from 0 to 60 per hour, see above) brought to broods. For 9 broods for which feeding observations were available, including prey items and sizes and brood ages, during a total of 71 observation periods the mean feeding rate was only 0.5 feeds per chick per hour (Table 7.3 b), compared to 1.9 in the larger sample above. Furthermore, feeding rate significantly increased with brood age.

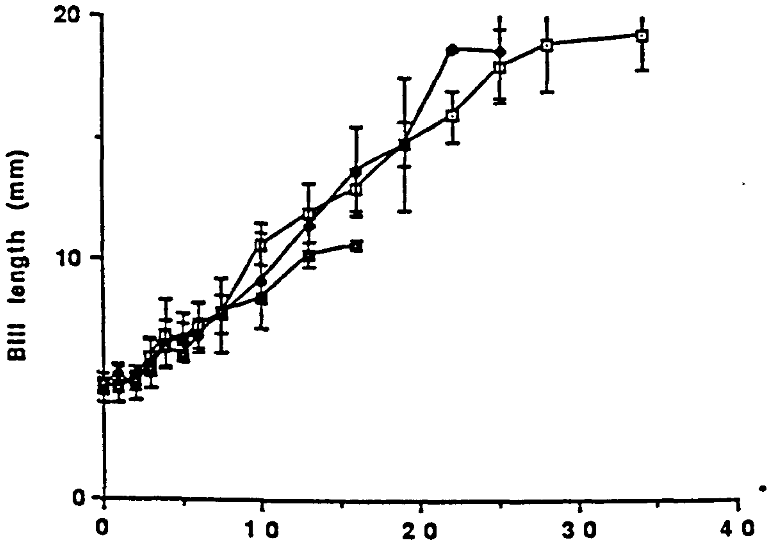
7.3.3 Nestling growth and age

Growth patterns were examined for nestlings in different ranks in the size hierarchy. The best-fitting Principal Component representing nestling body size was compared to single size variables in its usefulness for ageing nestlings with growth curves.

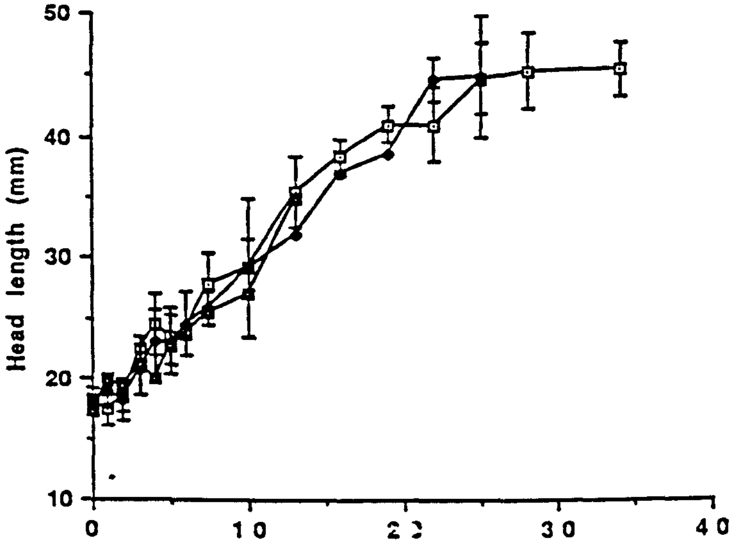
Growth pattern: rate and absolute size

Bills and heads grew at similar rates regardless of hatch sequence (Fig. 7.5 a and b). Although there was some variation in size of nestlings at hatching, different older nestlings of the same age varied more in size because nestlings grew at different rates (see Fig. 7.6). Most measures of growth were therefore heteroscedastic, i.e. larger nestlings were more variable in size than smaller nestlings. This was so particular for wing length (WING) and mass (Fig. 7.5 c and d). Wing length differed slightly between first, second and later hatched nestlings. Second-hatched chicks showed significantly retarded growth and low mass after the age of 6-8 days (Table 7.4 a and b, columns 5 and 6). Runts started to experience reduced mass (compared to the first nestling) sooner than the second-hatched chicks, at 4-5 days (Table 7.4 b, columns 7 and 8), so that by the second week, the size hierarchy was further exaggerated by retarded growth of runts, particulary in their body mass (Fig. 7.5 d). Second-hatched chicks also grew more slowly and remained smaller than the eldest siblings, until the end of their third week, when the surviving second chicks caught up with the top ranking nestlings first in size (day 18, Fig. 7.5 a-c) and later also in mass (day 24, Fig. 7.5 d). It is possible that second hatched nestlings benefited from improved allocation of food once their elder siblings had reduced their energy requirements before fledging.

(Figure 7.5)


Bill length (mm)
20
10
0
0
10
20
30
40

A


Head length (mm)
50
40
30
20
10
0
10
20
30
40
Age (Days)

B

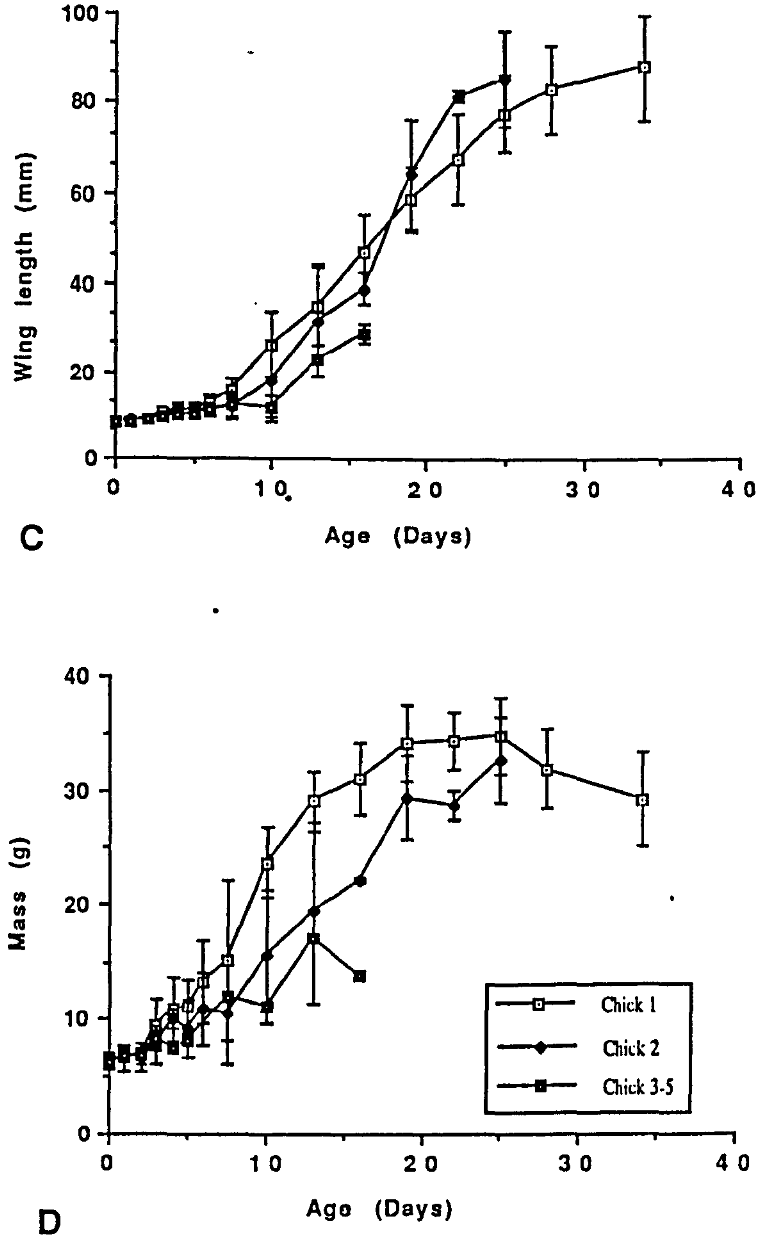


Figure 7.5 a-d: Bill length, Head & Bill length, Wing length and mass changes with age, seperately for each nestling in the size hierarchy. Means of repeat measurements (see text).

Figure 7.6: Two nestlings of the same brood: Asynchronous hatching produces a size hierarchy of nestlings within Blue-throated Bee-eater broods

Table 7.4: T-tests of nestling size (A; wing length) and mass (B; g) at different ages, between nestlings of different ranks (where nestling rank in the hierarchy and chick number are the same). Note that nestlings were re-measured not more than every other day, so any one 2-day-age-category only ever includes one measure per nestling.

p: (*) = nearly significant at the 5% level, * = significant at the 5% level, ** significant at the 1% level.
df: degrees of freedom; depends on whether variance was different for the ranks compared

A

	Mean wing lengths:			Differences between nestling ranks:					
Age (days)	Chick 1 (SD,N)	Chick 2 (SD,N)	Chick 3 (SD,N)	1->2 t (df)	p	1->3 t (df)	p	2->3 t (df)	p
0-1	8.29 (.83,14)	8.34 (.58,19)	8.28 (.44,9)	-0.23 (31)	0.819	0.03 (21)	0.979	0.29 (26)	0.771
2-3	9.58 (.99,12)	8.90 (.88,10)	9.13 (.64,8)			1.15 (18)	0.266	-0.61 (16)	0.552
4-5	11.00 (1.54,12)	10.79 (1.48,14)	10.00 (1.16,4)	0.36 (24)	0.721	1.18 (14)	0.256	0.97 (16)	0.344
6-7	13.80 (1.99,10)	11.14 (1.86,7)	12.00 (2.83,2)	2.78 (15)	0.014 *	1.11 (10)	0.292	-0.53 (7)	0.615
8-9	20.67 (3.06,3)	14.33 (3.06,3)	-	2.54 (4)	0.064 (*)	-		-	
10-11	27.67 (7.89,6)	17.75 (10.6,8)	11.80 (2.3,5)	1.92 (12)	0.080 (*)	4.68 (12)	0.003 **	1.52 (12)	0.166
12-13	32.40 (8.3,5)	29.50 (3.5,2)	22.00 (- ,1)	0.46 (5)	0.668	-		-	
14-15	39.00 (10.1,6)	32.50 (13.8,6)	23.00 (- ,1)	0.93 (10)	0.376	-		-	
16-17	48.29 (6.5,7)	41.00 (- ,1)	28.50 (2.1,2)	-		4.07 (7)	0.005 **	-	
18-19	57.60 (5.0,5)	63.50 (12.0,2)	-	-1.01 (5)	0.359	-		-	
20-21	63.17 (10.7,6)	-	-	-		-		-	
22-23	67.50 (9.9,6)	81.00 (1.4,2)	-	-1.83 (6)	0.117	-		-	
24-25	80.33 (7.2,3)	85.00 (16.9,2)	-	-0.45 (3)	0.685	-		-	
26-27	69.20 (25.4,9)	84.50 (7.8,2)	-	-0.81 (9)	0.437	-		-	

B

	Mean nestling mass:			Differences between nestling ranks:					
Age (days)	Chick 1 (sd,N)	Chick 2 (sd,N)	Chick 3 (sd,N)	1->2 t (df)	p	1->3 t (df)	p	2->3 t (df)	p
0-1	6.55 (.96,13)	6.64 (.78,20)	6.42 (.59,9)	-0.28 (31)	0.779	0.37 (20)	0.718	0.74 (27)	0.464
2-3	8.41 (2.1,13)	7.27 (1.5,10)	7.65 (1.3,8)			0.93 (19)	0.366	-0.56 (16)	0.582
4-5	11.08 (2.4,12)	9.68 (1.8,13)	8.04 (1.7,7)	1.65 (23)	0.113	2.95 (17)	0.009 *	1.99 (18)	0.062 (*)
6-7	13.76 (3.6,10)	10.95 (3.5,8)	12.05 (2.9,2)	1.65 (16)	0.118	0.62 (10)	0.550	-0.40 (8)	0.697
8-9	23.37 (2.9,3)	13.27 (2.9,30	-	4.28 (4)	0.013 *	-		-	
10-11	23.72 (3.1,9)	15.60 (6.5,9)	11.06 (8.4,5)	3.39 (12)	0.006 **	7.96 (12)	0.000 **	1.49 (12)	0.163
12-13	29.13 (1.9,6)	20.45 (2.1,2)	14.20 (- ,1)	5.56 (6)	0.001 **	-		-	
14-15	28.98 (4.0,6)	19.38 (8.7,6)	19.80 (- ,1)	2.47 (10)	0.03 *	-		-	
16-17	31.36 (2.5,8)	22.20 (- ,1)	13.80 (.42,2)	-		9.20 (8)	0.000 **	-	
18-19	34.26 (3.6,5)	29.33 (3.7,3)	-	1.85 (6)	0.114	-		-	
20-21	33.73 (2.4,7)	-	-	-		-		-	
22-23	34.73 (3.1,6)	28.65 (1.2,2)	-	2.55 (6)	0.43 *	-		-	
24-25	34.83 (3.8,3)	35.25 (2.8,2)	-	-0.13 (3)	0.903	-		-	
26-27	32.79 (4.5,9)	30.15 (3.0,2)	-	0.77 (9)	0.463	-		-	

The slight wing length retardation of chick 2 towards the end of the first week and at the beginning of the second week (Table 7.4 a) was accompanied by a much larger and more significant discrepancy of mass (Table 7.4 b), indicating that the deterioration was mainly in mass. In Chicks 3-5, mass discrepancy with chick 1 clearly went along with size retardation (shorter wing length than chick 1; Table 7.4 a). Second-hatched nestlings therefore seemed to deteriorate mainly in condition, whereas runts (chicks 3-5), lacking these reserves and getting even less food, showed stunted growth.

Growth pattern: shape

Nestling mass increased slowly until about the third or fourth day. Relatively unretarded growth in the eldest nestling continued at high rate of mass gain from day 7 to day 20. The eldest nestling loses mass prior to leaving the nest (Fig. 7.5 d; also Fig. 1 in Bryant and Tatner 1990).

The growth curve for wing length also followed a 4th order polynomial for all nestlings, in particular the eldest (Fig. 7.7 a-c). Bill length (BILL) and Head length showed a less pronounced sigmoidal growth pattern than wing length and mass. The first and second nestling had similar growth patterns in BILL and Head (with clearly overlapping standard deviations, Fig. 7.5 a and b). All runts that were aged in the field died before their 20th day, after general retardation in growth around day 13 (Fig. 7.5 c). The wings of runts grew slowly at first but faster later; this pattern was not repeated for BILL and Head, however. Too few of the aged runts survived long enough for a quantitative comparison with the first two hatchlings beyond the early growth phase.

Using growth data of aged chicks to estimate nestling age

Principal Component analysis was used to determine which nestling size measures are most indicative of nestling age. These size variables were then used to age nestlings where the age was not known.

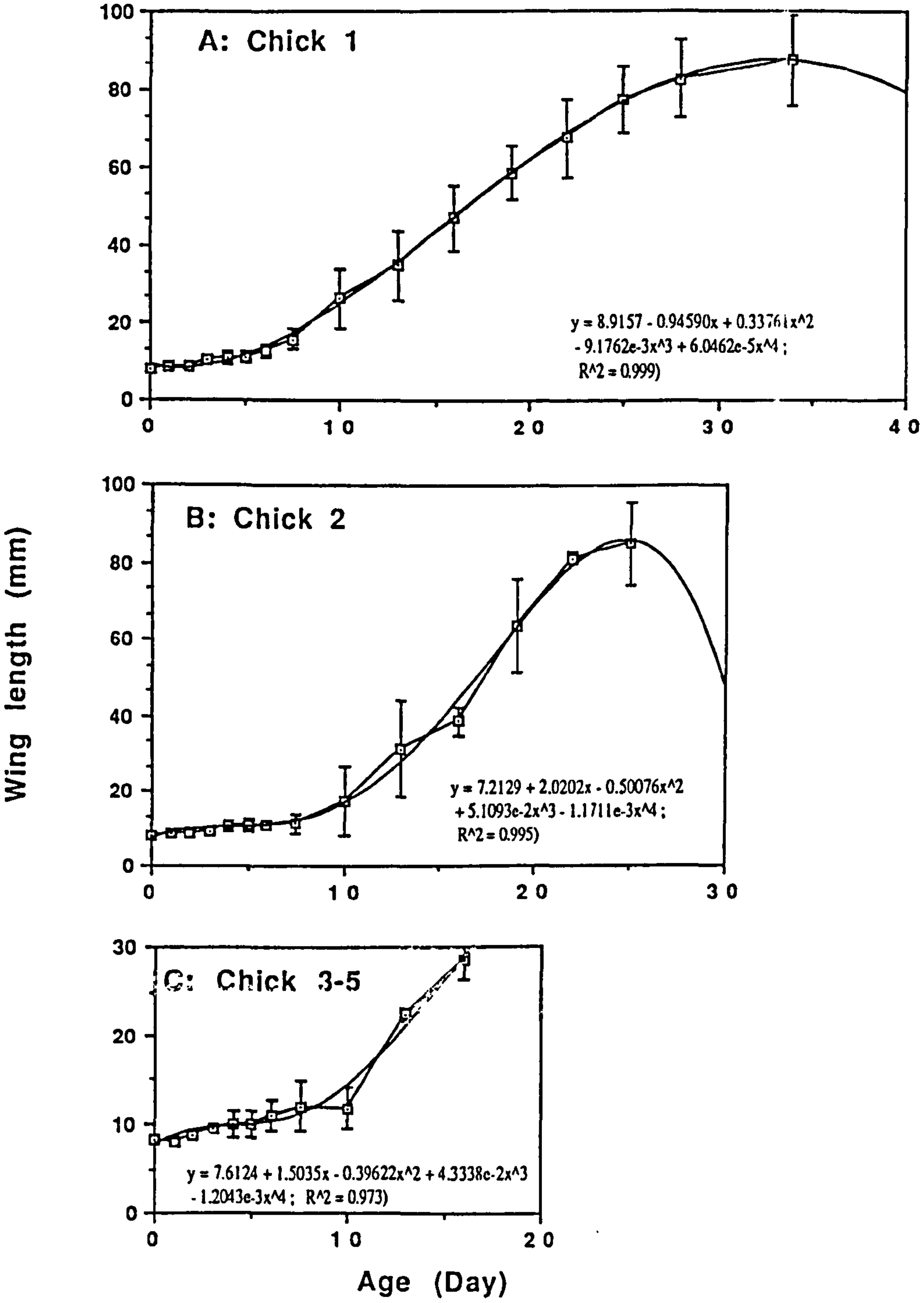


Figure 7.7 a-c: 4th order polynomial curves fitted to wing growth, separately for first, second and later-hatched chicks.

Principal Component Analysis

The general methodology of Principal Component Analysis (PCA) is introduced above (Chapter 2). When used for ageing growing organisms, the first principal component (PC1) should be a combination of measures that highly correlate with age. All body size measures were highly correlated with age as expected (Table 7.5). I used the 4 biometric measures in various combinations to find the PC1 that explained the highest amount of variation. Table 7.6 summarizes the results: wing length and BILL combined give the best PC1. The vector score for a nestling's combination of wing length and BILL measurements on any one capture was calculated as follows:

$$\text{PC1} = 0.51\ (\text{BILL}) + 0.51\ (\text{wing length}) \qquad \textbf{(7.4)}$$

For each nestling on a given day, a PC1 score was calculated using equation 7.4. For first and second hatched nestlings, wing length and BILL produced the best fitting PC1, whereas for later hatching chicks, the amount of variation explained by PC1 was higher if mass and Head were included. Table 7.7 summarize and equations 7.5 to 7.7 the PC1s derived for first hatched, second hatched and third to last hatched respectively:

$$\text{PC1}_{\text{I}}\ (\text{Chick } 1) = 0.99\ (\text{wing length}) + 0.99\ (\text{BILL}) \qquad \textbf{(7.5)}$$

$$\text{PC1}_{\text{II}}\ (\text{Chick } 2) = 0.98\ (\text{wing length}) + 0.98\ (\text{BILL}) \qquad \textbf{(7.6)}$$

$$\text{PC1}_{\text{III}}\ (\text{Chick } 3\text{-}5) = 0.93\ (\text{wing length}) + 0.93\ (\text{BILL}) + 0.98\ (\text{Head}) + 0.99\ (\text{mass}) \qquad \textbf{(7.7)}$$

Evaluation of the use of PC1 for ageing nestlings

The PC1 calculated from wing length and BILL (equation 7.4) correlated better with age than any of the single variables (Table 7.5), but all size variables correlated highly and significantly with age. The improvement on correlations of wing length, BILL and head length on age achieved by PC1 was negligible. When I compared PC1 of the first hatched nestling - the chick that is most likely to grow relatively unrestrainedly (see Emlen *et al*, 1991) - with its components BILL and wing length (Figs. 7.8 d and c, 7.7 a), the improvement in smoothness and linearity of the growth curve achieved by PC1 was so slight that it did not justify using a multivariate factor. Indeed, if fitted with a polynomial curve, age was expressed most closely by wing length (see below).

Table 7.5: Spearman correlation of body size and mass with age

	coeff	p	N
wing length	0.958	***	235
BILL	0.958	***	237
Head	0.954	***	165
Keel	0.780	***	72
Mass	0.911	***	247
PC1	0.964	***	164

Table 7.6: PCA summary: components, Eigenvalues and percent variance explained by the first Principal Component (PC1) using different combinations of body size measurements. PCs are ordered by the % variation they explain.

Components used in PCA	Eigenvalue of PC1	% variation explained by PC1
Wing length, BILL	1.962	98.1
BILL, Head	1.949	97.4
Wing length, Head	1.937	96.8
BILL, wing length, Head	2.900	96.6
BILL, Head, mass	2.862	95.4
BILL, mass	1.906	95.3
Wing length, Head, mass	2.846	94.9
BILL, wing length, Head, mass	3.897	94.8
Wing length, mass	1.896	94.8
BILL, wing length, mass	2.842	94.6

Table 7.7: **Components, Eigenvalues and percent variance explained by the best-fitting first Principal Component (PC1) for first, second and later hatched nestling biometrics** For Nestling 1 and 2, PC1 is composed of wing and bill length, whereas in later hatches chicks, weight and head length are also included in PC1 (see text)

Number in hatch sequence	Parameters used	Eigenvalue of PC1	% Variance explained by PC1
1	WING, BILL	1.94	97.2
2	WING, BILL	1.94	96.8
3-5	WING, BILL, Mass, head	3.66	91.5

Ageing young nestlings by wing length

Wing length in relatively unrestrained growth (the eldest nestling, Emlen *et al*, 1991) is best fitted with a 3rd or 4th degree polynomial curve (Figs. 7.8 b and 7.7 a) when compared with a linear or second order polynomial model (Fig. 7.8 a). The amount of variance explained by either model, however, was only useful for comparisons between the models and could not be used for absolute considerations because the data were heteroscedastic. For the same reason I cannot test whether the 4th degree polynomial curves that model the wing growth data of later-hatched nestlings (Fig. 7.8 b and c) differ significantly from unrestrainedly growing chicks or from each-other. Because of the possibility of stunted growth, however, I aged eldest, second and later hatched nestlings separately.

The age of nestlings (in days) was determined from wing length with the following fourth-order polynomial equations,

for chick 1, $\text{age} = 8.92 - 0.946\ \text{WING} + 0.338\ \text{WING}^2 - 0.00918\ \text{WING}^3 + 6.05e^{-5}\text{WING}^4$ (7.8)

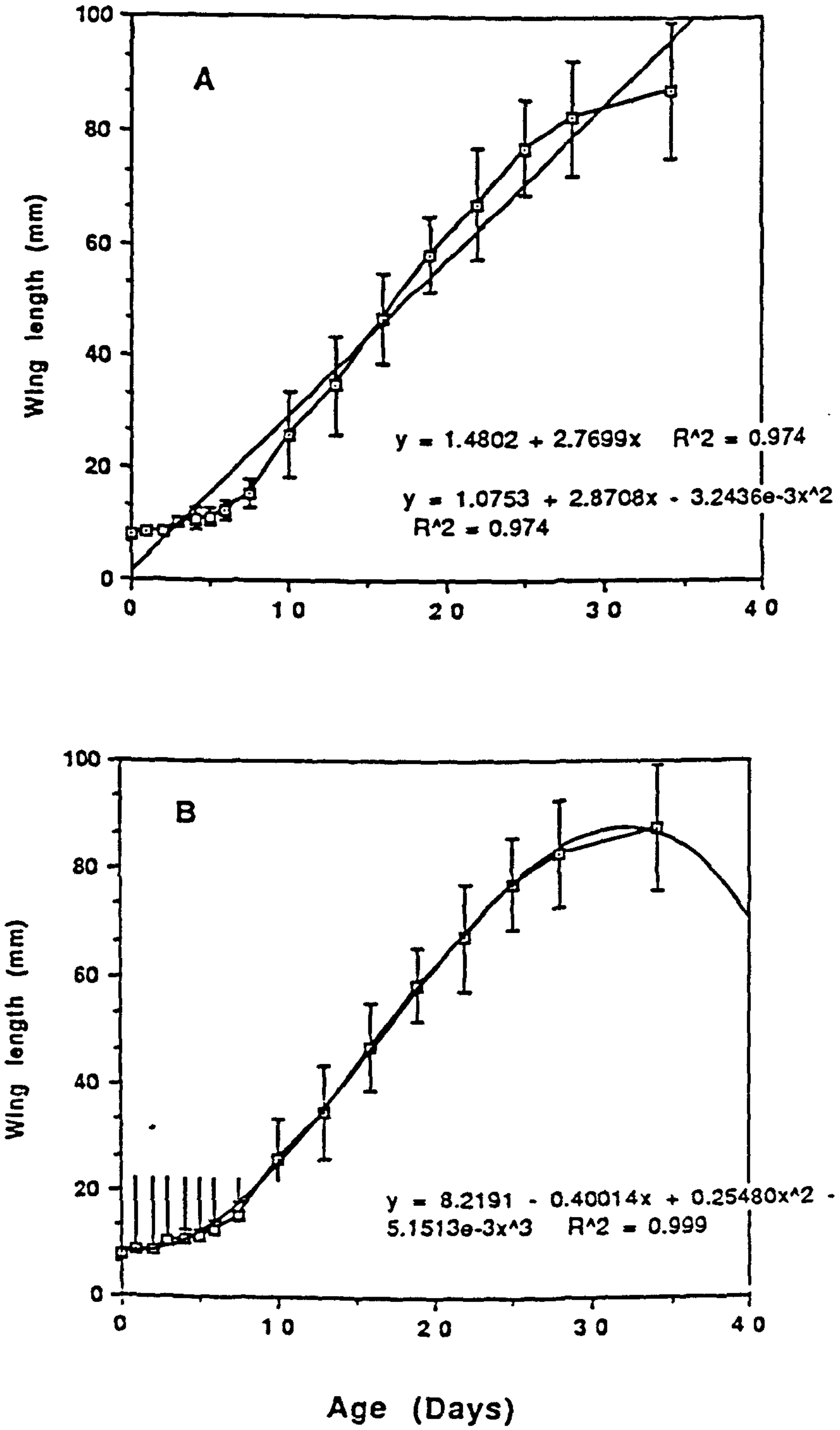
for chick 2, $\text{age} = 7.21 + 2.02\ \text{WING} - 0.501\ \text{WING}^2 + 0.00511\ \text{WING}^3 - 1.17e^{-3}\text{WING}^4$ (7.9)

for chicks 3-5, $\text{age} = 7.61 + 1.50\ \text{WING} - 0.396\ \text{WING}^2 + 0.00433\ \text{WING}^3 - 1.20e^{-3}\text{WING}^4$ (7.10)

Variation in wing length increased with age, so that the estimate of a chick's age from wing length becomes less reliable with age. The day of hatching for each nestling was therefore calculated from its earliest capture, and only if that capture turned out to be within the first two weeks after hatching (up to day 14; see query in Appendix 4.9). With this method, the age of 97 nestlings was estimated. For these nestlings, chick age at first capture was used to estimate the chick's hatch date which was used in turn to calculate an estimated age of the chicks at later captures by subtracting the hatch date estimate from the day of capture.

The high natural variation in body size between nestlings of the same age produces error when ageing nestlings by their wing length. To investigate if it is possible to age nestlings older than 14 days from a single wing length measurement, nestling age was calculated directly for each capture from the corresponding wing length using the curves in equations (7.8 - 7.10; see also Fig. 7.7 a-c), and compared to the previous age estimates (made either in the field or from wing length at first capture, as above). Age derived by using wing length

(Figure 7.8)


A
Wing length (mm)
100
80
60
40
20
0
0
10
20
30
40
y = 1.4802 + 2.7699x R^2 = 0.974
y = 1.0753 + 2.8708x - 3.2436e-3x^2
R^2 = 0.974
B
Wing length (mm)
100
80
60
40
20
0
0
10
20
30
40
y = 8.2191 - 0.40014x + 0.25480x^2 -
5.1513e-3x^3 R^2 = 0.999
Age (Days)

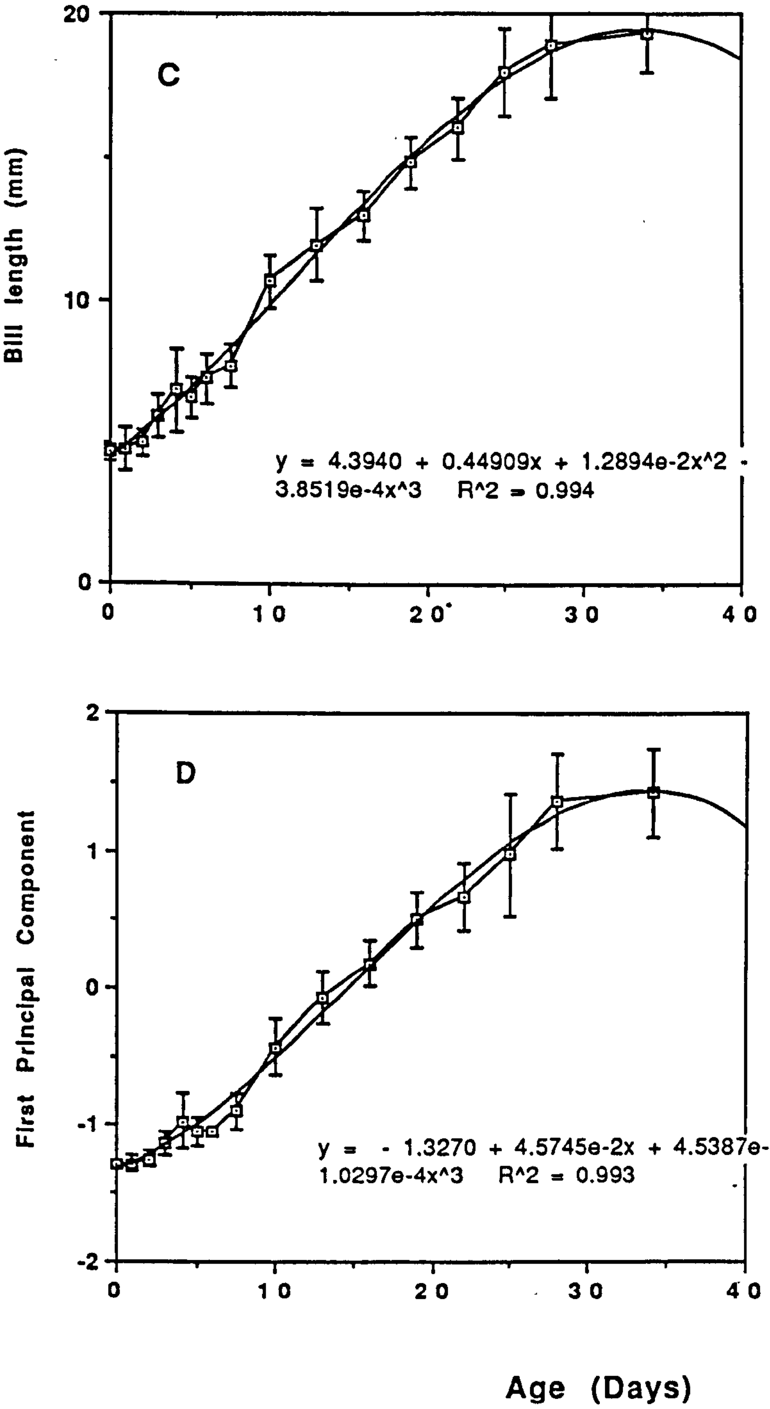


Figure 7.8 a-d: Unrestrained growth (first-hatched nestling growth curve): a selection of different models fitted to the growth of different size parameters, including linear and 2nd order polynomial curve fitted to the increase of wing length (A), a 3rd order polynomial curve fitted to wing length increase (B), a 3rd order polynomial curve fitted to the bill length increase (C), and a 3rd order polynomial curve fitted to the first principal component (see text). The best-fitting model, however, is a 4th order polynomial on wing length increase (Fig 7.7 a).

was significantly between the two groups (Wilcoxon matched-pairs signed-rank test; $Z = -8.34$, $p < 0.0001$, $N = 164$). Wing length estimates of age were consistently too low (139 cases, compared to 16 over-estimates), suggesting that stunted growth may be common in the second half of the nestling period. It is therefore not reliable to age nestlings older than two weeks by using only a single measurement of wing length.

7.3.4 Chick mortality during the nestling period and age of death

The median age of nestling death was 11 days (range = 4 - 35; Fig. 7.9). Not many fourth-hatching chicks were aged before their corpses were discovered, but of those that were, many died before day 11, as did third-hatched chicks (Fig. 7.10). First-hatched chicks died any time during the nestling period. Those chicks that died late were probably deserted by their parents (Fig. 7.9 a). Nestlings were significantly more likely to starve during the first half (up to day 11) of the nestling period (43 compared to 6; $\chi^2 = 27.939$, $p < 0.001$). If the mortality pattern is adjusted to different food supplies in different seasons, there might have been a difference between these proportions in 1990 compared to 1991, but no such difference was detected (Fig. 7.9 b; χ^2 with Yates Correction = 0.0888; $p > 0.40$), possibly because there were too few records from 1990.

Most nestlings died during the nestling period did *not* show a decrease in body mass independent of their rank during the early nestling period (Table 7.8). At the age of 13 days, however, those nestlings that did perish, had a lower mass compared to those that lived to fledge. It seems therefore that the effects of starvation show themselves as a loss of body mass only close to death and there is no prolonged period of mass loss beforehand. If death is not preceded by a long period of relative loss of absolute mass, then either the nestlings did not starve until immediately prior to their death, or starvation did not affect nestling condition which remained stable until a point of 'no return', when they died whether or not feeding conditions improved. Mean Cond2 differed significantly for nestlings that subsequently died, from those that fledged (Table 7.8), most of the variation being due to the second ranking nestling whose mean condition was lower if it was destined to die (Table 7.9). The condition of the second nestling in particular was also lower if measured as pectoral muscle thickness (Cond1), and in relation to the growth of the first-ranking nestling (Cond3).

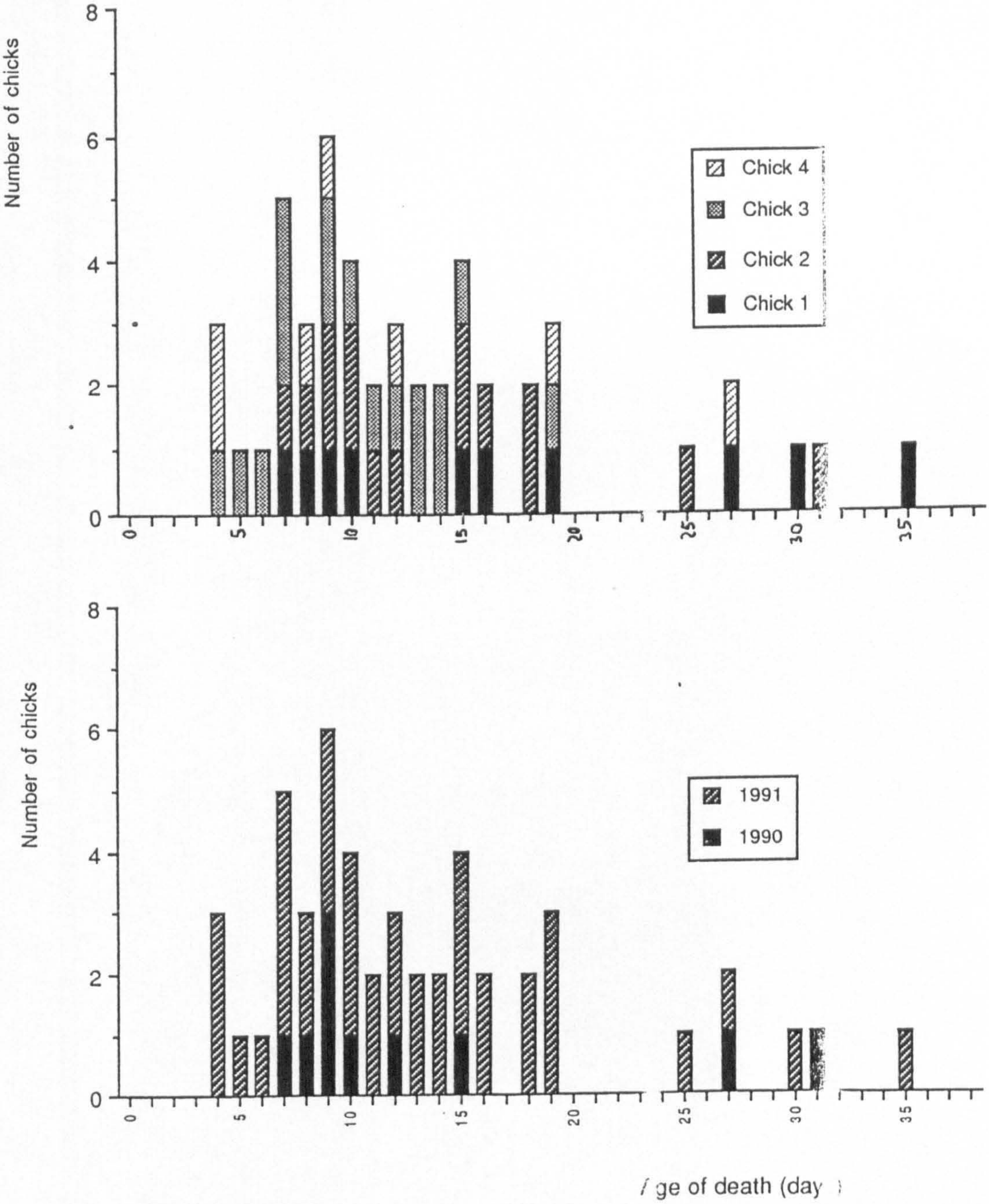


Figure 7.9: Frequency distributions of the age of death of starving nestlings (nestlings that died due to predation or desertion of the whole brood were excluded), separately for (a) rank and (b) years of study (no chicks were aged reliably enough in 1989). (See text for statistical comparisons)

Figure 7.10: A runt which perished within the first few days of hatching. The bruises on its back and the back of its head are probably inflicted by its elder sibs.

Table 7.8: ANOVAs of nestling mass and condition at different ages and over the whole nestling period, controlling for hatching sequence (chickno), for nestlings that survived versus nestlings that perished (survive).
interact = interaction of chickno and survive

	F (chickno)	p	F (survive)	p	F (interact)	p
Mass (day 3) (24)	0.735	0.493	1.603	0.221	0.629	0.437
Mass (day 5) (24)	3.368	0.057	0.119	0.734	8.817	0.002 **
Mass (day 7) (16)	0.288	0.601	1.532	0.241	0.308	0.589
Mass (day 9) (16)	0.047	0.954	3.268	0.098 (*)	0.836	0.380
Mass (day 11)(39)	6.615	0.004	2.389	0.132	1.016	0.373
Mass (day 13)(32)	2.543	0.098	5.500	0.027 *	0.977	0.390
Mass (day 15)(30)	0.875	0.429	3.536	0.072 (*)	0.186	0.670
Cond2	9.776	0.000 ***	9.554	0.002 **	0.148	0.862
Cond3	18.102	0.000 ***	7.755	0.006 **	0.711	0.493

Nestling mortality was not significantly related to the extent of feather mite infestation (see Chapters 2 and 5) or to nestling rank independently of hatching sequence (see methods). The maximum number of wounds recorded for any chick (Fig. 7.11) did not influence whether it was more likely to die (Table 7.9). Third- and later-hatched nestlings with 2 or more wounds were more likely to die than those with less than 3 wounds (Table 7.10), but the fledging success of second-hatched nestlings was not affected by whether or not they had more than 2 wounds in my study. Nestling with more than 4 wounds never fledged, while about half of the nestlings with 4 or fewer wounds survived (Fig. 7.11).

Weekends and chick mortality

At Nam Heng during 1991, the golf course was used at weekends without interruptions from the time of sunrise until near sunset. Because adult birds are reluctant to descend into their burrows during any kind of disturbance in or near the colony, the nestlings went virtually unfed during most weekends in 1991. No data are available on the time it takes for a chick to die when it is not fed at all, but insufficient food supply probably affects the youngest nestlings almost immediately, with only about one or two days delay. The number of nestlings dying on or immediately after a weekend in Nam Heng in 1991 should then be higher than that of nestlings dying during the remainder of the week. This hypothesis was tested but nestling mortality could not be conclusively shown to have increased during or after weekend golfing (Table 7.11).

Table 7.9: Summary of correlations of nestling survival with nestling characteristics, including means (medians) and variation (sd or range), controlling for nestling rank in the hatching sequence (chickno). N = total number of repeat measurements of all nestlings of the category. The 18 measurements of surviving 3rd hatched nestlings are mainly from broods with early mortalities of the first and/or second nestling.

Variable	Chick No	Survived: Mean/Median ± sd/range (N)	Died: Mean/Median ± sd/range (N)	Test	Statistic	p
Cond1 (pectoral)	1	3.0 (2.0-4.0) (47)	2.5 (0.5-3.5) (14)	Kruskal-Wallis ANOVA	13.382	0.0003 ***
	2	2.5 (1.0-4.0) (34)	2.0 (1.0-3.0) (20)		8.905	0.0028 **
	3	2.0 (1.5-4.0) (14)	2.0 (1.0-3.0) (18)		2.159	0.1417
Cond2 (mass cf each chickno)	1	0.8421 ± 3.454 (55)	-1.2630 ± 3.733 (14)	student's t-test	-2.00	0.0490 *
	2	1.7680 ± 3.378 (42)	-0.2709 ± 2.141 (20)		-2.88	0.0060 **
	3	-1.8362 ± 5.232 (18)	-3.1628 ± 2.891 (18)		-0.94	0.3550
	4	-2.4640 ± 0.431 (3)	-2.4619 ± 4.939 (4)		0.00	0.9999
Cond3 (mass cf chick 1)	1	0.8421 ± 3.454 (55)	-1.2630 ± 3.733 (14)	student's t-test	-2.00	0.0490 *
	2	-2.3704 ± 3.192 (42)	-4.8527 ± 2.295 (20)		-3.11	0.0030 **
	3	-4.0775 ± 5.893 (18)	-4.6524 ± 4.664 (18)		-0.32	0.7480
	4	-2.8378 ± 1.259 (3)	-5.8772 ± 5.545 (4)		-0.91	0.4040
Mass at age 13 days	1	29.8 ± 5.0 (18)	27.2 ± 5.5 (2)	student's t-test	-0.68	0.5030
	2	27.7 ± 4.8 (7)	19.9 ± 11.4 (3)		-1.59	0.1490
	3	25.1 - (1)	10.4 - (1)		-	-
Max no of Wounds	1	3.0 (1.0-2.0) (6)	- (0)	Kruskal-Wallis ANOVA	-	
	2	3.0 (1.0-4.0) (9)	2.0 (1.0- 8.0)(13)		0.171	0.6789
	3	1.0 (1.0-2.0) (6)	2.0 (1.0-12.0)(9)		2.666	0.1025
Mean Rank	1	1 (1-1) (55)	1 (1-1) (14)	Kruskal-Wallis ANOVA	0.000	1.0000
	2	2 (1-2) (42)	2 (2-2) (20)		3.681	0.0550 (*)
	3	3 (2-3) (18)	3 (2-3) (18)		0.535	0.4645
Max No of Mites	1	0.5 (0.0-4.0) (20)	0.0 (0.0-3.0) (3)	Kruskal-Wallis ANOVA	0.157	0.6920
	2	0.0 (0.0-4.0) (13)	0.0 (0.0-0.0) (7)		3.343	0.0675 (*)
	3	0.0 (0.0-2.0) (3)	0.0 (0.0-0.0) (5)		1.667	0.1967

Table 7.10: The number of nestlings that died and fledged compared to the number of wounds (0-2 or 3 or more). Only the lower-ranking nestlings' survival is significantly affected by significant wounding.

	0-2 wounds		3 or more wounds				
Rank	died	fledge	died	fledge	χ^2	N	p
1	0	6	0	0	-	6	-
2	8	4	5	5	0.127	22	0.7216
3-5	5	6	6	0	(Fisher)[a]	17	0.0427 *
all	13	16	11	5	1.507	45	0.2196

[a](Fisher) = Fisher's exact Test; All χ^2 are yates-corrected

Table 7.11: Number of chicks estimated to have died on or after the weekend compared to the rest of the week

Days vs. rest of the week	χ^2	p
Sunday and Monday	3.125	0.077 (*)
Sunday to Tuesday	1.667	0.197
Mondays	2.133	0.144
Monday and Tuesday	2.880	0.090 (*)

7.3.5 Supplementary Feeding Experiment and Induced Recovery

In the supplementary feeding experiment, the first two top-ranking chicks were given supplementary food in experimental nests but no food in control nests. In broods of 2 chicks, only the first-hatched nestling was given additional food. The effect of additional food given to top-ranking nestlings was investigated on fledging success, the age at which runts perished and growth and condition of top-ranking chicks and runts.

Fledging success

In the supplementary feeding experiment, the largest chick (chick 1) fledged in all 8 experimental broods and all 8 control broods. In broods of 2 chicks, where the second nestling (chick 2) was defined as a runt (and therefore was not fed in the experimental nests), 2 out of 5 experimental broods fledged the second nestling compared to only one of the 5 control broods (not significantly different; Fisher's Exact Test, $p > 0.90$). For most fledglings, the exact fledging day could not be established. Two of the 3 second nestlings that *were* fed experimentally did not fledge, but neither did their control counterparts. All 8 third and all 4 fourth hatchlings died. In summary, I was not able to demonstrate any differences in fledging success between experimental and control broods.

Chicks classified as runts invariably died at a more advanced age in experimental nests than in controls, i.e. when their elder siblings were fed experimentally, the runts perished later (Fig. 7.12; Table 7.12). This difference was significant between experimental and control broods in a pair-wise non-parametric comparison of the sum of all days survived by runts which eventually perished in both (control *and* experimental) broods (4 pairs of broods; Wilcoxon matched-pairs signed-ranks test, $Z = -2.0226$, $p < 0.0431$).

Growth and condition

To test whether the first one or two chicks in the nestling hierarchy benefited from supplementary feeding, I compared growth rates and condition of the experimentally fed chicks and their controls. For each individual nestling, the slope of the growth of the wing

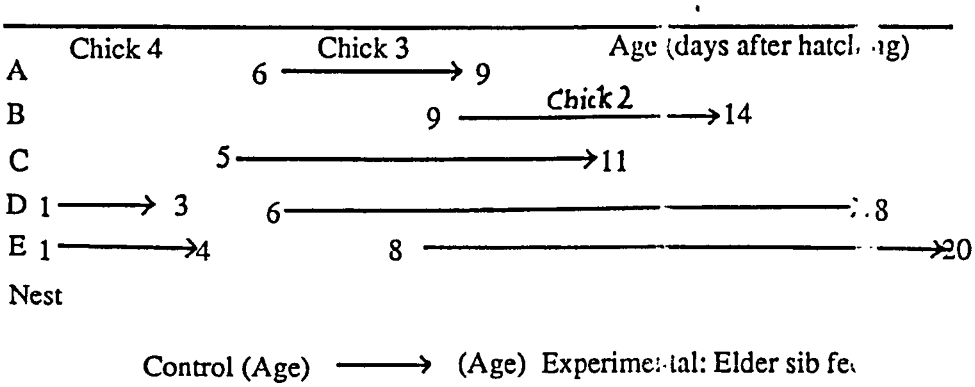


Figure 7.12: The age at which runts died, seperately for each 'case' (A-E) constituting a pair of control and experimental nest. The age at which runts died was invariably higher in experimental nests (shown by arrows), where the elder sibs received supplementary food.

during asymptotic growth (before day 16, see Bryant and Tatner, 1990) was calculated separately (see Table 7.13), but not many of the rates were significant. No valid statistical comparison could therefore be made, but growth rates did not seem to improve overall for the experimentally fed chicks (Table 7.13 a and b, first column). Cond2 probably improved for first-hatched nestlings that received about 20% of their DME in supplementary food (see methods; 2-way ANOVA, controlling for case, F was nearly significant at $p = 0.058$) and improved clearly for second-hatched nestlings that were supplementary fed ($F = 15.651$, $p < 0.01$). Amongst the control top-ranking nestlings, a few had poor condition (Fig. 7.13 a), whereas none of the experimentally fed first-hatched nestlings had low mass per size at any stage (Fig. 7.13 b). It looks therefore as though the supplementary feeding did stabilize mass gain in growing top-ranking nestlings, although the effect showed up only as a trend (Note that regressions are not valid here since different numbers of repeated measures were used for each nestling). Top ranking nestlings did not benefit in growth rate from increased provisioning, which indicates that their growth was probably not stunted in the control nests either. This is in line with the results from the previous section (7.3.4).

Mass, condition and growth rate of runts

It is possible that there is a threshold of nestling mass per age for fledging, i.e. once a chick falls below this threshold it cannot recover, regardless of whether conditions improve again later. This could happen, for example, if a chick cannot obtain any more food, either because it cannot compete with its siblings, or because it becomes too weak to feed. The reason why runts may have lived longer in experimental nests may then have been that they could sustain growth consistently at a rate above the threshold for successful fledging, like first-hatched chicks. This is suggested by Fig. 7.14, where the runt of a control nest perishes after nearly 10 days without mass increase whereas the second-hatched sibling of an experimentally fed chick grows at a similar rate to both first-hatched chicks. (Fig. 7.14 shows the expected results under the above model, but the effect shown in this figure is an arbitrary selection of a control and a different experimental nest). It is possible that runts did have improved growth rates in experimental nests, but because they perished so early in control nests, they were not re-measured often enough to assess their growth rates (Table 7.13). Cond2 for all runts did not overlap entirely for experimental and control nests. Control runts had some lower scores

Table 7.12: The mean ages (in days from hatching; datapoints in brackets) at which experimental runts (chicks whose elder siblings were fed experimentally but which were not fed themselves) and the corresponding chicks in the control broods died. Datapoints are ordered for corresponding pairs, e.g. chick-2 died at 9 days in the experimental brood and at 6 days in its control; in the brood where chick-3 died at the age of 20 days, its control died when 8 days old. See text for statistical evaluation.

	Chick 2 mean N=2	Chick 3 mean N=3	Chick 4 mean N=2
Experimental	11.5 (9,14)	16.3 (11,18,20)	3.5 (3,4)
Control	7.5 (6, 9)	6.3 (5, 6, 8)	1.0 (1,1)

Table 7.13: The effect of experimental feeding on mean growth rates (mass (A) and wing length (B)) of fed chicks and runts, respectively. Growth rates were calculated for each single nestling separately, as the slope of the regression of mass (g) or wing length (mm) on chick age (days from hatching). Only significant slopes ($p<0.050$) were included, of nestlings less than 16 days old (see text).

A: mass growth rates

	Fed chicks and controls (chick 1 and 2)	**Runts (chick 2 only; too few data for chick 3 and 4)**
exp	2.076 (SD=0.129) N=3	1.323 (SD=0.701) N=4
contr	2.152 (SD=0.009) N=2	0.451 (no SD) N=1

B: wing growth rates

	Fed chicks and controls (chick 1 and 2)	**Runts (chick 2 only; too few data for chick 3 and 4)**
exp	2.846 (SD=0.300) N=3	2.090 (no SD) N=1
contr	2.762 (SD=0.006) N=2	--- [1]

[1] no significant increase in wing length for any control runt due to early death

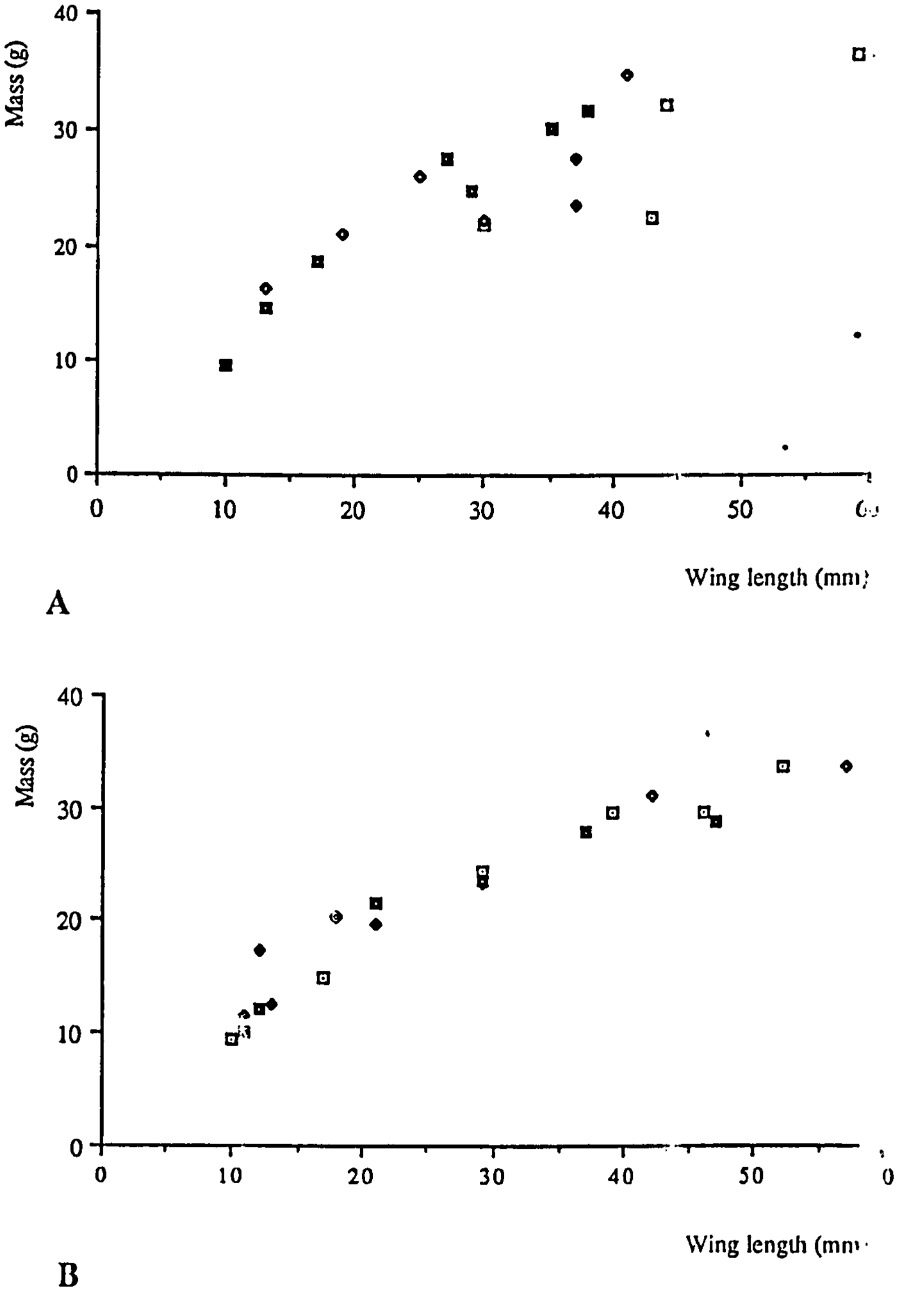


Figure 7.13: Measurements of mass and wing length to indicate the condition of the first-hatched nestling which were (A) not fed (control) and (B) receiving supplementary food (experimental).
Note: These are repeat measurements from re-captures of 5 birds. Different style dots were used for each bird.

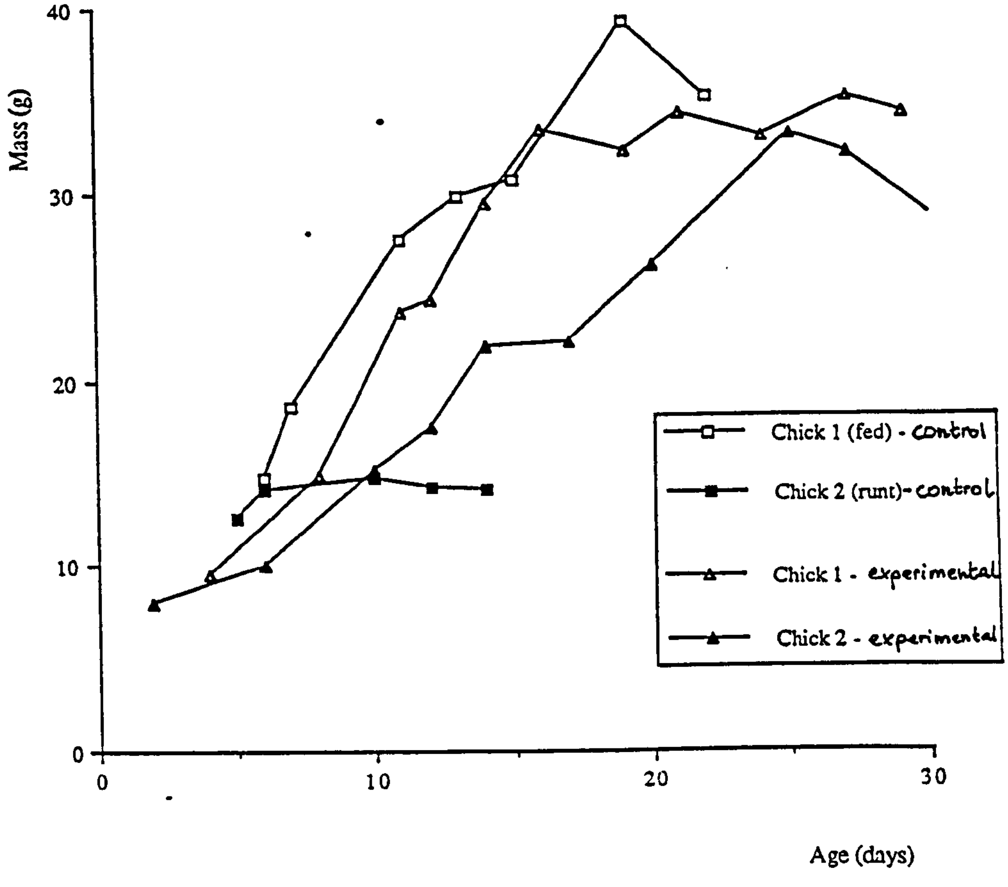


Figure 7.14: Examples of mass increases with age in a control nest and an experimental nest with 2 chicks each but not from the same case. Chick 1 grew at similar rates in both nests. In the experiental nest, the second chick caught up with chick 1. In the control nest, the second chick did not gain mass and perished.

for mass per wing length than runts in experimental nests (Fig. 7.16 a and b; again, regressions of mass on wing are not permitted here, because of unequal numbers of repeat measurements). Experimentally fed top-ranking chicks weighed heavier for their size. Runts suffered less in cond2 when their eldest nestlings received additional food experimentally (2-way ANOVA of chick 2 runts, controlling for case; $F = 3.819$, $p < 0.01$; for ANOVAs of chicks 3 and 4 there were too few data points).

Number of wounds of runts

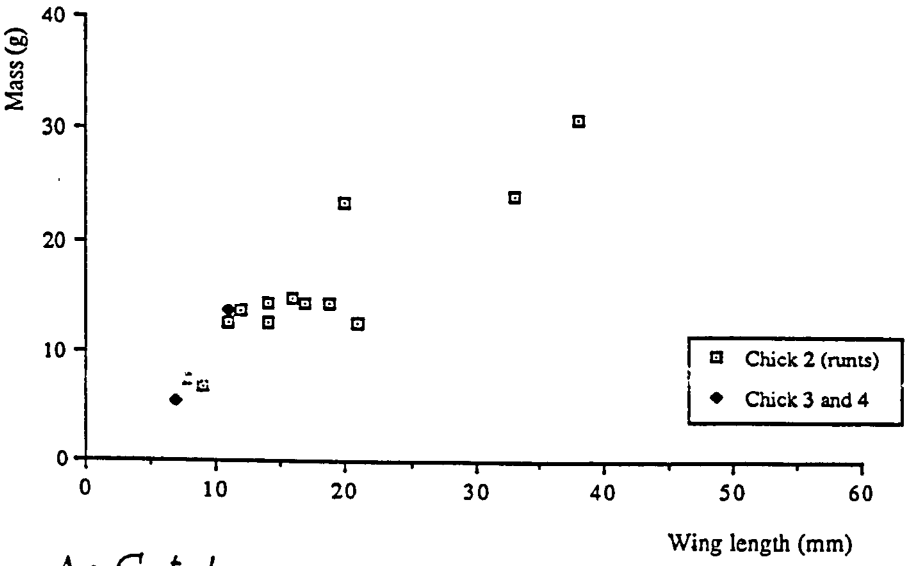
The maximum number of wounds or scabs (summed for each nest for all runts) in pairs of experimental (median = 8 wounds, 0-12) and control nests (median = 4 wounds, 0-12) were not significantly different (Wilcoxon matched-pair signed-ranks test, $Z = -0.135$, $p > 0.80$, $N=5$ pairs of nests). In 6 out of 9 experimental nests (66%), runts had some wounds, whereas in 4 out of 5 control nests (80%) runts had some wounds. This is again not significantly different (Fisher's Exact test, $p > 0.90$). Therefore, if the level of aggression towards runts was lowered by supplementing the food of the higher ranking nestling(s), this could not be demonstrated here.

Induced Recovery Experiment

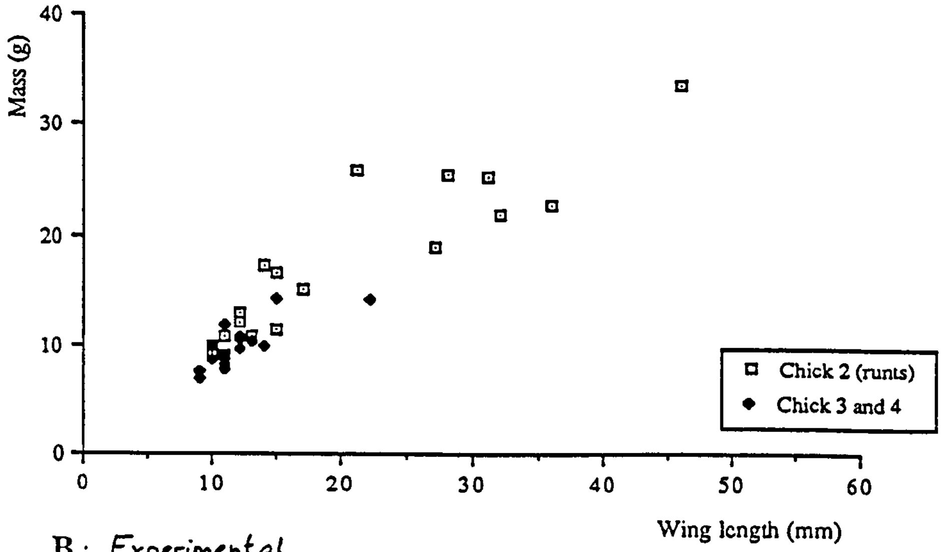
All nestlings included in the Induced Recovery Experiment died on the same or next day despite the supplementary food ingested. They were probably past the stage for recovery, so that if they had been fed earlier, they might have survived longer. Alternatively, these nestlings may not have recovered regardless of the supplementary food received, for example if brood reduction was obligatory.

7.3.6 Nestling Behaviour and Experiments in an Artificial Nest

In this sub-section, the main investigation is concerned with how nestling behaviour, as observed in the artificial nest (see methods), was affected by nestling hunger and condition. For this, I first describe the behaviours observed and then study the effect of some possible



A : Control



B : Experimental

Figure 7.15: Measurements of mass and wing length (cond2) to indicate the condition of runts, (A) in control and (B) in experimental nests. Runts with older siblings receiving supplementary food have slightly higher values. Note: These are repeat measurements from re-captures of 5 or less birds. Different style dots were used for each rank.

co-variates (trial, time, nestling rank and whether its eyes were open), before looking at the effect of abdomen depletion and experimental feeding on behaviour.

Chick Behaviour in the Nest

During the preliminary trials, several behaviours were observed and scored on a 0-5 integer scale according to variation in frequency and intensity.

1. Attentiveness: When the adult's call sounded, the chick raised its head, shuffled around, or stiffened or erected its body. This behaviour had a duration of at least several seconds after each call. Scores: no such reaction = 0, occasional response to call = 1, some response but not intense = 2, regular intense response = 3, prolonged intense response = 4, extremely intense and prolonged = 5.

2. Position: Before each trial, chicks were placed at the back-end of the chamber. During each trial, the position to which the chick moved and the orientation it assumed with respect to the tunnel was scored. Some older chicks ran straight to the end of the tunnel (position = 5), some stayed at the back but with their bills directed at the tunnel (position = 1) or moved as far as the middle of the chamber (2), the start of the tunnel (3), or entered the tunnel (4). If the bill was not pointed towards the tunnel exit, position was assumed to be random (0).

3. Vocalizing: The chicks usually answered to the recorded adult call, sometimes with the very distinctive begging 'trill' (see Chapter 4). No vocal response = 0, a single, low-key call = 1, meek but regular response to adult call = 2, always clearly responding to adult, occasionally also in the intervals between adult calls = 3, loud and with few interruptions after the first play of the adult call, but with increased level when the adult call sounds = 4, or quite continuous and loud = 5.

4. Scuffle: the chicks of *M. viridis* stand on their legs from the day of hatching and sway back and forth. Often, the blind nestlings also turned in circles, and when they encountered each-other, two (or three) siblings pushed against each-other sideways in a circle or one chick was pushed to one side by one or two others. A small chick can occasionally push aside a

larger one. I scored scuffle as > 0 only if chicks did encounter each-other (although before each trial, all chicks were placed close together into the 'chamber', they moved apart sometimes). Scuffling was scored as one or two short encounters = 1, clear but infrequent or low-key scuffle = 2, much time spent clearly in scuffling = 3, aggressive and scuffling most of the time = 4, clearly scuffling all of the time = 5.

5. Pecking: A rare but very marked behaviour of chicks is pecking directed at the nest or at other chicks. I counted clear bouts of pecks (1 = one distinct or several weak pecks, 2 = two distinct pecks or few medium pecks, 3 = three distinct pecks or many medium pecks, 4 = four distinct pecks or strong pecks, 5 = more than four pecks or pecks including pinching). Score 5 included a strong, repeated pinch given to my hand by a near-fledgling which rushed to the burrow exit during the play-back experiment. The pinching movement included scraping with its medium-sharp hook. This behaviour was observed only once during three seasons of handling nestlings.

6. Open bill: Some chicks opened and closed the bill repeatedly; I counted this behaviour similarly to pecks.

Some of the nestling characteristics were significantly correlated, in particular condition, abdomen and eyes with nestling rank; condition with abdomen; and eyes with condition (Table 7.15). In all subsequent analyses of the effect of any of these variables on nestling behaviour, correlating variables were therefore controlled for. Chickno was used rather than rank because it is expected to be more relevant, because nestling behaviour is likely to be influenced by their prior social experience with each-other.

Effect of nestling characteristics on behaviour

Different nestling characteristics were tested with respect to behaviour. There were rank, eyes, condition and abdomen depletion. Habituation (trial number) was also examined. Amongst nestlings with closed eyes and of medium condition and abdomen, runts reacted generally more actively to the recorded adult call than higher ranking chicks (Table 7.16). The behaviour of chicks 1 and 2 in the artificial nest was similar (first test, Table 7.16), and the

Table 7.15: Spearman rank correlation coefficients of variables that may affect behaviour (N = 181 observation periods)

First row: correlation coefficient
Second row: (p)
third row: significant correlations are marked with *, ** or ***

	Trial	Chickno	Cond	Abdomen	Eyes
Chickno	0.096 (0.194)				
Cond	-0.045 (0.543)	-0.405 (0.000) ***			
Abdomen	0.125 (0.095)	-0.492 (0.000) ***	0.311 (0.000) ***		
Eyes	-0.191 (0.009) **	-0.258 (0.000) ***	0.546 (0.000) ***	0.162 (0.029) *	
Time	0.042 (0.572)	0.003 (0.963)	0.102 (0.168)	0.150 (0.044) *	0.050 (0.495)

Table 7.16: The effect of position in the hierarchy on nestling behaviour (attentiveness, positioning, vocalization, scuffle, pecking and open bill) for medium condition chicks, with closed eyes, with medium or full abdomen.

Test	Effect on behaviours	p	N
chick 1 vs chick 2	none	(all ns)	59
chick 1 vs chicks 3/4	runts were more attentive than chick 1	*	
	runts vocalized more than chick 1	***	57
	runts pecked more than chick 1	*	
chick 2 vs chicks 3/4	runts were more attentive than chick 2	**	
	runts vocalized more than chick 2	***	61
	runts pecked more than chick 2	*	

Note: only significant effects are listed. Those behaviours which are not listed here were not significantly affected. Mann-Whitney U tests used throughout behaviour of both was significantly different in similar ways from chicks 3 and 4 (second and third test). Therefore, chicks 1 and 2 were grouped together in the following analyses where applicable.

Attentiveness and the levels of vocalizing and scuffle all decreased with habituation (trial), when controlling for 'eyes' ('eyes closed' was a larger sample than 'eyes open'; Table 7.17). This may be because once the chicks can see, they are more affected by the unusual surroundings. Alternatively, chicks that can see may be able to position themselves more directly at the tunnel entrance. Positioning did not improve, however, when nestlings could see: dominant nestlings may have moved further towards the back of the 'nest' rather than towards the entrance, but since lower-ranking nestlings did not change their positioning once they could see, this is not likely to be an effect of the experimental set-up. Scuffling could perhaps be a strategy more for young nestlings, but there is no consistent strategy change between young and older nestlings (all Table 7.17). Because of the effect of habituation on chick behaviour, I used only the first trial where applicable in the following analyses.

Condition (measured as pectoral muscle thickness) did not have much effect on nestling behaviour (Table 7.18). Only the vocalization of top-ranking nestlings changed with poor condition: begging was more intense when condition was poor. This is in support of the suggestion that top-ranking nestlings beg more and that this may eventually help to further exaggerate any size differences between high-ranking and low-ranking chicks (Ricklefs, 1965; Magrath, 1990).

Effect of abdomen depletion on behaviour

Nestling hunger (measured as the extent of repletion of the abdomen) was confounded in effect with Cond1 (see Table 7.15), so that most chicks were either hungry and of poor condition, or not hungry and of good condition, and there were in particular few low-ranking nestlings of poor condition that had depleted abdomens. Nestling hunger increased the frequency of several behaviours, for chicks of poor condition, at least where the sample of observations was large enough (Table 7.19): in particular, indirect competition through begging (vocalizations), direct competition (scuffle) and aggressive pecks were more intense

Table 7.17: The effect of Trial and Eyes on all observed behaviours (attentiveness, position, vocalization, scuffle, pecking and open bill), controlling for correlating variables (see Table 7.3.6.1).

Main effect	Controlled	Effect on behaviours	p	N
Trial	Eyes=closed	attentiveness decreased with trial number vocalizations decreased with trial number scuffling decreased with trial number	* * *	116
Trial	Eyes=open	scuffling decreased with trial number	*	45
Eyes	Chick 1+2 Abd=full Cond=med Trial=1	position was further back when eyes were open	(*)	27
Eyes	Chick 1+2 Abd=notfull Cond=med Trial=1	scuffling decreased when eyes were open	(*)	27
Eyes	Chick 3+4 Abd=full Cond=med Trial=1		small sample	2
Eyes	Chick 3+4 Abd=notfull Cond=med Trial=1	vocalizing decreased when eyes were open	(*)	14

Notes:

1. Only significant effects were listed (including (*), which is $0.05 > p > 0.10$). Those behaviours which are not listed here were not significantly affected.
2. Mann-Whitney U tests used throughout

Table 7.18:The effect of low condition (pectoral muscle score) on the behaviour of nestlings in reaction to the call of a feeding adult tested in the artificial nest, controlling for confounding variables (abdomen and eyes).

Chick	Abdomen	Eyes	Effect of poor condition	p	N
1	full	closed		all ns	8,14
1	full	open		small sample	1,14
1	not full	closed	vocalizing increased	*	4,5
1	not full	open		small sample	0,6
2	full	closed		all ns	10,7
2	full	open		small sample	1,8
2	not full	closed		all ns	18,4
2	not full	open		small sample	1,5
3+4	full	closed		small sample	0,0
3+4	full	open		small sample	0,2
3+4	not full	closed		all ns	31,10
3+4	not full	open		all ns	2,2

Note: only significant effects were listed. Those behaviours which are not listed here were not significantly affected. Mann-Whitney U tests used throughout

Table 7.19: The effect of hunger (abdomen not full) on the behaviour of nestlings in reaction to the call of a feeding adult tested in the artificial nest, controlling for confounding variable (condition).

Chick	Condition	Effect of Hunger	p	N
1	good	less attentive	*	4,11
1	poor	increased scuffling	**	7,24
2	good		all ns	3,8
2	poor	increased vocalizing increased scuffling increased pecking	* * **	25,17
3+4	good		small sample	1,2
3+4	poor		small sample	44,1

Note: only significant effects were listed. Those behaviours which are not listed here were not significantly affected. Mann-Whitney U tests used throughout in hungry second-hatched chicks of poor condition. Note, however, that for many of these condition cases, the sample size was too small for drawing indicative conclusions.

Top-ranking nestlings were tested in the artificial nest before and after being given supplementary food. Two pairwise trials were made for four nests, and six replicate pairwise trials were made for the brood of one nest (brood 168-91). In both cases the behavioural responses to feeding lent experimental support to the results of the previous section, namely that several competitive behaviours were enhanced by hunger (Table 7.20). Attentiveness probably decreased due to habituation in the second trial after feeding. Pecking was not observed frequently enough to be included in this analysis, because most trials were without pecks. Of 7 pecks observed during the feeding experiments, none was after feeding. This is confirmed as a trend when compared to the number of trials without pecks (Table 7.21).

7.3.7 The Hook Experiment

To test whether the mandibular hook has a function in siblicide, the hooks of all but the youngest nestling were regularly abraded in 7 experimental nests and fledgling success, wounding and nestling condition was monitored.

Number of fledglings

The number of fledglings was compared for the 7 matched pairs of experimental and control nests. Altogether, 6 chicks fledged from experimental nests and 9 from control broods, but this was not significant (Wilcoxon matched-pairs signed-rank test of number of fledglings; $Z = -1.6036$, $p = 0.1088$). In experimental nests, two broods did not fledge any nestlings at all. If the presence of a hook in the elder nestlings increases the number of fledglings per brood (assumingly, by efficient brood reduction; see below), this could not be shown here.

Number of wounds on nestlings

The number of wounds (means of the maximum wounds recorded for any one chick) was reduced in experimental nests for nestlings of all ranks, but significantly only for second-

Table 7.20: The influence of supplementary feeding on nestling behaviour in reaction to the call of a feeding adult tested in the artificial nest

	Nest 168-91 only (6 replicates)			Two replicates each from 4 nests		
Behaviour	effect of feeding	Z	p	effect of feeding	Z	p
Attentiveness	decrease	-2.023	0.043	increase	-0.548	0.584
Position	further back	-1.153	0.249	further back	-0.674	0.500
Vocalizations	fewer	-1.782	0.075	fewer	-0.838	0.402
Scuffle	decrease	-1.826	0.068	decrease	-2.023	0.043

Note: Only first hatched chicks (i.e. the largest in the nest) were tested, before and after feeding. Note that attentiveness is also affected by habituation (trial number, see section 7.*) which is unavoidably confounded with trials before and after supplementary feeding.
Wilcoxon matched-pair signed-rank tests were used throughout

Table 7.21: Pecking and supplementary feeding: the incidence of pecking in trials of nestlings before and after feeding.

	before feeding	after feeding
No pecks	13	10
Pecks	7	0

χ^2 (Yates Correction) = 2.818, p = 0.0932 ranking nestlings, from a mean of 4.3 wounds per nestling to 1 wound per nestling (Table 7.22). Second-ranking chicks also had the largest number of wounds in control nests, where the oldest sibling had an intact hook.

Runt survival

The number of days each nestling survived was summed for all nestlings which died in each nest. For all 7 pairs of control and experimental nests, the sum of runt survival days was higher in experimental than in control nests (Fig. 7.17; Wilcoxon matched-pairs signed-rank test: $Z = -2.0226$, $p < 0.0431$), i.e. in nests where the elder nestlings had an intact hook, runts died at a younger age, and therefore the presence of intact hooks on the high-ranking nestlings facilitated efficient brood reduction.

Runt condition

For each nestling of the broods of the 7 experimental broods (see methods), mean Cond2 was compared to the corresponding values of their counterpart chick in the control broods. For 3rd- and 4th-ranking nestlings there were not enough datapoints, but second-ranking nestlings clearly improved in condition when their elder sibling's hooks were abraded ($p < 0.05$; Table 7.23), whereas the condition of first-ranking nestlings was unaffected ($p > 0.10$).

Condition of the top ranking chick

The condition of the top-ranking nestling did not decrease significantly when its hook was abraded (Table 7.23). A decrease would be expected if chick 1 can disadvantage chick 2 more efficiently with a hook (i.e. in control nests) so that either more resources are allocated to the eldest chick, or the eldest chick has to spend less energy to disadvantage the second nestling; furthermore, if the hook helps to eliminate younger siblings more effectively, the reduction in competition by their earlier death should result in an increase in condition of the top-ranking chick. This, however, could not be shown in this study.

Table 7.22: Wounds on nestlings in experimental nests (older nestlings' hook abraded) and control nests

Kruskal-Wallis one-way ANOVA used to compare wounds of chicks in experimental and control nests

	Mean number of wounds (± SD) (N)				
	Experimental	Control	χ^2	p	Total
Chick 1	0.0 (± 0.0) (7)	0.9 (± 2.3) (7)	1.0000	ns	0.5 (± 1.2) (14)
Chick 2	1.0 (± 0.9) (8)	4.3 (± 2.9) (6)	5.2902	*	2.4 (± 2.5) (14)
Chick 3-5	1.0 (± 1.1) (9)	1.7 (± 3.3) (9)	1.0000	ns	1.3 (± 2.3) (18)
Total	0.7 (± 1.0) (24)	2.2 (± 3.1) (20)	1.1490	ns	1.4 (± 0.3) (44)

Table 7.23: Condition of nestlings of broods where eldest nestlings either had (control) or had no (experimental) mandibular hook. The condition of the second nestling was better when its sibling had no hook.

Condition = (observed mass - expected mass from the growth curve for the same age and rank) / expected mass.
Student's paired T-test to compare condition of nestlings in control and experimental broods

	Control		Experimental				
	Mean	± SD	Mean	± SD	T	p	N
Chick 2	-4.00	± 2.91	1.62	± 1.44	4.21	0.024	4
Chick 1	2.71	± 2.65	0.48	± 3.23	-1.48	0.190	7

7.4 DISCUSSION

7.4.1 Incubation and nestling size hierarchy

If incubation starts before the ultimate egg is laid, the nestlings hatch asynchronously. In the following, I discuss whether hatching asynchrony is a result of incubation onset during laying in the Blue-throated Bee-eater.

The hatching spread in this study was 3.5 days (range 2-9) for broods of up to 4 chicks, which is was shorter by 1 day than the value of 4.3 reported by Bryant and Tatner (1990). A similar and significant but unexplained difference in hatching spread (4.4 and 3.6 days) was found in different years at the same colony of European Bee-eaters (Lessells and Avery, 1989). There may be several reasons for such a difference here, the most obvious being the exclusion of broods above 4 chicks in my study. Secondly, the broods used here were mostly at the Nam Heng colony, which may have shown more synchronous hatching than the population at Sungei Buloh which was used in the previous investigation. A further difference may have arisen from inaccuracies in estimating the onset of laying. This bias was 1-3 days in general but did not produce a consistent under- or over- estimate of the date of onset of laying (Chapter 4). Fourthly, chicks may have been aged wrongly by up to 2 days from their wing length growth curve (section 7.3.3, Table 7.4).

The estimate of hatching time of 20-24 days is much longer than the 17 days predicted from adult mass by Rahn *et al* (1975) for Blue-throated Bee-eaters, with adult mass of 34g (pers obs). This could have been explained by part-incubation as indicated by lukewarm egg temperatures (section 7.3.1). Part-incubation may have been due to food shortages for example. Part-incubation seemed to commence immediately after the first egg was laid at least sometimes, because I found clutches of one egg (i.e. during laying) which were lukewarm. Another line of evidence for the timing of incubation onset comes from the observed hatching spread itself. Nestling 1 and 2 hatched one day apart, whereas chick 3 and 4 hatched about 2 and 3 days after chick 2 (Table 7.1). The hatching time, from when the egg was presumed to have been laid to when it was estimated to have hatched, was 24 days, 23 days and 20 days or less for 1st, 2nd and later hatched respectively. For European Bee-eaters, Lessells and

Krebs (1989) found that parents delayed feeding their newly-hatched broods occasionally for up to 2 days, which would produce a pattern as if the first 2 chicks had hatched closer to each-other. The data in this study, however, were derived independently and suggest that a delayed onset of incubation suspended embryonic development of the first chick for one day on average, so that first and second chick hatch one day apart, 24 and 25 days after the first egg was laid. Accordingly, if later-hatching chicks are incubated more consistently, they would develop faster.

The observed hatching spread was calculated under the assumption that nestling size or embryo age at hatching does not vary with hatch sequence. Eggs might, however, hatch at different stages of embryonic development. Furthermore, size differences of nestlings within broods may be enforced by spells of food shortages during laying which result in a decline in egg quality with laying sequence (O'Connor, 1979; Bryant, 1978). Egg size is affected by food availability for example in African Marsh Harriers *Circus ranivorus*, which lay a larger last egg under usual conditions, but they increased clutch size and laid smaller last eggs when given additional food during laying (Simmons, 1994). Heavier eggs may hatch into fitter chicks as suggested for example by O'Connor (1979) and Howe (1976), but this was disputed by Williams (1994) who suggests that chicks from heavier eggs survive better only during the first few days after hatching (but not subsequently), probably because they have more yolk reserves (see also O'Connor, 1979). Although no data on egg size or quality were available for Blue-throated Bee-eaters, differential investment into eggs may nevertheless be an adaptation for brood reduction alternative (or additional) to hatching asynchrony (e.g. Simmons, 1994). Egg size can increase or decrease with laying sequence. In species where egg size decreases with laying sequence, differential investment into eggs rather than asynchronous hatching can explain size differences of nestlings within broods (Simmons, 1994; Jover *et al*, 1993; Parsons, 1970). In those species where egg size increases with laying sequence on the other hand, such as the Tree Swallow, any effect of egg size on nestling size is usually swamped by asynchronous hatching (e.g. Zach, 1982).

Although Blue-throated Bee-eaters lay an egg every second day during un-disrupted laying (Bryant and Tatner, 1990), most of the broods for which laying intervals could be inferred (3 out of 5) had a gap of longer than 2 days between later eggs. It is therefore possible that eggs are laid at different intervals depending on position in the laying sequence. Laying gaps have been associated with food shortages during laying in House Martins (Bryant, 1975) and Blue Tits *Parus caeruleus* (Nilsson and Svensson, 1993 a). Lessells and Avery (1989) report that in European Bee-eaters, hatching more synchronous than laying, so that the laying schedule itself contributes more to hatching asynchrony than incubation during laying. This could be an alternative explanation for the observed pattern of hatching also in Blue-throated Bee-eaters.

Since all of the tended clutches of one egg which I visited were lukewarm (see above) and there was no increase in temperature either between successive eggs laid or before and after any particular clutch size had been reached, part incubation probably started at the onset of laying. It is likely that eggs were not incubated consistently, which could affect the hatching pattern and was observed also for European Bee-eaters (Lessells and Avery, 1989). My observations on clutch temperatures suggest that eggs were left unattended for nearly half of the time during the day (section 7.3.1), but probably not for several days at a stretch as seems to be the case for some other tropical hole-nesters as reported by Gaston and Powell (1989). These researchers argue that ambient temperature may be high and constant enough for neglect to have little affect on hatching success. Although bee-eater burrows may be warm enough to allow some embryonic development to occur (see 7.1.2), hatching success was affected adversely by incubation neglect in the Blue-throated Bee-eaters (section 7.3.1), so that incubation does seem necessary for undisturbed embryonic development to occur, and that inconsistent incubation during laying is thus likely to affect the hatching pattern.

If full incubation commences just after the second egg is laid (Fig. 7.1 e), third and later nestlings should hatch every 2 days, which is similar to the hatching pattern calculated from chick ages. This pattern, where the first two chicks hatch close together followed by longer intervals between the later hatchlings, is common amongst species with hatching asynchrony and was also observed by Stouffer and Power (1990) in broods of Starlings, by Mead and Morton (1985) for White-crowned Sparrows, and by Lessells and Avery (1989) for European Bee-eaters. For Blue-throated Bee-eaters in this study, the hatching data are compatible with the model of incubation onset in Fig. 7.1 e.

Mead and Morton (1985) propose that egg-laying and incubation may be controlled by the same hormone, prolactin, so that the transition between laying and incubation would then depend on how sharply the level of prolactin increases during laying (see introduction). They argue further that hatching asynchrony may be incidental, a consequence of the change in hormone level, rather than adaptive. Magrath (1990), however, denies that the underlying hormone level is the single most important factor that governs laying and incubation, because of the observed variation in incubation patterns regardless of a possible underlying phylogenetic constraint (Magrath, 1990). This view is also upheld by Lessells and Avery (1989), who restate the hormonal hypothesis as adaptive, since the cost of using two separate hormones to control laying and incubation can be compared to the benefits of hatching asynchrony. Nevertheless, they argue that the hypothesis has limited explanatory power because it does not account for between-species variability in hatching asynchrony. Furthermore, the hormonal hypothesis is mostly relevant to species in which females incubate alone (Magrath, 1990). In species where both sexes incubate, incubation could start earlier despite hormonal constraints in the female. This the case in hirundines (Nilsson, 1993): Nilsson (1993) shows that in hirundines, only the species where the male shares incubation start incubating during laying. He suggests that incubation during laying may be too costly for females which incubate on their own, but equally well, females may face a constraint on incubation onset due to hormones (hormonal hypothesis). The hormonal hypothesis predicts that the early incubation is done mostly by the male. As I have reported in this study, both sexes in Blue-throated Bee-eaters incubate. Observations of incubation, however, did not lend themselves to test if males incubate more during laying than females. Male help with incubation, however, is likely to allow Blue-throated Bee-eaters to start incubating during laying, regardless of whether or not the female is constrained hormonally to incubate during laying.

In conclusion, a 'mixed model' of incubation pattern, as in Fig. 7.1 e can explain the observed hatching patterns of a greater difference in hatching interval between the 2nd and later chicks than between chicks 1 and 2. Several other factors which I did not investigate may influence the hatching pattern or nestling size hierarchy with similar effects and cannot be ruled out. My data on laying dates and incubation are insufficient to distinguish between alternative hypotheses. More information on egg size and quality, and direct observations of laying and incubating adults are needed to unravel the role of laying, egg quality and incubation for hatching pattern and size differences between nestlings.

7.4.2 The brood reduction hypothesis and resource tracking

There may be reasons why it is costly for incubation to start before the end of egg laying, such as the need for self-feeding during laying, for example, or seeking opportunities for intra-specific parasitism (see Chapter 6). Nilsson (1993) argues that incubation during laying may be very costly for females (see above). If an early onset of incubation, and asynchronous hatching as its consequence, take place despite such opposing selection pressures, the early onset of incubation must carry a selective advantage which could be explained by the brood reduction hypothesis. Here I discuss the evidence for (and against) this hypothesis.

Brood reduction is only advantageous if, at least in some years, there is not enough food for all hatchlings to fledge. On average, only about 40% of the energy requirements of chicks aged 11-18 days were provided by the adults (7.3.2). Feeding rate calculations were based on observations of parental provisioning visits which may under-estimate visit rate (see Chapters 2 and 5). I used mean feeding rates for all pairs and circumstances, not taking account of individual differences in feeding abilities between parents or periods of varying food abundance (for all pairs). Furthermore, eldest nestlings are likely to monopolize more than their 'share', which was not taken into account: the provisioning rate at each nest was simply divided by brood size, so that the share taken by lower-ranking siblings was probably over-estimated. Different aged broods are probably fed at different rates. Bee-eater chicks grow faster on a mixed diet (Krebs and Avery, 1984), so apart from the amount of food brought to the chicks by the parents, the variation in prey spectrum may also play a role in how much of the brood's energy and nutrient requirements are met. Despite these flaws in the estimate, its low value suggests there is a persistent deficit of amount of energy provisioned to broods in relation to their requirements. This must be compensated for by adjusting either feeding rates or insect sizes, otherwise some or all nestlings will starve.

A common finding in Meropidae is the occurrence of 'helpers-at-the-nest' (see Chapter 4) who feed the young together with the parents, improving the fledgling rates or condition of the brood (Emlen and Wrege, 1991, for White-fronted Bee-eaters; Lessells, 1990, for European Bee-eaters, and Dyer, 1982, for Red-throated Bee-eaters). Few Blue-throated Bee-eater nests had 'helpers' (Chapter 4). In the absence of 'helping', brood needs are aligned to food abundance by starvation of the youngest nestlings which reduces their growth rates in White-fronted Bee-eaters (Emlen *et al*, 1991) for example, or results in brood reduction. As reported in this chapter, flexible growth rates (size retardation) were also found for Blue-throated Bee-eaters. Efficient brood reduction predicts that in times of limited food, 'surplus' nestlings die quickly so that more resources are available for the survivors (Ricklefs, 1965). Runts of Blue-throated Bee-eaters showed retarded growth and sometimes did not perish immediately: this may have been a sign of a slow decline due to starvation which seems on first sight mal-adapted (see e.g. Magrath, 1989). Rather than perish, however, as soon as food becomes limited, Blue-throated Bee-eater runts 'resource track' (Bryant and Tatner, 1990; see also introduction): they delay growth in times of temporary food shortage, which presumably reduces their energy requirements (Emlen *et al*, 1991), and resume growth once conditions improve. The growth pattern of the runts (third- and later-hatched chicks) reported here (e.g. Fig. 7.7 c) suggests that reduced growth is used as a strategy by Blue-throated Bee-eater runts during the period when the elder siblings assimilate most of the available energy. Second-ranking Blue-throated Bee-eater nestlings were less starved, probably because they were able to secure at least some food, and accordingly had reduced condition but not stunted growth.

Developmental retardation in response to food stress is reported for White-fronted Bee-eaters by Emlen *et al* (1991; see above). For Red-throated and European Bee-eaters, this flexible growth rate was not reported (Dyer, 1979 and Lessells and Avery, 1989), and Emlen *et al* (1991) attribute this to more predictable breeding conditions and higher mean reproductive success in these species. They argue that morphological retardation is a specialized adaptation in White-fronted Bee-eaters, similar to flexible growth-rates reported for other aerial insectivores such as House Martins (Bryant, 1975), with similarly unpredictable and patchy food supplies. This is probably true also for Blue-throated Bee-eaters.

The main source of evidence for resource tracking lies in runt recovery, after a period of retarded growth when additional food is received. The recovery experiment did not have conclusive results, but in the supplementary feeding experiment runts took longer to perish and improved in condition (Cond2) when their elder siblings were given additional food. Although the runts did eventually succumb even in experimental nests, their reduced rate of doing so suggests that they may have recovered if more food had been given to their elder siblings or if the food supply had improved earlier. Runt mortality may therefore be a reversible response to limited food. The threshold energy requirement for runts to live may act via a threshold size difference between runts and elder chick(s): if elder chicks are satiated, younger nestlings get a chance to make up some of the difference in size imposed on them as a result of hatching asynchrony. They may, however, still not reach the minimum requirement in which case they will perish. If they do obtain this threshold in size difference they are more likely to survive the nestling period. Fledgling brood size may thus be controlled by such a threshold in size differences between the first hatchling and later ones. Under this interpretation, the observed response of runts in the feeding experiment was an incomplete response that would eventually have resulted in fledging, if the experimental food supply had been high enough or had started earlier. In this light it would therefore seem that runt mortality in Blue-throated Bee-eaters depends at least to some extent on the food supply.

7.4.3 Alternative hypotheses to explain nestling mortality

An adaptive explanation for nestling mortality alternative to the brood reduction hypothesis is the insurance hypothesis against hatching failure (see section 7.1). It is possible that runt mortality is observed as a consequence of insurance, where over-production leads to elimination of 'surplus' nestlings that would raise the brood size above the threshold energy requirement for successful fledging (see introduction). The rate of hatching failure was high at 26% (Chapter 4), compared to the overall 8% established for example by Ricklefs (1969) for 3226 eggs of 9 species. On average, therefore, one egg per clutch did not hatch, which is in line with the insurance hypothesis. Furthermore, Blue-throated Bee-eaters only rarely raised their median brood size of 3 to fledging (this study, and Bryant and Tatner, 1990) and have never been known to fledge the potential of 4 or 5 chicks. The fact that nestling mortality was very common, also stressed by Bryant and Tatner (1990), makes it consistent with the insurance hypothesis. Therefore insurance against hatching failure cannot be rejected as a partial explanation for nestling mortality in Blue-throated Bee-eaters.

Asynchrony was costly in Blue-throated Bee-eaters in terms of nestling energy expenditure (but lower in 'peak' expenditure; both Bryant and Tatner, 1990). This cost of asynchrony is consistent with the hurry-up hypothesis. This hypothesis is relevant mainly for single-brooded species which have very pronounced breeding seasons, such as those found in temperate climates where food supply and temperature decline rapidly towards the end of the season (Magrath, 1990): if the male partner helps to incubate, birds can start to incubate early (Nilsson, 1993), which saves time if they are in danger of late breeding. Blue-throated Bee-eaters are single-brooded with both partners incubating, and they have a pronounced breeding season, exploiting a particular weather 'window' of sunshine after the rainy season (Chapter 4); there was also a tendency by the earlier birds to synchronize breeding during the digging phase by delaying burrow completion (Chapter 5). Earlier breeders can then perhaps also afford to delay incubation until after laying, so that their broods would hatch more synchronously; asynchronous hatching is then a cost associated with late breeding. If this is the case, asynchrony should increase with season (Magrath, 1990), as has been observed in Blue Tits, Great Tits and Pied Flycatchers (Perrins, 1979; Clark and Williams, 1981 and Slagsvold, 1986 b; all in Magrath, 1990). In this study, I did not look at asynchrony with respect to season; nor did Bryant and Tatner (1990), so that for Blue-throated Bee-eaters this prediction remains untested.

We have seen that some of the results presented here are consistent with alternative interpretations of nestling mortality. None of these alternatives, however, explains the evolution of siblicide in Blue-throated Bee-eaters (Bryant and Tatner, 1990). For this, a functional explanation is still needed, which so far could only be provided by the brood reduction hypothesis. In the following I describe some proximal causes and effects of nestling behaviour and discuss its possible functions with respect to nestling competition.

7.4.4 The role of food in sibling competition

If sibling aggression is an adaptation for more efficient brood reduction, then the nestlings should show increased aggression towards each-other once the food supply falls below a threshold of food needed to raise all chicks in the brood (threshold hypothesis, 7.1.4). In this study, evidence for the proximate role of food in sibling aggression was sought by increasing the amount of food available to top-ranking chicks, which were assumed to be under food constraint (i.e. in a 'bad' year). The number of wounds which bear witness to attack on runts by their elder siblings (Bryant and Tatner, 1990) was not reduced when I increased the food supply to their elder siblings by 20% (7.3.5), probably because this increase was not large enough to decrease competitive behaviour of the top-ranking chick in the long-term. When observed in the artificial nest, however, the top ranking Blue-throated Bee-eater nestlings in experimental broods did show a marked and consistent decrease in several competitive behaviours (and no other activities) when they were satiated after being fed. As predicted, all competitive behaviours increased in level also when chicks had an empty abdomen (which was used as a measure for nestling hunger). Food amount therefore did have a short-term effect on nestlings' aggressive behaviour. Moreover, I could demonstrate that this proximate effect of food on competitive behaviour is mediated by nestling hunger.

Food was also shown to have an ultimate role in nestling mortality and siblicide. Runts had improved body condition and died later when their elder siblings received supplementary food. Their parents probably allocated more food to them, but they also survived longer because their older sibs, being less hungry, attacked and bullied them less. The mechanism of recovery was therefore a decrease in attacks and competition as well as a change in food allocation. This suggests that siblicide is not obligate but depends on the amount of food as suggested by the food amount hypothesis (Mock *et al*, 1987; see 7.1) and by resource tracking (7.1.4). The relationship between nestling competition and food amount is mediated by hunger in Blue-throated Bee-eaters. The effect of hunger on different aspects of nestling behaviours is discussed below.

7.4.5 The proximate role of food on behaviours: hunger affects sibling aggression

The argument that aims to settle why a food deficit results in chick mortality easily becomes circular: an energy deficit is necessary to set the scene for brood reduction, or it may be the result of a larger-than-viable brood size due to hatch-failure insurance. The proximate part played by food in nestling competition can throw some light on the direction of the causality.

When a parent arrives at the nest with food, nestlings may enhance their chances of receiving the food item either by begging, by moving towards the best position, by jostling and shuffling for the best position or by intimidating each-other by shuffling or pecking. Begging is the best-known avian nestling strategy of indirect competition. In American Robins, begging increases not only with hunger but also with the begging of the siblings (Smith and Montgomerie, 1991). Since Blue-throated Bee-eater broods are in dark burrows, begging is probably expressed by vocalizing. Begging behaviour was more pronounced in high ranking Blue-throated Bee-eater nestlings. If parents respond to these increased begging calls (as they do, for example in American Robins, Smith and Montgomerie, 1991), then the nestling that begs most intensively or calls loudest gets the food item. Ricklefs (1965) argues that if top-ranking nestlings beg more, they then receive more food and grow faster, which in turn accentuates nestling size difference achieved by asynchronous hatching.

In species where parents arrive with food at a predictable position in the nest, chicks close to that position have a better chance of receiving the food item (see McRae *et al*, 1993, for review). In Blue-throated Bee-eaters, nestling position at the burrow exit should thus be important, and parents of older broods often wait at the exit for a chick to take the food item (pers obs). The first position at the burrow exit might correlate with rank or nestling hunger if, for example, the largest or hungriest chick runs faster to the burrow exit upon hearing the adult arrive. The equivalent behaviour 'position', tested here by observations in the artificial nest, was not affected by nestling rank, condition or abdomen repletion, since nestlings stayed towards the rear of the burrow after being fed. One interpretation of this behaviour is that replete chicks give up their favourable position, and perhaps their siblings can then move further towards the burrow exit where the food is expected to arrive. Greig-Smith (1985) showed that in large broods of Stonechats *Saxicola torquata* chicks compete for better position, which is towards the rear of the nest where nestlings can stretch over their siblings to receive the food item. Forbes and Ankney (1987) show that Grebe chicks fight for the position near arriving adults, influencing food allocation in asynchronous broods. American Robin chicks jostle for position at the nest side where the adults are expected to arrive (McRae *et al*, 1993). In Blue-throated Bee-eaters, begging and positioning behaviour are not the main behaviours affected by hunger, condition or nestling rank. Instead, experimentally fed high-ranking nestlings decreased their directly competitive and siblicidal behaviours (scuffle and pecking) rather than their indirect competitive behaviours (vocalization and position; Tables 7.19 and 7.20).

Pecking and begging increased in the top-ranking chick of Blue-footed Boobies when they were deprived of food (Drummond and Chavelas, 1989). Extending the resource tracking hypothesis to include nestling competition, the top-ranking siblings would be expected to stop harassing the runts once the food supply increased above the threshold energy requirement, assuming that there were no constraints against a flexible response to food abundance. Aggressive behaviour in Blue-footed Boobies reverted back to the normal levels after deprivation to below the threshold level (Drummond and Chavelas, 1989). Both in this study (Table 7.21) and in the study by Drummond and Chavelas (1989), pecking, the most obvious siblicidal behaviour, was very much lower after nestling food intake was increased. To summarize therefore, nestling hunger, although influencing begging and direct competition, dramatically increases siblicide behaviour.

7.4.6 Nestling dominance

Social dominance may be fought-out between nestlings anew each time the parent feeds the brood. Since hunger makes nestlings more aggressive, this may directly influence their social status, i.e. a chick may become more dominant if it is hungry. This was experimentally shown for adult Dark-eyed Juncos *Junco hyemalis*, where opponents were more likely to be dominant when they had not been previously fed (Cristol, 1992). The opponents had, however, similar 'resource holding potential', i.e. there were no great asymmetries in competitive abilities. If chicks in the same brood are of similar size, fights over food may similarly be decided on the basis of the relative value of the resource to the chick, i.e. how hungry each chick is. Alternatively in asynchronous broods, a social dominance may develop between the nestlings, and each chick behaves according to its social status, so that aggression is only expressed (in relation to hunger) by high-ranking nestlings, as observed for the Blue-throated Bee-eaters. Drummond and Osorno (1992) show that the second-hatched Blue-footed Booby chick usually remains sub-ordinate to the top-ranking sib, even if it becomes larger than the dominant chick, because it has been conditioned into behaving submissively early in the nestling period.

The existence of an established social hierarchy between nestlings in a brood may have further implications. It is possible that size differences between nestlings arise because of nestling gender (reviewed by Drummond *et al*, 1991) rather than because of asynchronous hatching or offsetting asynchronous hatching. If the sex-ratio varies with laying sequence as in Lesser Snow Geese *Chen caerulescens caerulescens* (Ankney, 1982), or if one sex hatches earlier than the other as in Blue-footed Booby nestlings (Drummond *et al*, 1991), then nestlings of the first-hatching sex can have social dominance over nestling of the other. Although Blue-footed Booby males are smaller than females, in mixed-sex broods they hatch first and remain dominant even if the later-hatching females outgrew them later (Drummond *et al*, 1991), because of the social conditioning of nestlings during their early nestling phase (Drummond and Osorno, 1992). The influence of sex on sibling competition is usually expected to be limited to sexually dimorphic species, where the larger sex is not only more vulnerable to food shortages but also has social dominance over the smaller sex (Drummond *et al*, 1991). Although Bee-eaters are not sexually dimorphic, social dominance could still be dependent on sex if aggressive behaviour, for example, is expressed more fully by one sex. Since Bee-eater chicks were not sexed in this study, this idea could not be tested.

7.4.7 Function of the hook

The reduction of wounds in nests where the hooks of high-ranking chicks had been abraded shows that the mandibular hook is a weapon to aid nestling aggression (see also Bryant and Tatner, 1990), although it is possible that wounds are reduced in experimental nests for other reasons. If hooks are used for securing food items rather than pecking or pinching for example, then the competitive ability of higher ranking siblings might have been impaired in experimental nests. Runts might then have improved their condition through their relative enhancement in competitive ability, the decrease in runts' wounds may then have been a result of improved condition of the runts. I observed strong pinching behaviour (under 'pecks') in older chicks. This behaviour, in combination with the hook, produces a severe scratch. This lends strong support for the hypothesis that the hook has a function in siblicide, even if the hook can have a use in direct competition, as squabbling over food items and agrees with the conclusions of Bryant and Tatner (1990). Raptors are the only other birds reported to have weaponry which can be used against siblings (see Bryant and Tatner, 1990, and McRae *et al*, 1993, for reviews).

Broods in which top-ranking nestlings had abraded hooks tended to fledge fewer chicks, while at the same time runts died later. This evidence from the hook experiment showed that the presence of hooks in the elder nestlings probably enhances breeding success by making brood reduction more efficient. The beneficiaries seem to have been second-ranking nestlings, which had less wounds in experimental nests and more wounds in control nests. Assuming that Cond2 is a measure of nestling quality and that the top-ranking chick is the most likely to fledge, I showed in section 7.3.7 that the presence of the hook, although helping brood reduction by eliminating runts more quickly did not enhance the quality of fledglings.

7.4.8 Conclusions

Nestlings have evolved a combination of behavioral and morphological traits which aid either direct competition (scuffle) or siblicide (pinching and pecking with the special mandibular hook). These adaptations may be supplementary to that of male cooperation which allows an early onset of incubation, which seems to be at least partly responsible for asynchronous hatching. It is not clear whether asynchronous hatching is a breeding cost for late-arriving Blue-throated Bee-eaters, associated with the need to start incubating early to avoid breeding late. The function of asynchronous hatching may be to aid runt mortality by hastening their decline when there is too little food to support the entire brood (brood reduction hypothesis). This is accelerated by wounding of runts with the mandibular hook in direct aggression by its elder co-nestlings, which in turn is mediated by hunger. If the food supply is increased, runts are allowed to recover at least partly and perhaps fully, if the food amount surpasses a threshold of the amount needed to support the runts ('resource tracking').

The evidence presented here is consistent with brood reduction, but additional or alternative explanations for nestling mortality include insurance against hatching failure and the hurry-up hypothesis. As in raptors and egrets, Blue-throated Bee-eaters regularly hatched more chicks than they are known to raise, and the insurance hypothesis can probably explain some runt mortality in *M. viridis*. Aggressive behaviour was more efficient with the mandibular hook which is probably especially evolved to aid sibling aggression, which speeds up the demise of later-hatched victims. Although the hook in Blue-throated Bee-eaters is similar to the weapons which raptor chicks have, nestling aggression and runt demise is related proximately and ultimately to food in Blue-throated Bee-eaters, and they probably do not practice obligate siblicide. In this, they are more like Boobies and other non-raptors. Sibling aggression is therefore adaptive in Blue-throated Bee-eaters, but it is not possible to ascertain whether this is because runts hatch despite being surplus to the viable brood size (insurance) or because they cannot be sustained because conditions turn out to be unfavourable and clutch size could not be adjusted (brood reduction).

CHAPTER 8: DISCUSSION

In this chapter I draw together the implications of results from earlier chapters on aspects of the social ecology and the mating and breeding behaviour in Blue-throated Bee-eaters. In particular, I shall discuss coloniality, followed by cooperative breeding and the mating system. Brood reduction and siblicide are re-examined as strategies against egg 'dumping', and egg 'dumping' is discussed as a strategy for breeding females to increase their reproductive output.

Strategies of breeding behaviour which may be adopted by individual Blue-throated Bee-eaters to increase reproductive success were discussed in previous chapters and are summarized in Table 8.1. I use Table 8.1 in the following discussions when referring to each aspect of the Blue-throated Bee-eater breeding behaviour in turn. This table also contains strategies which I have not investigated here.

8.1 Coloniality in Blue-throated Bee-eaters

The encounter rate amongst potential breeding partners could be enhanced by staying paired over the winter or by re-assembly at the same colony (Table 8.1). Pairs can meet-up at the beginning of the breeding season, because successful breeders returned to exactly the same site in the colony (Chapter 5). There was some anecdotal evidence that pairs returned to the colony together from the wintering grounds (Chapter 4), but an investigation of wintering birds was beyond the scope of this study (see Table 8.1). In any case, return rates were so low that most birds had to find a new partner each year.

Bee-eater species which have been studied extensively are all highly colonial (Table 8.3). They all exploit large insect food like the Blue-throated Bee-eater (e.g. Fry, 1984). Hegner (1982) argues that the distribution of the large insect food of White-fronted Bee-eaters, although still overall patchy, is predictable enough for the central place foraging theory to be applicable: the birds benefit by having reduced travel distance and search times to where the food is most abundant (Brown *et al*, 1992; Ward and Zahavi, 1973; Horn, 1968) and colony members may exploit each-other's success (Brown, 1988 and 1986; Ward, 1965). It is likely

Table 8.1: Components of fitness relevant for *M. viridis* and options of behaviours for individual birds to increase them (see Table 1.1)

Component of fitness	Individual	Options for increasing component	this study
encounter rate	M+F	- assemble at breeding grounds to meet with previous or new partner	x
		- stay paired during the winter	(x)
fertilization rate	M	- see EPCs	x
		- exclude other males by guarding partner	(x)
		- control insemination by timing or frequency of copulation or amount of sperm transmitted	
		- behavioural and physiological adaptations (sperm plug, sperm removal)	
timing of laying	M+F	- incubation feeding	(x)
		- helping in digging or induce partner to dig	(x)
		- arriving early	(x)
nestsite for eggs	M+F	- return to nest site of the previous year if successful	x
		- dig burrow and defend it	x
		- steal burrow	(x)
	F	- 'dump' eggs	x
Predator avoidance	M+F	- synchronize breeding at colonies to swamp predator (see below)	(x)
		- breed solitary so as not to attract predator attention	(x)
egg survival	M+F	- help to incubate	x
		- 'dump' eggs in host clutch (INP)	x
parental effort	F	- guard partner or mate repeatedly with him to avoid him siring EPO	x
	M+F	- desert eggs or chicks: partner has to increase effort (but may desert too)	(x)
	chicks	- begging behaviour, wait at entrance etc	x
nestling survival	M+F	- invest in care	(x)
		- recruit helper to provision young	(x)
		- reduce competition for food by breeding solitarily	(x)
		- use colony as 'information centre' to forage more efficiently	
		- 'dump' egg at the right time wrt when host eggs are laid	x
		- reduce broods to viable number of chicks as early as possible	x
	chicks	- obligatorily prevent future competition from sibs for food	x
		- kill or exclude competing sibs only when food is scarce, facultatively	x
post-fledgling survival	M+F	- choose good quality mate to pass its genes on to offspring	(x)
		- chose mate compatible in age or size	(x)
		- choose mate of good condition/ ability/ experience to provide care	(x)
adult survival	M+F	- defer breeding if conditions are unfavourable (and help relatives[1])	(x)
		- dilute risk of predation by living in groups	
		- migrate to avoid competition with Blue-tailed Bee-eaters	(x)
		- desert eggs or chicks if conditions deteriorate	

[1] especially the philopatric sex (more likely to have relatives in the colony)

x dealt with in the present study (x) investigated anecdotally in the present study

M male F female

that coloniality has evolved in Blue-throated Bee-eaters at least partly in response to food distribution (Table 8.2). Competition for food in large colonies (e.g. Brown *et al*, 1990; Møller, 1987 d; Shields *et al*, 1988) is the most likely explanation for the tendency for fewer fledglings per nest in the large NH91 colony; similarly, reduced competition for food in the small SB90 colony was the most probable reason for the tendency of more chicks fledging per nest there (Chapter 4). The situation at NH91 was probably aggravated further by excessive disturbance from golfers in that year.

Limited nesting habitat has been proposed as a cause of colonial nesting in Swallows (Shields and Crook, 1987; Snapp, 1976). I encountered many seemingly suitable colony sites throughout the Peninsula Malaysia (where there is an abundance of golf-courses and large park-gardens with restricted access to the public, near relatively undisturbed forest or mixed vegetation) which were not used by Bee-eaters. It is likely that other factors like familiarity, closeness of forest patches or of other foraging areas are limiting, or that even those sites which are used by the Blue-throated Bee-eaters are sub-optimal, if changes in habitat during the last century of development in Malaysia have pushed the species into more unsuitable habitats (see Chapter 4). I could find no clear evidence for the notion that suitable nest sites are limited for Blue-throated Bee-eaters, which is also what Hegner *et al* (1982) argue for White-fronted Bee-eaters.

A recent move to more sheltered, 'man-made' colony sites may have resulted in reducing predation to a negligible level: only 2 or fewer nests were predated in each colony (see Chapter 4). The probability of predation for each nest decreased drastically in larger colonies, from 25% in small colonies to less than 10%, where the number of nests monitored was higher (all Chapter 4). Reduced risk of predation may be a benefit of coloniality through the 'selfish herd' effect (Watt and Mock, 1987; Hamilton, 1971).

The risk of becoming a victim of intraspecific brood parasitism (including both extra-pair copulations and egg 'dumping') is expected to be higher in colonies (Møller and Birkhead, 1993; Shields *et al*, 1988; Hoogland and Sherman, 1976) and thus represents a potential cost of coloniality for the Blue-throated Bee-eater (Table 8.2). There were no confirmed extra-pair offspring (Chapter 6; this is discussed in more detail below), and although extra-pair

Table 8.2: Some potential costs and benefits of coloniality for Blue-throated Bee-eaters (see text for explanations of concepts and Chapter 1 for references)

Costs	Benefits
Increased competition for food	Reduced travel time to unpredictable food resources because follows distribution of clumped resources
	Reduced travel time because colony acts as 'information centre' for food distribution, or according to central place foraging economics
Increased competition for nest sites	High quality habitat for nest site (which are limited)
Conspicuous to predators	Swamp predators
	Safe site from predators
	Predator detection faster
	Predator mobbing
Increased infestation of ectoparasites	Presence of relatives for cooperative breeding
Increased competition for mates	Encounter rate for mate choice increased, search time decreased
For pair members: increased danger of EPCs of partner	for EP males: increased opportunity for EPCs
for breeders: increased risk of INP	for 'dumpers': increased opportunity for INP

copulations did occur they are probably quite rare (see below). There was no evidence for an increase in intra-specific nest parasitism in the larger colonies of Blue-throated Bee-eaters (section 6.2.9). Intra-specific nest parasitism, however, is as high as reported for other colonial species, including White-fronted Bee-eaters (Table 8.3). Unless solitary Blue-throated Bee-eaters experience similarly high levels of nest parasitism, intraspecific nest parasitism is a cost of coloniality in the Blue-throated Bee-eater.

Compared to the three other Bee-eater species which have been studied most extensively, Blue-throated Bee-eaters are less obligatory in their coloniality (Table 8.3). Two likely costs of coloniality were identified as competition for food in large colonies and intra-specific nest parasitism in colonies of all sizes, including small colonies. Coloniality in Blue-throated Bee-eaters is likely to have originally evolved in response to several selection pressures; one of these is predation which, since their probably recent move into a more sheltered environment, is nowadays probably not a problem in Blue-throated Bee-eater colonies any more. If Blue-throated Bee-eaters were originally colonial to avoid predation in their original habitat, coloniality itself may have become a cost they carry-over from their recent past. This may be the reason why their coloniality is not obligatory, and it is perhaps to be expected that they are in the process of becoming less colonial as competition for scarcer insect food increases.

8.2 Cooperative breeding in Blue-throated Bee-eaters

According to the territory saturation model of helping (reviewed e.g. by Hegner *et al*, 1982), young birds become helpers rather than breeders if there is lack of breeding space (Table 8.2). Apparently suitable Blue-throated Bee-eater colony sites, however, seemed common in semi-urban areas all over the Peninsula Malaysia (see above, section 8.1). Instead, habitats with suitable food supplies may be limited (Emlen, 1991), and competition for these food supplies might deter prospective helpers from breeding themselves (Emlen, 1991; also Emlen, 1982 a and b). Hegner and Emlen (1987) argue that the temporal patchiness and unpredictability of insect food explains the incidence of helping in White-fronted Bee-eaters. In bad years after droughts, when there may not be enough food for all potential breeders to raise young, sub-adults are increasingly recruited as helpers (Emlen, 1982 a). The foraging observations of Blue-throated Bee-eaters in this study suggested that there were patches of suitable

Table 8.3: Comparative breeding structure in well-studied species of Bee-eaters

Bee-eater species (*Merops sp*)	Coloniality/ no. breeders	Extent of cooperation	Foraging	IBP*: type & extent	Philopatry, Ad return	Sex ratio M/F	Habitat/ Environment	Migration	Starvation	Predation
White-fronted (*M. bullockoides*)[a]	obligatory 40-450	Clans of 2-11 birds 50% + helpers (M,F)	stable Clan territories	EPF: 1%, 1/5 EPCs (per F and season); INP: 16% of nests (7% of eggs)	both sexes return, F joins M breeding group		Seasonal tropical savanna, river-banks	no	48% of nestlings	4% (eggs), 7% (pre-fledging)
Red-throated (*M. bullocki*)[b]	sub-colonies 10-200 1000s per area of riverbank?	Units of 2-5 birds 30% + helpers					Seasonal tropical savanna type, river-banks			5% of eggs and nestlings
European (*M. apiaster*)[c]	200	Units of 2-6 birds 20% + helpers (only M)	non-territorial	EPF: 1% (1/100 chicks), no INP.	both sexes return M > F, F joins M breeding group	M > F first year, M = F later	Seasonal sub-tropical savanna type, river-banks	long-distance ?		
Blue-throated (*M. viridis*)[d]	1-400	Units <= 3 <5% + helpers	non-territorial ?	no EPFs 20% 'dumped' some quasi-parasitism	both sexes return (to site; M > F?)	(F>M sexed)	tropical urban grass-lands	within tropics		2.2% (eggs) 7% (broods) 25% (in small colonies)

[a] Emlen and Wrege, 1994, 1991, 1986; Hegner and Emlen, 1987; Hegner *et al*, 1982; Wrege and Emlen, 1991

[b] Fry, 1984, 1972; Dyer and Fry, 1980; Crick and Fry, 1986.

[c] Lessells, 1990; Jones *et al*, 1991.

[d] Bryant and Tatner, 1990; Green, 1990(?); Medway and Wells, 1976; P.T. Green, pers com; this study

*: includes Intraspecific nest parasitism (egg 'dumping', Extra-pair copulations and 'Quasi-parasitism'

M = Male; F = Female

foraging habitat within 1-2 km of both colonies which were not utilized, or at least were never seen to be used. At those sites that were used regularly (e.g. *REM Rubber*), there may have been a regular supply of insect food, but it was my impression that most of the insect food was very patchily distributed, available for only short periods of time (e.g. assemblages of dragonflies over a field; swarms of ant and termite alates). With insect food being unpredictable in time *and* in space, many returning Blue-throated Bee-eaters may be unable to breed during years with low overall food availability.

Helping at the nest is a behaviour widely reported amongst bird species (see reviews by Emlen, 1984; Skutch, 1961; see also Chapter 1 and 4) and is common amongst Bee-eaters (Table 8.3), where relatives breed in the colony and coloniality may enhance the opportunity to recruit a 'helper' from a pool of related birds (see Tables 8.1 and 8.2). For some individuals (depending on sex and age), helping a relative can be preferable to breeding (Emlen and Wrege, 1994; Lessells, 1990; Lessells and Krebs, 1989). For young Bee-eaters who are deciding whether to breed, to help or to become floaters, the last is considered the most costly option because of the missed breeding opportunity on one hand, and of not adding to its inclusive fitness by raising related chicks on the other (Emlen, 1994). Only very few helpers, however, were found amongst Blue-throated Bee-eaters (Chapter 4). There were floater populations of non-breeders and failed breeders at Blue-throated Bee-eater colonies, which foraged nearby and could presumably have been recruited, but which neither helped nor bred. Competition for food could partly explain why juveniles might have become floaters rather than breeders or helpers, if the constraint is so great that even self-feeding becomes difficult for these potential helpers. In Emlen's (1994) model, however, extreme constraints act to push young White-fronted Bee-eaters further towards helping. Some explanation is therefore needed as to why cooperation is not more common in Blue-throated Bee-eaters.

Potential helpers may have been deterred by early disturbance. Since return rates were exceptionally low in the first year of this study, perhaps due to the high disturbance levels and use of patagial tags in the previous year, those birds that did return may have found too few relatives to help or to recruit as helpers. Although most floaters and unsuccessful breeders visited the colony only rarely and were therefore probably not detected as returns, all returning breeders showed great allegiance to the site of their previous nesting attempt, so that it is unlikely that returning birds bred elsewhere in the vicinity where they would have gone undetected. Perhaps most breeders did not come back because of low success rates in the previous years, since only successful breeders returned to breed the next year (all returning breeders had raised fledglings in the year before; Chapter 4). It is possible helping is low overall because during favourable years both in environmental terms and return rate, most birds breed rather than help, whereas during bad years, many birds that are not able to breed would help instead but can only do so if there are relatives present at the colony (see above).

To summarize, helping is favoured in bee-eater-saturated environment (see above; Emlen, 1982 a; König, 1981) and in birds that are long-lived so that young birds which in general reproduce less well (Curio, 1983; see also Lessells and Krebs, 1989) can defer breeding to a later season. Because of high season-to-season mortality (50% or more; Chapter 4), the cost of a missed opportunity to breed is presumably very high in Blue-throated Bee-eaters. There did not seem to be a limitation for potential breeding sites. If competition at the colony is too high for the young birds to breed, they could strike off on their own, provided that coloniality is not obligatory. Whereas White-fronted Bee-eaters always nest in colonies of about 200 or more birds (e.g. Emlen and Wrege, 1994), and Red-throated Bee-eaters are described as living in colonies of hundreds of birds (Fry, 1984), Blue-throated Bee-eaters were occasionally found nesting solitarily (pers obs; Table 8.3). Therefore, Blue-throated Bee-eaters should breed if they can, even solitarily, and the expected level of cooperative breeding is low. The low numbers of helpers reported for Blue-throated Bee-eaters in this study is probably typical rather than exceptional for this species (e.g. D.M. Bryant, pers comm, for Sungai Buloh in 1981 and 1985 and P.T. Green, pers comm, for Sungai Buloh in 1986-1988). Cooperative breeding is prevalent in colonial Bee-eaters (Fry, 1984). White-fronted Bee-eaters live in family units or 'clans' with up to 4 helpers per nest and are highly social (Table 8.3). Blue-throated Bee-eaters, with non-obligatory coloniality, also have a low level of cooperation (few had helpers, none more than one) and are clearly not as social as some other Bee-eater species.

8.3 The mating system of the Blue-throated Bee-eater

Male monogamous birds have various options to increase their fertilization rate: they can seek extra-pair copulations (EPCs) and try to guard their partner against EPCs (Table 8.1). Sometimes they do both literally at the same time, as reported for White-fronted Bee-eaters, where mate-guarding males at the colony comprise the majority of those which give sexual chases to extra-pair females (Emlen and Wrege, 1986). Since no extra-pair offspring (EPO) were established unambiguously for Blue-throated Bee-eaters (Chapter 6; see Table 8.3), EPO are probably uncommon in Blue-throated Bee-eaters for either of four reasons:

(1) there are no EPC attempts,

(2) there are no EPCs because of (a) effective mate guarding or (b) because the female avoids EPCs,

(3) EPCs do occur but do not lead to EPO because they get out-competed by PCs, or

(4) females participating in EPCs lay the next egg in the nest of the extra-pair male, i.e. EPO are attributed to 'quasi parasitism'.

I observed one definite EPC during this study. Although this means that EPCs do occur, it is not clear whether they are common, since relatively few copulations could be assigned to either pair males or extra-pair males (Chapter 5). Pairs spent more time within sight of each other during pre-laying and laying (even outside the time when they were digging, which is nearly always done in pairs) than later in the season during incubation and chick feeding. Even during pre-incubation, however, only about 40% of sightings of pair members were within view of each-other (Chapter 5). If males do try to mate-guard, therefore, their behaviour alone is not very effective at excluding EPCs. (Mate-guarding in Blue-throated Bee-eaters is discussed more fully in section 5.4.3).

Ramo (1994) reports that male Grey Herons *Ardea cinerea* have few EPC attempts at low densities, but more at higher densities (see also Venier and Robertson, 1991). The author concludes that EPC is a mixed reproductive strategy in male Grey Herons. It is possible that Blue-throated Bee-eater colonies in this study were less dense than typical (which is discussed in Chapters 4) and that EPCs are an alternative mating strategy used by Blue-throated Bee-eaters in very large colonies. This could not be confirmed in this study.

It is possible that EPCs do occur commonly, perhaps away from the colony at the feeding site (Venier and Robertson, 1991) or in the nest chambers (Riley, 1992). EPCs might occur despite mate-guarding, as in Blue Tits *Parus caeruleus* (Kempenaers *et al*, 1992), but that they might not result in EPO. In Fulmars *Fulmarus glacialis*, 2.4% of copulations observed were EPCs, but 9 females with EPCs (out of 15 families with assigned paternity) had not a single EPO (Hunter *et al*, 1992), perhaps because PCs are more frequent than EPCs, or EPCs are followed by PCs. Møller and Birkhead (1993) show that colonial bird species with monogamous mating systems practice frequent copulation to ensure paternity (see their appendix), some together with and some without mate-guarding (see also Møller and Birkhead,1991; Venier and Robertson, 1991). In this study, the EPC I observed was followed immediately by a forced PC, which was never observed under any other circumstances (Chapter 5). This is circumstantial support for the notion that even when EPCs do occur, they do not commonly lead to EPO because of copulation patterns (timing or frequency) of the female with the pair male (see Møller and Birkhead, 1991, and Chapter 5). To summarize, mate-guarding could therefore not have been the only mechanism for pair-males to avoid being cuckolded. If EPCs did occur, they could have been out-competed by pair copulations.

Mate-guarding may be ineffective because females are actively seeking EPCs for different reasons: to obtain 'good genes' for her offspring from males of high social status (Smith, 1988) or quality (Kempenaers *et al*, 1992), as a pre-amble to mate-switching (Heg *et al*, 1993; Colwell and Oring, 1989), as an insurance against their mate's infertility (Wetton and Parkin, 1991) or to actively increase sperm competition for the fertilization of her eggs (Sheldon, 1994). In most bird species where copulation has been studied in detail, the cooperation of the female is needed for successful cloacal contact (Mills, 1994; Wagner, 1991; Birkhead *et al*, 1990), presumably because most male birds do not have a penis-like organ for intromission (Sheldon, 1994). 'Rape' or forced copulations are thus rarely successful in birds (Sheldon, 1994; Smith, 1988; Hatch, 1987; Butler, 1982). The picture emerging from the most recent literature is that it is not uncommon for EPCs to be controlled by female choice (Heg *et al*, 1993), from which two possibilities arise which will be discussed in turn: either, female Blue-throated Bee-eaters choose not to partake in EPCs, or they do solicit EPCs which do not, however, lead to EPO (see below).

In species where EP rape is common, mate-guarding by the pair male reduces harassment of females by EP males (e.g. Mineau and Cooke, 1979; see Birkhead, 1988). If the females themselves, however, can and do avoid EPCs, mate-guarding may not be necessary. In colonially nesting Cliff Swallows, for instance, males do not mate-guard despite copulation attempts from EP males, because the females successfully avoid EPC attempts (Butler, 1982; see also Björklund *et al*, 1992). If the Blue-throated Bee-eaters I DNA fingerprinted therefore did not have any EPO, this may be because my particular sample of females did not accept EPCs. This could be, for example, because they were paired to high-quality partners and would not have improved their offspring's genetic parentage (as reported by Smith, 1988), or because it is advantageous for females to copulate only with males of known fitness and they cannot easily asses the quality of potential EP partners (Butler, 1982). The former could be true, for instance, if the only chicks that survived long enough to be blood-sampled (taking blood from very young chicks proved too difficult) were from nests where high-quality parents look after them better. The latter case of difficult assessment could be true, if Blue-throated Bee-eater males do not have clear signals for quality (plumage, ornament or behaviour), by which a female can choose a potential EP partner. Females may avoid EPCs furthermore to avoid infection with diseases she could catch from the extra-pair male (see Birkhead and Møller, 1992). The Blue-throated Bee-eater is sexually monomorphic, and the male probably does not signal his quality (or of being free of diseases) extensively in plumage brightness or tail length, as is common in sexually dimorphic bird species (Harvey and Bradbury, 1991; Hedrick and Temeles, 1989).

Females may control whether or not EPCs result in fertilizations. Circumstantial evidence suggests that the extent of mate-guarding and whether there is female control of EPCs determines the mating system in some colonial seabirds. Wagner (1991) compared EPC and EPO occurrence between two closely related colonial seabirds, the Razorbill *Alca torda* and Common Guillemot *Uria aalge*. Guillemots mate-guard more vigilantly and forced EPCs are regularly achieved by interruption of pair-copulations, whereas Razorbill females control the success of EPCs and they are not very closely guarded. In the Northern Fulmar *Fulmarus glacialis*, females successfully solicit some EPCs despite moderate mate-guarding (Hatch, 1987). There was, however, no evidence for EPO in Fulmars in a subsequent DNA fingerprinting study by Hunter *et al* (1992). A lack of EPO despite observed EPC was reported also for two species of Warblers *Phylloscopus spp* (Gyllensten *et al,* 1989) and in the typically monogamous Oystercatcher *Haematopus ostralegus* EPO were similarly much rarer than EPCs (Heg *et al,* 1993). The same may also be true for Pied Flycatchers, where lack of mate-guarding and 29% EPCs were reported in one study (Alatalo *et al,* 1984), but only 4% of offspring could be assigned to EPO with DNA fingerprinting in another, albeit at a lower density of breeding birds (Lifjeld *et al,* 1991). In their recent review of the predictability of EPO from EPC rates, Dunn and Lifjeld (1994) report that there was no positive relationship between EPO and EPCs across species (but see Birkhead and Møller, 1992), which, they propose, is as expected with female control of paternity. Hunter *et al* (1992) attempt to explain the discrepancy between observed EPCs and confirmed EPO for Fulmars with the observation that the pair male was always the last to copulate with his female after the last EPC. They conclude that paternity is assured by frequent copulations (see also Birkhead and Møller, 1992). Similar observations are reported for Guillemots by Hatchwell (1988; in Birkhead, 1988). Lifjeld *et al* (1991) conclude that in Pied Flycatchers, lack of female cooperation in EPCs rather than frequent pair copulations were responsible for the low success rate of EPCs. This lack of cooperation may be more subtle in this species, such as refusing complete cloacal contact (Lifjeld *et al,* 1991). Lifjeld *et al* (1993) argue that female Tree Swallows control whether or not sperm is transferred successfully during copulations. Dunn and Lifjeld (1994) venture that forced or passively accepted EPCs might be less likely to result in fertilization in some species.

It seems that the Blue-throated Bee-eater conforms to the 'Fulmar-Razorbill' pattern: firstly, all copulations in Blue-throated Bee-eaters involved the consent of the female by 'ducking', except for a single pair-'rape' which occurred after the EPC (Chapter 5). This EPC was, secondly, female-solicited and with full female cooperation, lasted a long time and had cloacal contact, whereas the pair-'rape', without female cooperation, did not have cloacal contact. Thirdly, mate-guarding in Blue-throated Bee-eaters was too moderate to avert such EPCs by females. It is likely that EPCs do occur occasionally in Blue-throated Bee-eaters, and that they are female-solicited. The reason why they did not lead to EPO is perhaps dilution of foreign sperm, or last-sperm-precedence, by the pair male (see above).

In species where pair cooperation and a strong pair bond is imperative for successful breeding, female partners of high quality males resist EPC attempts, as in the Red-billed Gulls for example, where PCs were 8 times more successful than EPC attempts because of lack of female cooperation in EPCs (Mills, 1994). It is argued elsewhere that Blue-throated Bee-eater pairs probably cooperate at all stages in the breeding cycle. Cooperation and a strong pair bond often coincides with a monogamous mating system (e.g. Mills, 1994; Decker *et al*, 1993). Perhaps therefore, EPCs are, in Blue-throated Bee-eaters, a rare behaviour solicited by the female, associated with benefits other than fertilization of her eggs, such as mate-switching (see also Chapter 5 - 'The function of copulations').

The evidence from DNA fingerprinting points towards a monogamous mating system in the Blue-throated Bee-eater, where pair cooperation and synchronous breeding assures that most nestlings are actually sired by the pair male. DNA fingerprinting has revealed that exclusively monogamous mating systems, as for example in Black Vultures *Coragyps atratus* (Decker *et al*, 1993), are quite rare in birds and also in mammals (Ribble, 1991). Moderate monogamy is typical for Bee-eaters, for instance in the European Bee-eater (Jones *et al*, 1991; Table 8.3), but in White-fronted Bee-eaters, monogamy is less exclusive than for the Blue-throated Bee-eater (Table 8.3). It is possible that the ecology of the Bee-eaters produces an adaptive radiation in mating systems similar to that found in the birds of paradise: Beehler (e.g. 1990) describes how specializations in unpredictable, temporarily abundant food resource such as figs, may produce a monogamous mating system in a bird family where polygyny is wide-spread, because the female cannot bring enough nutrients to the brood on her own. Blue-throated Bee-eaters seem to specialize on dragonflies (see Chapter 4), which may be similarly temporary when abundant and may have helped to shape the monogamous mating system of the Blue-throated Bee-eater.

8.4 Early incubation and siblicide as strategies to counter INP

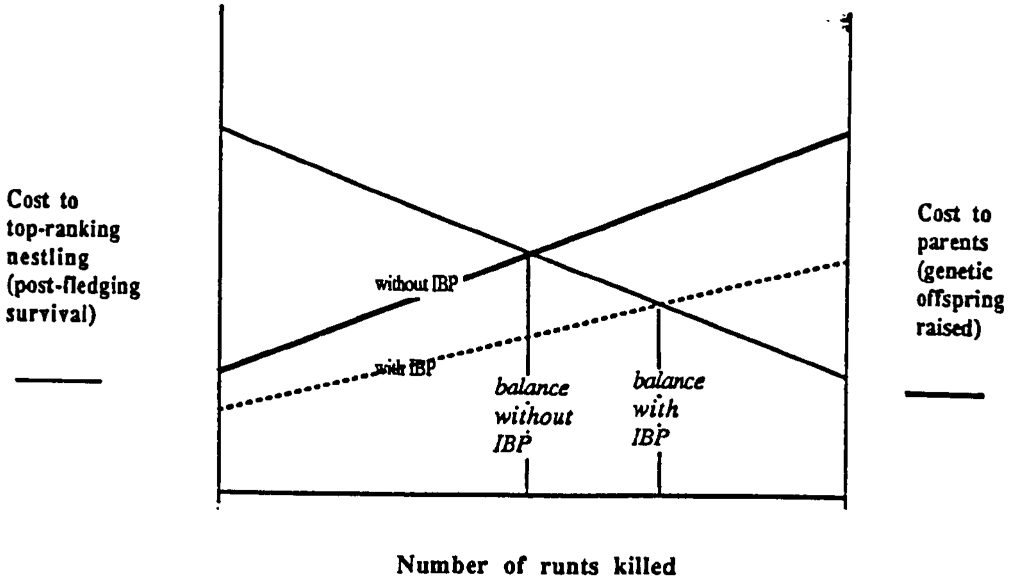
An early onset of incubation and siblicide may be adaptations against INP (see Bryant and Tatner, 1990). If 'dumped' eggs are expelled before the onset of laying in their own nest, an early onset of incubation assures that the first-hatching nestling is a true genetic offspring and has a size advantage over the later-hatching chicks most of which are eliminated by starvation and siblicide. This was suggested for instance by Feltham (1987). I shall refer to this notion as the '*anti-INP hypothesis*'.

The following findings are expected under this hypothesis. (1) Birds expel eggs before they start laying themselves. (2) Birds accept eggs after their own eggs appear in the nest. (3) Top-ranking nestlings are the genetic offspring of both putative parents and a higher percentage of illegitimate offspring is found amongst later-hatched nestlings. (4) As a consequence of an early onset of incubation a pronounced hatching asynchrony persists. (5) Frequently only the top-ranking nestlings survive to fledge. (6) Siblicide or other nestling competitive behaviour aid speedy elimination of the younger nestlings. (7) A high level of egg 'dumping' persists in the population.

Although some of the hypotheses discussed in Chapter 7 for hatching asynchrony cannot be discounted as being relevant to the evolution of nestling aggression and siblicide (in particular 'insurance', 'hurry-up' and 'brood reduction'), Blue-throated Bee-eaters behave in a way which is largely consistent with the anti-INP hypothesis. (1) In Chapter 6, I showed that Blue-throated Bee-eaters nearly always expelled eggs experimentally 'dumped' into their nest before their first egg was laid and (2) invariably accepted 'dumped' eggs thereafter. (3) Lower-down in the hatching order, up to one-third of eggs were the result of one or other form of INP in Blue-throated Bee-eaters (possibly by individuals of varying degree of relatedness to the host birds; Chapter 6). (4) Blue-throated Bee-eaters have a pronounced hatching asynchrony which was exaggerated further by top-ranking nestlings growing faster (Chapter 7). (5) Nestling mortality was so pronounced in this study, that most nests fledged only one nestling which was nearly always the top-ranking chick. (6) Blue-throated Bee-eaters have evolved a mandibular hook with which runts were wounded which makes them more likely to die (Chapter 7). (7) The level of INP in Blue-throated Bee-eater colonies was high (Chapter 6).

More subtle predictions of the above hypothesis include the effect of food abundance. The predictions are rather similar to those of the brood reduction hypothesis, with the addition that the selection pressure is much higher if the nestlings which are eliminated are more likely to be non-kin. In fact, the anti-INP-hypothesis is probably best viewed as an addition to the brood reduction hypothesis in Blue-throated Bee-eaters. In poor conditions, where only one nestling can usually be raised, it would be very costly to risk raising a nestling which is not the true offspring, but if conditions are favourable, this risk can be taken, especially since there is a 2/3 chance that each subsequent chick is a true genetic offspring.

In Blue-throated Bee-eaters there should thus be a shared interest of parents and their true offspring, to eliminate illegitimate later-hatched nestlings in poor conditions. Jackson (1993) suggests that it might be possible that parents discriminate against parasitic young and selectively starve them. Nevertheless, since numerous experiments of egg and nestling exchange have shown that birds generally accept eggs and even young chicks as their own, it is unlikely that parents can distinguish between legitimate and non-genetic offspring hatching in their nest. Therefore, the likely anti-INP strategy adopted by parents is restricted to incubation, whereas the anti-INP strategy of chicks is siblicide. From the parents' point of view, top-ranking nestlings may 'overshoot' the ideal target brood size with their siblicidal behaviour (Bryant and Tatner, 1990) because those runts which are legitimate offspring and can be raised successfully, should not be killed. From the point of view of the first-hatched chick(s), siblicide should continue to eliminate younger siblings until the costs to the elders' own survival as well-nourished post-fledglings meets that of loosing a chick for the parents (plus their own inclusive fitness of losing a full relative). This could result in a parent-offspring conflict of how many chicks to kill (see Forbes, 1993, for review). The compromise, which is expected to lie somewhere in the middle (Figure 8.1), is different if some of the later-hatched chicks are expected to be non-kin to both the patents and the top-ranking nestling. By ensuring that the surviving, top-ranking chick is their own offspring, siblicide is also in the parents' interest and the balance in the parent-offspring conflict is pushed further towards favouring siblicide (Figure 8.1). Egg 'dumping' may thus have been important for the evolution of siblicide in the Blue-throated Bee-eater. The elimination of non-genetic offspring as a function of siblicide has important implications for the optimum strategy of egg 'dumping' in Blue-throated Bee-eaters, and is discussed in the next section.



<u>Figure 8.1</u>: **The parent-offspring conflict of siblicide in Blue-throated Bee-eaters:** a model of the effect of intra-specific brood parasitism (IBP) on the outcome of the parent-offspring conflict. The cost to the top-ranking nestlings of retaining other nestlings (thin line) is balanced against that to the parents in losing their offspring due to siblicide (thick line; the model does not take into consideration that siblicide is also be useful to the parents under the *brood reduction hypothesis*, see text). Cost to the top-ranking nestling is measured either in terms of food lost for post-fledging survival for the top-ranking nestling, which is assumed to be maximal when it is remains alone in the nest and to decrease linearly with each chick retained in the nest (in reality it may start-off level, if enough food is available to raise more than one well-nourished fledgling). Cost to the parents is measured in terms of chicks lost: with each chick killed, the parents raise one chick less until only the top-ranking nestling remains. The cost to the parents of losing chicks balances the cost to the top-ranking nestling's post-fledgling survival where the two lines intercept. The cost to the parents of losing any one chick is reduced by one-third if the probability of this chick being a full genetic offspring is only two-thirds (as estimated in Chapter 6 from DNA fingerprints; dotted line). The balance reached in the parent-offspring conflict of siblicide then moves towards killing more runts.

8.5 Intraspecific nest parasitism (INP)

Blue-throated Bee-eaters have quite a high level of INP (Chapter 6.2) and of corresponding anti-cuckoldry behaviour by birds with nests (Chapter 6.3). Egg 'dumping' as a reproductive strategy in Blue-throated Bee-eaters is discussed in this section.

8.5.1 Why do birds 'dump' eggs?

To understand INP it is necessary to know the identity of egg 'dumpers', i.e. whether they have nests of their own or not (Jackson, 1993) and thus, whether INP is done by birds which have suffered a failed nesting attempt or which are unmated ('best-of-a-bad-job' hypothesis, e.g. Jackson, 1993), or whether INP is a sophisticated mixed reproductive strategy (Petrie and Møller, 1991).

INP as the 'best of a bad job'

Females may 'dump' eggs because they have no nest of their own, perhaps because they are unmated but have been fertilized by a male who is paired to a different female (Lyon, 1993 a and b, Brown and Brown, 1988; Yom-Tov, 1980) or perhaps because available nest sites are limited (Horn and Rubenstein, 1984). Although most burrows are washed-in from previous years, Blue-throated Bee-eaters do not generally re-use the few intact burrows from the previous year (personal observations). This may have evolved as ecto-parasite avoidance (e.g. Duffy, 1988), but it could also indicate that there is no shortage of burrows for breeding, and that the cost of burrow construction is low. Blue-throated Bee-eaters often dig three burrows before laying (Chapter 5) which might again indicate a surplus of burrows. There was, however, some indication that many attempted burrows were discarded as being non-viable and that birds arrive early to be able to have more digging attempts (Chapter 5). A limitation on breeding sites can therefore not be wholly discarded as a possible reason for egg 'dumping' in Blue-throated Bee-eaters.

Failed nesters may 'dump' already formed eggs (Pinxten *et al,* 1991 a; Evans, 1988; Yom-Tov, 1980; Emlen and Wrege, 1986; Andersson, 1984). If birds have to desert a nest during laying, they are unlikely to dig or find another empty burrow to lay into. They then either have to contest ownership of an occupied burrow, discard their already formed eggs or lay into another pair's burrow. If nest loss is the main cause for INP, then the incidence of INP should be connected with specific cases of nest loss (Lyon, 1993 b). There was some evidence for nest desertions in this study during laying in the 1991 breeding season at Nam Heng (NH91), probably due to weather or human interference (Chapter 4), but NH91 did not have a high proportion of INP. There was therefore no circumstantial evidence for the hypothesis that eggs 'dumpers' are mostly failed nesters.

INP as a mixed reproductive strategy

If INP is a strategy, individuals can be specialist egg 'dumpers', as an alternative to tending a nest ('pure parasite hypothesis', Kendra *et al*, 1988, in Jackson, 1993; but see Lyon, 1993b, who states that there is no evidence to date on lifelong pure parasites in INP). Alternatively, individual females can 'dump' some of their eggs into other nests and also tend their own nest (e.g. Jackson, 1993; Lyon, 1993 a and b; Gibbons, 1986; Hogland and Sherman, 1976).

Recent literature on parasitoid insect species (Hardy, 1994, reviewing Ridley, 1993, therein) suggests that multiple matings by females may be a strategy to reduce sibling competition. Many parasitoids deposit several eggs into the same host, and the more closely related the young are, the more similar they are and the more they should therefore compete with each-other. Multiple matings create genetic diversity between siblings which may reduce competition amongst the siblings (this is a similar argument to the 'reduced sibling competition' hypothesis of hatching asynchrony). Following this hypothesis, intraspecific brood parasitism could reflect a similar strategy in birds, by one or both parents to increase the genetic distance between nestlings and thus decrease fighting between them, or to supplement the function of the size hierarchy with additional differences in nestling quality. In Blue-throated Bee-eaters, a paired male might encourage an extra-pair female carrying an egg fertilized by him to 'dump' her egg into his nest, which would increase the genetic distance between his nestlings without carrying less of his own genes.

To distribute eggs between nests can be tactical for avoiding catastrophic predation losses or nest failure ('nest failure hypothesis'; see Lyon, 1993 b; Brown and Brown, 1989; Payne, 1977). One likely reason for nest failure in Blue-throated Bee-eaters is flooding, as observed in the colony of at Sungai Buloh (P.T. Green, pers comm). If eggs are spread across nests to ensure survival of some offspring in case nests fail because of flooding or other losses, we would expect eggs appearing in any nest to be from individuals with nests further away, not of close neighbours as in the Cliff Swallow (Brown and Brown, 1988). Egg 'dumping' by neighbours was reported for Swallows by Shields *et al* (1988) and Møller (1987 g). In Blue-throated Bee-eaters, there was some evidence that relatives are neighbours and might 'dump' eggs on each-other (both Chapter 6), which would be in disagreement with the predictions from the nest failure through flooding hypothesis of INP for Blue-throated Bee-eaters.

A further reason for egg 'dumping' was found by Lyon (1993 a) for American Coots *Fulica americana* and by Gibbons (1986) for Moorhens *Gallinula chloropus*. Both studies found that many nesting females laid eggs parasitically prior to initiating their own clutches. Gibbons (1986) argues that the early egg was laid parasitically because, since male Moorhens did not cooperate over incubation during the early laying stage (see also Power *et al*, 1981), the females had to delay breeding. Lyon (1993 a) concludes that American Coots 'dump' their early eggs, because brood reduction in their own nest limits the number of fledglings produced, and females attempt to increase their reproductive output by laying additional eggs into other nests. This was also found by Jackson (1993), except that in her study species, the Northern Masked Weaver *Ploceus taeniopterus*, it is the last and not the first egg(s) that should be laid parasitically for the same reason; namely that the last (fourth) nestling in a nest usually starves. In these birds, as in Blue-throated Bee-eaters, the last chick has a severe disadvantage due to hatching asynchrony and almost never fledges. Jackson (1993) coins this as the 'brood size constraints' hypothesis of INP.

In section 8.5.3 below, I consider the notion that a breeding female Blue-throated Bee-eater should 'dump' her 4th to last eggs, because the chick it would produce would not be viable in her own nest (see Chapter 7) but might survive in another nest if the egg is 'dumped' at the right stage of the host laying sequence. INP by breeding females not only assumes that (1) her usual clutch size is larger than the viable brood size but also that (2) the cost of producing an egg is balanced against the cost of 'dumping' it. I therefore first consider briefly other reasons why clutch size in Blue-throated Bee-eaters may be larger than the viable brood size.

8.5.2 Clutch size and cost of laying

Lack (1954) states that "clutch size has been evolved through natural selection to correspond with the largest number of young for which the parents can on average find food" (p.22). Two trade-offs mould clutch size: one between future and present reproductive effort, and another between survival and number of offspring (Godfray *et al*, 1991; Lessells, 1991). Apart from food availability (Lack, 1954; see Chapter 4), factors like daylength (Crick *et al*, 1993) and competition with other species may influence clutch size from year to year, as reported for mid-latitude breeders (Yom-Tov, 1994). The optimal clutch size is a compromise between all of these considerations.

Sibling competition sometimes has the effect that smaller clutches are produced by parents (Godfray & Parker, 1992). This is probably not true for the Blue-throated Bee-eaters, which had a mean clutch size of 3.7 eggs but rarely fledged more than 1 or 2 chicks. I have attempted to explain this discrepancy with the brood reduction hypothesis and alternatives (Chapter 7). Forbes and Ydenberg (1992) show that only very few 'good years' are necessary for clutch size to remain higher than the usual fledging brood size. The brood reduction hypothesis assumes that in good years, most nestlings fledge (Chapter 7). Perhaps too few of these 'good years' have been witnessed during studies on the Blue-throated Bee-eater (Bryant and Tatner, 1994; and Chapter 7 of this study), and the brood reduction hypothesis has to be viewed over a longer time-span for Blue-throated Bee-eaters.

These hypotheses assume, however, (1) that egg production and laying *per se* are costly to females (Perrins, 1970), (2) that large clutches are more costly to the female in terms of weight loss (Moreno and Carlson, 1989; Moreno *et al*, 1989) and (3) that extra eggs do not fulfil a purpose. Afik and Ward (1989) suggest that dead eggs slowed down cooling rates of a clutch of Hoopoes *Upupa epops* and thus additional eggs may serve as a 'buffer' rather than being a waste.

In Blue-throated Bee-eater clutches, 61% of broods had one or more eggs which failed to hatch because they were infertile, neglected or broken. It may not be so much more costly to lay a larger clutch: in a study of the energetics of laying and incubation, Ward (1992) found that the mean daily energy expenditure did not increase significantly with the number of eggs in wild Swallows. This is because the added deposition of nutrients into each egg usually increases to a peak and then flattens off, so that more eggs do not necessarily increase peak daily nutrient deposition. It is therefore possible that the production of 'too many' eggs is not very costly for Blue-throated Bee-eater females. Blue-throated Bee-eaters may have been subjected to a recent change in habitat (which is discussed in Chapter 4). They perhaps have not yet adjusted their clutch size to less favourable circumstances, such as might be presented by the recent forest decrease over much of lowland Malaya, and their clutch size may be a remnant of Meropidae clutch size which is larger than their present optimum.

8.5.3 To 'dump' or not to 'dump' - a model

If there is a redundancy of eggs that a Blue-throated Bee-eater female can lay in each season, then the extra eggs could be 'dumped' (e.g. Jackson, 1993). INP could then be a mixed reproductive strategy practised by breeding females who also have their own nest (as found by Lyon, 1993 b, and Jackson, 1993, as discussed above in section 8.5.1). In the following, I propose a model of INP as a mixed strategy for laying females, to show whether they should retain each egg in their own nest or 'dump' it, depending on its place in their own laying sequence and on the laying sequence of the host. Nestlings are assumed to hatch asynchronously in the same order the eggs are laid, because incubation starts before the last egg is laid. It is further assumed that eggs are 'dumped' without prior incubation (but see Jackson, 1993; Brown and Brown, 1988 b) and that a 'dumped' egg therefore takes the place in the hosts' laying sequence of the egg laid by the host directly after the 'dumped' egg.

The number of eggs (X) which the female should retain rather than 'dump', given that X+1 and later eggs are not likely to survive in her own clutch if retained, will depend on the brood size at fledging and the number of eggs she needs for insurance against hatching failure. (This model does not include insurance against genetic defects apparent after hatching or predation or similar failure of chicks which could result in a loss of top-ranking chicks). Given that hatching failure is the proportion of eggs failing to hatch,

$$\text{insurance against hatching failure} = \text{hatching failure} * \text{full clutch size} \tag{8.1}$$

Thus, for the egg in the female's own sequence,

$$X = \text{fledgling number} + \text{insurance against hatching failure} \tag{8.2}$$

or

$$X = \text{fledgling number} + (\text{hatching failure} * \text{full clutch size}) \tag{8.3}$$

Eggs 'dumped' into a host nest before the host's own onset of laying are assumed to be always expelled. An egg can only survive in a host nest if it is 'dumped' in a 'dumping window', which opens after the host's first egg is laid and closes as soon as the Xth egg is laid in the host laying sequence. X thus also defines egg number in the host laying sequence before which a parasitic female should 'dump' her egg.

Based on the breeding data of the Blue-throated Bee-eater, this model can be adapted as follows (Figure 8.2). Since the mean clutch size was 3.7 (section 4.3.1), and hatching failure was about one in three (Section 4.3.1), insurance = 3.7 x 0.3 = 1.1. In a good year, up to 2 nestlings (the first two) nestlings can usually be fledged (Chapter 4). X is therefore 2 + 1.1 = 3.1 In practice, therefore, 3 eggs should be retained and the laying female has one egg, the fourth, to spare: since the chick hatching from the 4th egg is not expected to survive the nestling period in the female's own nest, her 4th egg should be 'dumped' (Figure 8.2, inset A). Since X also defines the point at which the 'dumped' egg becomes non-viable in the host laying sequence, the egg must be 'dumped' before the 3rd egg in the host laying sequence (Fig. 8.2, inset B). If the host's first or second egg fails to hatch, a 'dumped' egg may still survive as the third egg in the sequence. In order for the 'dumped' egg to hatch as one of the first two chicks, the ideal is that the female should 'dump' her 4th egg into a nest containing only one host egg and at most 2 (Figure 8.2, inset B). If an egg is 'dumped' after the 3rd egg in the host sequence, it becomes the 4th egg in the host nest, for which the benefit is zero (Fig. 8.2, inset A). Therefore, the benefit of 'dumping' after the 3rd egg in the host sequence is also zero (Fig. 8.2, inset B).

The area in which it is more beneficial to 'dump' than to retain an egg is therefore probably quite small in Blue-throated Bee-eaters (Figure 8.2, inset C). Blue-throated Bee-eaters lay an

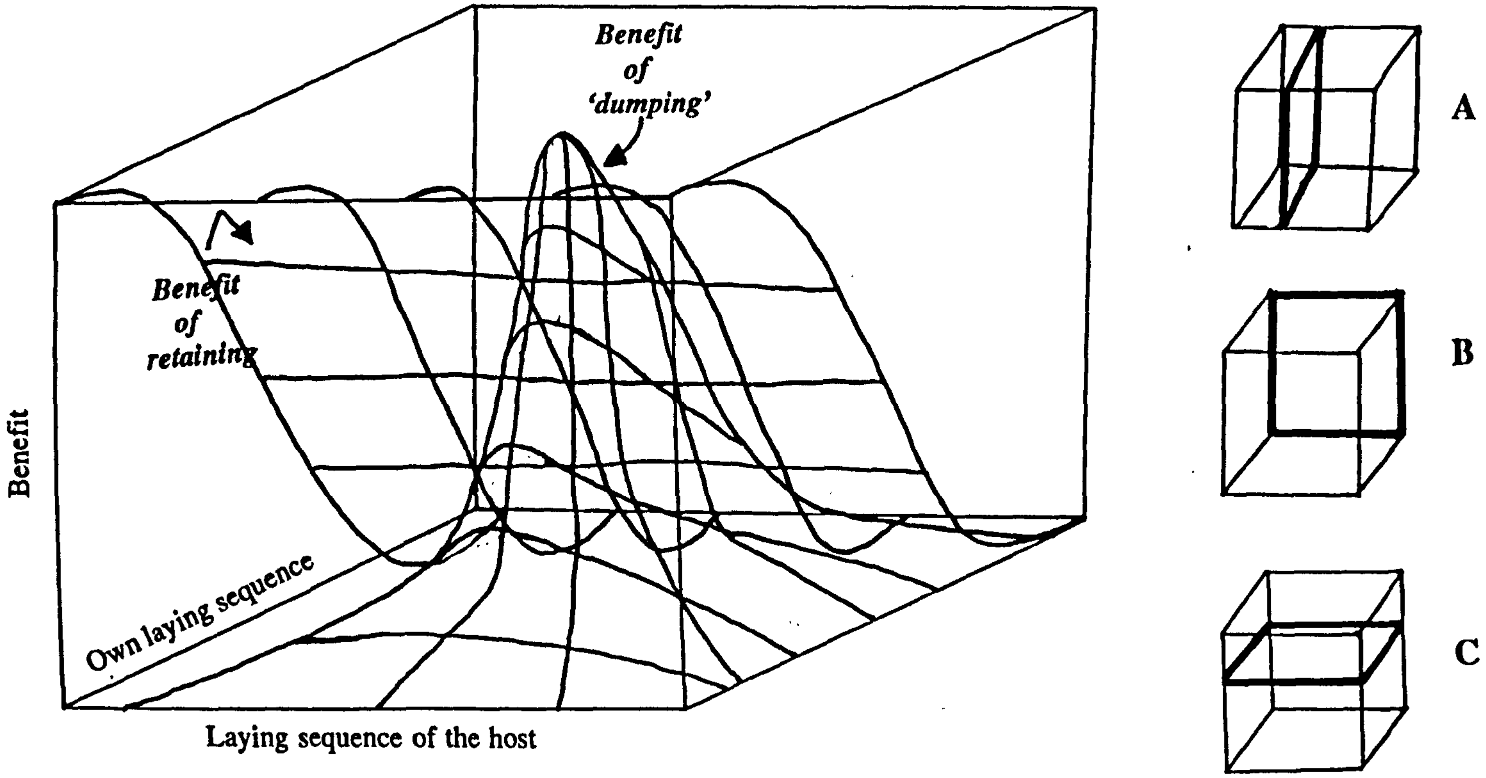
Figure 8.2: Model of the benefit of egg retention versus egg 'dumping' for breeding female Blue-throated Bee-eaters. Whether an egg should be retained or 'dumped' depends on the laying sequence both in the female's own nest and in the host nest.

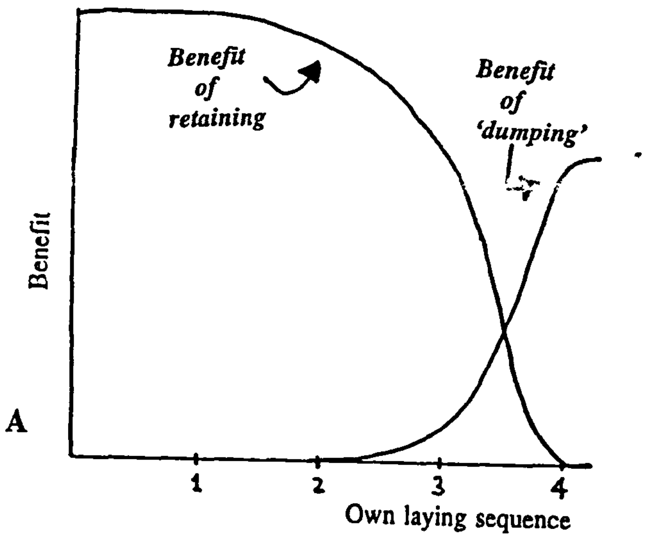
Insets A-C represent different 'slices' of the model which is shown in the main picture. Egg numbers in the laying sequence refer to the actual deposition of each egg, e.g. '1' is the onset of laying in the nest.

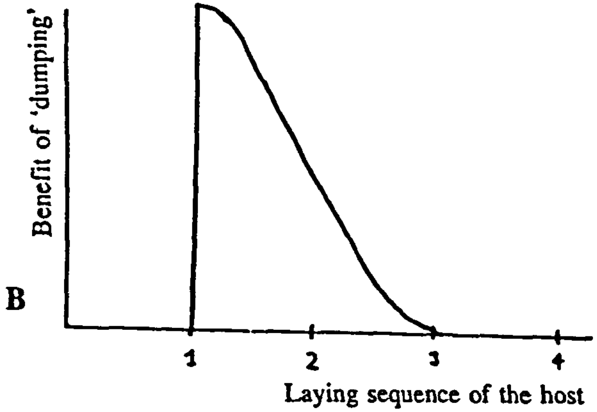
A: Benefit of 'dumping' (curve on the right) and retaining (curve on the left) depending on the female's own laying sequence.

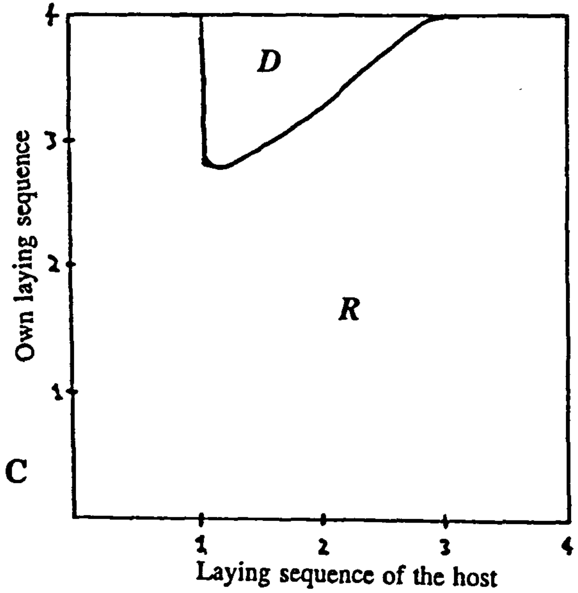
B: Benefit of 'dumping' depending on the host laying sequence (benefit of retaining is independent of the host laying sequence, see main picture).

C: Net benefits of 'dumping' and retaining an egg. D: benefit of 'dumping' > benefit of retaining. R: benefit of retaining > benefit of 'dumping'.


Benefit of 'dumping'
Benefit of retaining
Benefit
Own laying sequence
Laying sequence of the host
A
B
C


A
Benefit
Benefit of retaining
Benefit of 'dumping'
1
2
3
4
Own laying sequence


B
Benefit of 'dumping'
1
2
3
4
Laying sequence of the host


C
Own laying sequence
4
3
2
1
D
R
1
2
3
4
Laying sequence of the host

egg roughly every two days, so out of 7 days of laying 4 eggs (during which there is at least one egg in the host nest), there are 3-4 days during which 'dumping' an egg could lead to success, in terms of producing a fledgling. The timing of 'dumping' is therefore crucial to the success rate of 'dumped' eggs. First-hatched nestlings are the only chicks surviving in most broods (Chapter 4), but no 'dumped' egg can become the first-hatched chick in a host nest unless the host's first egg does not hatch (or unless the host's first chick dies early - failure of the top-ranking chick has not been taken into consideration in this model). This is why 'dumped' eggs have a lower success rate relative to the retained first egg(s) in the laying sequence of the breeding female (the overall peak of benefit of 'dumping' is lower than the peak of retaining in Figure 8.2). This sets the strategy for 'dumping' late eggs rather than early eggs (as in Jackson, 1993).

The evidence in support of this model in Blue-throated Bee-eaters is difficult to assess. In practice, for example, hatching failure for an individual will not be 1/3 but anything from 0 to many. Therefore, it is necessary to know (say) the number of eggs that 95% will hatch. Complications to the model occur if Blue-throated Bee-eaters 'dump' eggs which have been part-incubated elsewhere and hatch together with the clutch (Jackson, 1993; Brown and Brown, 1988). This is perhaps unlikely, however, since egg-carrying behaviour has never been observed. The model would be further complicated when the reverse situation is included, namely that the parasitic female is perhaps parasitized as well, when INP is a mixed strategy of breeders in the population. This risk would further limit the number of viable eggs the female herself lays in her clutch, so that she should start 'dumping' eggs earlier, which may have presented 'positive feedback' for the evolution of INP. If INP is common between relatives because they are more likely to nest together (e.g. in ducks, Triggs *et al*, 1991), then INP is more likely to evolve as a mixed strategy, but inclusive fitness then has to be considered in the model. The model predicts that INP should be a mixed reproductive strategy for breeding females for at least some of her eggs. This prediction could be tested with single locus probes (see Chapter 6). These can be scored across whole populations of individuals so that the identity of parents might be established to find out whether breeding females practice INP, and establish if INP is a mixed strategy by individuals or whether it is performed mainly by unpaired females or failed nesters.

8.5.4 The evolution of INP in the Blue-throated Bee-eater

Yamauchi (1993) introduces a model which predicts that INP evolves if nestling competition intensity exceeds the cost of parasitising a nest. The cost of parasitizing a nest is smaller in colonial species (Yamauchi, 1993; Hamilton and Orians, 1965; see Chapter 6) because, for example, it is less difficult to find and monitor nests at the right stage (Jackson, 1993) and to enter nests unnoticed (Davies, 1991). If the 'dumper' is related to the host pair, it might be tolerated in or near the host nest (as in White-fronted Bee-eaters; Emlen and Wrege, 1986), which would facilitate 'dumping'. I found evidence from DNA fingerprints that relatives not only roost in the same burrow occasionally, but the fingerprints also suggest that some of the non-genetic offspring had been 'dumped' by relatives of the putative parents (Chapter 6.2). This would represent a further reduction of the cost of INP - that of raising illegitimate young for the host - through kin selection. There are therefore several indications for the cost of INP to be relatively low in Blue-throated Bee-eaters.

The level of sibling competition is particularly high in Blue-throated Bee-eaters (Chapter 7). I therefore argue that according to Yamauchi's model (1993), conditions in Blue-throated Bee-eaters were probably favourable for INP to evolve. Further to this is the argument used by Jackson (1993) that if (1) the 4th nestling in broods of 4 is likely to starve and (2) lower-ranking nestlings have reduced growth rates, then the brood size constraints hypothesis for the evolution of INP is supported. Evidence for brood size constraint has been shown conclusively in Chapter 7 for Blue-throated Bee-eaters.

To summarize, conditions seem particularly favourable for INP to have evolved in Blue-throated Bee-eaters, for some or all of the reasons discussed in this section (8.5). These are (1) coloniality may reduce search and monitoring cost for prospective 'dumpers'; (2) INP of relatives (a) might reduce monitoring costs to the 'dumper' if it is tolerated at the prospective host nest and (b) reduces the cost of raising an illegitimate offspring through kin selection; (3) there is almost obligatory brood reduction which eliminates the last nestling(s) in a pronounced hatching hierarchy and produces selection pressure for breeding females to 'dump' their last egg(s).

I conclude that although INP represents the 'best-of-a-bad-job', at least for some individuals of many species, INP might be a mixed reproductive strategy in Blue-throated Bee-eaters, practised by at least some nesting females who lay some of their eggs parasitically to increase their reproductive output.

8.6 Conclusions

Blue-throated Bee-eater are, compared to other open-country bee-eaters, only moderately social, moderately colonial and have a low incidence of 'helping-at-the-nest' (Table 8.3). Coloniality itself may be a more recent behaviour in the social system of Blue-throated Bee-eaters, which lack the gregarious habit and extensive cooperative breeding system of the more colonial Meropidae. *M. viridis* is perhaps more similar to the Bee-eater species of the African equatorial forest zone, which are sedentary and less colonial (Fry, 1984). The Malayan Blue-throated Bee-eater may thus have changed its behaviour very recently, including migration which might have been imposed on Malayan breeders by other migratory species and might have had far-reaching consequences for its social and breeding behaviour. Breeding seasonality is, in White-fronted Bee-eaters, probably enforced by a rigid molt schedule (Emlen and Wrege, 1991). In Blue-throated Bee-eaters, it is perhaps a result of a very regular migration schedule combined with a weather 'window' which may temporarily enhance insect abundance or availability advantageous for breeding.

The mating system in Blue-throated Bee-eaters is essentially monogamous, both behaviourally and genetically with no or few extra-pair offspring. The predominant mixed reproductive strategy appears to be egg 'dumping', as in other colonial bird species (Birkhead *et al*, 1993; Lank *et al*, 1989; Brown and Brown, 1988 a and b; Emlen and Wrege, 1986). It is argued that conditions in Blue-throated Bee-eaters have been particularly favourable for INP to evolve, not only because of colonial breeding, but perhaps also because eggs are 'dumped' by relatives, and because the number of fledglings per nest is limited. It is predicted that egg 'dumping' might therefore be a mixed strategy for breeding females to increase their reproductive output, and not just a 'best-of-a-bad-job' strategy for failed breeders or unmated females. Recent changes in habitat which may have caused *M. viridis* to colonize more unsuitable habitats may have increased nestling competition further, decreased the viable brood size and increased the selection pressure towards 'dumping' the extra eggs. Since the largest cost of nest parasitism to the hosts is to raise unrelated young in place of its own, the extreme advance of hatching in first- and second- laid eggs and the almost obligatory elimination of the youngest nestlings by siblicide observed in this study of Blue-throated Bee-eaters, may have co-evolved with the increasing practice of INP (*anti-INP hypothesis*). Brood size at fledging is probably controlled by a combination of brood reduction (with resource tracking; see Chapter 7), insurance (e.g. Forbes, 1993), and anti-INP strategy.

SUMMARY

1. This study is concerned with the social behaviour of breeding Blue-throated Bee-eaters *Merops viridis* with particular emphasis on pair behaviour, the mating system, mixed reproductive strategies and nestlings competition and siblicide. Blue-throated Bee-eaters usually nest in colonies in self-dug burrows in level, well-drained soil with good visibility where they can hunt from perches, as is found on golf-courses and park-gardens in South-east Asia. Two colonies, one at Sungei Buloh in Selangor (SB) and one on Nam Heng Complex in Johor (NH) were studied on Peninsula Malaysia during three breeding seasons. Methods included: behavioural observations, regular monitoring of nest contents, regular capture and measurements of adults and nestlings, individual marking of adults with patagial wing-tags, colour tape and paint on tail feathers. Several experiments were conducted, including (1) egg 'dumping' of artificial eggs ('egg dumping experiment'), (2) supplementary feeding of nestlings ('feeding experiment'), (3) behavioural observations after supplementary feeding ('artificial nest') and (4) abrading the mandibular hook of nestlings ('hook experiment').

2. Problems encountered were: early disturbances which apparently caused desertions in many cases; patageal wing-tagging which decreased return-rates from 50% to 10%; occasionally, clutches or eggs were destroyed when digging into a nest (2 clutches and about 3 single eggs). No interference was encountered from measuring burrow lengths. Of three different methods to capture adults, mist-nets, 'decoy loops' and net-traps placed at the burrow entrance, only the latter proved to be successful. No injuries were incurred by birds when caught or extracted from traps, except in 3 cases where adults died in nets or during capture.

2. I designed a conceptual model of the Blue-throated Bee-eater data which is independent of the physical implementation (which is an Oracle database). The conceptual model shows the ideas and documents the implementation. The data collected in the field were converted to the data model of the database which could then be readily manipulated using the Oracle relational database management system (rdbms) and query language (SQL) for statistical analysis which was done in SPSSX. For other researchers it is useful to have a well-designed relational database to supplement their own data collections. For example, previous data on

Blue-throated Bee-eaters which had been available could have been accessed with great ease if they had been already stored in a database.

3. Colony sizes at the main sites varied from 5 to 150 pairs during the study period, with smaller sub-colonies and solitary pairs nesting nearby the main colony site. The Blue-throated Bee-eaters had an overall mean clutch size of 3.7 (SD=1.5). Hatching success was 2.99 (SD=1.0) or 78% of eggs hatched. Predation rates were 2.2% of all eggs or 2.8% of clutches and 7% of broods. Of all broods, 565 fledged one chick, only 19% fledged more than 1 (in most cases probably 2). The nestling period was estimated as 30-31 days. The mean onset of laying was on 13th May with a spread from 8th April to 13th July, but most pairs laid near the mean onset of laying. Breeders of intermediate dates had the highest fledging success.

4. The climate in Malaysia is only mildly seasonal. Blue-throated Bee-eaters choose to breed during a sunny (but not entirely dry) season from march to August, after the most pronounced period of long rains which is in January to February in most parts. This probably coincides both with a high insect food abundance (after long rains) and good foraging weather (sunny conditions) during their main nestling feeding period in June. Recent changes in breeding habitat might have occurred for the Blue-throated Bee-eater both from deforestation and through new openings in man-made environments like golf-courses and large private gardens.

5. Return rates from one season to the next were 10-50% (see point 2), and those returns for which breeding success was known, all had fledglings in the first season. Breeders returned to within several metres of their nest-site of the previous season. They re-nested with the previous partner if present, but because of low overall returns, there was necessarily a lot of re-mating. Populations differences in body size, plumage coloration and central tail-streamer length were tested, but the only difference between the two colonies was that some SB birds had very bright throats with contrasting colour which was not found at the NH colony. Particular behaviour with social significance were described, including calls and their social context, kleptoparasitism and tail-flicker ('greeting' behaviour). Blue-throated Bee-eaters practice 'helping-at-the-nest', but only about 5% of nests or less had a 'helper', and never more than one 'helper' was recorded for any brood.

6. Blue-throated Bee-eater adhered to their breeding season with strong year-to-year conservatism, regardless of yearly differences in weather. This was achieved during digging by synchronized burrow completion, and early arrivals may have the advantage of attempting more than one burrow and improve nest site quality, whereas late-arriving breeders may dig shallower burrows.

7. Blue-throated Bee-eaters are monomorphic and a discriminant function was calculated from size variables to help sex birds. The male is on average slightly larger than the female. Males had more variable lengths of central tail-streamers. There was no correlation of size and plumage coloration with breeding dates, except perhaps that the brown coloration on the nape extended further down the back in birds with intermediate breeding dates.

8. One seemingly successful, female-solicited extra-pair copulation was observed, followed immediately by an unsuccessful pair-rape attempt. Sexual interactions were solicited by females early in the season by 'ducking' which is similar to the begging behaviour of newly-fledged, dependent young and did less often result in copulations than sexual interactions initiated by males closer to laying which is the presumed fertile period. Females solicited probably in the context of mate choice and pair formation. A male soliciting a sexual interaction always (except in the pair-rape) attempted to allofeed the female. Male solicited sexual interactions were probably mostly in the context of fertilization or sperm competition.

9. Pairs excavated their burrows preferably in pairs, and one partner was vigilant while the other dug. Pair members commonly took turns while digging and had a special contact call used for digging. Pairs had to be established before nest excavation could commence.

During and just prior to laying, birds spent more time together than in any other breeding phase, but even then only about 40% of sightings (other than digging) were of partners together. If the male was mate-guarding, he therefore did not do so very efficiently.

Provisioning rates varied from 1 to 60 feeds per brood per hour, peaking between 10:00 and 13:00hrs and depended on nest, broods size and brood age. Different size food items were brought to broods of different ages. Individual provisioning adults had different strategies of visiting their broods, which may reflect different hunting distances or success rates and were independent of the partner. Some pairs might have combined their visiting patterns, but this was not consistent across pairs.

Because at most stages in the breeding cycle, pair members did not spend much time together (apart from during digging which they did in pairs), it seems on first impression that pair cooperation is low. The truth is, however, probably the opposite, namely that pair members spend little time together because they are cooperating and are sharing labour very efficiently, taking turns in most tasks rather than following each-other.

10. Out of 59 nestlings, 11 (18%) were classified as illegitimate offspring of both putative parents, using 95% confidence intervals of the band sharing coefficient and number of unexplained nestling bands as criteria. Between 0 and 3 (5% or fewer) nestlings were sired by an extra-pair male. Four (7%) nestlings were the result of intra-specific nest parasitism (INP) and 4-7 (7-12%) of 'quasi' parasitism (the offspring of the pair-male and an extra-pair female); INP by relatives of the hosts could have explained some intermediate band sharing coefficients.

Anti-INP behaviour was demonstrated when experimentally 'dumped' eggs were almost always expelled before the onset of laying, but never afterwards.

DNA fingerprinting showed that relatives occasionally roosted in the same burrow and related males were more likely to nest close together. Compared to other colonial Bee-eaters, *M. viridis* had low levels of EPO, but similar or higher levels of INP.

11. Growth curves were used to age nestlings where the hatch date was not known, showing that Principal Components of body size measurements were not much better than wing length to reliably predict nestling age in the first two weeks after hatching. Growth patterns suggested that the second-ranking nestling gained mass more slowly than the first-ranking nestling but could make up for this by increasing mass after the top-ranking chick had fledged, whereas third and fourth-ranking nestlings had a period of retarded growth, and they

nearly always perished. Runts perished significantly more often during the first half of the nestling period, before or on day 11. Nestlings with more than 4 wounds never fledged.

12. The *brood reduction hypothesis* and *resource tracking* predict a mechanism by which surplus nestlings are eliminated efficiently when food decreases, but that starving runts can recover when conditions improve. Blue-throated Bee-eaters hatch asynchronously which produces a nestling size hierarchy where the last-hatching runts are injured by their elder sibs with a mandibular hook (Bryant and Tatner, 1990).

The 'feeding experiment' was conducted to test if runts can recover if conditions improve. Top-ranking nestlings received additional food in experimental broods, whereas control broods were handled but not fed. Additional feeding of top-ranking siblings prolonged the survival of their later-hatched siblings, but I could not demonstrate if this was because they received more food from the parents or because direct aggression from their elder sibs was reduced. It is likely that the amount of additional food given was not sufficient to show these effects. I provided experimental evidence that improved conditions (simulated by giving the elder siblings of starving runts additional food) can delay nestling mortality which perhaps eventually leads to complete recovery of starving runts.

Experimental broods from the feeding experiments were observed an the 'artificial nest' before and after feeding, which showed that begging, 'scuffling' between nestlings and pecking or pinching behaviour in response to an adult feeding call was all higher in hungry nestlings. Pinching was very effective when used in combination with the sharp mandibular hook. These results show that siblings show competitive behaviour as well as aggression towards each-other and that these behaviours are perpetuated by nestling hunger.

13. In the 'hook' experiment, only the youngest nestling was allowed to retain the sharp mandibular 'hook' in experimental broods. Control broods were handled, but the hook of all chicks was left intact. Fledging rates were lower in experimental broods but not significantly so. The absence of the hook decreased the number of wounds from 4 to 1 on average (which might decide whether a chick is to die or not, see point 11) for second-rank nestlings and increased the condition of runts, and the demise of runts was significantly delayed in

experimental broods. The hook therefore aids efficient brood reduction in the Blue-throated Bee-eater.

14. Blue-throated Bee-eater broods were severely limited by food. Under this severe brood size constraint, breeding females may increase their reproductive output by 'dumping' their last egg. This may lead to the high frequency of INP observed in Blue-throated Bee-eaters. An early onset of incubation gives the first-laid egg(s) a temporal developmental advantage over subsequently 'dumped' parasitic eggs. The 'dumped' nestlings are eliminated by starvation and siblicide, which may itself be an adaptation to INP to eliminate unrelated nestlings (*Anti-INP hypothesis*).

15. To conclude, Blue-throated Bee-eaters probably have a near monogamous mating system. Compared to other open-country bee-eaters, they have low levels of coloniality, of social interactions, of cooperative breeding and also of EPO. It is possible that environmental changes which have occurred in Blue-throated Bee-eater habitat in the past century or so (less forest edge and reduced food availability) has pushed Blue-throated Bee-eaters into sub-optimal habitat with increased competition from the slightly larger Blue-tailed Bee-eaters. This may in turn have caused Blue-throated Bee-eater to migrate locally and reduced overall breeding success. As a result, coloniality in Blue-throated Bee-eaters might carry large costs of competition for less food amongst nestlings and increasing practice of INP.

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APPENDIX 1: Alphabetic list of names and abbrevations, including variables

Alarm Call - Defined in Chapter 4
BL - Bill length (defined in Chapter 2)
BRIGHT - Throat brightness (defined in Chapter 2)
BROWN - Extent of brown on nape (defined in Chapter 2)
BSC - band sharing coefficient
BW - Bill width (defined in Chapter 2)
Chirp - Call, defined in Chapter 4
Colony-Year - any one colony per year; e.g. Nam Heng 1990, Sungai Buloh 1989.
Cooe - Call, defined in Chapter 4
Day0 - first egg date; onset of laying
DME - daily metabolized energy
EPC - *E*xtra *P*air *C*opulation (by male or female pair member)
EPF - *E*xtra *P*air *F*ertilization
EPO - *E*xtra *P*air *O*ffspring
EPP - *E*xtra *P*air *Paternity* (refers specifically to the male pair member)
HB - Head and bill length (defined in Chapter 2)
HRFR12 - for definition see Chapter 4
IBP - *I*ntra-specific *B*rood parasitism (EPC *and* INP)
INP - *I*ntra-specific *Nest* parasitism (refers only to egg 'dumping', not EPC)
IWM - insect wet mass
KEEL - Keel length (defind in Chapter 2)
LPHD - longest possible hatching date
MST - Malaysian Standard Time
NH - Bee-eater colony on *N*am *H*eng Complex, Johor, Malaysia (second study site)
NH Garden - Bee-eater foraging site (see Chapter 4)
NH River - Bee-eater foraging site (see Chapter 4)
NH Village - Bee-eater foraging site (see Chapter 4)
NH90 - *N*am *H*eng colony in 1990
NH91 - *N*am *H*eng colony in 1991
NS = $p > 0.05$ (non significant)
PC - *P*air *C*opulation/ Principal Component
PCA - Principal Component Analysis
PC1, PC2/3 - First (Second/ Third) Principal Component
rainday - for definition see Chapter 4
REM - estate neighbouring Nam Heng Complex
REM Clearing - Bee-eater foraging site (see Chapter 4)
REM River - Bee-eater foraging site (see Chapter 4)
REM Rubber - Bee-eater foraging site (see Chapter 4)
REM Swamp - Bee-eater foraging site (see Chapter 4)
RRI - Rubber research Institute
SB - Bee-eater colony in *S*ungai *B*uloh, Selangor, Malaysia (the original study site)
SB89 - *S*ungai *B*uloh colony in 1989
SB90 - *S*ungai *B*uloh colony in 1990
SB91 - *S*ungai *B*uloh colony in 1991
SPHD - shorted possible hatching date
SD - standard deviation
se - standard error
TS - Tail with streamers (defined in Chapter 2)
WING - wing length (defined in Chapter 2)
***** = $p < 0.05$
****** = $p < 0.01$
******* = $p < 0.001$

APPENDIX 2: Insect sizes

For each type of insect (I_SIZE) and its size (I_SIZE), the absolute size (ABS_SIZE) and number (N_SIZE) is stored in the database table Insect. For example, a BIG FLY and a SMALL BEE are both medium size insects (ABS_SIZE = MED, NSIZE = 4). Insect sizes are given below, as retrieved from the database (see Chapter 3 for an introduction to database querie language).

```
SQL>  select * from insect;

I_TYPE   I_SIZE   ABS_SIZE      NSIZE
-------- -------- -------- ----------
FLY      BIG      MED               4
BEE      SMALL      MED             4
BEE      MED        BIG             6
BEE      BIG        V.BIG           7
HORNET   SMALL      MED             4
HORNET   MED        BIG             6
HORNET   BIG        V.BIG           7
G'HOPPER SMALL      MED             4
G'HOPPER MED        MED-BI          5
G'HOPPER BIG        BIG             6
B'FLY    SMALL      SMALL           2
B'FLY    MED        MED             4
B'FLY    BIG        BIG             6
H'OPTERA SMALL      SMALL           2
H'OPTERA MED        MED             4
H'OPTERA BIG        MED-BI          5
CICAD    SMALL      MED             4
CICAD    MED        MED-BI          5
CICAD    BIG        BIG             6
FLY      MED      SMALL             2
FLY      SMALL    V.SMALL           1
ALATE    SMALL    V.SMALL           1
ALATE    MED      SMALL             2
ALATE    BIG      MED               4
ANT      BIG      MED               4
ANT      MED      SMALL             2
ANT      SMALL    V.SMALL           1
MOTH     SMALL    SM-MID            3
D'FLY    SMALL    SMALL             2
D'FLY    MED      SM-MED            3
MOTH     BIG      MED-BI            5
MOTH     MED      MED               4
BEETLE   MED      MED               4
BEETLE   BIG      BIG               6
BEETLE   SMALL    SM-MID            3
D'FLY    BIG      MED               4
```

APPENDIX 3: The data dictionary

A Listing of the database tables with field-names and datatypes, in the order in which their equivalent Entity Types are discussed in Chapter 3.

```
Adult

 Name            Type
 --------------  ----
 RING            CHAR(8)
 TAG             CHAR(8)
 SEX             CHAR(3)
 QUALS           CHAR(25)
```

```
Bird_Year

 Name            Type
 --------------  ----
 DAY             DATE
 RING            CHAR(8)
 R_N             CHAR(3)
 BREEDER         CHAR(8)
 BROWN           NUMBER
 GREEN           NUMBER
 KEEL1           NUMBER(4,2)
 KEEL2           NUMBER(4,2)
 TARSUS          NUMBER(4,2)
 H_B             NUMBER(5,2)
 B_W             NUMBER(3,2)
 B_L             NUMBER(4,2)
 EYES            CHAR(8)
 WING            NUMBER
 T_L             NUMBER(4,1)
 RINGER          CHAR(8)
```

```
Adult_Capture

 Name            Type
 --------------  ----
 DAY_TIME        DATE
 NESTID          CHAR(12)
 TAG             CHAR(5)
 RING            CHAR(8)
 NR              CHAR(3)
 TAGCOND         CHAR(8)
 BLOOD           NUMBER(3,1)
 BLOODTUBES      CHAR(12)
 OVARY           NUMBER(38)
 CLOACA          NUMBER(38)
 COND            NUMBER(3,1)
 TS              NUMBER(38)
 IA              CHAR(3)
 WT              NUMBER(5,2)
 MITES           CHAR(8)
 BRIGHT          CHAR(8)
 RINGER          CHAR(8)
 NEST            NUMBER(5)
 HEAD            NUMBER(5,2)
```

```
Chick

 Name            Type
 --------------  ----
 NESTID          CHAR(12)
 CHICKNO         NUMBER
 QUALCN          CHAR(8)
 HDAY            DATE
 QUALD           CHAR(8)
 EXACTD          NUMBER(38)
 COMMENTS        CHAR(25)
 EXPT            CHAR(8)
 DDAY            DATE
 QUALDD          CHAR(15)
 EXACTDD         NUMBER
 NEST            NUMBER(6)
```

```
Chick_Capture

 Name            Type
 --------------  ----
 DAY_TIME        DATE
 NEST            NUMBER
 CHICKNO         NUMBER
 RING            CHAR(8)
 N_R             CHAR(4)
 D_A             CHAR(4)
 BLOOD           NUMBER(3,1)
 BLOODTUBES      CHAR(12)
 ABDOMEN         CHAR(8)
 TF              NUMBER
 PINS            CHAR(8)
 COND            NUMBER(3,1)
 KL1             NUMBER(4,1)
 KL2             NUMBER(4,1)
 HB              NUMBER(4,1)
 HOOK            CHAR(4)
 B_L             NUMBER(4,1)
 EYES            CHAR(8)
 W_F             NUMBER
 WF              NUMBER
 WOUNDS          NUMBER
 WT              NUMBER(4,1)
 MITES           CHAR(8)
 WING            NUMBER
 DAYX            NUMBER(38)
 NESTID          CHAR(12)
 DAY0            DATE
 PLACE           NUMBER(3)
 DAYX_WING       NUMBER(3)
 MDSUM           NUMBER(5,2)
 SURVIVE         NUMBER(1)
 DAYD            NUMBER(2)
```

Brood

```
Name             Type
---------------  ----
NESTID           CHAR(12)
BROODNO          NUMBER(38)
ADULT1           CHAR(8)
ADULT2           CHAR(8)
ADULT3           CHAR(8)
START_DAY        DATE
QUALST           CHAR(12)
END_DAY          DATE
QUALE            CHAR(12)
SUCCESS          CHAR(25)
NEST             NUMBER(5)
MINEGG           NUMBER(3)
TOTEGG           NUMBER(3)
MINCHICKS        NUMBER(3)
TOTCHICKS        NUMBER(3)
EXP              CHAR(8)
HSPREAD          NUMBER(3)
FLEDGED          CHAR(3)
COLONY           NUMBER(3)
FPRINT           CHAR(3)
```

Nest

```
Name             Type
---------------  ----
NESTID           CHAR(12)
START_DAY        DATE
SUBLOC           CHAR(12)
SUBSTRATE        CHAR(12)
FGLOC            CHAR(12)
```

Hole_L

```
Name             Type
---------------  ----
DAY              DATE
NESTID           CHAR(12)
LENGTH           NUMBER(4,1)
N_R              CHAR(3)
STICKS           CHAR(3)
CURL             CHAR(3)
```

Nest_Entry

```
Name             Type
---------------  ----
DAY              DATE
NESTID           CHAR(12)
EGGS             NUMBER(38)
SPOILED          NUMBER(38)
DUMPED           CHAR(3)
CHICKS           NUMBER(38)
DEAD             NUMBER(38)
MAGGOTS          CHAR(12)
FOOD             CHAR(12)
NEST             NUMBER(3)
COMMENTS         CHAR(25)
TIME             DATE
NR               CHAR(3)
```

Location

```
Name             Type
---------------  ----
COLONY           CHAR(6)
LOC              CHAR(8)
SUBLOC           CHAR(12)
PGLOC            CHAR(15)
```

Ecology

```
Name             Type
---------------  ----
DAY              DATE
START_TIME       DATE
DURATION         DATE
INDEX_TYPE       CHAR(8)
SCORE            CHAR(8)
```

Insect

```
Name             Type
---------------  ----
I_TYPE           CHAR(8)
I_SIZE           CHAR(8)
ABS_SIZE         CHAR(8)
NSIZE            NUMBER(3)
```

Obs_Sched

```
Name             Type
---------------  ----
DAY              DATE
SUBLOC           CHAR(12)
START_TIME       DATE
END_TIME         DATE
OBS              CHAR(8)
OTYPE            CHAR(12)
```

Sighting

```
Name             Type
---------------  ---
DAY_TIME         DATE
PERCHLOC         CHAR(25)
BIRD_ID          CHAR(8)
ASSOCIATE        CHAR(15)
ACTIVITY         CHAR(25)
I_TYPE           CHAR(15)
I_SIZE           CHAR(8)
OBS              CHAR(8)
ABS_SIZE         NUMBER(3)
```

APPENDIX 3 B: Table Field names

Below is a list of the main field names and where they were used:

Attribute	Size	Type	Format	Database_Table.Column_Name
Bird_Id	8	char	xxx[*][?]; n00	Sighting./ Tail_Info. BirdId Flicker. Greeted/ Greeter Pair_Sched. Bird1/ Bird2 Sex. Male_Id/ Female_Id Initiator
NestID	12	char	nn-yy[-n]	Displacement./ Nest./ Nest_Entry./ Chick.NestID
Nest	3?	int	nn[n]	Chick.Nest
Ring	8	char	nnnn[n]; eg. 'lh last'	Adult./Chick.Ring
Tag	5	char	xxx	Adult.Tag
Perchloc	25	char	see list[nest] (mixed fields)	Sighting./Tag_Cond.Perchloc
Subloc	12	char	see list;grid	Obs_Sched./ Pair_Sched./ Scan_Sched./ Act_Scan./ Nest./ Adult_Death. Subloc
Activity	25	char	see list	Sighting. Activity Sex./ Pair_Sched. Behav_Type
Day	9	date	dd.mm.yy	Obs_Sched./ Pair_Sched./ Sex./ Ecology.Day/Chick.hday
Day_Time	15	date	dd.mm.yy hh.mi	Sighting./ Scan_Sched./ Displacement./ Act_Scan./ HoleL./
Time	6	date	hh.mi	Obs_Sched./ Pair_Sched./ Sex./ Displacement./ Ecology. Start_Time/ End_Time
NR	3	char	N;R	

APPENDIX 4: Examples of queries to retrieve datain from relational database

Queries and retrieved data arelisted in the format of when they are used in the database. SQL> is the 'prompt' of the oracle database at Stirling University. See Chapter 3 for an introduction to querie language SQL.

Appendix 4.1 Returns of sexed birds

Making use of the fact that there is only and exactly one record in the table Bird_Year for each bird each year that it was caught, we can find returns by looking for birds with more than one record in Bird_Year:

```
SQL> run
  1  /*  r 16: for each sexed adult, find if it is a return bird first */
  2  /*  and return its sex */
  3  select bird_year.ring, min(sex), count(bird_year.ring)
  4  from bird_year, adult
  5  where bird_year.ring = adult.ring
  6   and (adult.sex like '%M%' or adult.sex like '%F%')
  7  group by bird_year.ring
  8*  having count(bird_year.ring) > 1

RING     MIN  COUNT(BIRD_YEAR.RING)
-------- ---- ---------------------
0298     F                       2
5681     M                       2
```

This result was obtained with birds caught in 1989 and 1990. Two birds, one male and one female, were caught in both 1989 and in 1990, the rest were caught either in 1989 or in 1990 only. This takes no consideration, however, if the birds were caught earlier than 1989.

Appendix 4.2 Arrival dates of sexed birds

To find the date a bird was first observed in the colony (only data for 1989 were in the database at this stage, otherwise, an extra group by for year would have to be used), first I created a view sexarr, joining the date from Sighting with most data from Adult, for sexed birds. Then, for each ring, the minimum date was obtained:

```
create view sexarr as
select adult.ring, adult.tag, sex, sighting.bird_id, day_time
from Sighting, Adult
where (sex like '%M%' or sex like '%F%')
and Adult.tag = Sighting.bird_id
/* and to_char(day_time) like '%-89 %' */
/* order by tag, day_time */
```

```
SQL> run
  1  /* r14: return first day sighted, for sexed birds! */
  2  select ring, min(sex), min(day_time)
  3  from sexarr
  4  group by ring
  5* order by min(day_time) asc

RING     MIN MIN(DAY_T
-------- --- ---------
5965     F   30-MAR-89
3714     F   30-MAR-89
...
0283     M   01-JUL-89
0288     M   02-JUL-89
```

Appendix 4.3 Selecting and comparing streamer lengths for males and females

a. Select the longest streamer length reocrd for each of all sexed adults with intact streamers:

```
SQL> run
  1  /* longest streamer length for each of all sexed adults */
  2  select distinct a.ring,a.sex,a.quals, b.ts, b.ia,b.day_time
  3  from adult a, adult_capture b
  4  where a.ring = b.ring
  5  and (a.sex like '%M%' or a.sex like '%F%')
  6  and b.ts > 0 /* not null */
  7  and b.ia like '%I%'
  8* order by a.sex,a.ring

RING     SEX QUALS                              TS IA  DAY_TIME
-------- --- ------------------------ ---------- --- ---------
0284     F   ADULTCAP                          128 I   01-MAY-89
0285     F   -1.7335                           139 I   24-MAY-89
...
5995     M   ADULTCAP                          132 I   18-APR-87
5998     M   F 5965, OV + CL, WT               142 I   01-MAY-89

88 records selected.
```

b. Summaries per sex

i. for intact streamers only:

```
SQL> run
  1   select min(a.sex), count(a.ring), avg(b.ts), stddev(b.ts),
min(b.ts), max(b.ts)
  2  from adult a, adult_capture b
  3  where a.ring = b.ring
  4  and (a.sex like '%M%')
  5  and b.ts > 0 /* not null */
  6* and b.ia like '%I%'

MIN COUNT(A.RING) AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- --------- ------------- ---------- ---------
M              32  129.375   15.833305          99        154


SQL> run
  1  select min(a.sex), count(a.ring), avg(b.ts), stddev(b.ts),
       min(b.ts),max(b.ts)
  2  from adult a, adult_capture b
  3  where a.ring = b.ring
  4  and (a.sex like '%F%')
  5  and b.ts > 0 /* not null */
  6* and b.ia like '%I%'

MIN COUNT(A.RING) AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- --------- ------------ ---------- ----------
F              56  6.95960049        112        146
```

ii. abbrevated tails, all records (more than one per bird):

```
SQL> run
  1  /*  Do females work harder than males? */
  2      select   min(a.sex),    count(a.ring),    avg(b.ts),    stddev(b.ts),
      min(b.ts),max(b.ts)
  3  from adult a, adult_capture b
  4  where a.ring = b.ring
  5  and (a.sex like '%M%')
  6  and b.ts > 0 /* not null */
  7* and b.ia like '%A%'

MIN COUNT(A.RING)  AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- ---------- ------------ ---------- ----------
M             107 112.990654   16.4915618         78        158
...

MIN COUNT(A.RING)  AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- ---------- ------------ ---------- ----------
F             161 106.614907   15.9558226         13        146
```

iii. abbrevated tails, mean length per bird:

```
SQL> run
  2  /* - mean ts per bird */
  3       select   min(a.sex),    count(a.ring),avg(b.ts),stddev(b.ts),
      min(b.ts),max(b.ts)
  4  from adult a, adult_capture b
  5  where a.ring = b.ring
  6  and (a.sex like '%M%')
  7  and b.ts > 0 /* not null */
  8  and b.ia like '%A%'
  9  and b.ts = (select avg(c.ts) from adult_capture c
 10*                where c.ring = a.ring)

MIN COUNT(A.RING)  AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- ---------- ------------ ---------- ----------
M              53 114.924528   15.4631685         84        155

...

MIN COUNT(A.RING)  AVG(B.TS) STDDEV(B.TS)  MIN(B.TS)  MAX(B.TS)
--- ------------- ---------- ------------ ---------- ----------
F              51 106.764706   14.6691353         81        142
```

c an alternative, using a view to work with:

```
create view sexarr as
select adult.ring, adult.tag, sex, sighting.bird_id, day_time
from Sighting, Adult
where (sex like '%M%' or sex like '%F%')
and Adult.tag = Sighting.bird_id
/* and to_char(day_time) like '%-89 %' */

SQL> get vst2_cr
  1  /* vst_cr : view that holds t+s for all sexed birds */
  2  create view st2 as
  3  select adult.ring, adult.tag, sex, ts, ia
  4  from adult, adult_capture
  5  where adult.ring = adult_capture.ring
  6  and (sex like '%M%' or sex like '%F%')
  7* and ia like '%I%'
SQL> select * from st2;

RING     TAG      SEX         TS IA
-------- -------- --- ---------- ---
0284     A6G      F          128 I
0288     490      M           99 I
...
5808     S10      M          140 I
5846     MAO      F          128 I
5998     420      M          142 I

16 records selected.

SQL> run
  1  /* r1.sql : select average and all that of streamers */
  2  /*            for sexed birds.
  3  /* sextail : view that holds t+s for all sexed birds */
  4  select min(sex), avg(ts), min(ts), max(ts),
  5          variance(ts), stddev(ts), count(ts)
  6  from st2
  7* group by sex

MIN AVG(TS)  MIN(TS)  MAX(TS) VAR(TS) SD(TS)  COUNT(TS)
--- -------  -------  ------- ------- ------  ---------
F     130      121      164  134.181 11.583         12
M     133.75    99      154  574.916 23.977          4

  1  /* r1.sql : select average and all that of streamers */
  2  /*            for sexed birds.
  3  /* sextail : view that holds t+s for all sexed birds */
  4  select min(sex), avg(ts), min(ts), max(ts),
  5          variance(ts), stddev(ts), count(ts)
  6  from sextail
  7* group by sex

MIN    AVG(TS)  MIN(TS)  MAX(TS) VAR(TS) SD(TS)  COUNT(TS)
--- ----------  -------  ------- ------- ------  ---------
F   113.459          81      164 282.588 16.810         37
M   116.206          83      157 388.241 19.703         29
```

Appendix 4.4: Ageing chicks and getting their biometrics for growth curves (old version)

```
/* u6.sql - final version to include dayx of aged chicks into cc  /*
and selects only 1st/2nd chicks, with exactday < 2     /* (next: r21b)  */
  update chick_capture
  set dayx =
  (select (round(chick_capture.day_time) - round(chick.hday) )
            from Chick
            where round(chick.chickno)    =
                  round(chick_capture.chickno)
            and   chick.nestid = chick_capture.nestid)
```

r21b.sql retrieves biometrics etc from Chick_capture after ageing for chicks of known age (u6.sql) exact up to 1 day +/-, and only 1st or 2nd chicks.

```
select nestid, chickno,  dayx, b_l, wing, wt from chick_capture
      where dayx is not null  /* chicks with known age */
      and   2 >
            (select exactd
             from chick
             where chick_capture.nestid = chick.nestid
             and chick_capture.chickno = chick.chickno)
                        /* only chicks with good age-ing */
      and chickno < 3   /* only first and second chicks */
```

```
NESTID   CHICKNO        DAYX        B_L        WING         WT
------- ---------- ---------- ---------- ---------- ----------
30-90            1          4        4.4          8        5.8
23-90            1          7        6.3         11       11.9
23-90            2          6        5.3         10        9.4
23-90            1          9        6.8         14       16.6
23-90            2          8        6.9         12         13
30-90            1          6        5.6          9        9.3
30-90            2          4        4.8          9        7.3
2-90             2          7        5.7         10        7.5
128-90           1          2          5          8
128-90           2          4        5.3          9        6.2
128-90           1          5        5.2         10        6.4
131-90           2          6        8.4         14       10.9
30-90            1         29       21.8         95       31.3
30-90            2         27       21.2         97       37.2

14 records selected.
```

[These are all chicks 1 and 2 for which the age is known within one day, from 1989 and 1990. Analysis 1/91.]

Appendix 4.5 Find partners of sexed females

Sexed females are in table Adult. Nest and catching dates for these females (stored in table Adult_Capture) could then be used to look for their partners. I made a view 'Females' with this information first, joining the sexing info in Adult with the catching info for these females in Adult_Capture:

```
SQL> run
  1  create view females (dayf,nestid,ringf,sex) as
  2  (select day_time,nestid,adult.ring,sex
  3  from adult, adult_capture
  4  where sex = 'F'
  5  and (to_char(day_time,'yy') = '89'
  6   or to_char(day_time, 'yy') = '90'
  7   or to_char(day_time,'yy') = '91')
  8* and adult.ring = adult_capture.ring)

View created.

SQL> select * from females;

DAYF      NESTID       RINGF    SEX
--------- ------------ -------- ---
01-MAY-89 16-89        0284     F
24-MAY-89 28-89        0286     F
29-JUN-89 28-89        0286     F
14-APR-90 11-90        0492     F
06-JUN-90 37-90        0492     F
22-MAY-90 37-90        0492     F
07-JUL-90 37-90        0492     F
16-APR-90 19-90        0493     F
...(99 records selected)
```

Then catching dates and ring for corresponding males (caught within 2 days at the same nest) can be accessed by joining Females again with Adult_Capture:

```
SQL> run
  1  select females.nestid,ringf,dayf,ring,day_time
             /* ring,day_time is for Males */
  2  from females, adult_capture
  3  where females.nestid = adult_capture.nestid
      /* from same nest */
  4  and ringf <> ring        /* not the Female herself */
  5* and abs(dayf - day_time) <= 2
      /* within 2 days of each-other */


NESTID       RINGF    DAYF      RING     DAY_TIME
------------ -------- --------- -------- --------
16-89        0284     01-MAY-89 5995     01-MAY-89
28-89        0286     29-JUN-89 3922     29-JUN-89
33-89        0287     24-MAY-89 0288     24-MAY-89
14-90        0298     07-JUL-90 5145     07-JUL-90
  6-91       0488     05-MAY-91 0472     05-MAY-91
37-90        0492     07-JUL-90 0484     07-JUL-90
...(49 records selected)
```

Now, the males can be entered into Adult (from a table called Newsexed) using the following update querie after making sure there are no duplicate records:

Appendix 4.6 Using the discriminant function score to sex adults

To calculate the discriminant function (s) values for unsexed adults, I made first of all a view named 'calc_s' from unsexed adults and their biometrics needed for the calculation:

```
SQL> get calc-c
  1  create view calc_s as
  2  (select adult.ring,sex,keel1,h_b,wing,t_1,b_1,b_w,ringer
  3   from adult, bird_year
  4  where sex null     /* for unsexed adults */
 5* and adult.ring = bird_year.ring)
```

Then I prepared a table 'S' (another view would not let me use a column called 's' but I'd have to give it the whole equation)
to accomodate rings and s-values

```
SQL> get s-cr
  1  create table s
  2* (ring char (6),s number (7,4))
```

and calculated s-values as I inserted them from view calc-s:

```
SQL> get s-ins
  1  insert into s (ring,s)
  2  select ring, ( -30.2 + 0.576*keel1 + 0.0575*wing + 3
        0.0260*b_1 + 1.487*b_w  + 0.134*h_b   - 0.152*t_1)
  4  from calc_s
  /* view with biometrics for unsexed adults, see calc-c.sql */
  5  where
  6  (keel1 is not null
  7  and wing is not null
  8  and b_1 is not null
  9  and b_w is not null
 10  and b_w is not null
 11  and h_b is not null
 12* and t_1 is not null)
```

In all, there were 194 unsexed birds for which s-values had been calculated:

```
SQL> select * from s;

RING            S
------ ----------
0280       -.2686
0281          .02
0282       3.7273
0285      -1.7335
0290        .1319
... (194 records selected.)
```

Of these, 18 are females with 95% certainty:

```
SQL> select * from s where s < -1.70       /* females */;

RING            S
------ ----------
0285      -1.7335
0294       -1.882
06603   -106.2272
06638     -5.5999
06643     -3.5465
06667      -3.248
06671     -1.8315
06672     -3.2973
06686     -1.8884
06687     -2.1396
5132      -2.0283
5143      -3.1139
5146      -3.8615
5242      -2.1058
5466      -2.9484
5473      -3.3733
5479      -1.8473
5846      -2.2337

18 records selected.
```

And 26 are males with 95% certainty:

```
SQL> select * from s where s > 2.00       /* males */ ;

RING            S
------ ----------
0282       3.7273
0490       2.8447
0495       2.4272
06536      2.1066
06540      2.0702
06543      4.0297
06548      2.3241
06557      4.6392
06594      2.1477
06599      2.0909
06600      2.5759
06604      2.1582
06607      2.8926
06608      2.3525
06611       2.126
06628      2.4599
06629      2.1601
06681      2.0798
5134       2.0245
5139       2.2324
5240         2.45
5260       2.5905
5460       3.0284
5462       2.5105
5469        2.207
5821       2.2176

26 records selected.
```

Appendix 4.7 Entering newly sexed birds not yet in Adult, from another table (Newsexed), first checking if they are already in Adult:

To insert this information into table Adult, Im made table newsexed
with the 18+26 birds newly sexed by their s values

```
SQL> create table newsexed
  2  (ring char (6), sex char (3), s number (7,4));

Table created.

SQL> insert into newsexed
  2  (ring,sex,s)
  3  select ring,'F',s from s
  4  where s.s <= -1.70;

18 records created.

SQL> run
  1  insert into newsexed
  2  (ring,sex,s)
  3  select ring,'M',s from s
  4* where s.s >= 2.00

26 records created.

SQL> select * from newsexed;

RING   SEX          S
------ --- ----------
0285   F      -1.7335
0294   F       -1.882
...
06557  M       4.6392
06594  M       2.1477

44 records selected.
```

To insert table newsexed into adult, I checked first, if the birds are already in Adults, which they are:

```
SQL> run
  1  insert into adult (sex,quals)
  2  select sex, s from newsexed
  3  where not exists
     /* i.e., for birds that are not already in adult */
  4  (select adult.ring  from adult
  5*  where adult.ring = newsexed.ring)

0 records created.
```

However, if you simply did this:

```
SQL>
  1  insert into adult (ring,sex,quals)
  2* select ring, sex, s from newsexed
```

then there would be duplicate rings in Adult. So, we have to 'join' Newsexed and Adult:

```
SQL> run /* for females */
  1  update adult
  2    set sex =
  3   (select newsexed.sex
  4    from newsexed
  5    where newsexed.ring = adult.ring),
  6        quals    =
  7   (select newsexed.s
  8    from newsexed
  9    where newsexed.ring = adult.ring)
 10    where adult.ring in
 11   (select newsexed.ring from newsexed
 12*   where newsexed.s <= -1.70)

18 records updated.

SQL> run  /* for males */
  1  update adult
  2    set sex =
  3   (select newsexed.sex
  4    from newsexed
  5    where newsexed.ring = adult.ring),
  6        quals    =
  7   (select newsexed.s
  8    from newsexed
  9    where newsexed.ring = adult.ring)
 10    where adult.ring in
 11   (select newsexed.ring from newsexed
 12*   where newsexed.s >= 2.00)

26 records updated.
```

Appendix 4.8 Updating nestling place in hierarchy after fledging of elder sibs (assumes that each sib found is processed)

Chickno serves mainly to identify chicks within a nest. It is also are a record of succession at birth.In most cases therefore, chickno represents the real place each nestling has in the hierarchy in the nest at a given date. In cases where an elder sib has fledged or died however, the younger chicks move up in the hierarchy. Column 'place' in chick_capture takes account of the real place of the nestling in the hierarchy at a given day. Place is determined from chickno, by giving the smallest chickno (which is the eldest chick) in a nest at a given day the place no 1, the nestling with the second smallest chickno place 2, and runts (all leter nestlings pooled) take place 3.

Three queries are needed to update one place number each, and table chick_capture is joined with itself in order to group chicks in the same nest and at the same day. Date has to be given as days, because day_time includes times which would put captures from the same day but different times into different groups.

```
update chick_capture A
 set place = 1
 where A.chickno =
      ( select min(chickno) from chick_capture B
         where A.nestid = B.nestid
          and  to_char(A.day_time,'dd-mon') =
            to_char(B.day_time,'dd-mon')
      )
 and d_a = 'A'
            /* recorded dead runts would be placed 1 often!! */
/
update chick_capture A
 set place = 2
 where A.chickno =
      ( select 1+min(chickno) from chick_capture B
         where A.nestid = B.nestid
          and  to_char(A.day_time,'dd-mon') =
            to_char(B.day_time,'dd-mon')
      )
 and d_a = 'A'
            /* recorded dead runts would be placed 1 often!! */
/
update chick_capture A
 set place = 3
 where A.chickno >
      ( select 1+min(chickno) from chick_capture B
         where A.nestid = B.nestid
          and  to_char(A.day_time,'dd-mon') =
            to_char(B.day_time,'dd-mon')
      )
 and d_a = 'A'
            /* recorded dead runts would be placed 1 often!! */
/
```

Note that this querie was not used to determine place number; instead only nestlings who's elder sibs had died during their first week were upgraded for place (chapter 6.2)

Appendix 4.9 Updating hatch day for unaged nestlings from the earliest capture within the first two weeks, for which age was determined by wing length previously.

This querie involves three 'self-joins' of chick_capture by nestid and chickno:

```
/*
update every chick_capture record of each bird where not yet aged (day0), get
all records of that chick (key: nestid, chickno)
of those find the record with the smallest dayx. Day0-update is the (day_time
- dayx) of the records of that chick with the smallest dayx
*/
update chick_capture A
set A.day0 =
      ( select distinct(B.day_time - B.dayx) from chick_capture
        where
         B.chickno = A.chickno and
         B.nestid =  A.nestid and
         /* B is the record with the smallest dayx */
         B.dayx =
         /* find all records of that chick, get smallest dayx */
            ( select min(distinct C.dayx) from chick_capture C
              where A.chickno = C.chickno
              and A.nestid = C.nestid
            ) and
         B.dayx < 15 and
         /* if age chicks from late captures, inexact! */
         B.day_time =
         /* two different day_times may have same dayx */
            ( select min(distinct day_time) from chick_capture D
              where A.chickno = D.chickno
              and A.nestid = D.nestid
            )
      )
where A.day0 is null
/
```

Appendix 4.10 Number of different breeders caught per year and colony, using adult_capture and brood

```
SQL> run
  1  select count (distinct a.ring)
  2  from adult_capture a, brood b
  3  where to_char(a.day_time,'yy') = '89'
  4  and b.colony = 1
  5* and a.nestid=b.nestid

COUNT(DISTINCTA.RING)
---------------------
   41

SQL> run
  1  select count (distinct a.ring)
  2  from adult_capture a, brood b
  3  where to_char(a.day_time,'yy') = '89'
  4  and b.colony = 2
  5* and a.nestid=b.nestid

COUNT(DISTINCTA.RING)
---------------------
                    0
SQL> run
  1  select count (distinct a.ring)
  2  from adult_capture a, brood b
  3  where to_char(a.day_time,'yy') = '90'
  4  and b.colony = 1
  5* and a.nestid=b.nestid

COUNT(DISTINCTA.RING)
---------------------
                   30

SQL> run
  1  select count (distinct a.ring)
  2  from adult_capture a, brood b
  3  where to_char(a.day_time,'yy') = '90'
  4  and b.colony = 2
  5* and a.nestid=b.nestid

COUNT(DISTINCTA.RING)
---------------------
                   61

SQL> run
  1  select count (distinct a.ring)
  2  from adult_capture a, brood b
  3  where to_char(a.day_time,'yy') = '91'
  4  and b.colony = 2
  5* and a.nestid=b.nestid

COUNT(DISTINCTA.RING)
---------------------
                  142
```

Appendix 4.11 Food scans and cloud cover

Hypothesis: cloud cover affects insect behaviour and therefore Bee-eaters have better hunting in sunny condition. Question: does the proportion of birds carrying food, at any one time, vary with cloud cover? Task: The proportion of birds with food can be calculated from food scans. Observations for tagged birds during any one scan are in table sightings. These have to be counted per minute and added to table propn_tags, where the total number of untagged birds and the number of uintagged birds carrying food are stored. For those records, where a cloud cover (here called sunindex) was scored, this has to be extracted from table ecology and added to the counts. Result: a datafile that contains date and time (minute), the total number of birds, the number of birds carrying food and the score for cloud cover for that particular scan. The datafile is in standard format and can be used to calculate the proportion of birds caryying food.

```
/* add the sightings for that day_time into propn_tags (or a_s) */
update propn_tags pt
set s_tot =
      (select count(s.bird_id)
       from sighting s
       where s.day_time = pt.day_time
       and s.obs = pt.obs)
/
/* to get the total number of birds for propn_tag [or act_scan]  */
/* add the sightings for that day_time into propn_tags (or a_s) */
update propn_tags pt
set s_food =
      (select count(s.bird_id)
       from sighting s
       where s.day_time = pt.day_time
       and not i_type = ' 0'
       and not i_type = '0')
/
/* to get the total number of birds for propn_tag [or act_scan]  */
/* add the sightings for that day_time into propn_tags (or a_s) */
update propn_tags pt
set s_tags =
      (select count(s.bird_id)
       from sighting s
       where s.day_time = pt.day_time
       and not bird_id like '%00%') /* only marked birds */
/

/* pt-ecol.sql: */
/*   food scans (pt) and sunindex (ecol): put sun index on each pt record, */
/*   that is within the period in ecology. Adapted from nov1.sql */
column time format a10
column score format 9
column tot format 99.9
column food format 99.9
select e.day, to_char(pt.day_time,'hh24:mi') time,
   e.score,
   pt.no_food+s_food food,
   pt.no_total+s_tot tot
from propn_tags pt, ecology e /* from sighting and obs_sched */
where ( to_char(e.day,'dd.mm.yy') = to_char(pt.day_time,'dd.mm.yy')
        and                  /* same day */
      (to_char(pt.day_time,'hh24:mi') >= to_char(e.start_time,'hh24:mi')
      and to_char(e.end_time,'hh24:mi')
                             >= to_char(pt.day_time,'hh24:mi')
       )               /* within start and end of o_s */
       )
and e.index_type = 'SUN'
order by e.day,to_char(pt.day_time,'hh24:mi')
/
```

Appendix 4.12 Example of exploratory queries for birds with long streamers and very bright throats

1. Narrow down long streamers to just a few longest:

```
SQL> r
  1  select count (ts) from adult_capture
  2  where ts > 130
  3* and to_char(day_time, 'yy') > 88   /* to exclude PG's data */

 COUNT(TS)
----------
        50
  2* where ts > 140

 COUNT(TS)
----------
        25

  2* where ts > 150

 COUNT(TS)
----------
         8
```

2. Select the measurements of the few birds with the longest streamers:

```
SQL> r
  1  select day_time, nestid, ring, tag, ts,ia, bright from adult_capture
  2  where ts > 150
  3* and to_char(day_time, 'yy') > 88   /* to exclude PG's data */

DAY_TIME  NESTID       RING     TAG           TS IA  BRIGHT
--------- ------------ -------- ----- ---------- --- --------
09-APR-90 14-90        5601     XMY          164 I
10-APR-90 5-90         5681     T3R          154 I
06-JUN-90 26-90        5276     A2R          157 A
06-JUN-90 12-90        0461     S4G          153 A
28-MAR-89 0-89         0282     A3G          155 A
24-MAR-89 0-89         5263     A3W          172 I
26-MAY-89 30-89        5565     630          165 A    V.BR
08-JUN-91 192-91       06562     YRP         160 A     MED

8 records selected.
```

3. Birds with the brightest throats ('very bright')

```
SQL> select * from adult_capture where bright like '%V%';

DAY_TIME  NESTID       TAG   RING     NR  TAGCOND       BLOOD BLOODTUBES
--------- ------------ ----- -------- --- -------- ---------- ------------
    OVARY     CLOACA         COND          TS IA          WT MITES     BRIGHT
---------- ---------- ---------- ---------- --- ---------- -------- --------
08-APR-90 18-90        WOW   0490     N    NEW                   0 0
        1          1            3        110 N        38.2              V.BRIGHT

27-APR-89 9-89         400   5986     R    N
                                3        105 A        45.7                V.BR

26-MAY-89 9-89         400   5986     R    OK
                                3                     33.8                V.BR

24-MAY-89 18-89        0     0289     N
                                                                          V.BR

26-MAY-89 30-89        630   5565     N    N
                                2        165 A        34.7                V.BR

03-JUN-89 42-89        A9G   0292     N    N
                                2        141 I        37.4                V.BR

6 records selected.
```

Does throat brightness decline during the season for these birds?

```
SQL> r
  1  select * from adult_capture
  2 where ring = '0490' or ring = '5986'
  3* or ring = '0289' or ring = '5565' or ring = '0292'

DAY_TIME  NESTID       TAG   RING      NR  TAGCOND       BLOOD BLOODTUBES
--------- ------------ ----- -------- --- -------- ---------- ------------
     OVARY     CLOACA       COND          TS IA         WT MITES    BRIGHT
---------- ---------- ---------- ---------- --- ---------- -------- --------
08-APR-90 18-90        WOW   0490      N   NEW              0 0
         1          1          3        110 N         38.2          V.BRIGHT

07-JUL-90 35-90        WOW   0490      R   REPAINT        1.6 85,270
         0          2        2.5         83 0         32.8 SOMEE    MED-BR

27-APR-89 9-89         400   5986      R   N
                               3        105 A         45.7           V.BR

26-MAY-89 9-89         400   5986      R   OK
                               3                      33.8           V.BR

24-MAY-89 18-89        0     0289      N
                                                                     V.BR

26-MAY-89 30-89        630   5565      N   N
                               2        165 A         34.7           V.BR

03-JUN-89 42-89        A9G   0292      N   N
                               2        141 I         37.4           V.BR

12-JUL-86 084B-86            5565
                               3        158 I        33.25

18-APR-87 045Y-87            5986
                               3        121 I         40.5

10-JUN-89 30-89        630   5565      R   OK
                               2                      34.6           BR

10 records selected.

4. Exploration: Bright throats correlated with long tails?

SQL> r
  1  select day_time, nestid, ring, tag, ts,ia, bright from adult_capture
  2  where (ts > 150 or bright like '%V%')
  3* and to_char(day_time, 'yy') > 88   /* to exclude PG's data */

DAY_TIME  NESTID       RING     TAG           TS IA  BRIGHT
--------- ------------ -------- ----- ---------- --- --------
08-APR-90 18-90        0490     WOW          110 N   V.BRIGHT
09-APR-90 14-90        5601     XMY          164 I
10-APR-90 5-90         5681     T3R          154 I
06-JUN-90 26-90        5276     A2R          157 A
06-JUN-90 12-90        0461     S4G          153 A
28-MAR-89 0-89         0282     A3G          155 A
24-MAR-89 0-89         5263     A3W          172 I
27-APR-89 9-89         5986     400          105 A    V.BR
26-MAY-89 9-89         5986     400                   V.BR
24-MAY-89 18-89        0289     0                     V.BR
26-MAY-89 30-89        5565     630          165 A    V.BR
03-JUN-89 42-89        0292     A9G          141 I    V.BR
08-JUN-91 192-91       06562     YRP         160 A     MED

13 records selected.

...maybe it does, but not enough data to analyse.
```

Appendix 4.13 Query to exctract adult measurements and breeding data for analysis in SPSSX (incl the beginning of the SPSSX command file to read in the data)

```
clear columns
column nestid format a9
column keel1 format 99.99
column wing format 999
...
column brown format 9.9
column green format 9.9
select unique ac.nestid,
ac.ring,ac.tag,ac.day_time,
keel1, (bi.keel1+bi.keel2)/2 kl, wing,h_b,b_l,b_w ,t_l,ts,ia,wt,
cond,bright,mites,brown,green,head,b.success,b.start_day,b.fledged
from  bird_year bi, adult_capture ac, brood b
where
 bi.ring = ac.ring
 and b.nestid = ac.nestid
 and (b.qualst like ’%EGG%’ or b.qualst like ’%NE%’ or b.qualst like ’%hday%’)
order by ac.nestid
/

/*  ch593: all measurement details and season (day0), breeding success  */
data list file = ’ch593.dat’
 /nestid 1-9 (A) ring  11-19 (A) tag 20-25 (A) day 26-34 (date)
  keel1 37-41 (2) kl 44-48 (2) wing 51-53 (0) h_b 56-60 (2) bl 63-67 (2)
  bw 70-73 (2) tl 77-78 (0) ts 81-83 (0) ia 85 (A) wt 90-94 (2) cond 97-99 (1)
  bright 101-109 (A) mites 110-118 (A) brown 119-124 (1) green 125-130 (1)
  head 131-135 (1) success 136-160 (A) day0 162-170 (date) fledged 172-180 (A)
/* sort out mites: all different versions in ac here! */
recode mites (’     0 ’=0)(’0’=0)(’1E’=1)(’1 E’=1)(’1A’=2)(’1 AD’=2)(’2A’=3)
  (’FEW E ’=2)(’ FEW E’ = 2)(’ FEW ’=3)(’SOMEE’=2)(’SOMEA’=3)(’MEDE’=4)
  (’MED’=4) (’MANY E’=5) (’MED E’=4)(’ E’=3) into ms
/* sort out bright: all different versions in ac here! */
recode bright (’NOT    ’=1)(’ NOT  ’=1)(’NOTBR ’=1)(’BRIGHT’=5)(’ BRIGHT’=5)
  (’NOT-MED’=2)(’ NOT-MED’=2)(’   BR’=5)(’  NOT’=1)(’   NOT’=1)
  (’MED  ’=3)(’ MED ’=3)(’  MED’=3)(’MED-BR’=4)
  (’ MED-BR ’=4)(’BR’=5)(’BR?’=4)
  (’ BR’=5)(’V.BR’=6)(’ V.BR ’=6)(’V.BRIGHT’=6)
  (’ med-br’=4)(’  med’=3)
  into br
/* general breeding success into numbers 0=noeggs 1=eggsonly 2=chicks 3=fl */
recode success (’nobrood’ = 0)
 (’nobrood?’ =0) (’EXPELLED’=1)(’DESERTED?’=1)
 (’1exp/laidinbag/dted’=1)(’4sp/cool,damp,shallow’=1) (’clutch predated?’=1)
 (’sp/damp’=1)(’nochicks’=1) (’fledged2-3’=3)(’chicks’=2)(’fledged1’=3)
 (’FLEDGED?’=2)(’deserted?’=1)(’all sp?/deserted?’=1)(’fledged1’=3)
 (’alldied(mango?)’=2)(’deserted’=1) (’no brood’=0)  into nsucc
/* calculate means for each bird, by nest  */
aggregate outfile = *
 /break=nestid,ring
 /id = min(tag)   /* keep tag */
 /kl1 = mean(keel1)
...
 /mites = max(ms)
 /br = mean (brown)
 /gr = mean(green)
 /he = mean(head)
 /maxts = max(ts)
 /abb = max (ia)  /* I > A, so this should catch any 'I's */
 /succhar = min(success)      /* keep success as char variable for later */
 /gensucc = min(nsucc)  /* keep success as 0=no,1=eggs,2=chicks... (num) */
 /totsucc = min(fledged)      /* keep number of fledged for nests+chicks */
 /d0 = min(day0)  /* keep day0 */
 /N = N (ring)                /* number of orginal records */
```

APPENDIX 5: Observations of two Helpers:

A: All observations of X6W as the focal bird (Bird_Id), ordered in time (Date and Time), to show how this bird behaved during the season and when it became a helper.

DATE	TIME	PERCHLOC	BIRD_ID	ASSOCIATE	ACTIVITY	I_TYPE
30/MAR/1989	14:50	RH	X6W	VVR	S?	0
30/MAR/1989	14:59	RH	X6W	S1Y,1	S?	0
31/MAR/1989	13:58	RHENDDECK	X6W	S1Y,1	PROSPECT	0
01/APR/1989	12:30	RHENDWIRE	X6W	100,SMO	ARR,GREETED	I
01/APR/1989	12:32	RHENDWIRE	X6W	1,SMO	EATS?	I
01/APR/1989	12:34	RHENDWIRE	X6W	2	5CM	0
01/APR/1989	13:24	RHENDWIRE	X6W	S1Y	S	0
01/APR/1989	13:27	RHENDWIRE	X6W	0	S	0
01/APR/1989	13:28	RHENDWIRE	X6W	100,200	S	0
01/APR/1989	13:29	RHENDWIRE	X6W	S1Y	GREETS	0
01/APR/1989	13:30	RHENDWIRE	X6W	300	GREETS	0
01/APR/1989	13:31	RHENDWIRE	X6W	200	5CM	0
01/APR/1989	13:32	RHENDWIRE	X6W	S1Y,200	GREETS	0
01/APR/1989	13:33	RHENDWIRE	X6W	S1Y,200	GREETS	0
01/APR/1989	13:34	RHENDWIRE	X6W	200	S	0
01/APR/1989	13:35	RHENDWIRE	X6W	0	S	0
01/APR/1989	13:38	1	X6W	S1Y,100	D	
01/APR/1989	13:40	RHENDWIRE	X6W	1	S	0
01/APR/1989	13:41	RHENDWIRE	X6W	AMB	5CM	0
01/APR/1989	13:42	RHENDWIRE	X6W	0	S	0
01/APR/1989	13:58	RHENDWIRE	X6W	0	S	0
01/APR/1989	13:59	RHENDWIRE	X6W	AMB,2	5CM	0
01/APR/1989	14:02	RHENDWIRE	X6W	AMB,1	HUNTS	0
01/APR/1989	14:04	RHENDWIRE	X6W	0	S	0
01/APR/1989	14:05	RHENDWIRE	X6W	S1Y?	L'CALL,5CM	0
04/APR/1989	12:26	RHENDWIRE	X6W	0	ARRIVES	0
04/APR/1989	12:27	RHENDWIRE	X6W	0	S	0
04/APR/1989	12:30	RHENDWIRE	X6W	0	FLYOFF	0
04/APR/1989	15:18	RHENDWIRE	X6W	1	S	0
04/APR/1989	15:24	RHENDWIRE	X6W	0	S	0
05/APR/1989	09:52	RHENDWIRE	X6W	AMB	ARR,5CM,GREETED	0
05/APR/1989	09:53	RHENDWIRE	X6W	AMB	S	0
05/APR/1989	09:54	RHENDWIRE	X6W	AMB	PREENS	0
05/APR/1989	10:01	RHENDWIRE	X6W	0	S	0
05/APR/1989	10:14	RHENDWIRE	X6W	0	HUNTS	0
05/APR/1989	10:26	RHENDAIR	X6W	0	HIGHCIRCLE	0
05/APR/1989	11:50	RHENDWIRE	X6W	0	ARR	0
05/APR/1989	12:06	RHENDWIRE	X6W	0	S	0
05/APR/1989	14:29	RHENDWIRE	X6W	0	S	0
06/APR/1989	14:25	RHENDWIRE	X6W	0	S	0
06/APR/1989	14:36	RHENDWIRE	X6W	0	ARR	0
06/APR/1989	14:37	RHENDWIRE	X6W	100	S	0
06/APR/1989	14:38	RHENDWIRE	X6W	100	S	0
06/APR/1989	14:57	RHENDWIRE	X6W	0	S	0
08/APR/1989	09:25	RHENDWIRE	X6W	0	S	0
08/APR/1989	09:40	RHENDWIRE	X6W	0	HUNTS	0
08/APR/1989	09:46	RHENDWIRE	X6W	0	GREETS	0
08/APR/1989	09:55	RHENDWIRE	X6W	0	S	0
08/APR/1989	10:00	RHENDWIRE	X6W	0		0
08/APR/1989	12:15	RHENDWIRE	X6W	T?B,1	S	0
11/APR/1989	10:20	RHENDWIRE	X6W	0	S	0
11/APR/1989	11:10	RHENDWIRE	X6W	T9R,4	S	0
11/APR/1989	11:10	RHENDWIRE	X6W	S9R,4	S	0
11/APR/1989	11:12	RHENDWIRE	X6W	0	S	0
11/APR/1989	11:17	RHENDWIRE	X6W	SMB,2	GREETS	0
11/APR/1989	11:17	RHENDWIRE	X6W	OTB,2	GREETS	0
11/APR/1989	11:21	RHENDWIRE	X6W	XMO	S	0
11/APR/1989	11:23	RHENDWIRE	X6W	SVB	S	0
11/APR/1989	11:23	RHENDWIRE	X6W	SVB,1	D'PLACES	0
11/APR/1989	11:25	RHENDWIRE	X6W	0	S	0
11/APR/1989	12:56	RHENDWIRE	X6W	AMB	S	0
11/APR/1989	13:28	RHENDWIRE	X6W	0	S	0
11/APR/1989	13:42	RHENDWIRE	X6W	0	S	0
11/APR/1989	14:12	RHENDWIRE	X6W	0	S	0
17/APR/1989	15:53	RHENDWIRE	X6W	0	S?	0

17/APR/1989	16:01	RHMIDWIRE	X6W	0	S?	0
17/APR/1989	16:22	RHMIDWIRE	X6W	3	S?	0
19/APR/1989	14:00	RHENDWIRE	X6W	0	S?	0
19/APR/1989	14:30	RHENDWIRE	X6W	S6R	S?	0
22/APR/1989	16:22	RHENDWIRE	X6W	0	S	0
22/APR/1989	16:26	RHENDWIRE	X6W	??R	S	0
22/APR/1989	16:31	RHENDWIRE	X6W	0	S?	0
25/APR/1989	14:49	RHENDWIRE	X6W	S6R,1	D'PLACES	0
25/APR/1989	14:51	RHENDWIRE	X6W	1	S	0
25/APR/1989	14:52	RHENDWIRE	X6W	0	S	0
25/APR/1989	15:01	RHENDWIRE	X6W	0	S	0
28/APR/1989	11:55	RHMIDWIRE	X6W	0	S	0
28/APR/1989	13:31	RHENDWIRE	X6W	0	S	0
28/APR/1989	13:44	RHMIDWIRE	X6W	0	S	0
30/APR/1989	11:49	RHENDWIRE	X6W	??R	GREETS	0
30/APR/1989	12:02	RHMIDWIRE	X6W	0	S	0
03/MAY/1989	11:50	RHENDWIRE	X6W	1	S	0
03/MAY/1989	11:51	RHENDWIRE	X6W	0	S	0
03/MAY/1989	11:53	RHMIDWIRE	X6W	0	S	0
03/MAY/1989	12:02	RHENDWIRE	X6W	0	S	0
03/MAY/1989	12:04	RHENDWIRE	X6W	??R,2	5CM	0
03/MAY/1989	12:04	RHENDWIRE	X6W	T3B,2	S	0
03/MAY/1989	12:09	RHENDWIRE	X6W	T3B	S	0
03/MAY/1989	12:10	RHENDWIRE	X6W	0	S	0
03/MAY/1989	12:15	RHENDWIRE	X6W	0	S	0
04/MAY/1989	10:06	RHENDWIRE	X6W	0	S	0
04/MAY/1989	10:12	RHENDWIRE	X6W	0	S	0
04/MAY/1989	12:41	RHENDWIRE	X6W	0	S	0
04/MAY/1989	12:43	RHENDWIRE	X6W	0	BASK	0
04/MAY/1989	16:25	RHENDWIRE	X6W	??R	S	0
04/MAY/1989	16:30	31	X6W	??R	S	0
04/MAY/1989	16:32	RHENDWIRE	X6W	0	PREENS	0
04/MAY/1989	16:40	RHENDWIRE	X6W	P-XMW?	S	0
04/MAY/1989	16:40	RHENDWIRE	X6W	100	ATTACKED,OPENBILL	0
04/MAY/1989	16:42	RHENDWIRE	X6W	100	OPENBILL	0
04/MAY/1989	16:43	RHENDWIRE	X6W	0	S	0
04/MAY/1989	16:46	RHENDWIRE	X6W	??R	PLUSTER,GREETS	0
06/MAY/1989	10:25	RHENDWIRE	X6W	0	PREEN	0
06/MAY/1989	10:31	RHENDWIRE	X6W	0	L'CALL	0
06/MAY/1989	10:33	RHENDWIRE	X6W	2	PREEN	0
06/MAY/1989	10:36	RHENDWIRE	X6W	1	L'CALL	0
08/MAY/1989	09:22	RHENDWIRE	X6W	0	HUNT	0
08/MAY/1989	09:25	RHNDNWIRE	X6W	0	S	0
08/MAY/1989	09:28	RHENDWIRE	X6W	0	S	0
08/MAY/1989	09:33	RHENDWIRE	X6W	0	S	0
08/MAY/1989	09:38	RHENDWIER	X6W	0	S	0
08/MAY/1989	09:45	RHENDWIRE	X6W	0	S	0
08/MAY/1989	10:10	RHENDWIRE	X6W	0	S	0
08/MAY/1989	10:24	RHENDWIRE	X6W	AMB	5CM	0
08/MAY/1989	10:25	RHENDWIRE	X6W	AMB	PLUSTERS	0
08/MAY/1989	10:26	RHENDWIRE	X6W	0	S	0
08/MAY/1989	10:32	RHENDWIRE	X6W	0	S	0
08/MAY/1989	10:40	RHENDWIRE	X6W	0	S	0
08/MAY/1989	15:21	RHENDWIRE	X6W	0	S	0
08/MAY/1989	15:25	RHENDWIRE	X6W	1	S	0
08/MAY/1989	19:08	RHMIDWIRE	X6W	0	S	0
09/MAY/1989	07:52	RHENDWIRE	X6W	1	5CM	0
09/MAY/1989	07:53	RHENDWIRE	X6W	1	5CM	0
09/MAY/1989	07:58	RHENDWIRE	X6W	1	5CM	0
09/MAY/1989	08:01	RHENDWIRE	X6W	1	5CM, PREEN	0
09/MAY/1989	08:03	RHENDWIRE	X6W	1	5CM, PREEN	0
09/MAY/1989	08:06	RHENDWIRE	X6W	1	L'CALL	0
09/MAY/1989	08:08	RHENDWIRE	X6W	1	5CM, PREEN	0
09/MAY/1989	08:11	RHENDWIRE	X6W	0	S	0
09/MAY/1989	08:17	RHENDWIRE	X6W	0	S	0
09/MAY/1989	08:32	RHENDWIRE	X6W	0	S	0
09/MAY/1989	08:34	RHENDWIRE	X6W	0	S	0
09/MAY/1989	08:46	RHENDWIRE	X6W	0	EATS	I
09/MAY/1989	08:47	RHENDWIRE	X6W	300	S	0
09/MAY/1989	08:49	RHENDWIRE	X6W	0	S	0
09/MAY/1989	08:53	RHENDWIRE	X6W	0	S	0
12/MAY/1989	09:20	RHENDWIRE	X6W	0	S	0
12/MAY/1989	09:21	RHENDWIRE	X6W	0	S	0
12/MAY/1989	09:32	RHENDWIRE	X6W	0	BASKS	0

12/MAY/1989	09:34	RHENDWIRE	X6W	1	S	0
12/MAY/1989	09:35	RHENDWIRE	X6W	0	HUNT	0
12/MAY/1989	10:07	RHENDIWRE	X6W	0	S	0
12/MAY/1989	10:12	RHENDWIRE	X6W	0	S	0
12/MAY/1989	10:33	RHENDWIRE	X6W	0	S	0
12/MAY/1989	10:37	RHENDWIRE	X6W	0	S	0
12/MAY/1989	17:21	RHENDWIRE	X6W	0	S	0
12/MAY/1989	17:35	RHENDWIRE	X6W	0	HUNT	0
18/MAY/1989	18:53	RHENDWIRE?	X6W	1	S	I
18/MAY/1989	18:54	RHENDWIRE?	X6W	1	EATS	I
18/MAY/1989	19:00	RHENDWIRE?	X6W	0	S	0
18/MAY/1989	19:08	RHMIDWIRE	X6W	0	S	0
23/MAY/1989	12:06	RHENDWIRE	X6W	0	S	0
23/MAY/1989	12:10	RHENDWIRE	X6W	0	S	0
23/MAY/1989	12:15	RHENDWIRE	X6W	0	S	0
23/MAY/1989	15:09	RHENDWIRE	X6W	0	S	0
23/MAY/1989	15:10	RHENDWIRE	X6W	0	S	0
23/MAY/1989	15:13	RHENDWIRE	X6W	MXO	S	0
23/MAY/1989	15:15	RHENDWIRE	X6W	MXO	S	0
23/MAY/1989	15:19	RHENDWIRE	X6W	0	S	0
23/MAY/1989	15:23	RHENDWIRE	X6W	0	S	0
25/MAY/1989	10:35	RHENDWIRE	X6W	0	S	0
25/MAY/1989	10:40	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	10:45	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	10:50	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	11:21	RHENDWIRE?	X6W	0	EAT	I
25/MAY/1989	11:30	RHENDWIRE	X6W	0	S	0
25/MAY/1989	11:38	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	11:40	RHENDWIRE	X6W	0	EAT	I
25/MAY/1989	11:41	RHENDWIRE	X6W	0	S	0
25/MAY/1989	11:42	RHENDWIRE	X6W	0	S	0
25/MAY/1989	11:43	RHENDWIRE	X6W	0	S	0
25/MAY/1989	13:55	RHENDWIRE	X6W	0	S	0
25/MAY/1989	14:32	RHENDWIRE	X6W	0	S	0
25/MAY/1989	14:33	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	14:36	RHENDWIRE	X6W	0	PREEN	0
25/MAY/1989	14:37	RHENDWIRE	X6W	0	BASK	0
25/MAY/1989	14:38	RHENDWIRE	X6W	0	S	0
25/MAY/1989	14:44	RHENDWIRE	X6W	??O?	L'CALL	0
25/MAY/1989	14:45	RHENDWIRE	X6W	0	S	0
25/MAY/1989	14:47	RHENDWIRE	X6W	0	S	0
25/MAY/1989	14:50	RHENDWIRE	X6W	0	S	0
27/MAY/1989	12:36	RHMIDWIRE	X6W	0	S	0
27/MAY/1989	12:40	RHMIDWIRE	X6W	0	S	0
27/MAY/1989	12:44	RHMIDWIRE	X6W	0	HUNT	0
27/MAY/1989	12:45	RHMIDWIRE	X6W	0	EATS	I
27/MAY/1989	12:47	RHMIDWIRE	X6W	0	FLYOFF	0
27/MAY/1989	12:57	RHENDWIRE	X6W	0	S	0
27/MAY/1989	12:59	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:01	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:03	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:44	RHMIDWIRE	X6W	0	HUNT	0
27/MAY/1989	13:50	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:51	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:52	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:53	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:54	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:55	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:57	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:58	RHENDWIRE	X6W	0	S	0
27/MAY/1989	13:59	RHENDWIRE	X6W	0	S	0
27/MAY/1989	14:00	RHENDWIRE	X6W	0	S	0
31/MAY/1989	09:56	RHENDWIRE	X6W	0	S	0
31/MAY/1989	09:57	RHENDWIRE	X6W	0	S	0
31/MAY/1989	09:59	RHENDWIRE	X6W	0	S	0
31/MAY/1989	10:00	RHENDWIRE	X6W	0	S	0
31/MAY/1989	10:01	RHENDWIRE	X6W	0	S	0
31/MAY/1989	10:02	RHENDWIRE	X6W	0	PREEN	0
31/MAY/1989	10:03	RHENDWIRE	X6W	0	PREEN	0
31/MAY/1989	10:04	RHENDWIRE	X6W	0	PREEN	0
31/MAY/1989	10:05	RHENDWIRE	X6W	0	PREEN	0
31/MAY/1989	10:06	RHENDWIRE	X6W	0	PREEN	0
31/MAY/1989	10:07	RHENDWIRE	X6W	0	L'CALL	0
31/MAY/1989	10:08	RHENDWIRE	X6W	0	S	0

```
31/MAY/1989 10:09  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:10  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:11  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:12  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:13  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:14  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:15  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:16  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:17  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:18  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:19  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:20  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:21  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:23  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:24  RHENDWIRE   X6W       0                 HUNT           0
31/MAY/1989 10:25  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:26  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:28  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:29  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:32  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:35  RHENDWIRE   X6W       0                 S              0
31/MAY/1989 10:37  RHMIDFARWIRE    X6W   0                 PREENS         0
31/MAY/1989 10:39  RHMIDFARWIRE    X6W   0                 S              0
31/MAY/1989 10:43  RHMIDAIR    X6W       0                 HUNT           0
31/MAY/1989 10:44  RHMIDWIRE   X6W       0                 CALL           0
31/MAY/1989 10:45  RHMIDWIRE   X6W       0                 L'CALL         0
31/MAY/1989 10:46  RHMIDWIRE   X6W       0                 S              0
31/MAY/1989 10:48  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:49  RHENDWIRE   X6W       0                 PREEN          0
31/MAY/1989 10:51  RHMIDFARWIRE    X6W   0                 PREEN          0
31/MAY/1989 10:52  RHENDWIRE   X6W       0                 S              I
31/MAY/1989 10:53  RHENDWIRE   X6W       0                 FLICKERS       I
31/MAY/1989 10:54  RHENDWIRE   X6W       0                 EATS           I
31/MAY/1989 10:55  RHMIDFARWIRE    X6W   0                 S              0
01/JUN/1989 11:38  RHENDWIRE   X6W       T3R               5CM,GREETS     0
01/JUN/1989 11:39  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 11:40  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 11:44  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 11:48  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:23  RHENDWIRE   X6W       0                 PREENS         0
01/JUN/1989 12:24  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:25  RHENDWIRE   X6W       0                 HUNT           0
01/JUN/1989 12:26  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:27  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:28  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:31  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:32  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:42  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:45  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:46  RHENDWIRE   X6W       0                 PREEN          0
01/JUN/1989 12:47  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:48  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:49  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:50  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 12:51  RHMIDWIRE   X6W       0                 S              0
01/JUN/1989 12:54  RHMIDMIDWIRE    X6W   0                 S              0
01/JUN/1989 12:57  RHENDWIRE   X6W       46O?              S              0
01/JUN/1989 12:58  RHENDWIRE   X6W       0                 HUNT           0
01/JUN/1989 13:00  31          X6W       0                 ARR            0
01/JUN/1989 13:01  31          X6W       0                 OFF            0
01/JUN/1989 13:02  31          X6W       0                 ARR            0
01/JUN/1989 13:03  NEAR31      X6W       0                 ARR            0
01/JUN/1989 13:04  NEAR31      X6W       0                 OFF            0
01/JUN/1989 13:05  RHENDWIRE   X6W       S6R,??O           S              0
01/JUN/1989 13:15  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 13:21  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 13:22  RHENDWIRE   X6W       0                 CATCHES        I
01/JUN/1989 13:23  RHENDWIRE   X6W       0                 BASHES         I
01/JUN/1989 13:24  RHENDWIRE   X6W       0                 S              I
01/JUN/1989 13:26  31          X6W       0                 ARR,OFF        0
01/JUN/1989 13:28  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 13:29  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 13:31  RHENDWIRE   X6W       0                 S              0
01/JUN/1989 13:36  RHENDWIRE   X6W       0                 S              0
```

01/JUN/1989	13:38	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:40	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:42	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:43	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:45	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:46	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:47	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:48	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:52	RHENDWIRE	X6W	0	S	0
01/JUN/1989	13:53	RHENDWIRE?	X6W	0	S?	0
01/JUN/1989	13:55	RHMIDFARWIRE	X6W	0	S	0
01/JUN/1989	13:56	RHMIDFARWIRE	X6W	630	D'PLACED(SWOOP)	0
01/JUN/1989	13:57	RHENDWIRE	X6W	0	S	0
02/JUN/1989	14:10	RHMIDNEARWIRE	X6W	0	PREEN	0
02/JUN/1989	14:12	RHMIDNEARWIRE	X6W	0	PREENS	0
06/JUN/1989	13:22	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:24	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:25	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:27	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:29	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:30	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:31	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:32	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:33	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:35	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:37	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:43	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:46	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:47	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:51	RHENDWIRE	X6W	0	PREENS	0
06/JUN/1989	13:53	RHENDWIRE	X6W	0	PREENS	0
06/JUN/1989	13:54	RHENDWIRE	X6W	0	PREENS	0
06/JUN/1989	13:55	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:56	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:57	RHENDWIRE	X6W	0	S	0
06/JUN/1989	13:58	RHENDWIRE	X6W	0	S	0
12/JUN/1989	09:52	RHENDWIRE	X6W	0	S	0
12/JUN/1989	09:53	RHENDWIRE	X6W	0	S	0
12/JUN/1989	09:54	RHENDWIRE	X6W	0	S	0
12/JUN/1989	09:55	RHMIDFARWIRE	X6W	0	S	0
12/JUN/1989	09:56	31	X6W	0	S	0!
12/JUN/1989	09:58	31	X6W	0	INTO!	0
12/JUN/1989	10:00	31	X6W		INSIDE	0
12/JUN/1989	10:01	31	X6W	0	EMERGES	0
12/JUN/1989	10:02	RHMIDFARWIRE	X6W	0	S	0
12/JUN/1989	10:03	RHENDWIRE	X6W	0	PREENS	0
15/JUN/1989	11:50	31	X6W	0	INTO	I
15/JUN/1989	11:55	31	X6W	?	INSIDE	?
15/JUN/1989	11:57	31	X6W	?	INSIDE	?
15/JUN/1989	11:58	31; RHENDWIRE	X6W	0	FLYUP	0
15/JUN/1989	13:55	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:34	RHENDWIRE	X6W	0	S	I
15/JUN/1989	14:36	RHENDWIRE	X6W	0	S	0!
15/JUN/1989	14:39	RHENDWIRE; 31	X6W	0	S; INTO	I
15/JUN/1989	14:40	RHENDWIRE	X6W	0	ARRIVES	0!
15/JUN/1989	14:42	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:44	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:47	RHENDWIRE	X6W	0	BASHES	WASP
15/JUN/1989	14:48	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:52	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:53	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:56	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:57	RHENDWIRE	X6W	0	S	0
15/JUN/1989	14:58	RHENDWIRE	X6W	0	S	0
15/JUN/1989	16:50	RHENDWIRE	X6W	0	S	CICAD
15/JUN/1989	16:53	RHENDWIRE	X6W	0	S	CICAD
15/JUN/1989	16:54	RHENDWIRE	X6W	0	S	CICAD
15/JUN/1989	16:57	31	X6W	0	INTO	CICAD
15/JUN/1989	16:59	RHENDWIRE	X6W	0	S	0
20/JUN/1989	17:44	31	X6W	0	S	D'FLY
20/JUN/1989	17:47	31	X6W	0	S	D'FLY
20/JUN/1989	17:48	31	X6W	0	DROPSOFF	D'FLY
20/JUN/1989	17:50	RHENDWIRE	X6W	0	ARRIVES	0

APPENDIX 5 B: Querie and selected records to show all sightings of the Helper A4O and the breeding pair it helped (33O and 4OO), and sightings at their nest (9-89), to show the pattern of recruitment of this helper.

```
SQL> 1  select daytime, perchloc,bird_id,associate,activity,i_type,abs_size
  2  from sighting where (bird_id = '330' or bird_id = '400' or bird_id = 'A40'
  3* or perchloc = '9')  order by  day_time
```

```
DAYTIME            PERCHLOC      BIRD_I ASSOCIAT ACTIVITY       I_TYPE   ABS_SIZE
------------------ ------------- ------ -------- -------------- -------- --------
05/APR/1989 14:02  9             100    200      D              0
05/APR/1989 14:02  9             200    100      S              0
05/APR/1989 14:19  9             400    0        S              0
05/APR/1989 14:25  9             100    200                     0
05/APR/1989 14:25  9             200    100                     0
10/APR/1989 12:42  9             400    0                       0
11/APR/1989 11:30  9             200    300      D              0
11/APR/1989 11:30  9             300    200      S              0
11/APR/1989 11:50  9             100    200      S              0
11/APR/1989 11:50  9             200    100      S              0
11/APR/1989 11:52  9             100    200                     0
11/APR/1989 11:52  9             200    100                     0
11/APR/1989 14:09  9             100    0        D              0
17/APR/1989 13:43  9             100    0        D              0
17/APR/1989 14:40  9             100    0                       0
17/APR/1989 16:45  9             100    0        S              0
17/APR/1989 17:42  9             200    0        D              0
17/APR/1989 17:43  9             200    0        D              0
19/APR/1989 14:16  9             200    0                       0
28/APR/1989 10:58  9             S90    06B,2    5CM,PROSPECT   0
28/APR/1989 10:58  9             06B    S90,2    5CM,PROSPECT   0
28/APR/1989 11:00  9             S90    1        5CM            0
28/APR/1989 11:00  9             06B    0        BASKS          0
28/APR/1989 11:02  9             S6R    0        S              0
28/APR/1989 11:03  9             XMY    3        PROSPECT       0
08/MAY/1989 09:25  RHMIDTREE     330    0        PREEN          0
08/MAY/1989 09:28  RHMIDTREES    330    0        S              0
08/MAY/1989 09:33  RHMIDTREES    330    0        S              0
08/MAY/1989 09:38  RHMIDTREES    330    SSO      S              0
08/MAY/1989 09:40  RHMIDTREES    330    SSO      BILLLOCK       0
08/MAY/1989 09:41  RHMIDTREES    330    SSO      WRESTLE,FLYOFF 0
08/MAY/1989 09:42  AIR           330    SSO      AIRCHASE       0
08/MAY/1989 09:43  RHMIDTREES    330    SSO      DISPUTE        0
08/MAY/1989 09:44  AIR           330    SSO      AIRCHASE       0
08/MAY/1989 09:45  RHMIDTREES    330    0        S              0
08/MAY/1989 09:58  9             330    0        PROSPECT       0
08/MAY/1989 10:04  RHENDWIRE     330    ??R      HUNTS          0
08/MAY/1989 10:05  RHENDWIRE     330    0        HUNTS          0
08/MAY/1989 10:06  RHENDWIRE     330    ??R      5CM            0
08/MAY/1989 10:07  RHENDWIRE     330    0        HUNTS          0
08/MAY/1989 10:09  RHENDWIRE     330    ??R      5CM            0
08/MAY/1989 18:55  RHAIR         330    400      FLY            0
08/MAY/1989 18:55  RHAIR         400    330      FLY            0
08/MAY/1989 18:56  BEHINDRHMID   330    0        S              0
08/MAY/1989 18:56  BEHINDRHMID   400    0        S              0
08/MAY/1989 19:07  RHMIDTREE     330    SSO      S              0
09/MAY/1989 08:40  RHMIDAIR      330    1        D'PLACED       0
09/MAY/1989 08:42  9             330    0        S              0
09/MAY/1989 08:47  RHMIDTREES    330    0        S              0
09/MAY/1989 08:52  RHMIDTREES    330    0        S              0
11/MAY/1989 09:40  RHMIDTREES    400    0        HUNT           0
11/MAY/1989 09:40  RHMIDTREES    330    0        HUNT           0
11/MAY/1989 09:41  RHMIDTREES    400    0        HUNT           0
11/MAY/1989 09:42  RHMIDTREES    330    0        HUNT           0
11/MAY/1989 09:43  RHMIDTREES    400    0        HUNT           0
11/MAY/1989 09:43  RHMIDTREES    330    0        HUNT           0
11/MAY/1989 12:31  RHMIDTREES    330    0        PREEN          0
11/MAY/1989 12:34  RHMIDTREES    330    0        HUNT           0
11/MAY/1989 12:37  RHMIDTREES    330    0        S              0
11/MAY/1989 12:41  RHMIDTREES    330    0        S              0
11/MAY/1989 12:48  9             330    0        PROBES         0
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11/MAY/1989	12:49	RHMIDTREES	330	0	S	0
11/MAY/1989	12:50	RHMIDTREES	330	0	S	0
11/MAY/1989	12:51	9	330	0	PROBES	0
11/MAY/1989	12:52	RHMIDTREES	330	0	S	0
12/MAY/1989	09:05	RHMIDTREES	330	0	S	0
12/MAY/1989	09:06	RHMIDWIRE	330	0	HUNT	0
12/MAY/1989	09:30	RHMIDTREES	330	400	EATS,5CM	I
12/MAY/1989	09:30	RHMIDTREES	400	330	5CM	0
12/MAY/1989	09:32	RHMIDTREES	330	400	S	0
12/MAY/1989	09:32	RHMIDTREES	400	330	S	0
12/MAY/1989	09:45	RHMIDTREES	330	0	S	0
12/MAY/1989	09:50	RHMIDTREES	330	0	S	0
18/MAY/1989	16:41	RHMIDTREE	330	0	S	0
18/MAY/1989	17:10	9	S90	0	S	0
23/MAY/1989	14:02	RHMIDWIRE	330	0	HUNT	0
23/MAY/1989	14:05	RHMIDWIRE	330	0	PREEN	0
23/MAY/1989	14:10	RHMIDWIRE	330	0	S	0
23/MAY/1989	15:55	9	330	0	PROSPECT	0
23/MAY/1989	16:00	RHMIDTREES	330	0	S	0
25/MAY/1989	13:55	9	XVW	0	S	0
25/MAY/1989	13:55	9	330	0	INSIDE	0
25/MAY/1989	13:58	9	330	0	INSIDE	0
25/MAY/1989	14:10	9	330	0	INSIDE	0
25/MAY/1989	14:13	9	330	0	INSIDE	0
25/MAY/1989	14:14	9	330	0	INSIDE	0
25/MAY/1989	14:15	9	330	0	INSIDE	0
25/MAY/1989	14:18	9	330	0	INSIDE	0
25/MAY/1989	14:19	9	330	0	INSIDE	0
25/MAY/1989	14:20	9	330	0	INSIDE	0
25/MAY/1989	14:21	9	330	0	INSIDE	0
25/MAY/1989	14:26	9	330	0	EMERGES	0
25/MAY/1989	14:27	RHMIDWIRE	330	0	PREEN	0
25/MAY/1989	15:11	9	330	0	INTO	0
25/MAY/1989	15:17	9	330	0	INSIDE	0
25/MAY/1989	15:19	9	400?	0	INTO	0
25/MAY/1989	15:19	9	330?	0	INSIDE	0
25/MAY/1989	15:20	9	330	0	EMERGE	0
25/MAY/1989	15:21	RHMIDWIRE	330	0	S	0
25/MAY/1989	15:23	RHMIDWIRE	330	0	S	0
25/MAY/1989	15:25	RHMIDWIRE	330	0	S	0
25/MAY/1989	15:43	9	330	0	S	0
25/MAY/1989	15:44	9	330	0	INTO	0
25/MAY/1989	15:45	9	330		INSIDE	0
25/MAY/1989	15:48	9	330		INSIDE	0
25/MAY/1989	15:52	9	330		INSIDE	0
25/MAY/1989	15:53	9	330		INSIDE	0
25/MAY/1989	15:58	9	330		INSIDE	0
25/MAY/1989	16:01	9	330		INSIDE	0
25/MAY/1989	16:08	9	330		INSIDE	0
25/MAY/1989	16:10	9	330		INSIDE	0
25/MAY/1989	16:12	9	330		INSIDE	0
25/MAY/1989	17:23	RHMIDWIRE	330	0	PURR	0
27/MAY/1989	13:37	RHMIDWIRE	330	0	S	0
27/MAY/1989	13:39	RHMIDWIRE	330	0	CALL	0
27/MAY/1989	13:41	RHMIDWIRE	330	0	HUNT	0
27/MAY/1989	13:42	RHMIDWIRE	330	0	S	0
27/MAY/1989	13:43	RHMIDWIRE	330	0	PREEN	0
29/MAY/1989	08:31	30	330	0	PROBES	0
29/MAY/1989	08:32	30	330	0	PROBES	0
29/MAY/1989	11:40	9	330?	0	INTO	0
29/MAY/1989	13:59	RHMIDFARWIRE	330	0	PREEN	0
31/MAY/1989	10:20	9	330	0	EMERGE	0
31/MAY/1989	10:21	RHMIDFARWIRE	330	0	PLUSTERS	0
31/MAY/1989	10:23	RHMIDFARWIRE	330	0	PREEN	0
31/MAY/1989	13:12	RHMIDWIRE	330	0	S	0
31/MAY/1989	13:43	9	330?	0	PROSPECTS	0
01/JUN/1989	12:18	RHMIDNEARWIRE	330	0	EMERGE	0
01/JUN/1989	12:19	RHENDWIRE	330	0	S	0
01/JUN/1989	13:05	RHMIDWIRE	330	0	S	0
02/JUN/1989	13:48	RHMIDFARWIRE	330	0	RUFFLED,PREENS	0
02/JUN/1989	13:49	RHMIDFARWIRE	330	0	HUNCHED	0
02/JUN/1989	13:50	RHMIDFARWIRE	330	0	S	0
02/JUN/1989	13:51	RHMIDFARWIRE	330	0	S	0
02/JUN/1989	13:52	RHMIDFARWIRE	330	0	S	0

02/JUN/1989	13:53	28	330	0	S	0	
02/JUN/1989	14:27	9	330	0	S	0	
03/JUN/1989	16:01	9	330	0	ARRIVES; INTO	I	
12/JUN/1989	08:22	RHMIDTREES	330	0	S	I	6
12/JUN/1989	08:23	9	330	0	INTO	I	6
12/JUN/1989	08:24	9	330		INSIDE		
15/JUN/1989	09:04	9	330	0	INTO	D'FLY	4
15/JUN/1989	12:05	9	??G!	0	INTO	FLY	2
15/JUN/1989	12:28	9	430	0	PROBES	0	
15/JUN/1989	12:30	9	??0	0	INTO	0?	
15/JUN/1989	12:39	9	??G?	0	INTO	NA	
15/JUN/1989	13:55	9	330	0	INTO	CICAD	6
15/JUN/1989	14:42	9	A9G	0	INTO	BEE	7
15/JUN/1989	14:56	9	??G	0	INTO	0?	
15/JUN/1989	14:57	9	??G	?	INSIDE?	?	
15/JUN/1989	16:39	RHMIDTREES	330	0	S	D'FLY	3
15/JUN/1989	16:41	RHMIDTREES	330	0	S	D'FLY	3
15/JUN/1989	16:42	9	330	0	INTO	D'FLY	3
01/JUL/1989	16:08	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	17:07	RHMIDTREES	400	0	CALLS	BEE	6
01/JUL/1989	17:08	9	400	0	DROPSOFF	BEE	6
01/JUL/1989	17:09	RHMIDTREES	400	0	CALLS	0	
01/JUL/1989	17:10		400	0	FLYOFF	0	
01/JUL/1989	17:11	RHMIDTREES	330	0	ARRIVES;CALLS	0	
01/JUL/1989	17:18	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	17:19	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	17:20	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	17:23	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	17:24	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:25	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:26	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:27	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:28	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:29	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:31	RHMIDTREES	330	A4G	CALLS; 10CM	0	
01/JUL/1989	17:32	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:34	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:36	RHMIDTREES	330	0	PREENS	0	
01/JUL/1989	17:37	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:38	RHMIDTREES	330	0	PREENS	0	
01/JUL/1989	17:39	RHMIDTREES	330	0	PREENS	0	
01/JUL/1989	17:41	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:42	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:43	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:44	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:45	RHMIDTREES	330	0	PREENS	0	
01/JUL/1989	17:46	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:51	RHMIDTREES	330	0	BILLWIPES	0	
01/JUL/1989	17:52	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:54	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:56	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:57	RHMIDTREES	330	0	S	0	
01/JUL/1989	17:59	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:00	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:02	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:04	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:05	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:06	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:07	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:09	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:10	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:11	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:12	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:13	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:14	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:16	RHMIDTREES	330	0	CALLS	0	
01/JUL/1989	18:17	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:18	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:19	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:20	RHMIDTREES	330	0	S	0	
01/JUL/1989	18:21	RHMIDTREES	330	0	S	0	
02/JUL/1989	09:41	9	A4G	JUV	ARRIVES	0	
02/JUL/1989	09:48	9	A4G	JUV	FEEDS	I	
02/JUL/1989	09:54	9	A4G	0	DROPSOFF	FLY	1

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02/JUL/1989 09:56  9            A4G    0        DROPSOFF       I         2
02/JUL/1989 09:58  9            A4G    0        DROPSOFF       FLY       1
02/JUL/1989 10:08  9            A4G    0        DROPSOFF       H'OPTERA  2
02/JUL/1989 10:12  9            A4G    0        DROPSOFF       H'OPTERA  4
02/JUL/1989 10:21  9            490    0        CIRCLES        0
02/JUL/1989 10:28  9            A4G    0        DROPSOFF       I         4
02/JUL/1989 10:55  RHMIDWIRE    330    0        CALLS          0
02/JUL/1989 11:01  RHMIDTREES   330    0        CALLS          0
02/JUL/1989 11:03  RHMIDTREES   330    A4G      10CM           0
02/JUL/1989 11:04  RHMIDTREES   330    490      OPENBILL       0
02/JUL/1989 11:05  RHMIDTREES   330    A4G,330  D'PLACED       0
02/JUL/1989 11:08  RHMIDTREES   330    A4G      ARRIVES        0
02/JUL/1989 11:09  RHMIDTREES   330    A4G      FLYOFF         0
02/JUL/1989 11:55  RHMIDTREES   330    490      CALLS;10CM     0
02/JUL/1989 11:56  RHMIDTREES   330    490      10CM           0
05/JUL/1989 10:34  9            A4G?   0        S              0
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APPENDIX 6: Recipe for Los Alamos Buffer

Ingredients:

100mM TRIS base (pH8)
100mM EDTA
10 mM NaCl
0.5% SDS

Directions:

Weigh ingredients and mix in a beaker. SDS is added in a weight/volume percentage, so 0.5% is 0.5g in 100ml. Then add about 90% destilled water and mixed until dissolved; heat if neccessary. Adjust pH to 8 with concentrated HCl or NaOH. Keep cool.