Nest Structure and Related Building Behaviour in the Rook
Corvus frugilegus L.

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DECLARATION

I declare that this thesis, composed by myself, has not been accepted in any previous application for a degree. All sources of reference have been duly acknowledged.

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SUMMARY

1. The functions of animal artefacts and their importance in ethological study are discussed. The prominent role of nest building in the breeding biology of birds is then reviewed, emphasising its influence on avian reproductive biology. The central aim of the study, namely to establish the cost of nest building is introduced and the reasons for choosing the rook as a model species are stated.

The natural history of the rook is briefly described and the approach to studying the cost of nest building in this species outlined. The Cheap and Expensive hypotheses which form the basic model for the study approach are defined and the chapter concludes with a plan of the thesis.

2. The design features of rook nests and building materials used were studied in order to examine the extent of variability in the size and proportions of the whole structure. In addition, comparative data on twig material from nests and the rookery floor were analysed, i) to establish the principal source of nesting material and ii) to test for the preference of certain types of twigs for use in nest building. The conclusion is that rook nests are all built to the same design of a platform of twigs with a central, lined cup. However, it is shown that nests exhibit considerable variation in their size and weight: reasons for this are proposed. There is shown to be a significant preference for twigs in the size category 40.1-50 cms., as well for larch and highly branched twigs. The reasons why these may be preferred building materials are discussed.

3. Fluctuations in the number of nests within five colonies were recorded over the annual cycle. Nest numbers increased dramatically between early March and early April at all sites and then declined in every month after May. It was noted that the proportion of nests lost from within the colony varied between sites. There is no evidence, based on changes in nest state, to suggest that nests are refurbished

outside the building and breeding seasons. These conclusions support the Cheap hypothesis.

Data from the major study site at Milton Farm, show a differential rate of nest loss within the three major nest-containing tree species. Furthermore, disproportionately high numbers of nests were recorded in some species and disproportionately low numbers in others. On this basis, it is suggested that there may be a preference for nesting in certain types of tree.

4. The autumn resurgence of sexual behaviour was studied to quantify the extent of refurbishment. Repairs to the nest structure outside the breeding season would be regarded as being supportive of the expensive view of nest building. No evidence was found to suggest that nests were repaired or built anew in the autumn period, and the data therefore substantiated the predictions of the cheap perspective.

   The two alternative hypotheses for autumn sexuality, namely as a period of courtship or nest site prospecting were investigated, though it did not prove possible to resolve between these adaptive explanations. Recommendations are made for further study on rook behaviour during this period to confirm the functions of these behaviours and establish their role in the species' breeding biology the following spring.

5. Studies conducted at Milton Farm in the spring were aimed at establishing the effect of variation in building behaviour on reproductive performance. Predictions from the Cheap/Expensive model were made with regard to nest reuse, mode of material assimilation and choice of nest site, to examine their effect on reproduction. After the 1988 breeding season, the lack of any evidence supporting nest refurbishment outside the spring season and the absence of an

observed effect of building upon reproduction were two major conclusions in support of the cheap view of building. However, the conspicuous and frequent theft of nesting material and the increasing attendance at the nest site in relation to laying date were two anomalies to a total adoption of the cheap view. This prompted an experiment to remove a large proportion of twigs from the woodland floor in the vicinity of the rookery prior to the 1989 building season. The intention was to increase competition for nesting material and consequently, the cost of building. An increased incidence of stealing, a lower peak in nest numbers within the colony and a significantly lower fledging rate were recorded in the experimental year compared to the previous year. In the light of such findings, the effect of the perturbation experiment in increasing the cost of nest building to the rook is discussed.

6. The empirical evidence from this study is reviewed with the general conclusion supporting a low cost to nest building. The suitability of the rook as a model system is reviewed before making suggestions for further research on this species.

Proposals are made by which to study the cost of nest building in other bird species, both in the field and the laboratory. It is argued that the cheap view of nest building proposed for the rook should not be considered universally applicable throughout the avian class since birds exhibit a great diversity both in nest architecture and building behaviour. The importance of nest construction as a component of an individual's overall reproductive costs, and its influence on avian life history strategies are discussed.

1. INTRODUCTION

1.1. Animal Architecture

1.1.1. The Ethological Interest of Animal Artefacts

Animal artefacts occupy a special place of interest in ethological study for whilst most behaviour is transient, building behaviour offers an opportunity for study through the examination of the structures left behind. This is not to say that animal artefacts are to be regarded as permanent, some are extremely ephemeral such as the capture net of the ogre-faced spider *Dinopis longipes.* Others persist over several generations, for example the dam and lodge of the beaver *Castor fiber,* and under exceptional circumstances the artefact may end up in conditions conducive to fossilisation and become all but permanent. Such an occurrence has been documented by Berry (1923) who describes a caddis larval case from the Miocene.

Artefacts not only contain a wealth of information on the biology of their constructors, inherent in the choice of building material, the mode of construction and the function of the structure, but may also influence the biology of the constructors themselves. This is no more clearly illustrated than in the theory that nest paper quality may be an influential factor in the evolution of coloniality and hence eusociality in the Hymenoptera (Hansell 1984, 1989). Hansell proposes that the limited social behaviour observed in the Stenogastrine wasps may be attributable to their inability to produce paper strong enough to support a large nest. Paper quality in turn, may reflect a morphological limitation, jaw size. Stenogastrines feed on minute arthropod prey and have no need of strong jaws for feeding. If one compares this group to a group of wasps exhibiting a high degree of social structure, the Polistines, one finds that the latter are in general, strong jawed and builders of large paper nests suspended from a petiole. Van der Vecht (1977) sees the petiole to be an important feature of nest defence, limiting access to predators and permitting the development of large colonies. The inability of Stenogastrines to construct such a petiole he argues, is a limitation on nest defence and hence colony size.

In the Vespid wasps, comparisons of nest quality within the family has provided information on a broad evolutionary question, namely the factors influencing the evolution of their social systems. I mentioned that the nest petiole may be an important design feature providing the nest with increased security, in other words, selection may favour nests attached to their substrate by a petiole. Such a statement may be contested for it may be argued that the paper nest is inanimate and does not by any means, reproduce. One cannot therefore speak of selection operating at the level of the structure itself. I have said that paper quality may reflect wasp jaw design and nobody would question that this morphological feature is under genetic control. Similarly, few would question that features of building behaviour are under genetic control and therefore heritable (Dilger 1962), although this behavioural expression may be at the end of a long chain of causal connections. Animal artefacts are the end product of one facet of an animal's behaviour, its building behaviour, and can therefore be regarded as the phenotypic expression of genes controlling that building behaviour. This viewpoint is lucidly expressed by Dawkins (1982), who advocates that animal artefacts can be regarded as 'extended phenotypic traits'. His argument simply states that genetic change may produce phenotypic novelty in the resulting structure via changes in building behaviour and this variation will be subject to the forces of natural selection. Selection is therefore operating on the builders through the effectiveness of their structures. For example, suppose a chance genetic mutation was in some way manifest in the production of an artefact more efficient at protecting its constructor; selection will favour those individuals exhibiting the more efficient design and the 'gene' or 'genes' for that design feature will spread through the population.

Von Frisch (1975) and Hansell (1984) have both published books attempting to collate and order the diffuse literature on building behaviour. Hansell in particular, has shown building behaviour provides a heuristic approach to many lines of ethological study including adaptation and phylogeny. Analysis of the structure and design of artefacts themselves can be equally informative as they often play a very important role in an animal's biology. For example, in cases where the structure built is even semi-permanent, there exists the opportunity for inter- as well as intra-specific comparison. Birds are particularly suitable for studying building behaviour since nests and related structures have a very major influence on their biology. This thesis concentrates on the adaptive function (in the sense defined by Tinbergen 1963) of nest design and nest building in the rook *Corvus frugilegus* L. By examining the observed variation in both nest structure and building behaviour, I hope to illustrate its influence on rook breeding biology and discover what features of building have the greatest effect on an individual's reproductive performance.

1.1.2. The Functions of Artefacts

The construction of artefacts is an extremely wide practice throughout the animal kingdom, apparent in 19 classes spread across 9 phyla. Construction ranges from the delicate lorica of silicon rods built by some of the Zoomastigophoran protozoa (Norris 1965), to the monolithic communal structures of the sociable weaverbird *Philetairus socius* (Maclean 1973). When one considers that a major class of builders is the insects, then it would be safe to assume that the majority of living species build in one form or the other.

Hansell (1984) divides the functions of artefacts into four general categories.

1) Protection from the physical environment.

2) Protection from predators.

3) Food gathering.

4) Communication.

These categories are by no means mutually exclusive and some structures undoubtedly fulfil more than one of the above functions however, in this section I shall review some of the empirical evidence which illustrates the functional significance of artefact design and suggest ways in which such features may have evolved to emphasise my point that animal artefacts are subject to natural selection.

Protection from the environment - There are obviously a great many different environmental factors against which an animal may wish to protect itself and these factors will partly depend on the animal's habitat. Generally speaking, animals utilise artefacts to effect some form of temperature or humidity regulation, occasionally this may extend to facilitating gas exchange and ventilation. The example I have chosen is one of the temperature regulation afforded by the nest structure of the western harvest mouse, *Reithrodontomys megalotis dychei,* of North America. This choice is based not entirely upon my personal admiration of rodents but also because small homeotherms, with their high surface area to volume ratio, are particularly vulnerable to the effects of heat loss. The nest of the western harvest mouse is suspended in vegetation above ground level. The structure is essentially a ball of intertwined leaf strands lined with downy material. Shump (1974) made recordings of grass and ambient air temperatures in the immediate vicinity of the nest. He found that where external temperatures varied by 10-11^{o}C, the corresponding variation within an empty nest is approximately 6^{o}C. The selection of downy material specifically used to line the interior indicates that the nest is being used as more than just mechanical protection and is adapted to the function of insulation. It is difficult to say whether the ancestral harvest mouse nest was initially to protect the animal and incidentally functioned to conserve heat or whether insulation was the primary function and protection secondary. Whichever is true, nest structure has clearly become refined to buffer the effects of large-scale temperature change and this is likely to be very important in helping a small mammal conserve energy and thus meet its energy demands.

Protection from predators - In the previous section I mentioned that a nest petiole may be a design feature of Polistine nests intended to restrict the access of predators. The avian habit of constructing nests above ground is also obviously to restrict access to predators, however additional structural features are often necessary to safeguard against those capable of reaching the nest structure. The nest of the weaverbird *Malimbus scutatus* is in the shape of a retort with the downward-pointing tube being made of loosely woven strands of rattan leaf. Crook (1963) believes this design to be effective in preventing access to the brood chamber by snakes. Hansell refers to Crook's paper in his book, pointing out that the spiral orientation of the leaf strands causes the tube to lengthen and narrow when the snake exerts external pressure. Attempts to climb on the outside of the tube therefore only serve to increase its length. Crook's evidence is largely qualitative but *Malimbus* does provide a good example of the manner in which structural design confers protection. By making comparisons from within the genus he also suggests how the nest spout could have evolved from a spoutless design and as a structural characteristic is, 'a product of selection for its survival value in the habitat concerned'.

Food Gathering - Design features have also been shown to enhance prey capture efficiency and thus be adaptive. Dawkins (1982) describes the web of a spider as being, "a huge extension of the effective catchment area of her predatory organs" and trapping is certainly a widely used predatory strategy. A recent study by Lucas (1989) on second and third instar larvae of the antlion *Myrmeleon crudelis*, has shown that both pitfall orientation and the behaviour of the antlion in the pit bottom, serve to increase prey capture efficiency. The conical pit is asymmetrical with the wall opposite the larvae having the steepest slope as well as the finest sand grains. Both these design features retard escape from the front wall since fine particles are not only more stable on steeper inclines than coarser grains, but are less stable under the load of struggling prey (Lucas 1982). The other walls at the side and behind the antlion are shallower, with comparatively larger sand grains but are the regions within the pit where the larva is most efficient at grabbing its prey.

Lucas does not address the question of how antlion pits may have evolved but his studies do show that pit design and the behaviour of the larva in the pit bottom are adapted to maximise prey capture efficiency. It is possible to conceive selection refining pit structure from an initial rudimentary depression to an asymmetrical cone with walls of differential stability purely because these features enhance the prey capture abilities of the constructor and hence the its survival.

Communication - Artefacts perform a communicative function in two ways; by aiding signal transmission or by acting as signals themselves. In a later section of this chapter, I shall review evidence of structures acting as signals to birds, but the example I quote here is concerned with signal transmission. Bennet-Clark (1970) demonstrated that the double-mouthed burrow of the male mole cricket, *Gryllotalpa vineae*, has a morphology which maximises the amplitude as well as directs the male's song. I mentioned earlier in this section that structures may perform more than one function and I suggest it highly likely that the mole cricket's burrow may also confer some degree of protection to the animal during periods of such blatant self-advertisement. Burrows may therefore have evolved for protection and then become modified to amplify male song.

The studies quoted above illustrate the highly evolved design features apparent in artefacts. Such adaptations must mean that artefacts are subject to the forces of natural selection in the same manner as is the morphology and behaviour that governs them.

1.1.3. Birds as Builders

Amongst the vertebrates, birds can be considered the major building class. In the fish, amphibians, reptiles and mammals there do exist competent and effective builders, however in these groups, building behaviour is the exception rather than the rule. Collias and Collias (1984) approximate the number of avian species to be 9,021 divided into 28 orders and 166 families all of which contain builders. The species within the larger families, the Muscicapidae (incl. thrushes, babblers, warblers and flycatchers - c.1,375 sp.) and the Emberizidae (incl. buntings and tanagers - c.553 sp.) (taken from Gruson 1976) are almost all nest constructors. If Collias and Collias' review (1984) of the prevalence of building behaviour within the class is correct, then it would appear that it is only a very small minority of species which do not undertake some form of building. The class exhibits a variety in artefact construction that parallels the variation in morphology within the group. Furthermore, adaptive features of structural design reflect the diversity of habitats in which birds live.

Birds have adopted nest building as their strategy for protecting the clutch and, in the case of nidicolous species, the young. Location as well as design are adapted to protect the progeny from predation as well as the environment. Collias and Collias (1984) provide a fairly comprehensive review of the existing variation in nest design within the class and the manner in which these designs fulfil specific functions. Such a review is beyond the scope of this thesis, the point I wish to make is that the overriding function of nests, to protect the bird's progeny, has necessitated that nest structure become an integral part of avian breeding biology. Nests or related structures play a role in every aspect of the reproductive cycle, from mating and courtship to egg protection and incubation as well as in the final rearing of the young. By quoting studies that have focused on the function of avian artefacts in the various stages of bird breeding biology, I hope also to illustrate the variation apparent in avian construction.

1.1.4. The Influence of Nest Structure on Reproduction

Courtship - In some cases, the role of the nest in brood protection becomes negligible and the nest site and accompanying building behaviour serve just to consolidate the pair bond. Nelson (1968) describes the "symbolic nest building" of the Blue-footed booby *Sula nebouxii*. The male presents the female with nesting material with a very deliberate and elegant sweep of his head. He then places the pebble or twig in the nest structure and both birds incorporate it into the nest. This building is 'symbolic' because the nest itself has nothing to do with holding the egg or young. On the Galapagos, female *S. nebouxii* lay their eggs on the bare ground utilising little or no nesting material. To the Blue-footed booby, the initial nest structure serves no protective function and serves purely as a means of strengthening the pair bond.

The use of an artefact to facilitate pair bond formation is best illustrated by the bower birds (Ptilonorynchidae). Bowers are special avian edifices, built by the male, purely to attract a mate. The structure plays absolutely no part in the incubation or protection of the progeny since this function is performed by a nest built by the female after mating. Diamond (1987, 1988) has recorded intraspecific variation in bower style and decoration and Borgia (1985) has empirically demonstrated a relationship between bower quality and female preference in *Ptilonorhynchus violaceus*. Gilliard (1963) proposed that the bower had superseded the function of decorative male plumage since in interspecific comparisons within the family, he noted a positive correlation between increasing ornateness of bowers and reduced colouration and decoration in male plumage.

Borgia's demonstration that bower quality influences female choice and hence leads to an increase in male reproductive success is significant for the bower's 'phenotype' becomes as important a selection criterion as red throats are to three spine sticklebacks *Gasterosteus aculeatus* (Semler 1971) or the eyespots on a peacock's tail (Petrie et al. in press). In the case of bowers, selection is seen to be operating at an architectural level just as it does the phenotypic. In addition, the reduction in the ornateness of male plumage in response to increased complexity serves as another illustration of the way in which artefacts exert an influence on the animal's overall biology.

Egg protection and incubation - I have already mentioned in section 1.1.2., the manner in which nest structure is adapted to protecting the clutch of *Malimbus scutatus*. A contrast in complexity is provided by the Adelie penguin *Pygoscelis adeliae*, in this species the simple pebble nest around the egg is protection not against predators, but against the threat of flooding after a thaw (Sladen 1958).

In the majority of birds, incubation of the eggs is effected by the body heat of the adult birds. The Megapodiidae of Australia are an exception and have evolved a mound structure to act as an incubator. The mallee or 'temperature' fowl, *Leipoa ocellata*, utilises first the metabolic heat of compost and then solar radiation to incubate its eggs. Frith (1957) demonstrated that the male exhibits stringent behavioural mechanisms to ensure that the brood chamber is maintained at 34^{o}C, the optimum temperature for egg development.

Rearing - The role of nests in protecting nidicolous young during development is obvious and is the function most commonly associated with nest structures. However I wish to end this section by quoting Baeyens' study (1981) of roofing enhancing brood survival in the magpie *Pica pica*. Baeyen recorded that 91% of roofed nests (n=61) fledged young whereas only 17% (n=18) of open nests did so. Further experiments showed this to be attributable to predation from carrion crows *Corvus corone corone*. This study is significant on two accounts; first it illustrates that intraspecific variation in nest design influences clutch survival and second it is an example from only a small body of literature which focuses on the role of nest structure on bird breeding performance.

Both nest location (Nilsson 1984, Jackson 1988) and material selection have been shown to effect reproduction either by reducing predation (Møller 1984, 1987), buffering detrimental climatic conditions (e.g. Calder 1971) or minimising ectoparasites within the nest structure (Clark and Mason 1987, Bucher 1988).

Potential constraints imposed upon reproduction by nest design has been documented by Snow (1978), who has suggested that reduction in nests size in tropical birds such as the tree swifts (*Hemiprocne*) and the white-bearded manakin, *Manacus manacus*, is an adaptation to reduce predation by making the nest less conspicuous. This may have had the evolutionary consequence of reducing nest cup volume and hence clutch size. The evolution of clutch size, he argues, 'cannot be fully understood without considering the dimensions and other physical properties of nests'.

Nest design and structure are undoubtedly influential in reproductive performance and though the various aspects of building have been researched, no single study has considered all aspects of building behaviour namely, nest location, material selection and timing of building on the breeding performance of a single species. This project addresses all these questions to the building biology of the rook in an attempt to understand what features are most influential in an individual's reproductive performance.

1.1.5. The Trade-Off Approach

Early ethological studies emphasised the 'survival value' of morphology and behaviour. In more recent times however, the emphasis has shifted, realising the importance of both 'costs' and 'benefits' in the evolution of adaptive features. This concept is clearly illustrated by Fisher's (1930) description of balancing selection pressures affecting male secondary sexual characters. Phenotypic traits such as the length of a peacock's tail can be regarded as the compromise between sexual and natural selection. What is a benefit in increased attraction to females may be a cost in greater conspicuousness to predators. However costs need not be measured purely in terms of differential survival and reproductive success, a cost/benefit appraisal is equally applicable to temporal or energetic studies. Such an approach can and has been applied to nest building in birds. Weeks (1978) suggested there to be a reproductive advantage to the Eastern Phoebe, *Sayornis phoebe*, in reusing old nests compared to building nests anew. He concluded that building a new structure entails a significant drain on physiological resources as manifest in a reduced clutch size. Just as Weeks proposes a benefit to reusing old nests, Brown and Brown (1986) demonstrated that cliff swallows, *Hirundo pyrrhonota* assess the parasite burden in their mud nests and either reuse old nests or build anew depending on the level of infestation. In an extremely elegant experimental manipulation, they fumigated the nests of part of the colony, ridding the brood of its major ectoparasite the swallowbug, *Oeciacus oeciacus* (Fam.Cimicidae). Elimination of this bug significantly increased the body mass and survival of the fumigated broods compared to the untreated controls. The decision as to whether or not to reuse an old nest is therefore dependent on an assessment of the severity of cost in relation to potential benefits.

In adopting a cost/benefit (or trade off) approach in the analysis of building behaviour in the rook, I shall use the observed variation in nest structure and building behaviour to attempt to understand what factors of building behaviour contribute or detract most from breeding performance. The emphasis of this section has been to advocate the importance of animal artefacts to ethologists and evolutionary biologists as well as giving a few examples of the way in which avian structures perform their respective functions. Biological research begins with an understanding of the animal's natural history and I continue with this background information before further elaborating on my study objectives.

1.2 The Rook and Its Suitability as a Study Animal

1.2.1 The Literature.

'A Gentleman had returned from a distant climate to Trelawny, in a very imperfect state of health; in which it became necessary to prescribe for him a sort and degree of occupation which should lay him under constant attention, without inconvenience or anxiety. He was required to observe the actions and habits of the Rooks through the varying months of the year'.

So read the medical advice of Jonathan Couch physician to Lewis Harding who had returned from Australia suffering from an undiagnosed chronic malaise. Coombs (1978) believes Harding's resulting volume, written between 1847-8 though unfortunately never published, to perhaps be the first intensive study of a single species. Through personal experience, I am not entirely sure I could agree with Dr Couch's assessment of such a study being 'without inconvenience or anxiety' but maybe as a cure the prescription was vindicated for Lewis Harding died in 1893 at the age of 87.

Rooks featured in bucolic folklore long before Harding began his chronicle. This reflects the long and close association that the species has had with man and his agriculture. In more recent times, a great deal has been published on rook biology. Earlier work concentrated on the bird's basic natural history, (Burkitt 1936, Lockie 1955 & 1956, Marshall and Coombs 1957, Coombs 1960 & 1978, Swingland 1976 & 1978). During the late sixties and early seventies, Ian Patterson and co-workers at Aberdeen University published a series of papers in the Journal of Applied Ecology covering several aspects of rook ecology in north-east Scotland including; feeding ecology, dispersion, the recruitment and distribution of young in the population, juvenile mortality and perhaps of greatest applied importance, food intake and feeding behaviour.

The extent of damage done by rooks on freshly sown cereal crops was examined by Dunnet and Patterson (1968) and later by Feare (1974 & 1978). Dunnet and Patterson calculated an 'index of utilisation' for several potential agricultural food sources; grass, braird (sprouting grain), ploughed land, sown land, stubble, root crops and stock food. The results of their index showed the major impact to be on sown grain during April and May with a high percentage of birds feeding on stubble in the autumn months between September and November. My own communications with farmers in the Strathclyde region have shown that such autumnal damage is opportunistic. When fields have been partially flattened by storms, rooks are able to settle and feed on the ripening grain prior to harvesting. Feare (1974) supports the earlier work of Dunnet and Patterson and adds that the major spring damage is done to oat crops. He also points out that the presence of rooks on agricultural land may not be entirely destructive and that the birds may have a beneficial effect. Feare et al. (1974) and Coombs (1978) stress the importance of Tipulid larvae in the rook diet. The larva of *Tipula palidosa* are agricultural pests, feeding on the roots of cereal crops. Rooks feed communally, often in large numbers at high densities, this may significantly reduce the Tipulid population in the feeding area reducing crop damage and yield loss. Samorodov (1956) claimed that between 60-90% of the insects taken by rooks in Russia were agricultural pests.

Røskaft and co-workers at the University of Trodenheim in Norway have, in the last decade, published a great deal of work on the breeding behaviour of rooks and the exact references will be cited at the appropriate points throughout this thesis. Prior to their work, Owen (1959), Coleman (1972) and Richards (1976) all published work on rook breeding biology. However a notable omission from this field of research is any investigation into the influence of nest structure and building behaviour on reproductive success. I am therefore in the fortunate position of having at my disposal, a great deal of information on rook breeding biology and behaviour. The rook is proven to be an animal amenable to study and there is a body of information contained in the literature available for reference. The direction of this research will serve to fill the existing gap on the influence of nest structure and building behaviour on the reproductive performance of the rook.

1.2.2 Natural History

Distribution and Prevalence.

The rook's ability to capitalise on man's agricultural practices means it is found throughout much of Europe and western Asia. In the far east, *Corvus frugilegus* is replaced by its subspecies, *C.f.dastinator*, which has a partly feathered face and feathered chin. The northern part of the Iberian Peninsula, Italy and the mountainous areas of central Europe, are the only areas in the European continent devoid of rooks. To the north, the species occurs as far as central Norway. At this northern limit, birds fly south to avoid the Scandinavian winter where snow cover inhibits feeding. Rooks are a familiar sight around agricultural land throughout the British Isles, reaching very high densities on the west coast and in north-east Scotland. This is attributable to the fact that there are relatively large amounts of grain available over the winter, and spring sowings coincide with the breeding season ensuring a plentiful supply of food to chicks (Feare et al. 1974). The British Trust for Ornithology's 'Atlas of Wintering Birds in Britain & Ireland' records the presence of rooks in 83% of their 10km square quadrats, the breeding distribution being almost identical. The number of rooks in the inner Clyde area, which is the region incorporating the study sites of this project, has been estimated at 148,900 (Clyde Birds 1988). This is a density of approximately 11 pairs per km^2. In Renfrewshire alone, the district containing my main study site (see Section 2.2.1), calculations made from the above report estimate rook density to be at approximately 6 pairs per km^2. Such high densities mean that the lowland areas in and around Glasgow are an excellent place to study this species.

Annual Cycle

In order to understand the sequence of events in the rook building and breeding cycle, I shall briefly review the species' annual cycle beginning with the onset of building in early March. This is roughly two weeks later than the commencement of building in the south of England, a fact attributable to the milder spring conditions prevalent in the south at that time of year Coombs (1978 p.96).

Early March - Early/Mid April. This is the building period for the majority of pairs in the colony with a noticeable period of peak building activity in late March. New nests have been noted as late as early June.

Early/Mid April - Early/Mid May. Incubation period lasting approximately 30 days.

Early/Mid May - Early/Mid June. Brood rearing lasting approximately 28 days between the date of hatching and fledging. The majority of chicks having left the nest by the second week in June.

Early/Mid June - Mid/Late Sept. The post-breeding summer period. Fledglings are seen feeding in fields with adults and may continue to be fed by adults until six weeks after fledging. During this period, East (1986) noted a significant difference in the duration of feeding periods of adults compared to juveniles, with adults feeding for shorter intervals. He also noticed a difference in the allocation of time devoted to vigilance between the two classes. East concluded that adults feed more efficiently than juveniles and meet their dietary requirements quicker allowing them more time to devote to vigilance.

Late Sept. - Early Dec. An observed resurgence of sexual activity is seen in adult birds. In subsequent chapters I will refer to this as either the period of secondary or autumn sexual activity. This resurgence is characterised by the conspicuous attendance at the nest site by adult birds after a three month absence, the observed manipulation of nesting material, an increased rate of display in the rookery and the more frequent occurrence of ‘pursuit flights’ (Coombs 1960), an aerial form of display described by Burkitt (1935) as ‘mating flights’. In mid October the breeding colony moves to a communal winter roost and visits to the breeding rookery are mainly confined to dawn and dusk.

Mid Dec. - Late Feb. A quiescence in terms of sexual behaviour after the resurgence of sexual activity during the autumn and before the primary sexual period beginning in March.

1.2.3 The Reasons for Choosing Rooks as the Study Animal.

The decision to study nest building behaviour in rooks can be attributed to three main factors.

1) As mentioned in the previous section, the bird is present at high densities in the west of Scotland. This means that there is no problem locating your study animal as well as finding suitable study sites. This may seem a rudimentary point, applicable to all field-based biological research, but in a three year study with only three breeding seasons in which to collect information, an early decision on study site and rapid familiarity with study species are two great practical advantages.

2) Rooks are colonial nesters. Comparisons in building and breeding effort can be made between pairs within a single colony without having to take into consideration potential confounding variables such as local availability of nesting material, differences in food availability and even variation in local geography and climate. The influence of such factors on pairs that are geographically separated may cause a difference in reproductive performance but in a single rookery, these factors are negligible.

3) At the outset of the study it was clear that there were many aspects of rook nest building behaviour that were of potential ethological interest. The nests themselves are large structures, reportedly used perennially by the same birds (Coombs 1978). This implied that they were a relatively 'expensive' resource, a view supported by anecdotal reports of rooks building or renovating the nest structure in the autumn (Parfitt 1876, Morley 1943) and stealing nest material in the spring (Ogilvie 1951). Such observations point to there being a substantial 'cost' to nest production and by the extended phenotype perspective, selection would be expected to favour individuals most 'cost efficient' in their architecture and nest construction.

1.3. Outline of Study Objectives and an Introduction to the 'Cheap/Expensive' Paradigm.

1.3.1. Study Aims

As I briefly mentioned in section 1.1.5., I shall adopt a 'trade-off' approach to assess the biological cost of nest building to the rook. The measures of cost used in this study are the potential temporal or reproductive penalties incurred due to factors such as having to build an entirely new nest, competing for nesting material and safeguarding against material being stolen by conspecifics. If bird nests are 'extended phenotypic traits', selection will favour those individuals that minimise any cost of nest building or alternatively maximise beneficial aspects so as to increase their reproductive potential. There may be certain aspects of building behaviour that directly or indirectly enhance an individual's reproductive success for example, the refurbishment of the nest structure during the autumn, the selection of certain types of nesting material and maximal efficiency in the method of nest material assimilation during the spring. Any measure of cost may therefore be assessed by attempting to correlate observed variation in nest construction and building behaviour with variation in reproductive performance.

1.3.2. The Cheap/Expensive Paradigm

I have outlined the theoretical basis of the project, however in order to generate testable hypotheses it is necessary to have a more robust conceptual framework. My approach is to assess the biological cost of nest building in terms of two opposing hypotheses termed the Cheap and Expensive hypotheses. As the names suggest, these polarised perspectives represent the extremes of my cost assessment and are defined as follows:

CHEAP HYPOTHESIS- States that nests are a readily replaceable commodity. Their construction entails minimal energetic and temporal investment with the result that the effect on reproduction is minor.

EXPENSIVE HYPOTHESIS- States that nests are a valuable commodity. They are large and potentially time-consuming structures to build requiring substantial energetic investment from their constructors.

These two perspectives permit predictions to be made in various aspects of rook building behaviour during both the spring and the autumn. In addition, the pattern of appearance and disappearance of nests within the colony during the annual cycle can be interpreted within the paradigm since the extent of nest loss may be indicative of maintenance outside the breeding season. The predictions generated under each hypothesis will be detailed in the relevant chapters.

1.3.3 Thesis Plan

This study divides into two parts; the first deals with the nest structure itself and the second with building behaviour. The theoretical starting point for this study is a quantitative examination of the existing variation in nest structure, in terms of both morphometrics and the choice of constituent materials. It is only by gaining an appreciation of the inherent variability in both nest structure and building behaviour that an attempt can be made to correlate such variation with variable reproductive performance.

Chapter two outlines the method employed in the analysis of nest structure and details the approach used to answer fundamental questions about nest construction namely; i) where is the majority of nesting material collected from and ii) is there any evidence to suggest a preference for certain types of nesting material? Chapter three concludes the section on nest structure and details the changing pattern of nest numbers within a rookery over the year. As stated in 1.3.2., the pattern of nest change is indicative of the level of nest maintenance practised over the annual cycle.

The second part begins at chapter four which is an introduction to rook nest building behaviour. It outlines the facets of behaviour under study and makes the distinction between the spring and autumn field seasons. It describes the materials and methods used in the behavioural studies since these were common to the spring and autumn periods. Chapter five presents the data and results on my investigation of the adaptive function of autumn sexuality, attempting to discern which of the three proposed functions namely nest refurbishment, nest site selection or pair bond formation, is the principle objective of the birds in that season. Chapter six presents the data and results of the effect of observed variations in building behaviour on reproductive performance during the spring. It examines issues such as the adaptive function of stealing, its effect on the timing of reproduction, the effect of choice of nest site on reproduction as well as the possibility of new nests incurring a reproductive penalty compared to the use of old. The concluding chapter is the general discussion evaluating the results of the previous chapters. It attempts to answer at what point along the Cheap/Expensive continuum lies the true biological cost of nest building for the rook and addresses the general question of just how influential is nest building on the breeding biology of birds.

2. NEST STRUCTURE

2.1. Introduction

2.1.1. Outline of the Approach to Studying Adaptive Design

If nests are regarded as extended phenotypic traits then they will be subject to the forces of natural selection. One would therefore expect there to be adaptive features manifest in nest construction and in the selection of building material. If there is indeed a 'best' way to build a nest, then it might be expected that rooks will exhibit a conformity of nest design resulting from stabilising selection constraining variation in nest size, nest shape and the selection of building materials.

This chapter aims to investigate the design features that characterise a rook's nest, in order to determine just how stringent are the pressures constraining nest design. The study starts by looking at the size of nests and the nature of selected components of nest structures to show the extent of variation that exists in dimensions and in constituent materials. It then goes on to investigate evidence for selectivity in the choice of building materials since the characteristics of a preferred material type may act as an indicator of the design features important to the bird. The data presented will therefore address the following questions.

1) From measurements of intact nest structures, is there any evidence of consistency in size and weight?

2) Is there any uniformity in the type of materials used in nest construction and in the proportions in which they occur?

3) From the identification of constituent materials, can any inference be made as to the locations from which nesting material is collected.

4) Is there any evidence that birds are exerting a preference in the selection of nesting material?

Before dealing with my methodology and approach to these questions, I will briefly describe the mode of nest construction by a rook based on my own observations made at canopy level in the breeding seasons of 1987-89. An appreciation of the sequence of events involved in building will clarify the rationale behind my method of nest analysis. Such a description will also form the basis of a later discussion on nest design.

2.1.2. Nest Construction

The construction of a new nest can be discerned as occurring in three stages which are:

1) The formation of a nest platform.
2) The building up of the perimeter to form a raised outer ring with a central depression to act as a nest cup.
3) The lining of the cup interior with mud and insulatory materials.

The initial nest platform is formed by laying twigs in the fork of two or more branches. Where twigs are not actively wedged into place they remain in position only by being balanced in the crotch. Additional twigs are then piled on top or systematically pushed, threaded and lodged into place. The platform will gain in integrity with the addition of material since the 'foundation' twigs will be held in place by the weight of twigs above, and through the effects of a greater frictional resistance afforded by twigs wedged against one another and against the supporting branches.

The second stage of building involves the construction of the outer ring. This is normally achieved by a single bird standing on the platform and building up the perimeter by adding twigs to the platform circumference. The integrity of the outer ring, like that of the initial platform, can be attributed to the same frictional forces acting between twigs. Rooks manipulate collected material using their bills although twigs are occasionally held in the claws when the bird is perched. Its narrow and powerful bill, normally used to probe the topsoil for invertebrates when feeding, serves equally well to thread and lodge twigs, held in the beak tip, into gaps present in the structure.

As the outer ring is built up, it leaves a central depression to form the nest cup. The final stage of building is the preparation of the cup for laying. Mud, grass and other vegetation is added to the interior of the cup to fill existing gaps in the twig meshwork. The final interior lining is comprised of materials that would appear to serve as insulation for the clutch and young brood. My checks of nests to record reproductive data have shown that leaves, grass, feathers, strands of baling twine, bits of fleece and even paper are commonly used as insulatory material. During the addition of this final lining, the female is continually observed to mould the cup shape with her breast. This moulding is presumably to sculpt the nest cup to the female's shape thereby increasing the efficiency of incubation.

The next section begins with a brief description of the site and exact location from which nests were collected. It continues with a description of the methodology employed to quantify the constituent materials and concludes by detailing the approach to testing for selectivity in the choice of nesting material.

2.2 Materials and Methods

2.2.1. Study Site

All nests analysed were collected from a single rookery located at Milton Farm, nr. Kilmacolm, Renfrewshire (OS map. ref. 350/687). The rookery is denoted by the circled area in figure 2.1 which also details the surrounding geography. Milton Farm was also the major study site at which a hide at canopy level was used to observe nest building behaviour and collect behavioural data. The reasons for choosing this site as the behavioural study rookery are detailed in section 4.3.1. The colony size varied between 350-390 breeding pairs and was situated in a mixed species wood occupying an area of approximately 1.28 hectares. Surrounding land was used predominantly for grazing sheep and cattle though there was a sileage field immediately to the south of the rookery and a barley field approximately 0.5km to the east. This combination of pasture-land and cereal field provide an ideal feeding habitat for the colony.

A total of eight nests were removed from the rookery for analysis. Of these, six were collected from within the tree canopy whilst the remaining two were nests that had recently fallen to the rookery floor. Of these two 'windfalls', one was brought down in the bough of a large elm broken from the main trunk in a storm. The nest was still lodged in its fork and was removed undamaged. The second of the fallen nests came from a Scots pine. Though still intact at the bottom of the tree, the structure was greatly loosened by the fall and disintegrated during collection. All the nesting material was collected although it was not possible to subsequently measure parameters of the whole structure.

When nests were taken from their location in the tree canopy, care was taken to gather all material that fell to the ground while the nest was being removed and lowered. This was to minimise the amount of material lost during collection. Further details on the method used in the selection of nests for analysis are given in Appendix 3.

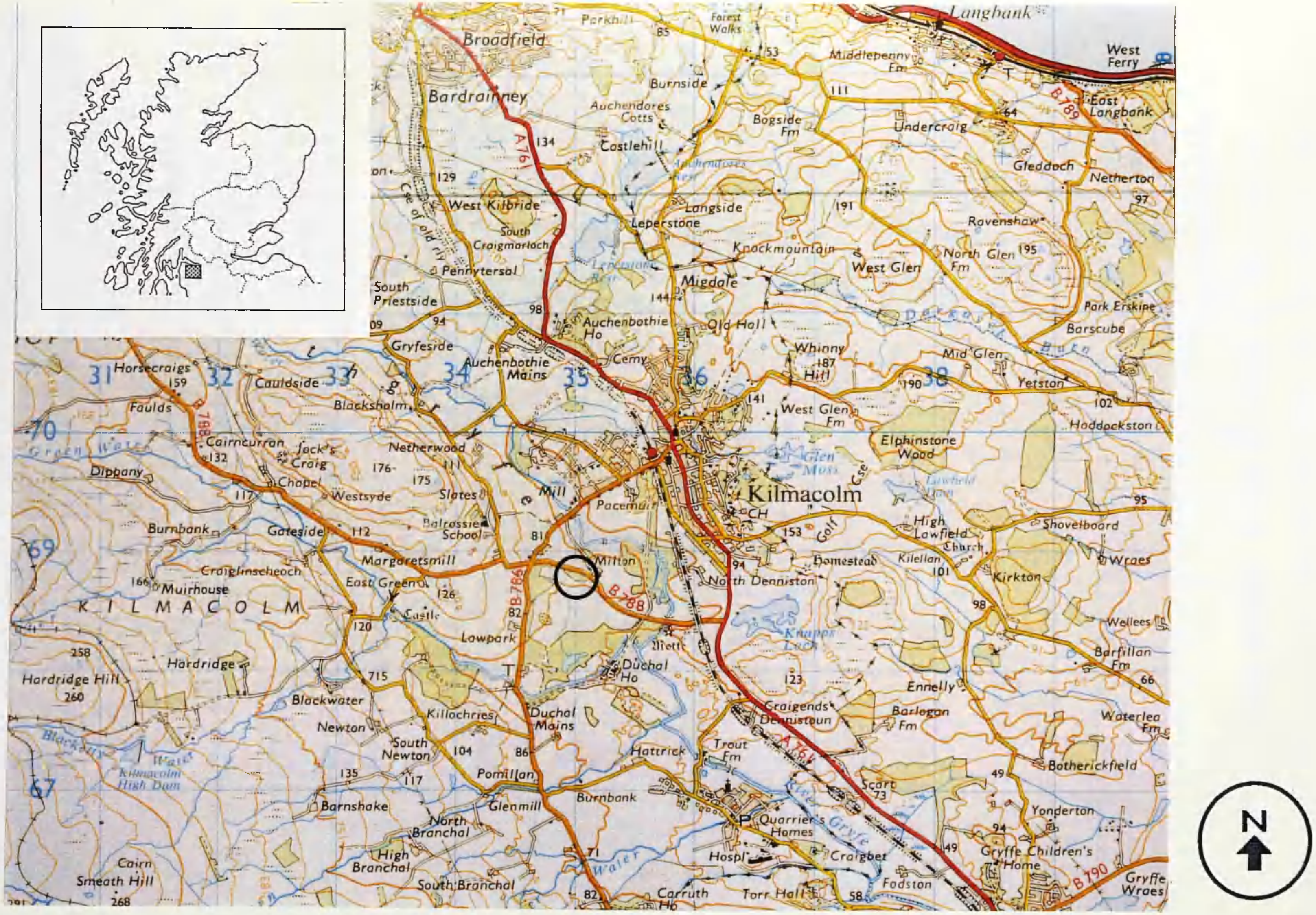
2.2.2. Quantification of nest structure

1) Estimating Nest Size

In order to investigate the design features important in the construction of a rook's nest, it was necessary to have a method of a) recording parameters of entire nest structures and b) have a system by which to quantify the component materials. A

Figure 2.1 The location of the main study rookery (denoted by the circled area) at Milton Farm nr. Kilmacolm. The hatched area of the inset approximates to the detailed map shown.

Scale; 2 cm. = 1 km.


Kilmacolm
KILMACOLM
Langbank
West Ferry
East Langbank
Broadfield
Bardrainney
Parkhill
Forest Walks
Middlepenny Fm
Burnside
Auchendores Cotts
Bogside Fm
Undercraig
Castlehill
Gleddoch
Netherton
West Kilbride
South Craigmarloch
Langside
Leperstone
Ravenshaw
Knockmountain
West Glen
North Glen Fm
Pennytersal
South Priestside
Migdale
Park Erskine
Barscube
Auchenbothie Ho
Old Hall
Whinny Hill
Mid Glen
Yetston
Gryfeside
Auchenbothie Mains
Cemy
Horsecraigs
Cauldside
Blacksholm
Faulds
West Glen Fm
Haddockston
Elphinstone Wood
Glen Moss
Cairncurran
Jack's Craig
Netherwood
Dippany
Chapel
Westsyde
Slates
Mill
Pacemuir
CH
Golf Cse
High Lawfield
Church
Shovelboard
Burnbank
Gateside
Balrossie School
Craiginscheoch
Margaretsmill
Milton
Homestead
Kilellan
Kirkton
Wraes
Muirhouse
East Green
Castle
North Denniston
Knapps Loch
Wellees
Lowpark
Duchal Ho
Barfillan Fm
Hardridge
Hardridge Hill
Blackwater
Ennelly
Killochries
Duchal Mains
Craigends
Denniston
Barlogan Fm
Waterlea Fm
Newton
South Newton
Hattrick
Trout Fm
Blackety Water
Kilmacolm High Dam
Pomillan
Burnbank
Bothericksfield
Scart
Barnshake
Glenmill
Quarrier's Homes
Yonderton
North Branchal
High Branchal
South Branchal
River Gryfe
Gryfe Water
Hospl
Craigbet
Gryffe Children's Home
Cairn
Smeath Hill
Carruth Ho
Torr Hall
Fodston
Gryffe Wraes
A761
B789
B788
B786
B790
31
32
33
34
35
36
38
70
69
67
N

uniformity of some construction feature may itself be indicative of an adaptation in response to selection pressure. By identifying features common to nest construction within the species, it may be possible to gain an understanding of the selection pressures governing nest design.

To establish how much variation is apparent in the size and shape of complete nests, measurements were made of intact structures. Their irregularity and pliability meant that only a limited number of parameters could be measured objectively and with a degree of accuracy. These were as follows:

1) Outer Ring:- Circumference, Length, Width
2) Nest Cup :- Circumference, Length, Width, Depth (where possible)
3) Nest Cup Dry Weight
4) Total Nest Dry Weight: - Calculated by summing the dry weights of nest cup material and the twigs from the outer ring
5) Total Number of Twigs in Outer Ring

Measurements of the outer ring and nest cup were made using a length of string to obtain the desired parameter. In the case of the outer circumference, the string was wrapped around the main body of the nests which was easily identifiable. This means that the ends of twigs which protruded out of the tight-knit structure did not influence the measurement. The obtained length was then aligned to a metre rule in order to convert the length to centimetres. To minimise inaccuracies of measurement, each variable was measured five times and the mean value taken as the final of representation of each parameter.

Measurements of nest cup depth were not always possible because some of the nests had had the cup flattened since incubation. The former position of the cup was however, still discernible as an area of mud in the centre of the twig outer ring. Total dry nest weight and total twig numbers were calculated for each of the eight nests analysed.

The initial stage of quantifying structure was to separate the nest cup from the outer ring. The cup remained a discrete structure with the mud binding the fine twigs, vegetation and lining material. This was dried under a Tullgren funnel and weighed. During the sorting and identification of the outer ring, the component twigs were weighed and counted. The total dry weight of the nests can be calculated by adding together the weights of the outer ring and nest cup.

The results of measurements made on intact structures are shown in section 2.3.1.

2) The Type and Proportion of Materials in the Outer Ring

In order to quantify the materials used in construction of the outer ring and examine the proportions in which they occurred, the twigs were sorted three times; first into pre-defined size classes, and then within each size class into their tree species of origin and finally, still within their size classes, into categories dependent on the number of forks they possessed. A full description of the method of assigning twigs into categories within the size, species and forking criteria will follow shortly, however, I think that I must first briefly explain why the above criteria were selected as being potentially important design features of nesting material.

Size - Twigs of a critical length and thickness may be important to provide the nest with a degree of strength and rigidity. As building proceeds, there may be a shift in preferred twig size from large twigs for support to finer ones that are more pliable and easier to manipulate into the outer ring. A quantification of the size distribution of the twigs incorporated into the nest may provide an insight into the structural requirements for a certain proportion of large twigs for support and for finer twigs for manipulating into the outer ring.

Species - Twigs may also differ in their architectural properties depending upon the species of tree from which they originated. Twigs from different species may therefore fulfil different structural roles, for example larch, *Larix decidua*, by virtue of the fact that it possesses numerous spur-like shoots along its length, may provide a greater opportunity for frictional cohesion between twigs. Alternatively silver birch, *Betula pendula*, possesses fine, pliable twigs that may be particularly suitable for forming the tight, concentric nest cup. It is therefore possible that there may be preferential selection for twigs of certain species dependent upon their physical properties.

Degree of Branching - The rationale behind quantifying the degree of forking in selected twig material is based on an initial premise that if adult birds were exerting some element of choice in the selection of nesting material, they might select twigs with greater cohesive properties. Forked twigs may interlock better with adjacent twigs and provide the nest with greater integrity and strength.

Quantification of twig type into categories within the three selected criteria, namely size, species and degree of branching, is a useful means of determining the design features involved in the selection of twig material. A consistently high proportion of twigs of a given category may be indicative of a selection for twigs exhibiting that character. My approach to testing for the exertion of choice in the selection of certain twig types is to make a comparison between the proportion of the identified categories occurring within nests with the proportional occurrence of the same categories on the rookery floor. The proportion of each size, species or forking category recorded on the rookery floor is assumed to reflect the level of twig availability. To clarify my point I shall phrase the rationale as a null hypothesis where H_0 states that if no preferential selection for twig types exists, then the proportion of each twig category observed in the nests will not differ significantly to the proportional occurrence of the same category on the rookery floor. In other words, the type of twigs used in building would simply be a direct reflection of the twigs available.

I shall continue by describing the method used to sort and quantify the twigs of the outer ring. The same method was used for quantifying the proportions of each twig category in the nests as for samples taken from the rookery floor. Finally, I shall describe a 'choice' experiment to directly test for the selection of twigs of a certain size.

Size - The length of each twig was measured in centimetres and assigned to one of the following size categories; 0-10, 10.1-20, 20.1-30, 30.1-40, 40.1-50 and >50cms. The number and weight of twigs in each size class was recorded. Twigs in the smallest category (0-10 cms.) were excluded from subsequent analysis because I had never observed rooks to bring such small twigs to the nest during building. This size category comprised a very small percentage of both total twig numbers and total nest dry weight, suggesting that they were probably fragments broken off larger twigs prior to collection or during the handling and transportation of the nest.

By obtaining a size profile of twigs incorporated into the nest it was possible to discover which size class of twig was most abundant both in terms of weight and number. By comparing the size distribution of twigs in the nest with the distribution of twigs on the rookery floor (see section 2.2.3.) it would be possible to test for a preference for twigs of a certain length.

Species - Once sorted into size classes, each twig was identified according to the species of tree from which it originated. This was done with the aid of identification guides and keys (A.Mitchell 1974, Prime & Deacock 1935, Phillips 1978, Rushforth 1980) and reference to the herbarium at the Botany Department of Glasgow University. Some twigs were in an advanced state of decay or were utterly devoid of bark or buds to act as distinguishing characteristics. These, along with species represented only in very small numbers (less than 5) were classed as 'miscellaneous'. The number and weight of twigs of each species in each of the six size classes (0-10, 10.1-20 cm. etc.), was recorded for the eight nests.

This species profile not only provides information on the frequency with which twigs of various species occurred in the nest structure but when correlated to twig availability (see section 2.2.3.) would provide evidence for choice being exerted in the selection of certain twig species as nesting material.

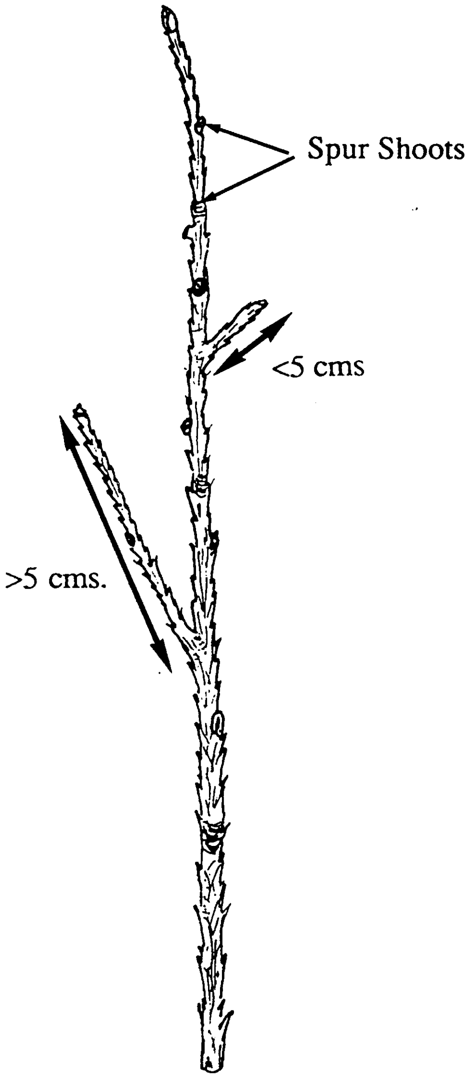
Degree of Branching - The twigs of the outer ring were sorted for a third time according the number of forks each twig possessed. A standard method was used to record the number of forks present on each twig. According to this method, both protrubrances after the divide had to exceed 5 cms. for a fork to be recorded. The choice of this figure was arbitrary but a standardised procedure was necessary in order to make comparisons a) between nests and b) with twig availability. The twigs were then assigned to categories within each size class, according to whether they possessed 0, 1, 2, 3, 4 or >4 forks. The weight and number of twigs in each of these categories was recorded.

As with the other two criteria, a comparison can be made with the twig material available to test for a disproportionately high incidence of forked twigs occurring within the nest structure. Figure 2.2 shows a larch and sycamore twig, illustrating how each was categorised a) according to size, b) according to species and c) according to the number of forks it possessed.

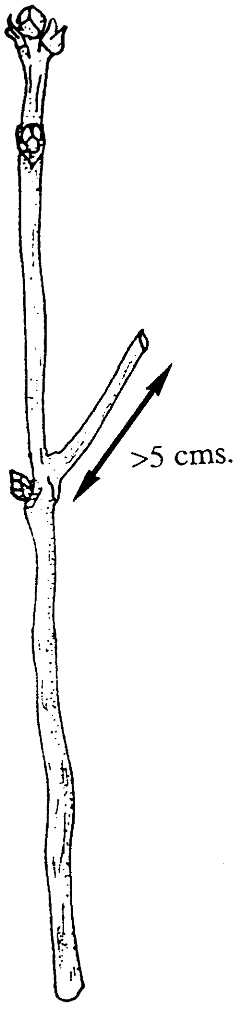
All twig weights were made using an Ohaus 700 series triple beam balance. This had a capacity of 2610g with a sensitivity of 0.1g.

The results and analysis of outer ring composition are detailed in section 2.3.

Figure 2.2 An illustration of the method used to categorise twigs of the outer ring. Both twigs fall into the size category 40-50 cms. The spur shoots on the twig on the left are characteristic of larch (*L.decidua*) and the scaled, ovoid buds of the twig on the right, indicate it to be from a sycamore (*A.pseudoplatanus*). Both twigs have one fork; the second protrubrance on the larch is < 5 cms. and is not therefore scored.



Larch
Larix decidua



Sycamore
Acer pseudoplatanus

3 cm.

2.2.3. Quantification of Twig Availability - Sampling the Rookery Floor

In order to test for an element of choice in the selection of twig material, it is necessary to estimate the relative availability of each twig category on the rookery floor. A disproportionately high frequency of any one category in the nests, may be indicative of preferential selection. This section details the methodology employed to determine the relative availability of twig categories by sampling the proportion of each category that occurs in $1m^2$ quadrat samples taken from the rookery floor.

The area of the rookery from which the nests were collected could be encompassed by a rectangle running the width of the rookery, east to west. This rectangle measured approximately 50x150 metres. This area was then subdivided into five 10x150 metre strips. Within each strip, four $1m^2$ quadrat samples were thrown onto the rookery floor at approximately 30m intervals. A total of 21 quadrat samples of the area were made just prior to the building season during late February and early March; fourteen of these were done in 1988 and the other seven in 1989.

Once the quadrat had been thrown, it was emptied of all twigs greater than 10cms, twigs partially enclosed in the sample area were included if more than half their length lay within the quadrat and were excluded if it did not. The twigs were then sorted in exactly the same manner as twigs from the nest outer ring, first into size class and then within each size class, into species and degree of branching. Testing for the existence of choice in the selection of nesting material by adult rooks is therefore based on a comparison between the proportion of twigs in each of the defined categories present on the rookery floor, with the proportion of twigs in the same categories, occurring in the eight nests analysed. The results of this quadrat sampling are summarised in section 2.3.

2.2.4 Ground Experiment

In addition to comparing twig availability with observed proportional occurrence in nests, a second method was employed to examine the question of whether there exists a preferential selection for twigs of a certain size. An experiment was conducted to test for a preference in the selection of twigs of a particular size category by adult birds. This involved setting up a simple choice experiment on the rookery floor. The experiment was conducted between March and May 1988. Inspection of the data on the size categories most common in the nest structure showed the three most prevalent classes to be 20.1-30, 30.1-40, 40.1-50cms. The total number of twigs in these size classes comprised approximately 68% of the outer ring. The aim of the experiment was to investigate directly whether or not there was a preferential selection for one of these three size classes. If choice is being exerted in the selection of twigs of certain sizes, then one would predict that the favoured size class within the quadrat would be over represented in the nest structure.

A $3m^2$ patch of rookery floor was raked clear of vegetation and debris. This was subdivided into 1m strips giving three strips of 3x1m. In each strip, 30 unforked larch twigs of each of the three size categories were arranged parallel to one another along the length of the 3x1m strip. By choosing the same species without forks, any confounding effect due to preference for species or forking is eliminated. Larch was chosen because it is easily identifiable and collectible. By laying twigs in an ordered line it was hoped to make any one twig as obvious as any other as well as perhaps providing an indication of the presence of birds in the quadrat due to a disruption of the ordering. The numbers of twigs present in each strip were checked at daily intervals and any losses replaced so that 30 twigs of each category were always present within the strip immediately after checking.

The 3x1m strip occupied by each size category within the quadrat was changed every alternate day to eliminate a positional effect influencing twig choice. The experiment was run twice at different times during the breeding season, these are described below.

Period 1 - The Experimental Period

This period ran from 18/3/88 to 12/4/88 and coincided with peak building activity.

Period 2 - The Control Period

This period was from 4/5/88 to 18/5/88 when building in the rookery had ceased. This period was aimed at assessing possible losses from the quadrat by factors other than the removal by rooks, for example by wind action or the activities of grazing sheep.

Section 2.3.4. presents the results of the losses of twigs in each size category during both periods 1 and 2. It also presents the data to show the pattern of twig loss from each size category over time and tests whether there was a significant difference in the numbers lost from the different size categories.

2.3. RESULTS

2.3.1. Variation in Nest Dimensions

Table 2.1 summarises the measurements taken of intact nests. It reveals there to be a great deal of variation in the size and weight of rook nests. Parameters of the outer ring indicate overall nest size; in the fourteen nests measured, circumference ranged from 130-198 cms., length from 36.0 - 78.6 cms. and width from 26.2 - 54.6 cms. The shape of the nest can be envisaged by comparing the ratio of the outer ring length and width. The agreement of these parameters for nests 8, 11 and 13 indicates that the nests were roughly circular whereas 2, 9 and 14 were far more ovoid. Such a difference in nest shape may itself reflect the geometry of the nest site. I will return to the point about fork geometry determining nest size and shape in section 2.4.

<u>Table</u> <u>2.1</u>. A summary of the measurements made on intact nest structures showing the circumference, length and width of the outer ring and the circumference, length, width and where possible depth, of the nest cup. In addition, cup dry weight, total nest dry weight and the number of twigs in the outer ring are shown for the eight nests analysed in the laboratory.

± figures refer to the Standard Deviation.

Nest number		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tree Species		SYC.	SYC.	SYC.	SYC.	ELM	SYC.	SP.	SYC.	SYC.	SYC.	SYC.	SP.	SP.	SP.
OUTER RING (cm.)	Circum.	170.0 ± 3.7	198.0 ± 6.3	156.4 ± 7.2	152.4 ± 8.2	131.3 ± 4.1	194.4 ± 5.2	- -	167.6 ± 3.9	176.0 ± 2.5	158.2 ± 1.9	130.0 ± 1.9	168.6 ± 3.5	153.8 ± 4.4	131.3 ± 2.9
	Length	36.0 ± 3.6	76.6 ± 1.8	42.4 ± 2.7	47.6 ± 4.3	48.0 ± 2.3	56.0 ± 3.8	- -	43.2 ± 1.3	78.6 ± 3.1	56.2 ± 0.8	44.8 ± 0.8	58.4 ± 2.2	43.0 ± 1.6	49.7 ± 0.7
	Width	27.8 ± 3.4	54.6 ± 2.8	26.2 ± 3.0	28.4 ± 2.1	36.0 ± 2.6	49.3 ± 1.4	- -	41.0 ± 1.3	54.6 ± 1.5	49.2 ± 0.8	42.0 ± 1.0	44.6 ± 0.9	42.2 ± 0.8	32.6 ± 0.5
CUP (cm.)	Circum.	81.0 ± 4.4	108.4 ± 3.4	62.5 ± 2.7	89.2 ± 7.4	96.3 ± 6.1	79.0 ± 4.5	- -	84.0 ± 3.1	62.8 ± 1.8	57.8 ± 0.8	64.0 ± 1.4	66.0 ± 2.0	65.8 ± 3.0	54.0 ± 1.4
	Length	15.5 ± 2.1	44.4 ± 2.3	22.4 ± 2.7	33.3 ± 5.1	31.1 ± 1.4	16.0 ± 1.2	- -	13.3 ± 0.8	26.4 ± 0.5	19.0 ± 0.7	20.6 ± 0.5	33.2 ± 0.3	23.2 ± 1.5	21.7 ± 0.8
	Width	13.0 ± 1.6	43.0 ± 1.2	15.8 ± 1.3	14.5 ± 1.2	30.0 ± 2.2	11.0 ± 1.5	- -	10.7 ± 0.4	19.6 ± 0.5	18.8 ± 0.0	18.0 ± 0.2	26.1 ± 0.5	21.1 ± 0.5	18.9 ± 0.5
	Depth	8.8	-	14.2	-	8.2	-	-	11.7	9.0	7.0	-	-	8.0	11.0
CUP DRY WEIGHT (g)		864	4746	529	2086	387	317	417	497	-	-	-	-	-	-
TOTAL NEST DRY WEIGHT (g)		2209	7385	1915	3504	1092	2018	2604	1920	-	-	-	-	-	-
No. TWIGS IN OUTER RING		501	607	418	472	310	555	821	420	-	-	-	-	-	-

Key: SYC. = Sycamore, *Acer pseudoplatanus*; ELM = *Ulmus procera*; SP = Scots Pine, *Pinus sylvestris*

Despite the variation in overall nest dimensions, there are certain parameters that are positively correlated. Table 2.2 summarises the results of two-tailed Spearman Rank Correlation tests between parameters of the entire nest structure.

The two trends that emerge from these correlations are:

1) As the number of twigs in the outer ring are shown to be significantly positively correlated to outer ring circumference, outer ring weight and total nest weight, it is true to say that the more twigs, the bigger and heavier the nest.

2) As table 2.1 shows, there is a great deal of variation in the relative contribution of the weight of the nest cup to total nest weight. This is supported by the fact that there is no correlation between these two parameters. There is also no correlation between cup weight and outer ring circumference and between outer ring circumference and cup circumference. These results show that nest cup size and weight are entirely independent of the size and weight of the outer ring. Possible reasons for this are discussed in section 2.4.

2.3.2. Observed Frequency of the Type and Proportions of Materials Used in the Outer Ring

Figures 2.3 - 2.5 are stack histograms showing the relative contribution (expressed as percentage composition) of each of the size, species and forking categories in the construction of the outer ring. At the far right of each histogram is the percentage composition of the relevant categories for twigs on the rookery floor. This serves as an indicator of twig availability for those categories. A summary of the frequencies of each twig category recorded on the rookery floor is shown in table 2.3. To reiterate the null hypothesis proposed in section 2.2.2., one would say that if the proportions of each category found on the rookery floor were comparable to the proportions found in each of the eight nests, then the area occupied by each category within the stack would be the same for both the nest and the ground sample. This would indicate that no selection was operating and materials were

Table 2.2 A summary of the results of two-tailed Spearman Rank Correlation tests between defined measured parameters of the intact nest structure. For definitions of parameters see text.

Comparison	r^s	Significance
Outer Ring Circum. v's No. Twigs	0.893	* (n=7)
Outer Ring Wt. v's No. Twigs	0.810	* (n=8)
Total Nest Dry Wt. v's No. Twigs	0.857	* (n=7)
Total Nest Dry Wt. v's Cup Dry Wt.	0.643	ns (n=8)
Cup Dry Wt. v's No. Twigs	0.143	ns (n=8)
Cup Dry Wt. v's Outer Ring Circum.	0.214	ns (n=7)
Cup Circum. v's Outer Ring Circum.	0.268	ns (n=13)

Key: * = Sig. at P = 0.05; ns = not significant

Table 2.3. Twig availability - A summary of the data from 21 x $1m^2$ quadrat samples taken from the rookery floor at Milton Farm showing the total numbers (T) and percentage (%T) of twigs in each denoted category.

	SIZE (cms.)				No. FORKS						SPECIES				
	10.0-20	20.1-30	30.1-40	>40	0	1	2	3	4	>4	L.d	A.p	P.s	B.p	Misc.
Total (T)	711	264	78	66	966	104	23	8	4	8	251	146	128	178	409
Mean (x)	33.9	12.5	3.7	3.1	46.0	5.0	1.1	0.4	0.2	0.4	12.0	7.0	6.1	8.5	19.5
S.D.	27.8	8.5	3.1	2.8	30.3	3.4	1.1	0.7	0.4	0.6	8.9	5.8	5.6	6.0	19.5
% T	63.5	23.6	7.0	5.9	86.8	9.3	2.1	0.7	0.4	0.7	22.6	13.1	11.5	16.0	36.8

Species Key

L.d = Larix decidua

A.p = Acer pseudoplatanus

P.s = Pinus sylvestris

B.p = Betula pendula

Misc. = Miscellaneous

being collected in direct proportion to their availability. However it can be seen from the figures that a) there is a great discrepancy between the prevalence of the size, species and forking categories on the ground and in the eight nests and b) there is variation in the frequencies of the respective categories between the nests themselves.

Figure 2.3, which details the percentage of the outer ring that is comprised of each of the size categories, shows that the smallest size category, 10.1-20.0 cms., is grossly under represented. The three larger size categories all appear within the nest structure at a higher incidence than occurs on the rookery floor. In section 2.3.3., I will detail the statistical analysis used to test if this deviation is significant.

Figure 2.4 shows the proportions of twigs species present on the rookery floor (ground) next to the proportions of twig species found in the eight nests analysed. Note that there is considerable congruity between the species of twigs that are immediately available on the rookery floor and those used in nest construction. Within the 'Miscellaneous' portion of the ground stack, which accounts for c.37% of twigs on the rookery floor, many were from species of tree present within the rookery. These include beech, *Fagus sylvatica*, alder, *Alnus glutinosa*, ash, *Fraxinus excelsior*, and hawthorn, *Crategus* sp. They were included in the miscellaneous category because they occurred at very low frequency in the ground samples, however it can be seen from the figure that even twigs of these species, occurring at relatively low frequency, are still found within the outer ring. It would therefore appear that the majority of twig material used in nest construction is collected from the immediate vicinity of the rookery. The question as to whether there exists an element of preference for twigs of certain species is addressed in section 2.3.3.

Figure 2.5 shows the percentage composition of twigs separated according to the number of forks they possess and compares their incidence within the nests to that

Figure 2.3. Stack histogram showing the recorded percentage composition of twigs from the outer ring in each size class for the 8 nests analysed. The 'GROUND' stack shows the percentage of twigs in each size class recorded on the rookery floor (taken from 21 x $1m^2$ quadrat samples). This stack is therefore representative of twig availability. Figures in brackets denote sample sizes.

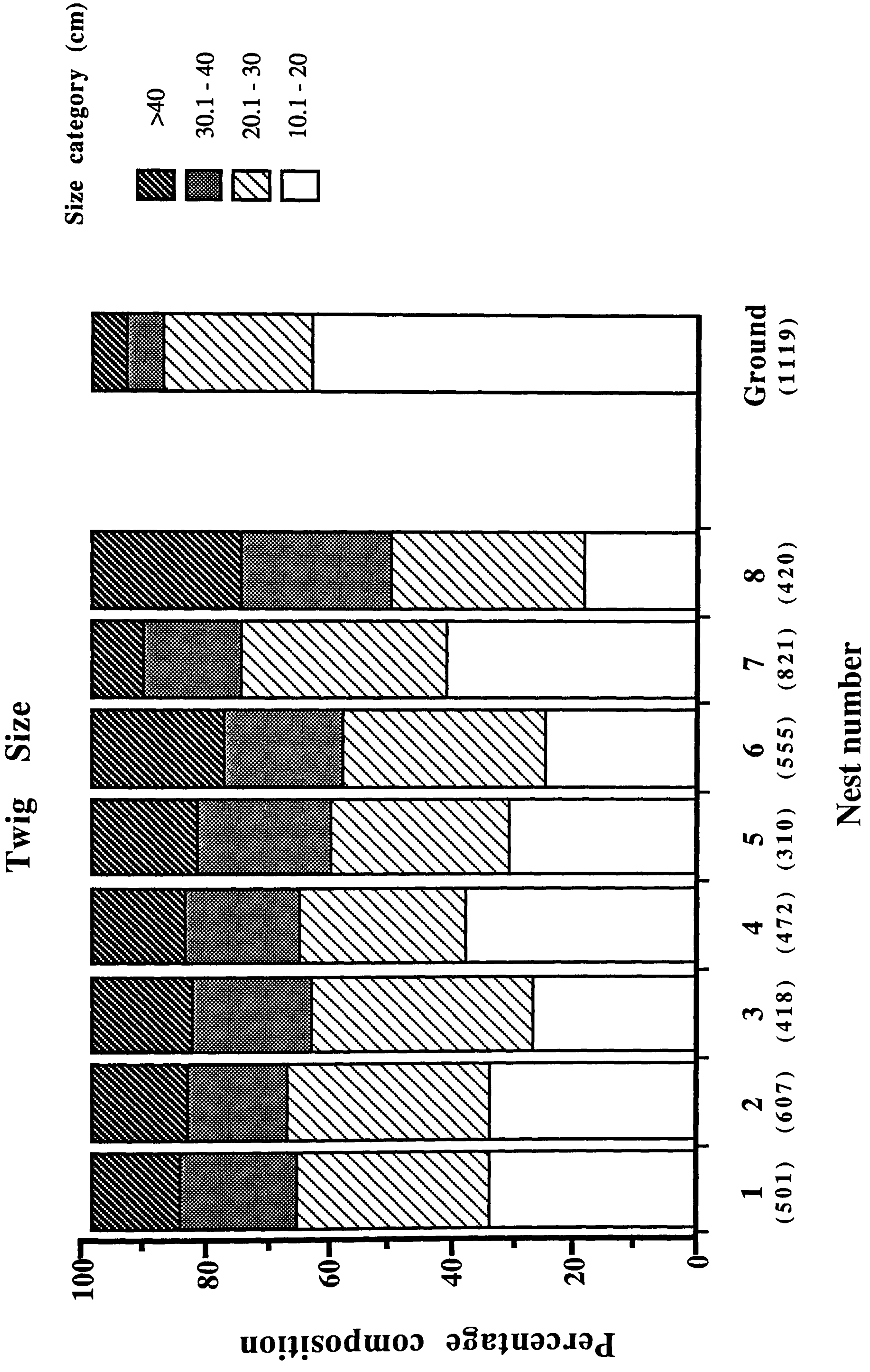

Twig Size
Size category (cm)
>40
30.1 - 40
20.1 - 30
10.1 - 20
Percentage composition
100
80
60
40
20
0
1 (501)
2 (607)
3 (418)
4 (472)
5 (310)
6 (555)
7 (821)
8 (420)
Ground (1119)
Nest number

Figure 2.4. Stack histogram showing the percentage composition of each twig species comprising the outer ring. The 'GROUND' stack represents the proportion (expressed as percentage composition) of each twig species occurring on the rookery floor (estimated from 21 x $1m^2$ quadrat samples). Figures in brackets denote sample sizes.

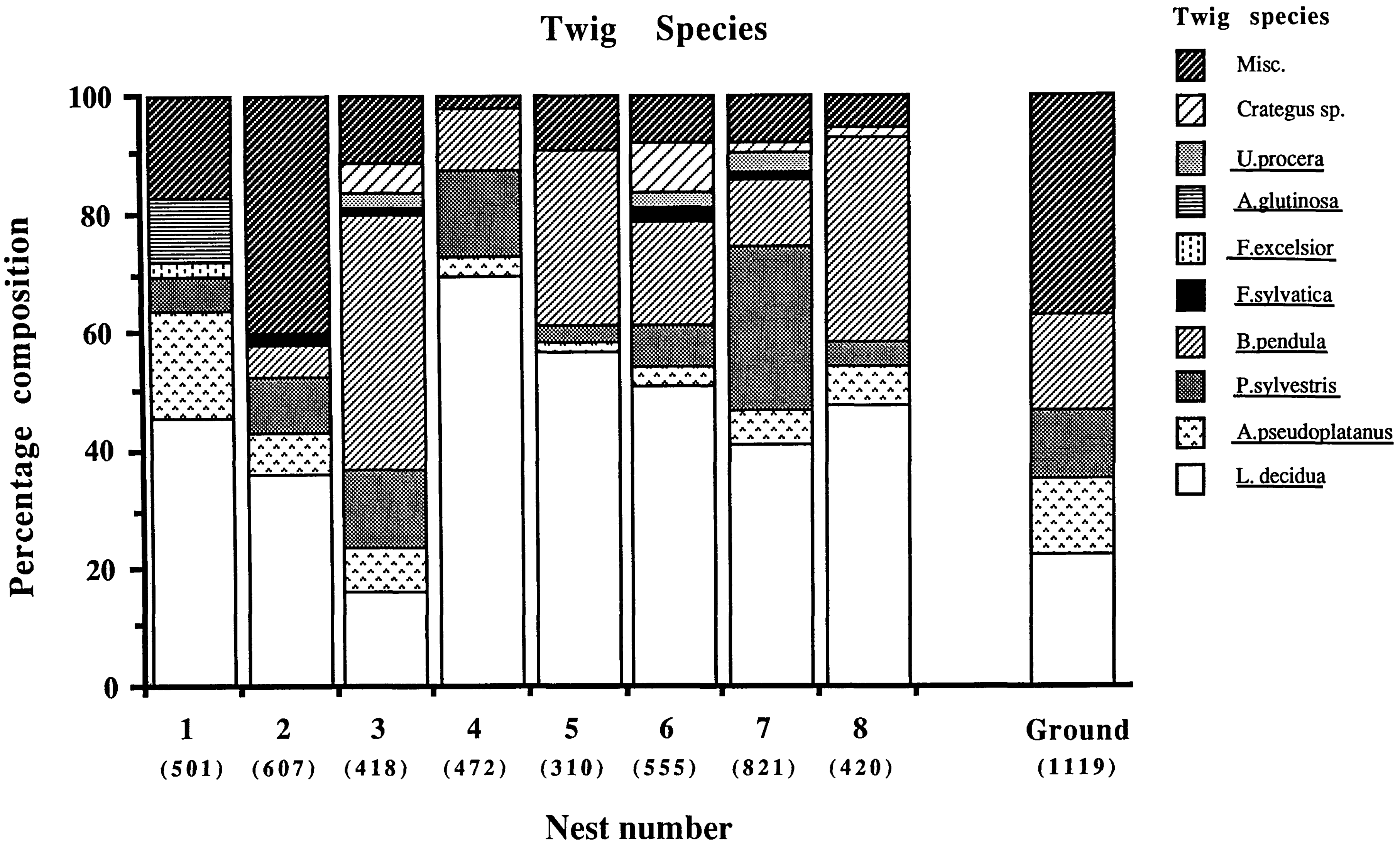
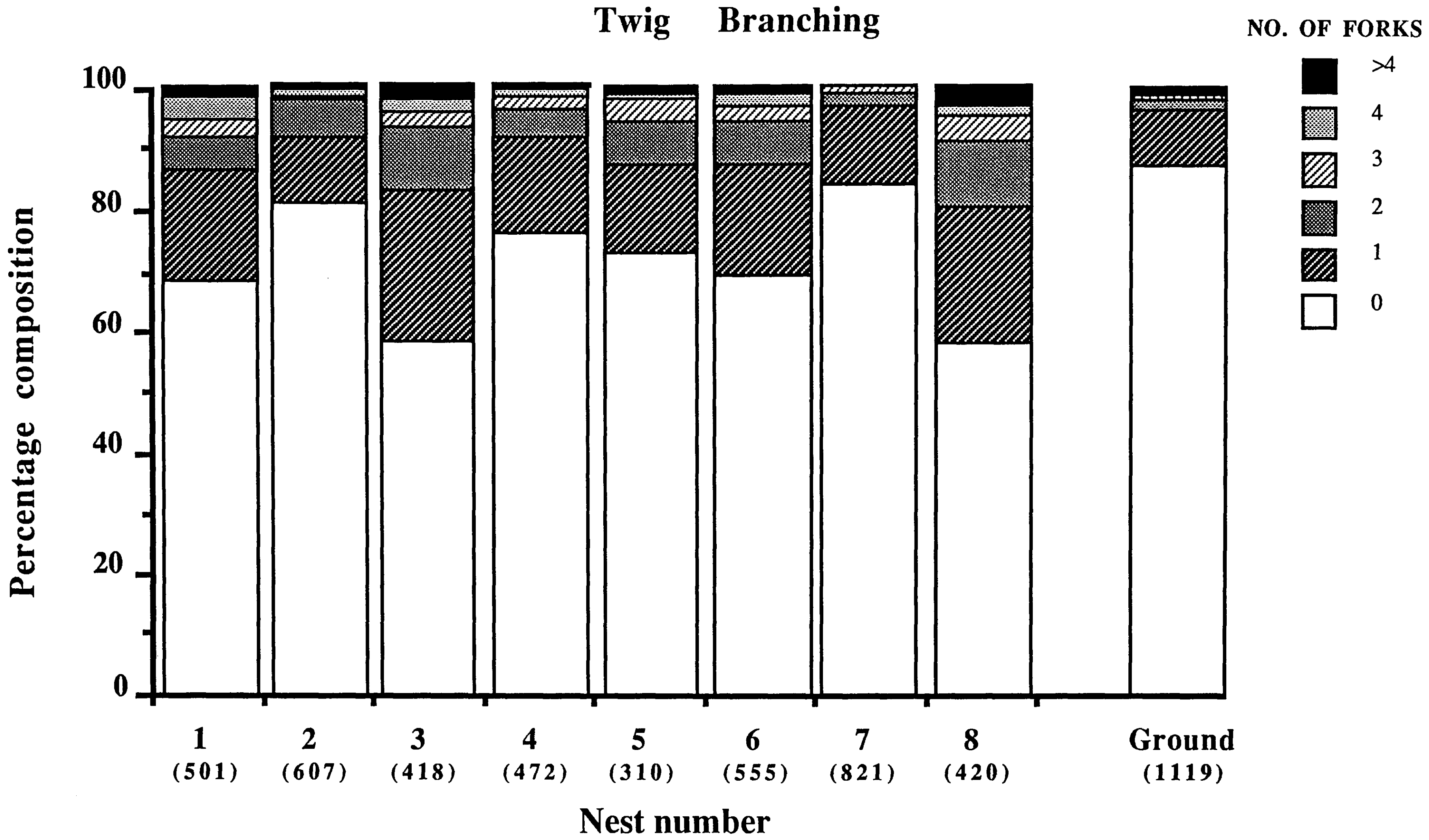

Twig Species
Percentage composition
100
80
60
40
20
0
1
(501)
2
(607)
3
(418)
4
(472)
5
(310)
6
(555)
7
(821)
8
(420)
Ground
(1119)
Nest number
Twig species
Misc.
Crategus sp.
U.procera
A.glutinosa
F.excelsior
F.sylvatica
B.pendula
P.sylvestris
A.pseudoplatanus
L. decidua

Figure 2.5. Stack histograms showing the proportion of twigs in the outer ring (expressed as percentage composition) sorted according to their degree of branching. The 'GROUND' stack shows the percentage of twigs in each branching category recorded from the rookery floor (data based on 21 x $1m^2$ quadrat samples). Figures in brackets denote sample sizes.


Twig Branching
NO. OF FORKS
>4
4
3
2
1
0
Percentage composition
100
80
60
40
20
0
1
(501)
2
(607)
3
(418)
4
(472)
5
(310)
6
(555)
7
(821)
8
(420)
Ground
(1119)
Nest number

on the rookery floor. The general trend suggests that there is a higher incidence of branched twigs within nest structures than is present on the ground since the percentage composition of branched twigs in the nests is greater than the percentage composition of branched twigs occurring in the ground sample. The importance of branching in the selection of twigs as nesting material is examined in the following section.

2.3.3. Evidence for Preference in the Selection of Nesting Material

There is a disparity in the proportion of twigs in each of the forking, size, and species categories observed on the ground compared to the proportions found in the nests. It also clear that the proportional contribution of each category in the three criteria (size, species and forking) varies between nests. The question arises as to which of these criteria is most important in the selection of nesting material. From such analysis it may be possible to draw an objective conclusion as to the most preferred type of twig material.

Any one twig will fall into one category of each of the size, species and branching variables. The problem is to first demonstrate that there is a significant deviation in the incidence of the chosen variables between sources (the ground and within nests) and second to discern which variable is most influential in the selection of that twig; was it its size, its species or the number of forks it possessed? In order to test which of these variables is most important, one can make pairwise comparisons between any two of the three criteria (e.g. species and size) hold one constant and then test whether there is a significant deviation in the expected frequency of the categories within the other criterion between the two sources.

This is the basic rationale behind Multiway Frequency Analysis which produces partial chi-square test statistics by comparing the observed and expected frequencies from multiple associations. In practise, results generated from associations between four or more variables become difficult to interpret so I have analysed three-way associations, two of the variables from the twig itself and the source from which it originated. Such an analysis shows a) whether there is a significant deviation in the incidence of the variable between sources and b) which of the two variables chosen is most influential in twig selection. The above analysis, is based on the data collected from the same eight nests used to show the frequency and type of materials used in the outer ring.

Comparison 1 - Size and Species of Twig v's Source (Ground or Nest).

Results of a loglinear multiway frequency analysis show:

i) That there is a highly significant difference in the size composition of twigs between the ground and in nests when controlling for species. (Partial $X^2 = 64.55$, 3 d.f., $p < 0.0001$).

ii) There is a significant difference in the species composition of twigs between the ground and in nests when controlling for size. (Partial $X^2 = 12.46$, 4 d.f., $p = 0.014$).

iii) The higher partial X^2 value for size against source (species held constant) compared to species against source (size held constant), indicates a greater selectivity for size compared to species (partial X^2 $64.55 > 12.46$).

Comparison 2 - Size and Degree of Branching of Twig v's Source.

Results of a loglinear multiway frequency analysis show:

i) There is a highly significant difference in the size composition between the ground sample and twigs in nests when controlling for extent of branching. (Partial $X^2 = 44.56$, 3 d.f., $p < 0.0001$).

ii) There is a highly significant difference between the composition of forked twigs on the ground compared to the composition of forked twigs in nests when controlling for size. (Partial $X^2 = 19.14$, 4 d.f., $p = 0.0018$).

iii) The higher partial X^2 value for size against source (when extent of branching is held constant) compared to extent of branching against source (when size is held constant) indicates a greater selectivity for size compared to the degree of branching exhibited by any one twig (partial X^2 44.56 > 19.12).

Comparison 3 - Inter-Nest Comparison of Size v's Species

A final test was run on the relative twig frequencies for each size and species category in the eight nests analysed. A non-significant partial X^2 for either size or species variable between nests would indicate that the proportion of twigs within the categories of that particular variable did not vary significantly between nests. In other words, the relative size and species categories did not significantly differ in their percentage contribution to the outer ring structure throughout the eight nests analysed. The results of the loglinear multiway frequency analysis were as follows.

i) There is a highly significant difference in the size composition of the eight nests when controlling for species (partial $X^2 = 197.601$, 21 d.f., $p < 0.0001$).

ii) There is a highly significant difference in the species composition between the eight nests when controlling for size (partial $X^2 = 1380.5$, 28 d.f., $p < 0.0001$).

The three way association between size, species and source (the eight nests) was also highly significant. This means that within the sample of nests there is significant variation in both size and species composition, the fact that the partial X^2 value for species against source is greater than for size against source (partial X^2 1380.5 > 197.6) is indicative that there was a much greater difference between the observed and expected values when comparing species composition between nests than when comparing size composition. This suggests that there is a greater variation in the selection of twig species between individual nests, than there is for twig size. This is in agreement with the conclusion made in comparison 1 no. iii), which states that size is more important than species when choosing material from the ground. If size is indeed the most important twig feature governing selection then one would expect the trend observed, namely a greater homogeneity in size composition than in species composition between nests. The implication is therefore that there is a greater selection pressure operating on twig size than on species. Significant differences in species composition may partly be explained by individual preference for particular species and partly by local twig abundance.

2.3.4 Ground Experiment

Table 2.4 is a summary of the number of twigs lost from within the quadrat during the building season (period 1) and during the control period outside the breeding season (period 2). During period 1 birds were seen removing twigs from the quadrat and losses were recorded.

The table shows that in period 1, twigs in the size category 40.1-50cm were selected more frequently than twigs in the other two size categories. This result is highly significant, $X^2 = 53.00$, 2 d.f., $p < 0.001$. No twigs were lost from the quadrat during period 2 which suggests that all twig losses during the experimental period were due to the action of rooks.

Figure 2.6 is a graph showing the cumulative loss of twigs in each size category from within the quadrat over time. In the size category 40.1-50 cms., twigs were regularly taken from the quadrat after day 9 (27/3/88) which was also the time of peak building activity in that year. The loss of twigs from the two smaller size categories occurs at a far lower rate starting at about day 5 (23/3/89) and losses continue at a lower rate throughout the duration of the experiment.

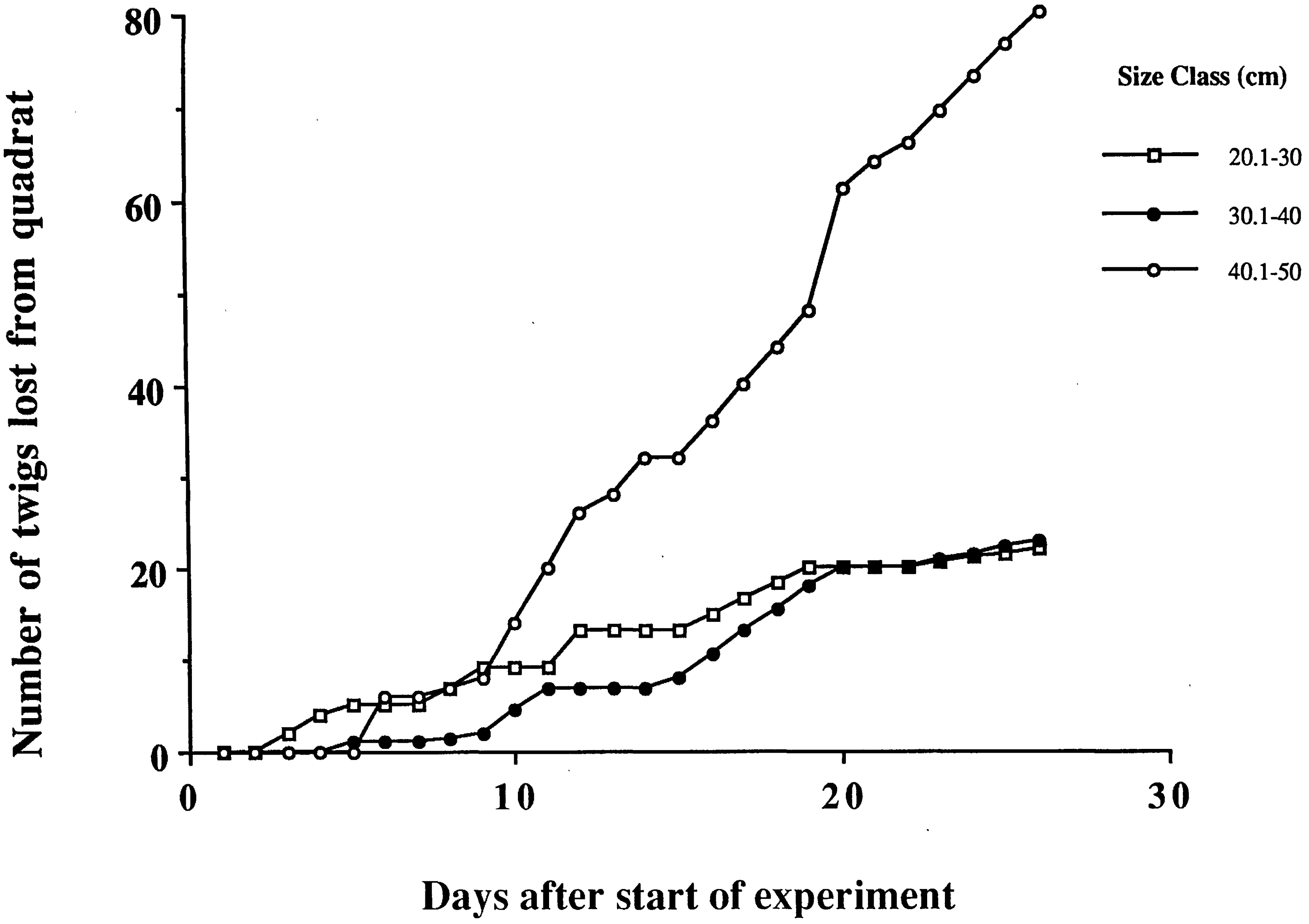
2.4. Discussion

Large variation in the size and proportions of rook nests has also been documented by Kulczyck (1973). In his paper he states that the outer diameter (what I have called outer ring length) varies between 26.5 - 85.0cm. Of all the external nest

Table 2.4. The number of twigs lost in each size category from the 3x3 m quadrat in the experimental period during peak building activity (Period 1 between 18/3/88-12/4/88), and the control period after the building season (Period 2 between 4/5/88-18/5/88).

Size Category (cm.)	Number Twigs Lost Period 1	Period 2
20.1 - 30	22	0
30.1 - 40	23	0
40.1 - 50	80	0

<u>Figure</u> <u>2.6.</u> The cumulative number of twigs lost in each size class from within the quadrat, shown in relation to the day after the beginning of Period 1 on 18/3/88.


80
60
40
20
0
Number of twigs lost from quadrat
0
10
20
30
Days after start of experiment
Size Class (cm)
20.1-30
30.1-40
40.1-50

parameters detailed in table 2.1, I found outer ring circumference to be a good indicator of nest size and the amount of twig material collected, since there is a significant positive correlation between this parameter and both total nest weight and total twig numbers.

More interesting though, are the correlations summarised in table 2.2 which show that there is little relationship between overall nest size and cup size since cup circumference and weight are independent of the weight and circumference of the entire structure. This may in part be due to the time of year when the nest is collected. Ideally, comparisons of nest cup dimensions should be made just before laying when the cup is of the dimensions suitable for breeding. Cup shape alters after hatching due to the effects of fledglings widening the perimeter and adults moving about on the nest. The influence of nest cup volume on reproductive success has been studied by Goodman (1982) in the barn swallow, *Hirundo rustica.* Goodman recorded the reproductive performance of pairs and made casts of nest cups to calculate volume. He concluded that nest cup volume was completely independent of fitness. Because rook chicks distort the shape of their cup after hatching (pers. obs.), a similar study would not be possible on this species. My data suggests however that cup size is independent of overall nest size and that in some nests such as numbers 2 and 4, far more cup material is added than in others. Since the angle of bifurcation of branches emanating from a fork is going to vary, I suggest that local fork geometry influences nest size. This may also account for the absence of any correlation between nest cup dimensions and total nest dimensions. Local geometry may cause outer ring circumference to vary greatly between nest sites whereas the circumference of the nest cup will largely be determined by the size of the female's brood patch which is relatively constant.

The question arises as to why there is such a difference in the extent to which individuals build? Since all the nests analysed presumably contained clutches, does this suggest some birds overbuild? It may be that the perennial use of nests causes an accumulation of building material over a number of years. The effect is to produce an annual increase in overall nest size as is the case for example, with eyries. Alternatively, as I have suggested, nest size may depend on nest site and more material may be required to secure the structure in its location.

A cost to building would clearly be demonstrated if it could be shown that birds building large and heavy nests had a reduced reproductive output compared to birds building smaller lighter structures. Such a comparison would be possible if the site of new nests was noted at the start of the building season, the reproductive performance of the resident pair recorded, and after the breeding season, the nest removed and analysed. The data could then be tested for a correlation between nest size and reproductive output. I shall return to the issue of the effect of building costs on reproductive output in chapter 6.

The congruity in the tree species composition of the rookery and the twigs used in nest building suggests that the woodland floor immediately beneath the rookery is the major source of twig nesting material. During March and early April, adult birds are commonly seen collecting twigs from the ground and incorporating them into their nests and as a casual observation, I have never seen birds holding nesting material in their beaks outside the vicinity of the rookery.

From my analysis it would appear that twig size is a more important factor governing twig selection than either species or extent of forking. Results of the ground experiment suggest a preference for twigs in the larger size categories (>30cm). Reference to the 'Ground' stack figure 2.3 and table 2.3 show that twigs in these size classes comprise a relatively small proportion of twig composition on the rookery floor though twigs longer than 30cm contribute to a substantial part of the outer ring (28-50%). I suggest that it is unlikely that birds are accurately evaluating the proportion of twig sizes being incorporated into the nest but may be simply fulfilling an architectural requirement by ensuring that a certain number of large twigs are collected to form a stable platform. A non-random arrangement in the size of twigs within the nest structure was noted by Kulczyck who said that in the platform, "thicker sticks up to 2cm in diameter and 20-50cm in length, prevail". The fact that there are a certain number of large twigs required in nest construction means that there may be competition for twigs of certain size classes during the building season. The question of potential competition for nesting material will also be raised in chapter 6.

Even when controlling for size, I have shown that there is some preference for twigs of certain species and for forked twigs. Selection by size alone does not fully explain the over representation of larch in all nests but nest 3 and of silver birch in nests 3, 5 and 8. Nor does size alone account for the high incidence of forked twigs compared to their availability. The reason behind these preferences is not certain though one can envisage characteristics of these materials that may be structurally desirable. For example, larch twigs have characteristic short spur shoots along their length (see figure 2.2) and these may provide plenty of purchase when lodged into the outer ring providing it with increased strength. Fine twigs of both larch and silver birch are also highly flexible which would readily permit them to be bent into a roughly circular structure, a feature which would make them a more manipulable material for nest construction. As I mentioned in section 2.2.2., selection for forked twigs may be due to the fact that branching confers greater potential for interlocking with other twigs and thus providing greater strength to the outer ring. Further ground experiments testing for species and branching preference would confirm the impression that these were the preferred types.

In summary: there is considerable variation in the size of nests built by rooks though each nest is constructed to the same design plan of an initial platform, followed by the outer ring and finally the nest cup. This variation in size may be due to the fact that structures are added to over several years or that some nests need more material simply to stay in the tree. The majority of nesting material is collected from the immediate vicinity of the rookery. Size seems to be the most important criterion in selecting twig material although results suggest that there is a preference for larch and to a lesser extent, silver birch. Forked twigs are also positively selected and I propose that this is because they are especially useful in maintaining outer cup integrity and hence nest strength.

3. CHANGES IN NEST NUMBER

3.1. Introduction

3.1.1. Past Surveys

In the last half century there have been three systematic surveys of the distribution, density and size of rookeries in Great Britain. The first of these, coordinated by James Fisher between 1944-46 was conducted at the request of the Agricultural Research Council under the auspices of the British Trust for Ornithology. Two more recent surveys have also been organised by the BTO, the first in 1975 (Sage & Vernon 1978) was in response to concern over diminishing rook numbers and the second in 1980 (Sage & Whittington 1985) was essentially a follow up census aimed at assessing the change in numbers over a much shorter time interval than the forty years that elapsed between the first two surveys.

The trend shown by the results of these studies is of a dramatic decrease in the breeding density of rooks between 1944/6 and 1975; a fact attributed to a change in agricultural management over that period. Between 1975 and 1980, Sage and Whittington recorded a continued decrease in the number of rookeries (by 8%) though an increase in the number of nests (by 7%). Their conclusion was that since 1975, birds had become concentrated into larger rookeries as manifest by a drop in the incidence of very small colonies (those containing between 1-25 nests).

The data from Scotland in the 1975 survey was assimilated by Castle and published in Scottish Birds in the same year. It was hoped that this survey would act as a core data set against which future changes in population and distribution could be measured. Local monitoring has been undertaken by the Nature Conservancy Council who have recorded breeding densities at regular intervals in the Loch Lomond area (Mitchell 1976, 1980 & 1987) and by the Clyde Ringing Group for a local atlas of species distribution in the Strathclyde area (Woods pers. comm.).

Such national surveys aim to evaluate the long-term changes in the density and distribution of rooks throughout the country. They are coordinated so as to record nest numbers at the supposed maximum, late in the building season, in the latter part of April. A synchronised count is important since Dunnet and Patterson (1965) have noted from their studies of rookeries in the Ythan valley of Aberdeenshire, that there is a substantial change in nest numbers within a rookery throughout the year, rising to a peak in April and then declining in May and June. No study has yet published results of the change in nest numbers within a colony over the annual cycle to show the extent or timing of such fluctuations. In addition, a comparison of the data between colonies would discern whether the pattern of change is similar between neighbouring rookeries.

3.1.2. Predictions of the Cheap and Expensive Hypotheses

In section 1.3.2., I mentioned that the Cheap/Expensive hypotheses would be used to generate predictions in an evaluation of a 'cost' to nest building. In this section I will describe the predictions made by each hypothesis pertaining to the pattern of change in nest numbers and use the data presented to answer three questions directed at establishing the biological cost of nest building to a rook. These questions are as follows:

1) Is there any evidence to suggest a refurbishment of the nest structure outside the breeding season?
2) To what extent are new nests constructed in the spring?
3) Is the pattern of fluctuation in nest numbers similar between neighbouring colonies?

The 'Cheap' and 'Expensive' perspectives would predict very different patterns in the change in nest numbers within a rookery over the annual cycle and forecast very different answers to the questions posed by 1 and 2. A summary of the predictions made by these two perspectives with regard to nest refurbishment and the intra-colonial change in nest numbers is shown below.

<u>Expensive</u>

1) Nests are a valuable commodity that merit refurbishment outside the breeding season in order to increase the likelihood of the structure persisting until the following spring.

2) As a consequence of 1), relatively few new structures appear in the rookery during early spring since refurbishment is essentially a strategy to offset having to build a new nest. There will therefore be relatively little change in the number of nests within a colony outside the breeding season.

3) The pattern of change in nest numbers will be similar at different colonies.

<u>Cheap</u>

1) Nests are a relatively cheap commodity, whose construction incurs little cost. Perennial persistence is not necessary and structures are not therefore maintained outside the breeding season.

2) The low cost of building means that new nests should be common in the spring and that a colony may exhibit considerable fluctuations in its nest numbers over the annual cycle.

3) The pattern of changes in nest numbers will differ between colonies.

In this chapter I will present data to show i) the pattern of change in nests numbers and ii) the pattern of change in nest state for five rookeries over the yearly cycle. This will determine which set of predictions are a better reflection of the actual observed pattern of changing nest numbers. By comparing the data from five colonies, it will be possible to determine whether the pattern of change is similar at different rookeries. As a secondary, but related issue, an examination of differential nest loss from the three major nest-containing tree species at Milton Farm was made, to determine if any species was more likely to lose its nest and therefore be regarded as an inferior nesting site.

3.2. Materials and Methods.

3.2.1. Study Sites

Changes in nest numbers were monitored at the major study site, Milton Farm in Renfrewshire. The map reference and general local geography for this site were detailed in section 2.2.1. In addition, four other rookeries were monitored across the Clyde Estuary in the Campsie Fells. These colonies are indicated by the circled areas in figure 3.1. The size of the colony, the type of wood in which it was situated and the local geography for these Campsie rookeries is outlined below.

Lernock nr. Fintry (OS map ref. 609/897) - an isolated copse surrounded by pasture-land. The number of breeding pairs varied between 166-209 nesting in Scots Pine, *Pinus sylvestris*, and a variety of deciduous species including, Oak, *Quercus robur*, Ash, *Fraxinus excelsior*, Alder, *Alnus glutinosa*, Beech, *Fagus sylvatica* and Silver Birch, *Betula pendula*. Heavy shooting of fledglings was carried out in the late spring in all three years of the study.

Old Manse. Balfron (OS map ref. 542/892) - cultivated, predominantly coniferous woodland bordering a cemetery. Land in the immediate vicinity of the rookery is mainly household gardens. There are however, fields suitable for feeding less than 0.5km to the north east. The number of breeding pairs varied between 94-116 nesting mainly in Scots Pine, *P.sylvestris* and Larch, *Larix decidua* with a few nests

Figure 3.1 The locations of the four rookeries in the Campsie Fells (denoted by circled areas) where nest numbers were counted at monthly intervals. The hatched area of the inset approximates to the detailed map shown.

Key: 1 = Lernock nr. Fintry
2 = Old Manse. Balfron
3 = Ballindaloch nr. Balfron
4 = Gartachorrans nr. Croftamie

Scale: 1.1 cm. = 1 km.


N
1
2
3
4
Fintry
Balfron
Killearn
Croftamie
Cameron Muir
Ballikinrain Castle
Ballindalloch Muir
B 822
B 818
B 834
A 875
A 81
A 811
C A M P S I E

in Oak, *Q.robur.* This rookery was not shot out in the spring.

Gartachorrans nr. Croftamie (OS map ref. 471/858) - a single species woodland comprised of oak, *Q.robur,* lining the Catter Burn. The rookery occupied a stretch of approximately fifty metres on private farm land. Fields either side of the burn are used for sheep grazing and birds were often seen feeding in this area. The breeding size of the colony varied between 82-89 pairs. This rookery was not shot out in spring.

Ballindaloch nr.Balfron (OS map ref. 541/883) - a planted wood in the grounds of private land surrounded by fields used for sheep grazing. The breeding size of the colony varied between 129-144 pairs nesting mainly in Scots Pine, *P.sylvestris* and to a lesser extent in Beech, *F.sylvatica* and Elm, *Ulmus procera.* The shooting of fledglings was a regular practise in this colony in a deluded attempt to control bird numbers.

3.2.2. Recording Nest Numbers

At all sites except Milton Farm, nest numbers within the colony were mapped at monthly intervals. At Milton, numbers were also recorded every month but in addition, counts were made at weekly intervals during the building season (March and early April) in order to get a more detailed idea of the changing pattern in nest numbers during peak building activity. Also at Milton, the number of nests lost from, or built in, each tree species at the time of each check was recorded to examine whether there was a difference in the rate at which nests were lost or gained from different tree species.

Counts were made by 'mapping' the nest-containing trees within the wood. The relative position of nests in the canopy were marked on a three by three grid drawn on a standard 10x15 cm. index card. This gave a two-dimensional representation of the three-dimensional distribution of nests within the tree. Every time counts were made, they were done from the same position on the ground so that recordings from that tree were made from the same perspective each month. This was achieved by hammering a plant tag into the trunk of the tree to act as the selected line of reference. A site code, tree number and the number of nests in the tree at the last time of monitoring, were all marked on the tag. In addition to the 3x3 grid, each index card bore the same information as on the tag so that a) it was possible to match the tree to its map and b) to act as verification that all nest-containing trees within the colony were monitored each month.

The results from monthly nest counts at the five colonies are shown in section 3.3.1.

3.2.3. Differential Nest Losses from the Three Major Nest-Containing Tree Species at Milton Farm

From the data on the number of nests lost each month from the three major nest-containing tree species, Scots Pine, *P.sylvestris*, Sycamore, *A.pseudoplatanus* and Larch, *L. decidua*, it is possible to calculate the cumulative percentage lost from each of these three tree species between building seasons (mid-April to mid-March). This can then be used to test for a disproportional rate of nest loss from one tree species compared to the others. The presentation of the observed results on differential nest loss between tree species and an analysis of whether this difference is significant is covered in section 3.3.2.

3.2.4 Evidence for the Preferential Selection of Certain Tree Species as Nesting Sites

In addition to analysing the pattern of nest loss from the major nest-containing tree species at Milton Farm, it was also possible to examine for preferential selection of certain tree species as nesting sites.

From the 'mapping' system described in section 3.2.2, one can calculate the number of nests built in each tree species. A null hypothesis can be formulated which states that if no preference for nesting in certain tree species exists, then the proportion of nests built in each species will be directly related to the incidence of that species within the rookery. This hypothesis makes the assumption that the canopy of the differing species offers equal scope for nesting. In reality, this is unlikely to be the case since I suggest the rather narrow pinnacle of a larch tree does not have as many suitable nesting sites as the broader canopies of sycamores and Scots pine. Nevertheless, the exercise can be of use in demonstrating a preference or avoidance of certain tree species for use as nesting sites if the observed proportion of nests occurring within it is greatly above or below the expected value predicted by the species' prevalence. This expected value is calculated by recording the number of trees of each species within the rookery and expressing it as a fraction of the total tree population. This fraction is then multiplied by the peak number of nests observed in the rookery (which in both 1988 and 1989 was recorded on 12/4). For example, if the peak in nests numbers was 300 and Scots pine comprised 0.5 of the tree flora, the expected number of nests in that species would be 150. Note that in recording the proportional occurrence of tree species, only trees > 20ft. were counted since rooks did not nest lower than this at Milton and trees of < 20 ft. were not considered to offer potential nesting sites.

The results of analysis on the disproportional distribution of nests in the major nest-containing tree species at Milton Farm are presented in section 3.3.3.

3.2.5. Categorisation of Nest Structure

In addition to recording just the number of nests in each tree, an assessment was also made of the size and integrity of each structure. Nests were categorised on an ordinal scale according to their size as being; very small, small, medium, large or very large. If the structure was loose such that one could see daylight through it when looking from below, it was classed as being 'ragged'. A nest at the rudimentary platform stage would be assigned this class. If the structure appeared as a solid, integrated structure, it was classed as being ‘tight’. Any one nest would then be classed for example as, Medium Ragged (MR), Large Tight (LT), Very Small Ragged (VSR) etc. On the subsequent month, if the structure was observed to have increased in size or changed from being ragged to tight, it was classed as a ‘Renovation’; if the nest had decreased in size or had changed from being tight knit to ragged it was classed as a ‘Deterioration’.

The results of changes in nest state within a colony over the annual cycle are detailed in section 3.3.4.

The categorisation of each nest structure provides an additional level of information to that of just a change in nest numbers since it permits an evaluation of the extent of nest maintenance undertaken by adult birds outside the breeding season. An evaluation of nest state is qualitative to the extent that the data is collected purely by observation and can be said to be non-repeatable, therefore one needs to be clear as to the extent to which one can draw conclusions from the results. Criticisms and limitations of these methods are the subject of section 3.2.6 below.

3.2.6. Criticisms of the Methodology

Nest Counts - Summer leaf cover presented the greatest difficulty in the all year round monitoring of nest numbers. Scots Pine, although an evergreen, did not pose a problem since its broad canopy and thin foliage did not obstruct a view of the nests which were obvious as silhouettes from below. The greater problem was posed by deciduous species where leaf cover prevented a clear view of nests between June and September. However, familiarity with the distribution of nests within the tree prior to leaf cover, enabled them to be located from angles other than the standard line of reference. Despite this, one site had to be abandoned in the first summer (1987) because the density of foliage made it impossible to record nest numbers with any degree of accuracy. No data has been presented from this site. In the other study sites I cannot discount a small but undefinable margin of error due to disappearances being recorded when the nest was in fact hidden.

A second source of inaccuracy can be attributed to what will be called 'multiple nests'. The outer rings of nests built in close proximity to each other often merge. If the portion of the circumference common to both nests is small, then two distinct lobes are apparent and there is no problem in discerning the presence of two nests. However, if two nests share a large part of their circumference, then the structure will appear from the ground to be a single, large, ovoid nest and the number of breeding pairs will be underestimated. Climbs into the tree canopy to get reproductive data or take measurements of nests have shown that large structures often contain more than one cup and this was not always obvious from the ground. One particular structure at Milton Farm during this study was approximately four feet in height. An impression of the number of cups contained in such a monolith could only be made by observing the number of pairs attending the site during the breeding and building season which in both 1988 and 1989, proved to be seven.

It is impossible to check each tree from within the canopy every month and so I must accept an inaccuracy in the method. However it is important to note that in large structures I was conservative in my estimate of the number of nests contained, guided principally by the number of birds I could see actually building or later, incubating in the structure. Secondly, if there is an error in the record of the number of pairs occupying a multiple structure then it will be constant since I was the only observer making the recordings.

A third source of error will be based on the assumption that all nests were used. Personal observations from canopy level indicate that some structures have not been used as nesting sites for two or more years and are overgrown with weeds, grass and assorted vegetation. In the present methods all nests visible were regarded as being occupied which will result in a potential overestimate of the breeding size of the colony.

The sources of error mentioned above namely , leaf cover, multiple nests and the assumption of 100% usage, are the same as those mentioned by Sage & Vernon (1978) when they conducted their national survey. As with many field methods, the only recourse is to appreciate these sources of error and make every effort to minimise their effects. Note however, that they are not simply additive and the degree of error is considered acceptable.

Monitoring Changes in Nest State - It is readily apparent that nests do change in size and shape during the year due to the action of birds or climatic forces breaking the nest apart. A method to quantify accurately this change from the ground in a large sample size is difficult to envisage. The assigning of nests to categories according to size and state is an attempt to monitor the changes that occur in nest structure. However it is still to some extent subjective because there is no definitive point at which a nest changes from being medium to large or vice versa. The scale is ordinal and comparative based on my assessment of relative nest size. Through experience, recording up to 1,000 nests a month, I believe my appraisal of nest size and state to be consistent.

In the results section, I have not used the categories described (e.g. VLT, MT etc.) in the analysis, since they were mainly a field technique serving as a record of a nest's condition in one month to act as a reference against which to compare its condition in the subsequent month. The data is presented purely as the number of nests which were renovated or deteriorated between checks.

3.3. Results

3.3.1. Changes in Nest Numbers at Five Separate Rookeries

Figure 3.2 shows the pattern of change in the number of nests at the four rookeries in the Campsie Fells between November 1986 and May 1989. These are regarded as neighbouring rookeries since the furthest direct distance between two colonies is 9.1 miles between Lernock and Gartachorrans. Two points arise from the observed pattern of change. The first is that all four colonies show the same trend in changing nest numbers over the annual cycle. There is a substantial increase occurring between February and April followed by a consistent loss in the months after breeding and prior to the next spring. Though the pattern is similar for all colonies, the proportion of nests lost from the colony varies between rookeries. The annual cycle is here defined as the time interval between mid-April and the following February. Table 3.1 summarises the percentage of nests lost from each of the five colonies in the two complete cycles covered by this study. This percentage loss is calculated by expressing the number of nests lost between April and February as a percentage of the original number of nests counted at the mid-April peak.

An examination of figure 3.2 shows that the rookery at Old Manse Farm fluctuated between a low of 59 nests in February 1987 to a high of 116 nests in April 1989. By contrast, the Lernock rookery fell to 29 nests in February 1989 but had 209 structures two months later representing a seven-fold increase during the building period. Factors accounting for such a dramatic difference in the number of nests lost between colonies will be discussed in section 3.4.

The second point to note from figure 3.2 is that each colony reached its own fairly constant peak in nest numbers by the mid-April of all three breeding seasons studied. This suggests that the rookery has a carrying capacity with regard to the number of nests it can support. Since there is a large non-breeding population (Richardson, et al. 1979), one must assume that the limiting factor regulating nest

Figure 3.2. The change in nest numbers as recorded at monthly intervals for four rookeries monitored in the Campsie Fells; Lernock, Old Manse, Ballindaloch and Gartachorrans. The monitoring period is from November/December 1986 to May 1989.

Key:
N = November
M = March
J = July

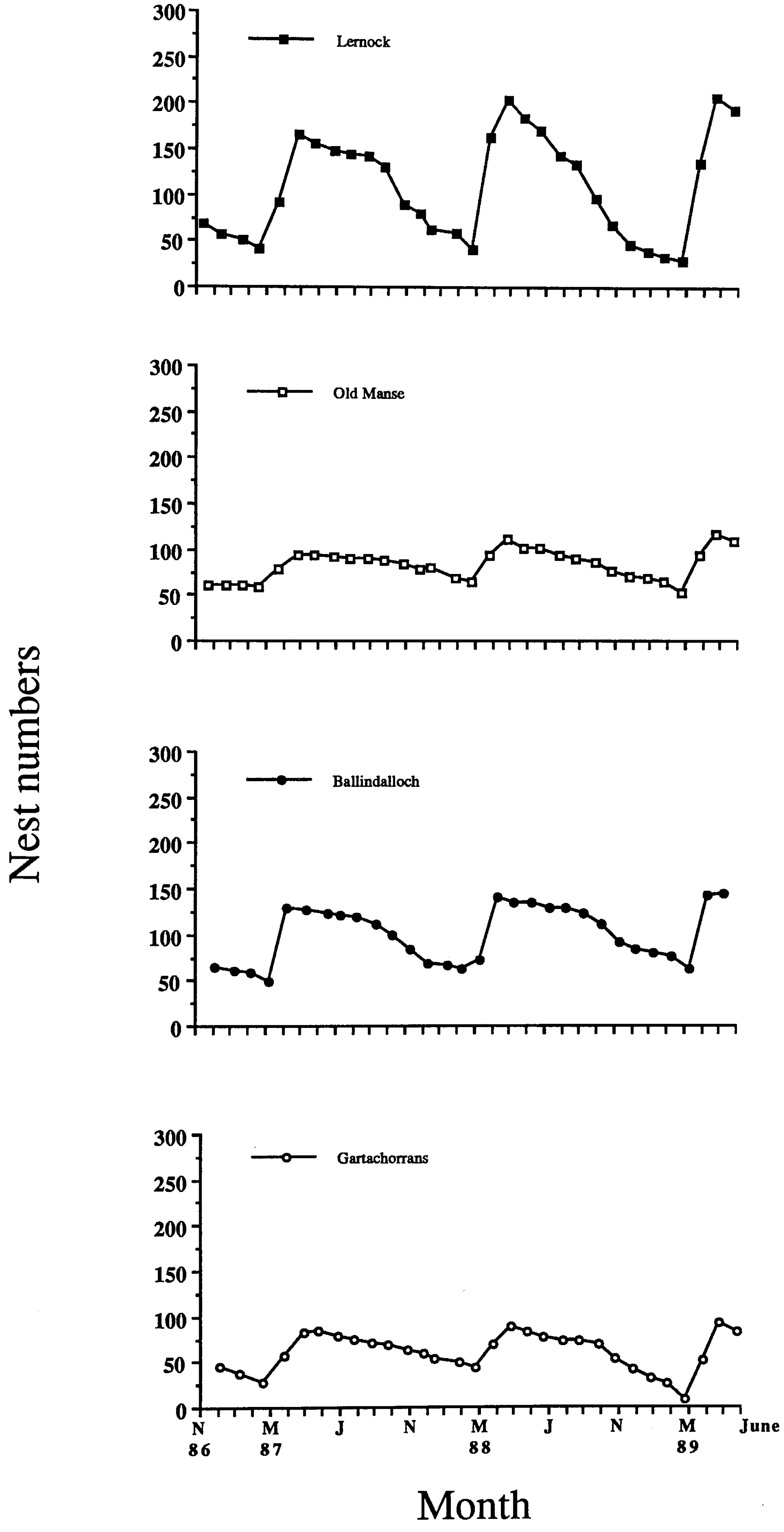

Nest numbers
Lernock
Old Manse
Ballindalloch
Gartachorrans
300
250
200
150
100
50
0
N 86
M 87
J
N
M 88
J
N
M 89
June
Month

Table 3.1 The percentage of nests lost from the four colonies in the Campsie Fells as well as the rookery at Milton Farm during a complete annual cycle from mid-April to the following February.

	% Nests Lost	
Rookery	1987/8	1988/9
Lernock	77.6	85.9
Old Manse	31.9	52.3
Ballindaloch	51.9	46.1
Gartachorrans	51.2	94.1
Milton Farm	-	41.0

numbers is either a shortage of suitable nest sites or perhaps local food supply dictating a critical density of breeding birds that may nest within the colony. The subject of annual changes in colony size and the recruitment of young birds into the colony, has been studied by Patterson & Grace (1984).

Figure 3.3 shows the changes in nest numbers at Milton Farm between December 1987 and May 1989. Checks were made monthly outside the building period and weekly during March and the first two weeks of April. During this period there is a consistently large weekly increase in nest numbers indicating a very high level of building activity. The observed annual trend apparent in the Campsie rookeries is repeated in this colony with a peak in numbers occurring in mid-April. Losses are then regularly recorded until the following spring. The number of nests varied from a low of 193 on 15/3/88 to a peak of 392 on 12/4/88, a 100% increase over a four week period.

3.3.2. The Extent and Pattern of Nest Losses from the Three Major Nest-Containing Tree Species at Milton Farm.

The proportional loss of nests from the three main nest-containing tree species, Scots pine, *P.sylvestris*, sycamore, *A.pseudoplatanus*, and larch, *L.decidua*, were compared using a chi-square analysis. Ninety-seven percent of nests in the colony were built in one of these three types of tree. In order to compare proportional loss, a comparison was made between the number of nests recorded in each species at maximum colony size (12/4/88, colony = 392) with the last count made before the building period of the following year (15/3/89, colony = 230). The number of nests in each species at these two dates are summarised in table 3.2.

The result of a Goodness of fit test show there to be a highly significant difference in the proportion of nests lost between the tree species; $X^2 = 15.72$, $p < 0.01$ at 2 d.f. Analysis of the component X^2 values show the largest discrepancy to be between the

Figure 3.3. Changes in nest numbers at Milton Farm rookery as monitored monthly outside the building season and weekly within it (during March and April). The monitoring period is from December 1987 to May 1989.

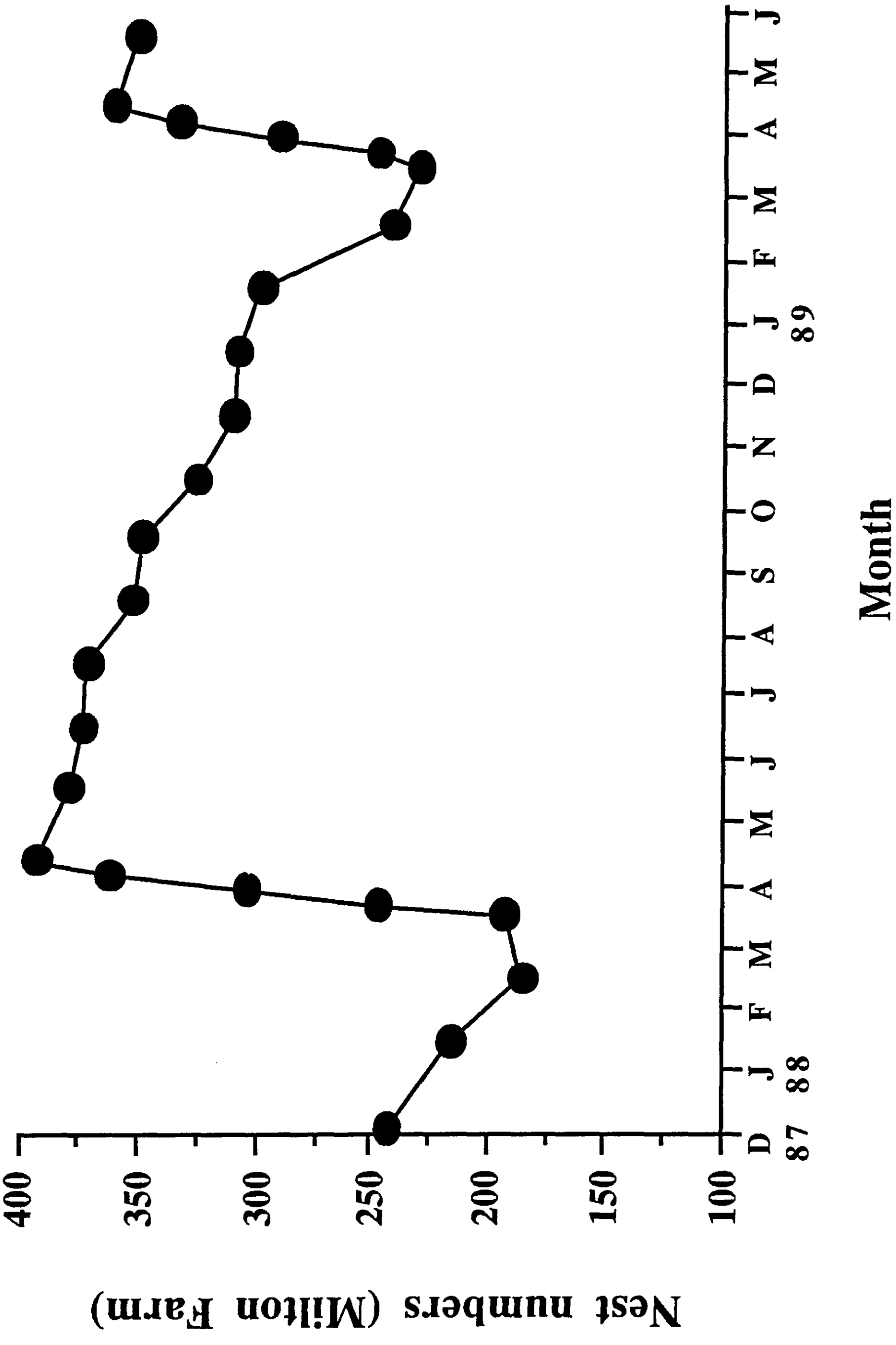

Nest numbers (Milton Farm)
400
350
300
250
200
150
100
D
87
J
88
F
M
A
M
J
J
A
S
O
N
D
J
89
F
M
A
M
J
Month

Table 3.2. The change in nest numbers observed in the three major nest-containing tree species, Scots pine, *P.sylvestris*, sycamore, *A.pseudoplatanus*, and larch, *L.decidua*, at Milton Farm during the defined annual cycle from 12/4/88-15/3/89.

	Nest Numbers	
Tree Species	12/4/88	15/3/89
P.sylvestris	218	142
A.pseudoplat.	128	78
L.decidua	33	5

observed and expected values for larch just prior to the 1989 building season (X^2 = 14). I therefore suggest that there is a disproportionate loss of nests from larch compared to Scots pine or sycamore. This is illustrated in figure 3.4 where the cumulative percentage of nests lost from within each tree species is shown against month. Note that the percentage of nests lost from larch is far greater than for either Scots pine or sycamore.

The timing of nest losses from the three tree species over the annual cycle, is shown in figure 3.5. On the y-axis, the '% of losses' is the percentage of the total number of nests lost from within that species since the previous check. Note that the graph does not provide any information on the absolute number of nests lost from each species, but merely the percentage of the total annual loss that occurred in each month. A Kolmogorov-Smirnov analysis was applied to test for a significant difference at the points of maximal separation between curves. Should a significant deviation exist, it would indicate a difference in the timing of nest losses between tree species however, no significant difference was found between curves and I therefore conclude that nests are lost from all the species at approximately the same time of year. Inspection of figure 3.5 suggests that the period of heaviest losses occurs between January and February in all three tree species.

3.3.3. Is the Distribution of Nests in Tree Species at Milton Farm Proportional to their Occurrence in the Rookery? Evidence for Certain Tree Species as Preferred Nesting Sites.

Table 3.3 summarises the data used in testing for a preference of certain tree species for use as a nesting site.

The difference between observed and expected nest numbers in the different species proved highly significant in both 1988 and 1989 (X^2_{1988} = 196.5, $p < 0.001$, 3 d.f.; X^2_{1989} = 177.8, $p < 0.001$, 3 d.f.: Goodness of fit test). Note that since nests persist

Figure 3.4 The cumulative percentage of nests lost from within Scots pine, Sycamore and Larch shown in relation to month, starting at the peak in nest numbers in 1988 on the 12/4/88, and finishing just prior to the onset of the building period on 15/3/89.

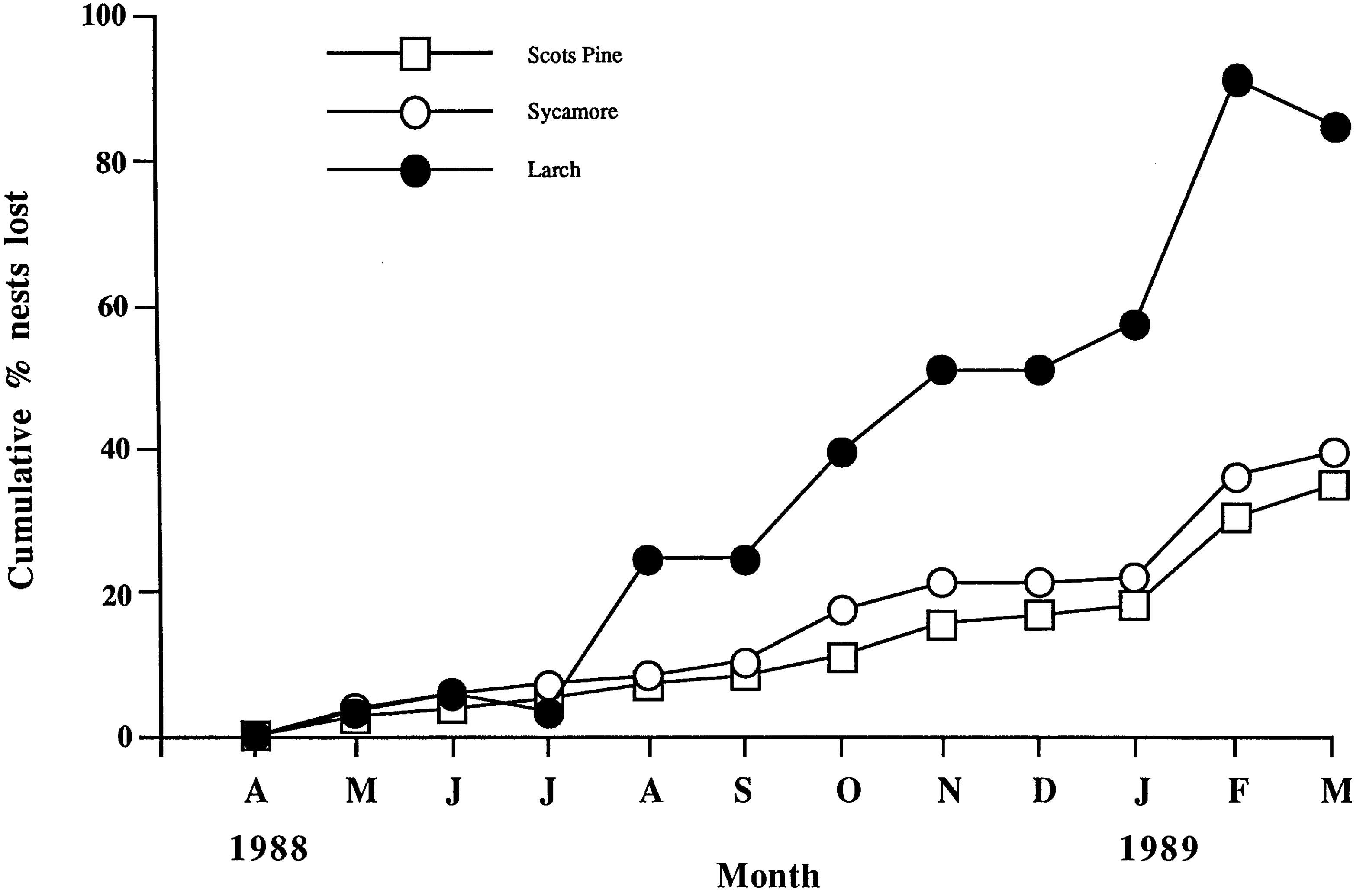

Scots Pine
Sycamore
Larch
Cumulative % nests lost
100
80
60
40
20
0
A
M
J
J
A
S
O
N
D
J
F
M
1988
1989
Month

Figure 3.5. The cumulative percentage of total nest losses from the three major nest-containing tree species; Scots pine, sycamore and larch between the period 12/4/88 - 15/3/89. The monthly pattern of nest loss is used to test for a difference in the timing of nest losses between species (see text).

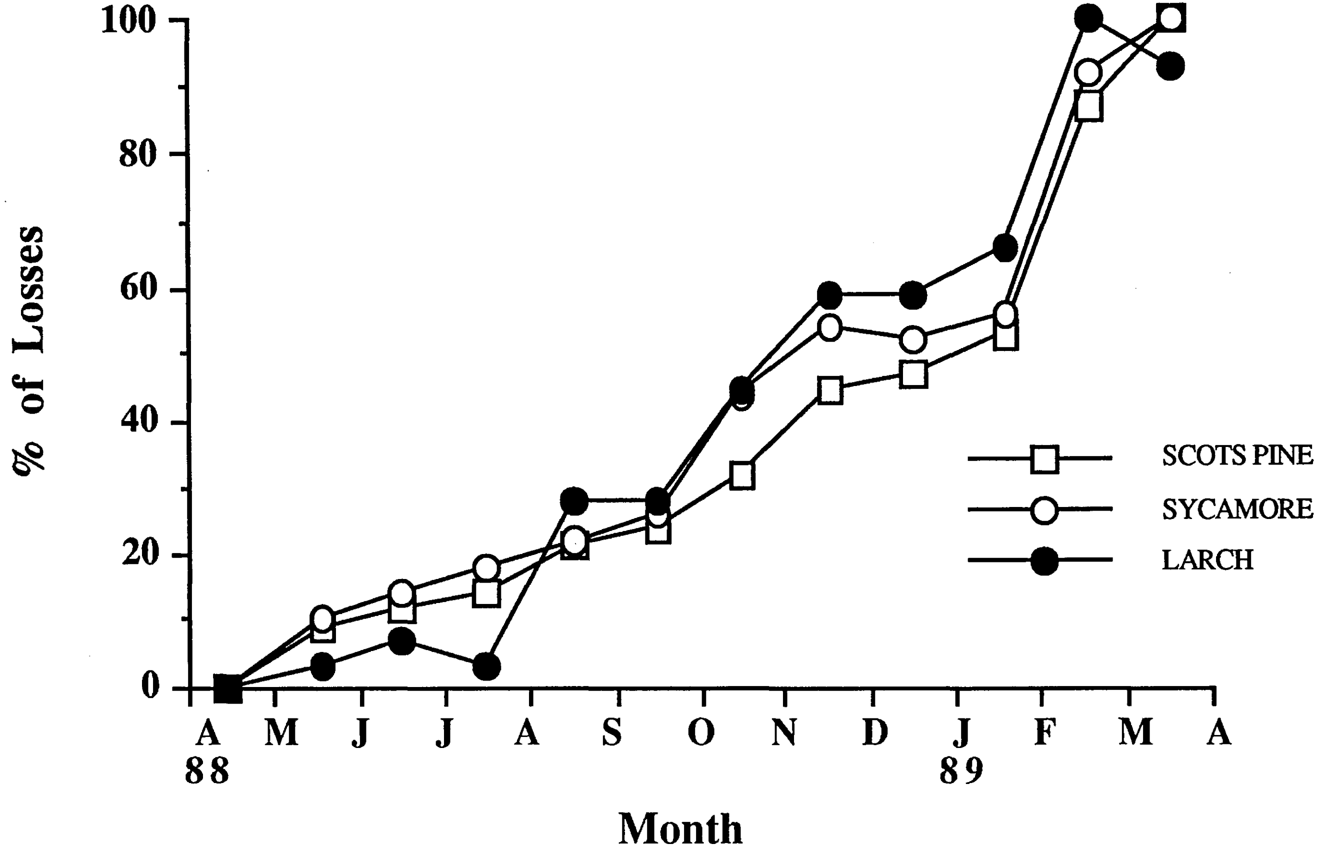

% of Losses
0
20
40
60
80
100
A
88
M
J
J
A
S
O
N
D
J
89
F
M
A
Month
SCOTS PINE
SYCAMORE
LARCH

Table 3.3 A summary of the data used to test for a preference in the choice of tree species as nesting sites. The observed number of nests in each tree species is that recorded at peak nest numbers on 12 April in both 1988 and 1989. The expected number is then calculated as being directly proportional to the prevalence of the tree species within the rookery.

Tree Species	P.sylvest.	A.pseud.	L.decid.	Misc.
Obs. nest nos.				
1988	218	128	33	15
1989	192	123	30	14
Prop. in rookery	0.32	0.21	0.20	0.27*
Exp. nest nos.				
1988	126	83	79	106
1989	115	75	72	97

* (Comprised of 0.18 Silver Birch, *Betula pendula*; 0.06 Ash, *Fraxinus excelsior*, 0.01 Lime, *Tilia europea*; 0.01 Beech, *Fagus sylvatica*; 0.01 Elm, *Ulmus procera*.)

KEY: *P.sylvest.* = Scots Pine

A.pseud. = Sycamore

L.decid. = Larch

Misc. = Miscellaneous

from year to year, the results are not independent. Inspection of the component X^2 values indicates the greatest deviations between observed and expected values in both years was for more nests to be built in Scots pine than was expected and for fewer to be built in species under the miscellaneous category. These conclusions will be discussed in section 3.4.

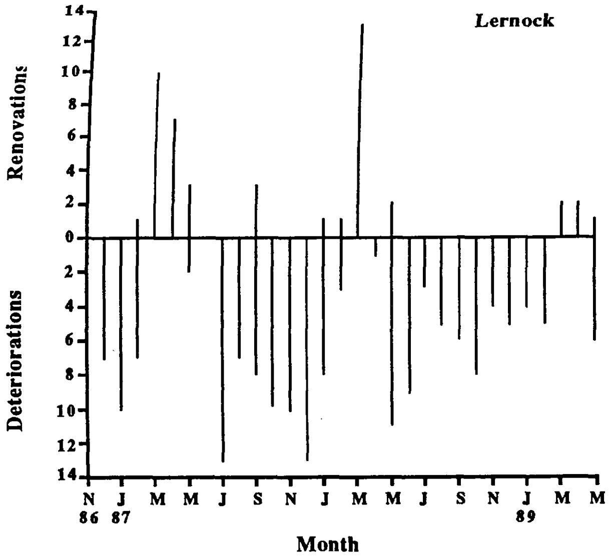
3.3.4. Changes in Nest State Between Breeding Seasons.

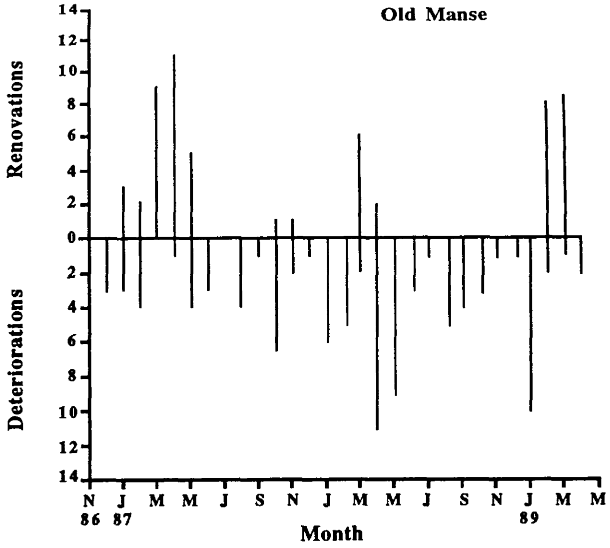
Figure 3.6 shows the number of 'deteriorations' and 'renovations' that occurred in each month at the four Campsie rookeries, and figure 3.7 shows the same information for Milton Farm.

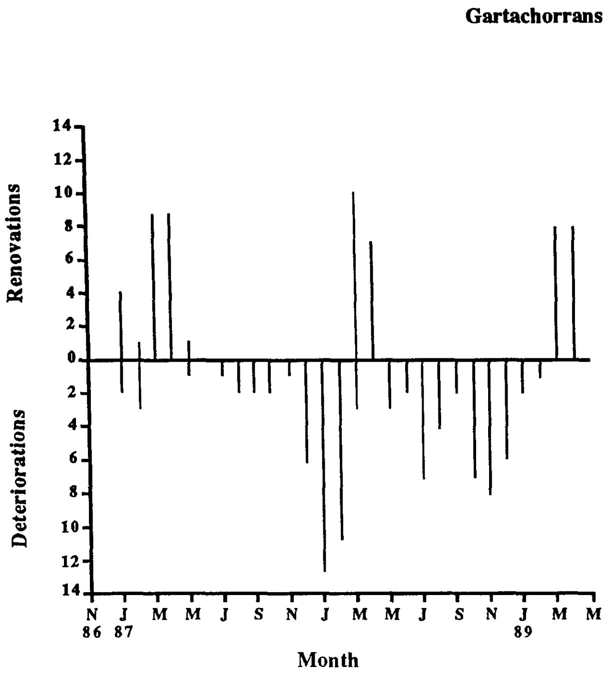
The pattern of changing nest state over time, is similar for all five sites showing renovations to be most common between March and May with some evidence of early building in February. Outside these months nests deteriorate, that is decrease in either or both size and integrity. The incidence of observed monthly deteriorations is particularly high for the rookery at Lernock compared to the other sites and it is this colony which displays the most dramatic change in nest numbers through the annual cycle (see figure 3.2). In any one month outside the breeding season, it is normally only a small percentage of nests (between 0-14%) within the colony that are observed to undergo a change in nest state. On two occasions a larger percentage were observed to have deteriorated, 21.4% at Ballindaloch in Nov.'87 and 27.7% at Gartachorrans in Jan.'88. The extremely strong winds in October 1987 may account for the observed damage at the Ballindaloch rookery although a similarly high incidence of deteriorations were not recorded at the other sites in this month. The high percentage of deteriorations at Gartachorrans in January 1988 does not seem to be related to particularly strong gales or high winds at that time and I cannot therefore attribute the observed high incidence of deteriorations to a particular period of adverse climatic conditions.

Figure 3.6 A summary of the changes in the state of nests at the four rookeries in the Campsie Fells, shown in relation to month. Nests which were reduced in size and/or integrity were classed as ‘Deteriorations’ whereas nests that increased in size and/or gained in structural integrity were classed as ‘Renovations’ (see text for details).

Alternate months are shown on the x-axis and the number of nests observed to have Deteriorated or Renovated within each colony at each monthly check are shown on the y-axis.


Lernock
Renovations
Deteriorations
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
N 86
J 87
M
M
J
S
N
J
M
M
J
S
N
J 89
M
M
Month


Old Manse
Renovations
Deteriorations
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
N 86
J 87
M
M
J
S
N
J
M
M
J
S
N
J 89
M
M
Month


Gartachorrans
Renovations
Deteriorations
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
N 86
J 87
M
M
J
S
N
J
M
M
J
S
N
J 89
M
M
Month

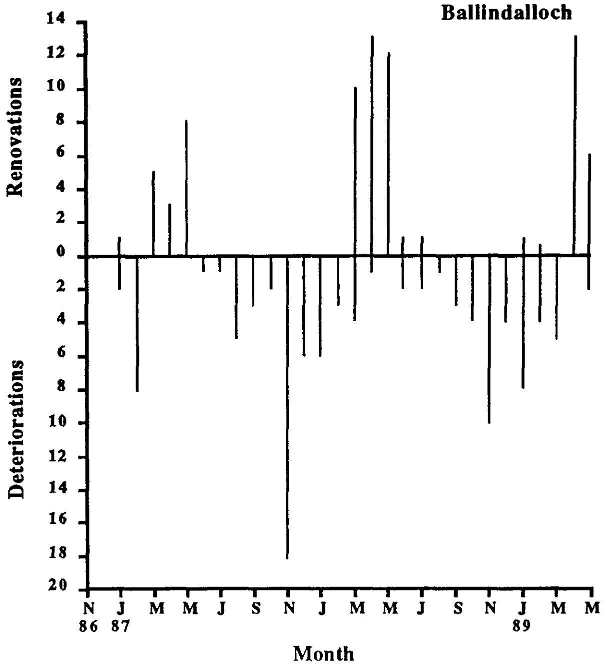
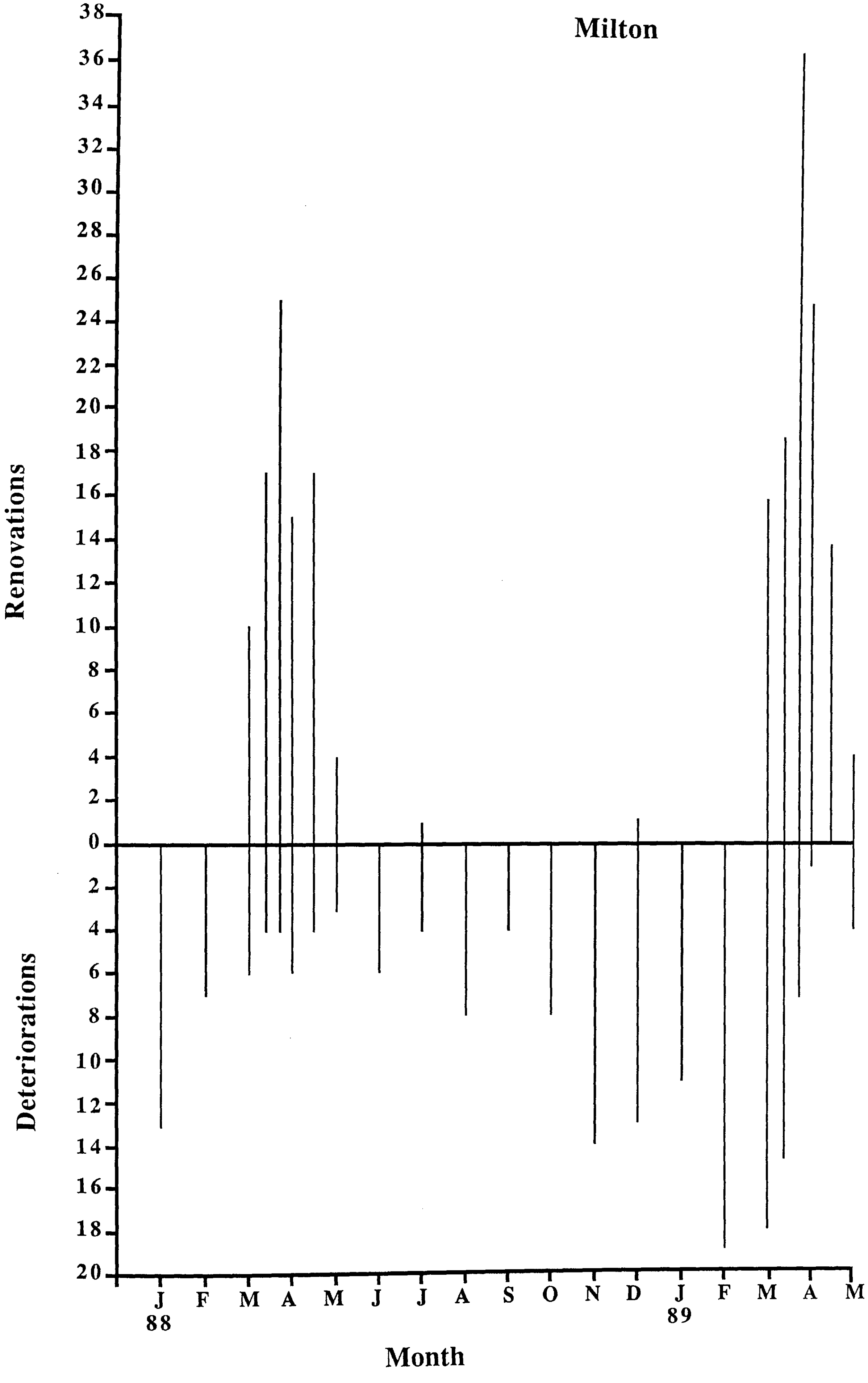

Ballindalloch
Renovations
Deteriorations
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
18
20
N 86
J 87
M
M
J
S
N
J
M
M
J
S
N
J 89
M
M
Month

Figure 3.7 The number of Deteriorations and Renovations observed to nests at the Milton Farm rookery shown in relation to month. The rookery was monitored at weekly intervals during March and early April to provide a more detailed impression of the extent of changes in the state of existing structures during the building period.


Milton
Renovations
Deteriorations
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
18
20
J
88
F
M
A
M
J
J
A
S
O
N
D
J
89
F
M
A
M
Month

During the building period, the maximum percentage of nests that were observed to have been renovated between checks was 14.9% at Gartachorrans in March 1988. The maximum percentage of nests renovated in any one month at the other four colonies were as follows; Old Manse 11.7% (April 1987); Ballindaloch 9.2% (March 1989); Lernock 7.9% (March 1988); Milton 12.8% (March 1989). The implications of this observation, that only a low portion of nests within the colony are renovated, is discussed in section 3.4.

3.4. Discussion

It is clear that rookeries suffer a depletion in nest numbers during the summer, autumn and spring. The proportion of nests lost from within the colony varied between rookeries and within rookeries, the extent of nest losses differed between 1987/8 and 1988/9. In both years, Lernock lost the great majority of its nests and at Gartachorrans, evidence of a rookery all but vanished in February 1989. At other sites, it was normal for between a third and a half of nests to disappear outside the building season.

The reason for a difference in nest losses between sites has not been thoroughly examined. There may be several factors which contribute to the survival of nests from one year to the nest; these include, i) the exposure of the site to adverse climatic conditions, particularly high winds or ii) the type of tree in which the majority of nests are sited. As the data from differential nest losses in different tree species showed at Milton Farm, some species lose their nests more readily than others. The disproportionately high loss from larch within this colony may be due to one or both of the following factors.

a) Unlike sycamore and Scots pine, larch has no broad canopy but thins to a point. There are therefore few large, stable crotches to act as nest sites. Instead nests tend to be wedged between a single branch and the tree bough with the result that the structure is not so well supported from beneath.

b) A thin pinnacle is going to be subject to greater lateral movement in strong winds than is a broad canopy. This could mean that nests in the top of larch trees may not only be less well supported but will be more vulnerable to the effects of gales.

Section 3.3.3 indicated that there was some evidence to suggest rooks preferred to build in Scots pine. This supports the view that birds may select tree species with wide, stable crotches as nest sites since they may be more secure. The under-representation of nests in the Miscellaneous category may be due to the fact that it is predominantly comprised of silver birch (0.18 out of a total of 0.27). This species typically has at its canopy fine, slender branches which I suggest are incapable of supporting a nest structure. Note however, the point made in section 3.2.4 which stated that an assumption was being made that the number of nesting sites available in the canopy was similar for all species. If this is not the case, and Scots pine offers greater potential for nesting, then the high number of nests in this species' would perhaps be expected.

A difference in the proportions of nests lost between sites may therefore occur because of a difference in the principle type of nesting tree as well as to differences in the degree of protection from adverse weather conditions. These factors may account for the heavy nest losses observed at Lernock since the site is isolated and exposed with no protection from high winds. Trees in the copse were old with many trees carrying dead wood. Nests were often found on the rookery floor after storms, still attached to a branch that had broken off the main trunk. Old Manse by comparison, was much more conservative in its pattern of change in nest numbers, with a smaller proportion of its nests being lost from year to year. Trees were planted close together at this site which meant that nests further into the wood gained some protection from wind from the trees on the outside. Houses to the south and east would also act as a wind break with the result that the Old Manse rookery was not as exposed as the one at Lernock.

A fuller examination of the effects of weather on nest persistence could be undertaken by measuring certain climatic variables that are thought to influence nest loss. For example, measurements of air speed at canopy level could be used to test if there was a correlation between the exposure of the site to wind and the numbers of nests lost. Multivariate analysis may then be used to separate the effects of exposure on nest losses from other potentially confounding variables such as tree species or height. A comparison of differential nest losses from nest-containing tree species between rookeries may confirm the initial findings that some species are more susceptible to losing their nests than others. It may therefore be possible to predict that woods containing 'precarious' tree species will suffer heavier losses during the annual cycle.

The observation that rookeries suffer a dramatic reduction in nest numbers outside the breeding season suggests that nests are not refurbished. This is confirmed by a) an almost complete absence of renovations to nest structures other than during the building season between March and May and b) the observed regular deterioration of a proportion of nests within the colony from month to month. The data in answer to the first of the three questions posed in section 3.1.2, are therefore supportive of the view that nest maintenance over the annual cycle is not a feature of rook breeding biology. I will elaborate on this subject in chapter five in the context of the proposed adaptive functions of autumn sexual behaviour. With regard to the second question, the dramatic increase in nest numbers that occurs over a relatively short time interval between mid-March and mid-April is indicative of a high level of building occurring each spring. During this period nest numbers normally double, or in the case of Gartachorrans in 1989, increase sixteen-fold. This means that at least every other pair is building an entirely new nest in the breeding season and if there is a reproductive penalty incurred by having to build a new nest, then it will be paid by the majority of individuals. Finally, it can be seen from figures 3.2 and 3.3, that the extent of nest losses, and hence spring building, is different between sites and therefore the pattern of fluctuation in nest numbers is not similar between colonies.

All of these above observations are in accordance with the cheap view of the cost to nest building. However, the observed absence of nest maintenance and the high incidence of spring building does not mean that one should discount the possibility of there being a penalty to nest building. It may be that birds cannot afford to invest the time or energy into nest refurbishment throughout the year. The cost of having to build a new nest in the spring is therefore unavoidable, endured because an individual has to compromise nest building with other maintenance activities such as post-fledging care, maintaining the pair-bond and foraging. Chapter six deals directly with the issue of a potential reproductive cost of having to build a new nest however, the evidence presented in this chapter conforms to the cheap perspective, advocating a relatively small cost to nest construction.

The fact that a degree of nest loss is recorded in all study sites and that the timing of nest deteriorations and losses is similar for all colonies, suggests that the absence of refurbishment and the high incidence of spring building are general phenomena typical of the species. This prediction could be confirmed by monitoring changing nest state and numbers in colonies throughout the rook's range.

In summary: It has been shown that there is a decline in both the numbers and state of nests within a colony outside the breeding season. This is indicative of an absence of nest maintenance. The high degree of building observed in the spring as well as the lack of refurbishment support a Cheap perspective of nest building though this may simply be an unavoidable penalty. There is some indication that choice of nesting tree may effect the likelihood of a nest persisting from one year to the next.

4.INTRODUCTION TO ROOK BUILDING BEHAVIOUR

4.1. General Introduction

In chapter one I advocated that artefacts should be regarded as extended phenotypic traits, their design having a genetic basis mediated via building behaviour. An assessment of the biological cost of nest building to the rook must therefore not only involve an analysis of the architecture of the nest itself but also a study of the behaviour behind its construction. So far, the Cheap/Expensive hypotheses have been used to generate predictions regarding the extent and pattern of nest loss within a colony. This approach is equally applicable when studying the adaptive features of nest building behaviour. The remainder of this thesis concentrates on the two periods of the year that involve nesting activity, the autumn and the spring. The conclusions drawn from studies of both periods will be used in a final evaluation of the biological cost of nest building.

This chapter introduces and distinguishes between the two separate field seasons; the spring breeding season and the autumn resurgence of sexual activity (alternatively named autumn sexuality or the period of secondary sexual activity). I will mention the facets of behaviour studied in the two periods. The bulk of the chapter however, is devoted to a general materials and methods section which will describe some of the equipment and techniques that were common to both seasons. The results and conclusions of my study on autumn sexual activity are presented in chapter five and those of the spring season in chapter six. These chapters will also detail materials and methods unique to the particular season in question.

4.2. The Autumn and Spring Seasons

4.2.1. The Autumn Resurgence of Sexual Activity

There are many anecdotal reports of rooks building in the autumn and several authors (e.g. Harding 1847, Marshall & Coombs 1957 and Holyoak 1967) have documented the marked resurgence of sexual behaviour that occurs between September and November. However, little attention has been directed at the adaptive significance of this autumn sexuality and of particular interest to my study were reported observations of autumnal nest building. Chapter five is therefore an investigation into the function of autumn sexual behaviour concentrating mainly on establishing the extent of autumn building since nest refurbishment is a potential adaptive explanation for this resurgence of breeding behaviour midway between breeding seasons. In addition, a piece of apparatus was developed (the design of which is described in Appendix 2 at the back of this thesis) to monitor the attendance of birds at the rookery. Rookery attendance was used as an indicator of the time invested at the nest site. This monitoring began in late summer 1988 and continued throughout the winter and into the following spring to discover not only how rookery attendance varied over the annual cycle, but also because a comparison between rookery attendance in the spring and in the autumn could provide a relative measure of commitment to the nest site during the latter period. The conspicuous breeding-related behavioural patterns displayed between September and November will be described in detail in the next chapter. I have focused on one particular behavioural pattern, the 'bow-caw' display since it is i) conspicuous, distinctive and common to both spring and autumn and ii) because it could be easily recorded from within a hide with minimal disturbance to the birds. Since it is such a characteristic behavioural feature of the autumn, it was hoped to discover what function this display performed and thereby provide an insight into the function of autumn sexuality. A description of the 'bow-caw' display is included in section 4.3.6.

4.2.2. The Spring

The major aim of behavioural studies conducted in the breeding seasons of 1987/8/9 was to discern what facets of building behaviour have the greatest effect on an individual's reproductive performance. The emphasis was therefore on correlating observed variations in building behaviour with the subsequent reproductive performance for that year. Sources of variation included the selection of nest site, whether an old or new nest was used and variation in the mode of material assimilation. Chapter six also includes a study into the motivation and potential benefits of stealing nesting material from conspecifics within the colony.

The focus of study is therefore different in the two seasons. For the autumn, it is establishing the extent of nest refurbishment and the possible adaptive function of a resurgence in sexual behaviour. In the spring breeding season, the most important issue is identifying the features of building behaviour that potentially influence fitness.

4.3. Materials and Methods Common to Both Autumn and Spring Seasons

4.3.1. The Suitability of Milton Farm as a Study Site

As mentioned in section 2.2.1, all behavioural studies were conducted at the rookery at Milton Farm which was chosen for the following reasons:

i) The colony was large and long-established (Lord Maclay pers. comm.) with nests occurring at a high density (c.305 nests/ha). The rookery was also located adjacent to the farm buildings so the birds were relatively accustomed to the movements of people and would therefore be unlikely to desert the rookery if disturbed on a daily basis.

ii) The rookery was situated on private land which meant that equipment left *in situ* was less likely to be vandalised or stolen. In addition, the land owner did not 'shoot out' the rookery each year which would cloud any conclusions drawn from comparative reproductive data as well as possibly affect the nesting pattern of adults within the colony.

iii) The presence of a small hill within the copse reduced the height of tower that would be required to produce a vantage point for the hide to overlook the nests.

iv) The copse contained several tree species, both coniferous and deciduous. This would permit an intra-colonial comparison of breeding performance in different tree species as well as providing the birds with an increased variety of material for nest construction.

4.3.2. The Tower

In order to study nest building behaviour it was necessary to observe birds at canopy level. To achieve this, a hide was constructed on top of an aluminium tower. The hide would remain in place for over two years so necessitating a structure that was strong and well secured. The selected site for the tower was on top of a hillock in the centre of the colony. The chosen site had a high density of nests in the immediate vicinity of the intended site, ensuring that there would be every opportunity to observe building at several nests during the spring.

Figure 4.1 shows the tower and hide which were erected in early February 1987. It can be seen that the tower is built in stages with interrupting platforms at seven foot intervals. Using a standard civil engineer's theodolite, the required height was calculated to be 50 feet. To provide additional support against lateral movement in the upper storeys, the tower was guyed at 14 ft. using steel guy ropes to four stakes buried in the ground. A further four guys were attached 30 ft. up the tower and these were secured to neighbouring trees. The slack was taken up in all cables resulting in the tower being securely anchored at eight points.

The hide was built of marine plywood and varnished so as to minimise warping and rot. The base area, formed by two platforms at the top of the tower, was 1.8 x 1.4 metres. As can be seen from figure 4.1, the hide was a triangular prism, 1.8 metres long with an interior height of 1.7 metres at the apex of the triangular cross section. The fact that the long axis possessed sloping sides ensured that an oblique face was

Figure 4.1. The tower and hide at Milton Farm. The hide was at canopy level (50ft.) enabling detailed observations to be made of between 25-31 nests during the autumn and spring seasons.

presented to the wind, so reducing wind resistance and minimising stress to the structure. Eight 35 x 25 cm. viewing panels were cut out, three along each of the two long-axes, facing north-east and south-west respectively, and a single panel in each of the ends which faced south-east and north-west. In order to minimise disturbance to the birds by the presence of an observer, each panel was fitted with a one-way perspex window. Access into the hide was via a trapdoor situated in the bottom platform.

The site of the tower permitted detailed observations to be made on between 25 - 31 nests located 2 - 15 metres from the hide.

4.3.3. The Assimilation of Nesting Material

Preliminary observations of nest building behaviour made in March 1987 suggested that the mode of nest material assimilation could be divided into three distinct categories. These were collecting stealing and manipulating. The definition of these three categories is as follows:

Collecting. - The incorporation of nesting material that is brought from outside the field of view or is not seen to have been stolen.

Stealing. - The acquisition of nesting material by an individual from the nest of another pair.

Manipulation. - The rearrangement of material already in the nest from one site within the structure to another.

The relative frequency with which each category was observed to occur during nest construction was recorded for individual nests in the vicinity of the hide. Each strategy was then expressed as a percentage of the total observed building effort for that nest. Note that by definition, an item is only regarded as being stolen if it is actually observed as having been removed from another nest. Birds may therefore steal nesting material from outside the observer's field of view but as the source is unknown, it will be recorded as having been Collected. The result is that the observed % Collecting is likely to be overestimated and the % Stealing underestimated. Further details on the methodology of recording mode of material assimilation are given in Appendix 3.

4.3.4. Obtaining Nest Measurements and Reproductive Data

Throughout the year it was necessary to climb trees either to take measurements of intact structures or collect nests for analysis. Regular climbs were made during the breeding season to monitor the clutch size, hatching and fledging success of different pairs. In many cases, nests on outer limbs could not be physically reached. However, it proved possible to record reproductive data from such nests using a 40cm. square piece of reflective plastic mounted on the end of an aluminium pole. The pole was in three sections which could be screwed together; this facilitated carrying whilst climbing. The mirror was mounted on a hinge joint which permitted the angle of reflection to be adjusted so as to view the nest cup. Safety is obviously a major factor in such exercises so climbing was never conducted when alone and ropes and harnesses were used.

4.3.5. Trapping and Ringing Rooks

A marked population was necessary in order to provide information on the following two issues.

1) The degree of nest site fidelity shown by pairs a) between autumn and the following spring and b) between consecutive springs.
2) A possible sex-related difference in behaviour during nest building.

The results of monitoring marked birds are detailed in the following two chapters.

The major objective was to ring birds nesting in the vicinity of the hide. This would have been guaranteed by snaring birds on the nests beside the hide. However, this is not a proven method of catching rooks and regardless of success rate, would be costly in terms of time and potentially harmful to the snared birds, which might subsequently desert the nest. A more reliable method of trapping rooks is the use of walk-in traps. These were sited in feeding fields adjacent to the rookery in order to try to ensure that the birds caught were those nesting in the study colony. The principle trap site was the sileage field 150m east of the rookery. The design used was that favoured by Green (1981) which is basically a cage made of 25mm mesh 'chicken' wire measuring 2m square and 1m tall. Access for the birds was via two tapering tunnels, each with an entrance span of 50cm and height of 25cm, narrowing to an inner arch of 15cm span and a height of 25cm. The end of the each tunnel was fitted with a one-way trap door. When the trap was set, the doors were propped open with a length of wire. The first birds entering trap would knock away this support and the presence of rooks within the trap then served to attract further birds (Green pers.comm.). These could enter the trap by pushing open the door but could not then use it to leave. A crawl flap, cut in one of the sides not incorporating a funnel, provided access for the removal of birds.

The trap was checked in the early morning and then again either in the afternoon or early evening. On days of heavy rain, the traps were not set to prevent birds getting their feathers waterlogged and becoming chilled. The majority of trapping was undertaken around the time of the breeding season, from February to June. In 1987, I attempted to extend the trapping season through the summer and autumn, positioning the traps where I noted large numbers of birds feeding. No birds were caught during this period and I am in agreement with Feare et al.(1974) and Green (1981), who state that rooks can only be caught in walk-in traps between March and June.

In addition to rooks, the following species were caught in small numbers; jackdaws, *Corvus monedula*, carrion crows, *Corvus corone* and a single lesser black-backed gull, *Larus fuscus.*

Trapped birds were ringed, weighed and had their wing length and head and bill length measured before being released. A fuller description of this process is given below.

Ringing: - Birds were individually marked with colour rings made from 'Darvic' plastic. The ringing programme incorporated six colours; red, yellow, dark blue, green, white and orange. Each bird had a single ring on its left leg and two on its right. With six colours this meant that there were 216 possible three-ring permutations.

Weighing: - The bird was weighed in a bird bag suspended from a spring balance. The bag was weighed again after the bird had been measured and released so that the weight of the bird itself could be calculated by subtraction. All bird weights were recorded to the nearest gram.

Head and Bill: - This measure was obtained using a pair of sliding callipers and is defined as the distance between the most posterior extremity of the cranium and the tip of the bill. The measurement was recorded to the nearest millimetre.

Wing Length: - This was obtained by sliding a wing rule beneath the folded wing held at ninety degrees to the body. The wing was then aligned along the edge of the rule and the distance between the carpal joint and tip of the longest primary feather measured to the nearest millimetre.

A summary of the morphometric data collected from trapped rooks is presented in Appendix 1 at the back of this thesis.

4.3.6. Monitoring Rookery Attendance

In the autumn of 1987, the monitoring of rookery attendance was confined only to the periods when I was in the hide collecting behavioural data. This totalled approximately fourty-eight hours of continuous recording in the combined months of October and November.

This method of recording rookery attendance is unsatisfactory on two accounts:

1) It was biased in terms of the time of day in which attendance was scored. Since I was in the hide to make observations on autumnal behaviour, I concentrated my sampling periods on dawn and dusk when rooks were most likely to be attendant. This will produce an artificially high score of attendance.

2) Forty-eight hours represents only a very small fraction of the total number of daylights hours during the months of October and November. A far more long-term method of monitoring is necessary in order to get a better idea of the birds' diurnal attendance pattern over consecutive months.

An instantaneous method of sampling (Tyler 1979, Martin & Bateson 1986) is suitable for such prolonged sampling. To achieve this, I built an automatic timer, (Rutnagur, Burns & Hansell 1989 - see Appendix 2), designed to repeatedly release a camera shutter at predesignated, fixed time intervals. Automated time-lapse photography has proved to be a useful method of collecting data (Mudge, Aspinall & Crooke 1987) since it can sample for very long periods with minimal disturbance to the subjects. Incorporated into the circuitry of the timer is a light-dependent resistor. As the light level falls, resistance in the circuit rises and the solenoid operating the camera shutter becomes inoperative. As the light level rises, resistance falls and once again the solenoid becomes operative. This system ensures that the timer continues its reiterated cycle but that the camera is only triggered during daylight hours.

The camera was set up in the hide and positioned so as to take a frame of a section of the rookery at canopy level. The timer was set to expose a frame at half-hour intervals. This means a standard 35mm, 36 exposure black and white film would last between twenty-four and seventy-two hours depending on daylength and thus the time of year. In the corner of the frame was suspended a large-figure digital clock which indicated the time of day at which the exposure was taken, as well as verifying that the preset timer was functioning correctly.

A fully exposed film was then developed and printed as a contact sheet. The presence or absence of birds was noted against the time of day to the nearest half-hour. For example, birds in frame at 1017 were scored as a positive attendance in the period 1000-1030. Several films exposed in the course of a calendar month provide several samples within each half-hour period. Attendance was expressed as the proportion of frames of each half-hour sample in which the birds were present. For example, if four out of eight frames taken between 1000-1030 in the month of October contained birds in picture, the calculated attendance during that period would be 0.5.

The results and discussion of rookery monitoring are presented in the following chapter and a copy of the published short communication detailing the timer design comprises Appendix 2 at the back of this thesis.

4.3.7. The Bow-Caw Display

The function of the bow-caw display was investigated by recording the rate and context in which the behaviour was observed.

The display, as the name suggests, involves the bird emitting a harsh *'kaar'* as it tilts forward on its perch with its neck slightly lowered. During the caw, the wings are often slightly lowered and spread, and as the bird bows, the tail is raised above the horizontal with its feathers fanned. I have observed both the intensity and the frequency of the display to vary although my investigation into the function of the display is confined solely to variation in call frequency in relation to season, pairing and group size.

5. THE AUTUMN RESURGENCE OF SEXUAL BEHAVIOUR

5.1. Introduction

5.1.1. The Proposed Adaptive Functions of Autumn Sexuality in the Rook

> "birds like our own rooks, leave their breeding places in autumn; and also, before departing, regularly repair their nests, carrying up sticks, sods etc. to fortify them against the violence of the winter storms. This indicates a very remarkable degree of prospective contrivance, irreconcilable, as it appears to us, with the common theories of instinct."
>
> (from the 'Architecture of Birds', 1831)

A period of sexual behaviour mid-way between breeding seasons seems paradoxical since there is a great deal of effort and time devoted to reproductive behaviour with no prospect of it resulting in reproduction. Autumn sexual behaviour is by no means unique to rooks, Morley (1943) reviews documented accounts in seventy British species, though in her own words she describes the autumn sexual behaviour of rooks to be, "developed to a greater extent than possibly any other British bird".

Lincoln and Racey (1980) established the physiological causation of the autumn resurgence in sexual activity, showing it to be linked to increasing concentrations of gonadotrophic hormones. The resulting breeding-related behaviour is well documented, yet the literature fails to support proposed adaptive explanations with field-based results. Harding (1847) first reported birds carrying twigs to the nest in the months of September and October and Brown (1928) suggested that the autumn may be a period of nest reconstruction. Coombs (1978) describes there being "frequent autumn nest-building activity", recording days in September and October when nest material is brought to the nest. The same author also expresses an opinion that the autumn period is one of nest site selection; a view shared by Ian Patterson (pers. comm.) and the Reverend E. Peake (1928). In the same year, the Reverend E.U. Savage proposed an alternative explanation for the observed autumnal behaviour, though as far as I am aware, this did not form the basis of a rift in the Anglican church. Savage suggested that this was the period when pair bonds were formed and that aerial displays were part of courtship. Richards' (1976) observations on his captive colony appear to support this suggestion by noting that his birds usually paired in the first few weeks of October.

In summary, the literature proposes three distinct adaptive functions to account for the observed autumn resurgence in sexual behaviour. These are summarised below:

1) That it is a period of nest refurbishment.
2) It is a period of pair-bond formation
3) It is a period of nest site selection.

Autumn nest refurbishment may be adaptive on two counts: a) If there is an energetic cost to building an entirely new nest, then this cost could be avoided by undertaking a period of nest maintenance midway between breeding seasons to ensure its persistence over consecutive years. b) Refurbishing the nest in the autumn may allow pairs to nest early in the spring since renovated nests would require minimal building to prepare them for eggs. Early breeding is considered an advantage because it increases the post-fledging survival of the young by ensuring a longer growth interval between fledging and the months of summer food shortage (Feare et al. 1974).

The selection pressure to breed early is also an adaptive explanation to account for the two other proposed functions of autumn sexuality, namely nest site selection and pair-bond formation. It may be true that since all three strategies would allow the prompt initiation of mating and breeding in the spring, they may all be adaptive features of the autumn resurgence of sexual activity.

5.1.2. Aims Behind an Investigation into the Adaptive Function of Autumn Sexuality.

Throughout this thesis, the central issue governing the study of both nest structure and building behaviour, is an assessment of the biological cost incurred by rooks in the building of a nest. The recorded incidents of rooks undertaking nest building in the autumn can be used to test between the predictions of the cheap and expensive perspectives since autumn refurbishment would indicate that the nest was a valued and 'costly' part of the spring reproductive effort. The extent of this cost may be lessened by a period of nest maintenance in the autumn. A full description of the predictions of the Cheap and Expensive hypotheses relating to autumn sexual behaviour are the subject of the following section. The major objective behind studying the autumn resurgence of sexual behaviour was to study the extent of nest building carried out in this period and incorporate the results into my evaluation of the biological cost of nest building. The literature also documents other facets of breeding-related behaviour apparent in the autumn and, in addition to investigating the extent of autumnal building, the behaviour of individuals at the nest site during the season was studied, in an attempt to discern whether birds were using it as a period of pair-bond formation, nest site selection or both.

5.1.3. The Cheap/Expensive Approach Applied to Autumn Sexual Behaviour

The Cheap and Expensive hypotheses make polarised predictions on certain features of autumn sexual behaviour which are summarised below.

Expensive

1) There is refurbishment of the nest to ensure its persistence until the start of the following breeding season.
2) There will be a high record of nest attendance indicative of substantial commitment to the nest site.
3) There will be high vigilance against stealers of nesting material or usurpers of the nest site.
4) Regular ownership: pairs investing time and energy in the maintenance and vigilance of the nest during the autumn will tend to utilise the same nest from autumn to spring the following year.

Cheap

1) There is no refurbishment or additional construction to the nest.

2) There is a low record of nest attendance during the autumn period.

3) There is little evidence of vigilance or aggression related to territoriality.

4) Pairs do not exhibit nest site fidelity between spring and autumn.

This chapter presents the results of field-based studies which are aimed at determining which set of predictions are a better description of autumn sexual behaviour in the rook. It thereby attempts to discern whether the autumn functions mainly as a period of nest refurbishment, pair-bond formation or nest site selection.

5.2. Materials and Methods

Much of the methodology used in studying autumn sexual behaviour was described in chapter four. This section serves to supplement information provided in the previous chapter and provide further detail on the question which the method was designed to address.

5.2.1. The Extent of Autumnal Nest Refurbishment

1987: - The primary aim of the first full autumn season was to quantify the extent of building by recording the incidence of the three defined modes of material assimilation (see section 4.3.3.) in the refurbishment or construction of the nest. Nests were individually labelled according to which panel of the hide they were viewed through. For example, if there were five nests visible through panel four, they would be labelled 4A to 4E respectively. In the autumn of this year, it was possible to record the relative frequency of collecting, stealing and manipulating for twenty-five nests in the vicinity of the hide. Observations were carried out at canopy level between 2/10/87 and 14/11/87.

1988:- The second autumn season adopted a slight change of approach whereby the emphasis shifted to contrasting the level of building in the autumn with that occurring in the spring. Two comparative studies were conducted; i) a marked twig experiment and ii) a photographic representation of the extent of building in the two seasons.

Marked Twig Experiment. This experiment was carried out in two parts, the first was undertaken in the autumn of 1988 and the second in the spring building season of 1989. Twigs were marked by wrapping either one or two bands of black insulating tape around their diameter. Doubly-banded twigs were placed horizontally on the top layer of the nest outer ring, whilst singly-banded twigs were inserted vertically into the outer ring until the bottom of the band was level with its height. These marked twigs acted as reference points denoting the height of the outer ring at the start of the autumn and spring seasons.

The subsequent addition or loss of material over these periods was recorded as a change in height of the outer ring, above or below the band of the marked twig. A minus reading indicated a reduction in the level of the nest (assuming that the marked twigs had not been actively pulled up by the birds), and a positive figure was indicative of an increase in the height of the nest in relation to the marker (assuming the marked twig had not been actively pushed further into the structure). Positive figures would therefore be a quantitative representation of building activity.

Between 30/9/88 and 13/10/88, marked twigs were placed in ten separate nests. Details of the number of twigs and their orientation in each of the structures are summarised in table 5.1.

The insertion of marked twigs into nests before the spring building season, was carried out between 1-3 March 1989. The rationale was identical to that of the

Table 5.1. The number and orientation of marked twigs placed in rook nests by the experimenter at the start of the autumn and spring seasons. 'Nest Number' refers to the mapping system described in section 3.2.2., the number referring to a specific tree in the rookery and the letter corresponding to one of the nests mapped within it.

Nest Number	No. Horizontal Twigs	No. Vertical Twigs
AUTUMN		
95A	1	1
95B	1	1
50B	2	2
50C	1	4
53B	2	0
53C	2	2
76C	0	2
76D	0	2
76E	0	2
76I	0	2
SPRING		
50A	0	3
50B	0	3
53A	0	3
76A	0	3
76B	0	3
76C	0	3
79A	0	3
79B	0	3
79C	0	3

autumn period although only vertically positioned twigs were used. On the basis of observations of nest building in the previous two springs, it was considered highly unlikely that horizontally placed twigs would be traceable because twigs on top of the outer ring will almost certainly be moved, buried or stolen.

Photographing Nest 5C. To act as an illustration of the comparative building effort in the spring and autumn, photographs were taken of a single nest, 5C, at the beginning and end of both seasons. All pictures were taken with 35mm, HP5 black and white film using a Canon A1 fitted with a 200mm lens. The photographs taken at the beginning and end of each period are shown in section 5.3.1.

5.2.2. Rookery Monitoring

In section 4.3.6., I described an automated method of monitoring rookery attendance. In resumé, daylight hours are divided into half-hour blocks, against which is recorded the diurnal pattern of rookery attendance. By sampling throughout autumn, winter and spring, it is possible to make a comparison in changing attendance patterns over consecutive months. Attendance at the rookery reflects the temporal investment to the nest site and therefore low and high levels of attendance in the autumn period are predicted by the Cheap and Expensive hypotheses respectively. Information on monthly changes in the pattern of rookery attendance is directed at answering two questions.

1) Is the autumn characterised by a change in the time of day when rooks are attendant at the colony compared to the months of late summer and winter?

2) Is the level of attendance in the autumn as great or less than that of the building season in early spring?

Section 5.3.2 presents the results of monitoring rookery attendance between August 1988 and April 1989. Note that in addition to this automated method, the arrival and departure of birds were always recorded during observational visits to the hide. This served to check if the diurnal pattern of attendance apparent in the photographic record was supported by personal observation. Observation times in the hide during the autumn totalled 49 hours in 1987 and 29 hours in 1988.

5.2.3. Bow-Caw Displays

Section 4.3.7. briefly described this behaviour. Several authors (Marshall & Coombs 1957, Coombs 1978, Bain 1982) have stated that bow-cawing functions as a self-advertisement display and that the frequency and intensity of bow-cawing peaks in the early spring and during the autumn. Taking the literature's proposed function at its word, the frequency of bow-cawing may be an indicator of the level of territorial or pair-bond related behaviour exhibited during the autumn since both behaviours require a high degree of self-advertisement. Consequently, if this season is a period of nest site selection or pair-bond formation, the expectation is that the rate of display should be high. Recording the rate of bow-cawing alone does not distinguish between these two functions, however a distinction may be possible by recording the variation in display rate in different contexts.

By comparing the rate of display between paired and unpaired birds, it is possible to draw some conclusions on the role of bow-cawing in relation to pair-bond formation. Alternatively, an investigation of the effect of group size on display rate would reveal an association between bow-cawing and territoriality.

The method and rationale of collecting data on the rate of bow-cawing may be summarised as follows.

1) To compare the display rate of individuals in the autumn and during the building

period in spring:- If the autumn is a period of mate selection and pair-bond formation, then it should be typified by a higher display rate than the spring. Individuals that secure their pair-bond and/or nest site in the autumn, will be at an advantage if there is a selective pressure favouring prompt mating and breeding in the spring.

2) To compare the rate of displaying by unpaired birds with that of paired birds:- If the function of the autumn period is for unpaired individuals to find a mate and establish a pair-bond, then one might predict that the rate of display in unpaired birds will be significantly greater than that of paired birds. There is a possible confounding effect that may cloud such a simple relationship since bow-cawing may also serve to consolidate an existing pair-bond. In this case, one would predict a comparable, high display rate for both paired and unpaired individuals.

3) To examine the effect of group size on display rate:- If bow-cawing is a demonstration of territoriality, then there will be a difference in the display rate between lone or paired birds, and birds in groups.

Several conspicuous perches were visible from the portholes of the hide which delimited a group of birds from others in adjacent trees. The same perches were observed in both autumn and spring so eliminating any bias in display rate arising from a difference in display location.

During each sample the variables collected were; Time, Date, Sample Duration (secs.), Number of Displays, Number of Birds in the Group, Number of Individuals in Group Displaying and whether these individuals were obviously Paired or Unpaired. Samples were started by the random selection of one of the perches and were terminated the instant any individual joined or left the group under observation. The logic of terminating the sample at this time is so as to be able to disregard the effects of a bird arriving or leaving the vicinity of a displaying rook. Display rate is defined as the number of displays per bird per minute (no. disp./bird/min.). This is calculated from the raw data by dividing the number of displays recorded in a sample by the number of individuals in the group that were displaying. This gives you the average number of displays per displaying bird (D). The rate per minute is then calculated by multiplying D by 60/Sample Duration.

The calculations and results of bow-caw rate in relation to season, pairing and group size are shown in section 5.3.3. Additional descriptive statistics for the variables measured are given in Appendix 3.

5.2.4 Movements of Marked Birds

The intention was to associate marked birds with particular nests in the autumn and record whether the same individuals returned to that site in the spring. This would provide a means of quantifying the extent of nest site fidelity between the two seasons. To recap, the Expensive hypothesis predicts that this should be high whereas conversely, the Cheap hypothesis predicts it to be low.

5.3. Results

5.3.1. The Extent of Autumnal Nest Refurbishment

Autumn 1987

This season was characterised by a complete absence of any nest construction. In 49 hrs. of observation from the hide between 2 October and 14 November 1987, birds were never seen to collect or steal twigs. However, on several occasions birds were seen manipulating nesting material; e.g. 23/10 (1512 hrs.), 26/10 (1605 hrs.) and 3/11 (1635 hrs.). These were single acts unlike the repeated manipulation that occurs in the spring. Three birds were also seen breaking twigs off from the tips of branches on 9/10, these were held in the beak for a few seconds before being dropped. Twice pairs were seen to pass nesting material from one to the other

(23/10 and 6/11) though this was not subsequently incorporated into the nest.

Such observations represent the total extent of building behaviour seen in the first autumn of the study with only singular, infrequent manipulations of nesting material being apparent. The collection or stealing of material was never observed.

The aim of the following autumn (1988) was to confirm the lack of autumnal building noted in 1987 and demonstrate this by designing experiments that would contrast the lack of building in the autumn with the primary building period in the spring.

Autumn 1988

Marked Twig Experiment

Table 5.2 summarises the position of marked twigs relative to the height of the outer ring at the end of the autumn and spring building seasons of 1988 and 1989 respectively. Negative figures represent a drop in the level of the outer ring in relation to the marked twig, whereas positive figures represent an increase in outer ring height. A zero indicates no change. The post-autumnal measurements of twig position were taken between 16-18 November 1988 and the post-building measurements in the spring, were made on 17 April 1989 when most females were incubating.

In the autumn, most of the horizontally placed twigs were missing from the nest by mid-November. If the general trend is toward the loss of nesting material (see section 3.3.3.), then it is likely that twigs loosely placed on top of the nest fell or conceivably, were removed.

The vertically-positioned twigs, by virtue of being more securely embedded, were not so vulnerable to the effects of wind or birds and were generally still present in

Table 5.2. The mean change in height (in cms.) of the outer ring of the nest cup in relation to horizontally-placed twigs (Height A) and vertically-placed twigs (Height B). Recordings were made after the autumn and spring building periods on the 16-18 November 1988 and 17 April 1989 respectively.

Nest Number	Height A	Height B
AUTUMN	(cms.)	
95A	0	- 0.4
95B	*	- 2.9
50B	*	- 1.4
50C	0	+ 1.4
53B	*	--
53C	*	- 1.2
76C	--	- 1.2
76D	--	0
76E	--	*
76I	--	- 0.4
SPRING		
50A	--	*
50B	--	*
53A	--	*
76A	--	*
76B	--	*
76C	--	*
79A	--	*
79B	--	*
79C	--	*

KEY: * = Twig not traced; -- = No marked twig inserted into nest mid-autumn. The trend shown by the autumn set of results is that there was little change in the height of the outer ring over the autumn. Six nests showed a slight reduction in outer ring height, two nests showed a slight increase, one nest showed no change and no marked twigs were traceable in the last. The recorded changes are small and may be unassociated with the actions of the birds themselves. Instead they may have been caused by the movement of branches supporting the nest, flattening by rain or disturbance by wind, all of which will cause the precise position of the markers to be altered.

An indication of whether the observed differences in outer ring height could be attributable to the sources of 'background movement' mentioned above, may have become clearer when autumn results were compared to the spring. Large positive changes in nest height in the spring period would have illustrated that the changes noted in the autumn were minor and architecturally insignificant. Unfortunately, the comparative experiment did not prove successful. As table 5.2 shows, no marked twigs could be found in nests in mid-April when the birds had completed building. I suggest that this is caused by the very high turnover of twigs positioned at the top of the nest in the spring and the fears over relocating horizontally placed twigs proved applicable to vertically positioned ones. Twigs are continually being repositioned (manipulated), built upon and stolen with the result that even if they were still present in the structure, they may have become deeply embedded within the nest and therefore not visible.

In summary, the placing of marked twigs into the nest structure did not fully succeed in demonstrating the lack of building in the autumn as I had intended. I attribute the failure to find marked twigs in mid-April to the fact that there is so much building activity resulting in the marked twigs being moved from their original position. This issue will be discussed further in section 5.4, but the benefit of hindsight does suggest improvements in the method most notably to ensure the persistence of the markers through the spring.

If markers are to be used in an attempt to quantify the extent of building activity in the autumn and spring periods, then they need to be made a permanent feature of the structure. Vertical marked twigs could be cemented to the side of the nest with an epoxy resin. This would at least ensure that its position was not altered, though it may it may conceivably be broken or covered. It would not be possible to discount that by altering features of the nest one would also alter the behaviour of the bird.

Several markers would be necessary to act as reference points of nest height because nests tend to be far from level and an external reference at one part of the nest may not be indicative of the height of the structure at another. This same problem confounds attempts to make direct measurements of nest height.

Photographing Nest 5C

Even if the difference in the amount of building undertaken in the autumn and spring periods has proved hard to quantify directly, it is possible to illustrate the comparative lack of building in the autumn. Figure 5.1 shows nest 5C on 14/10/88, two weeks into the autumn period, and on 15/11/88, at the end of the autumn period. The point to notice is that the nest cup is still flattened with no addition of material to the outer ring, the part of the nest most conspicuously built upon in the spring.

By comparison, Figure 5.2 shows the same nest on 3/3/89 before the start of the spring building season and on 15/5/89 when the completed nest contained two eggs. The side closest to the camera has been substantially built upon (by about 14cm) resulting in the formation of a central nest cup not visible from this camera angle. This series of photographs illustrate that the addition of twig material to the outer ring was not a feature of the autumn season.

Figure 5.1. Photographs illustrating the lack of structural renovation to nest 5C over the autumn period. Photograph A was taken on 14/10/88, approximately two weeks into the autumn resurgence of sexual activity, and photograph B was taken on 15/11/88 at the end of this period. The white arrow indicates a scar on one of the supporting branches which serves to act as a reference point against which to compare nest height.

A

B

Figure 5.2. Photographs of the same nest (5C) shown in figure 5.1, illustrating the renovation of the nest in the spring to a condition fit for laying a clutch. Photograph C was taken on 3/3/89 before nest building began in that year and photograph D shows the nest on 15/5/89 when it was complete and contained 2 eggs (not visible). The white arrows denote the same reference point as in the previous figure though in photograph D it is slightly obscured by twigs. Note however, that in this photograph the height of the outer ring has increased (by approximately 14cm.) such that it is now above the height of the reference point. The addition of twigs has resulted in the photograph only showing a view of the side of the nest with the position of the cup now facing away from the photographer.

C

D

5.3.2. Monitoring Rookery Attendance

Figure 5.3 shows the pattern of rookery attendance for the birds at Milton Farm from August 1988 to April 1989. Before drawing conclusions from the presented results, it is necessary to state two potential sources of error in the method.

1) The angle of vision covered in each frame represents only a certain sector of the rookery and therefore it is possible that birds may be at the rookery but not in the field of view.

2) Frames are taken at half-hour intervals, it is possible that birds may arrive and depart the rookery between two exposures.

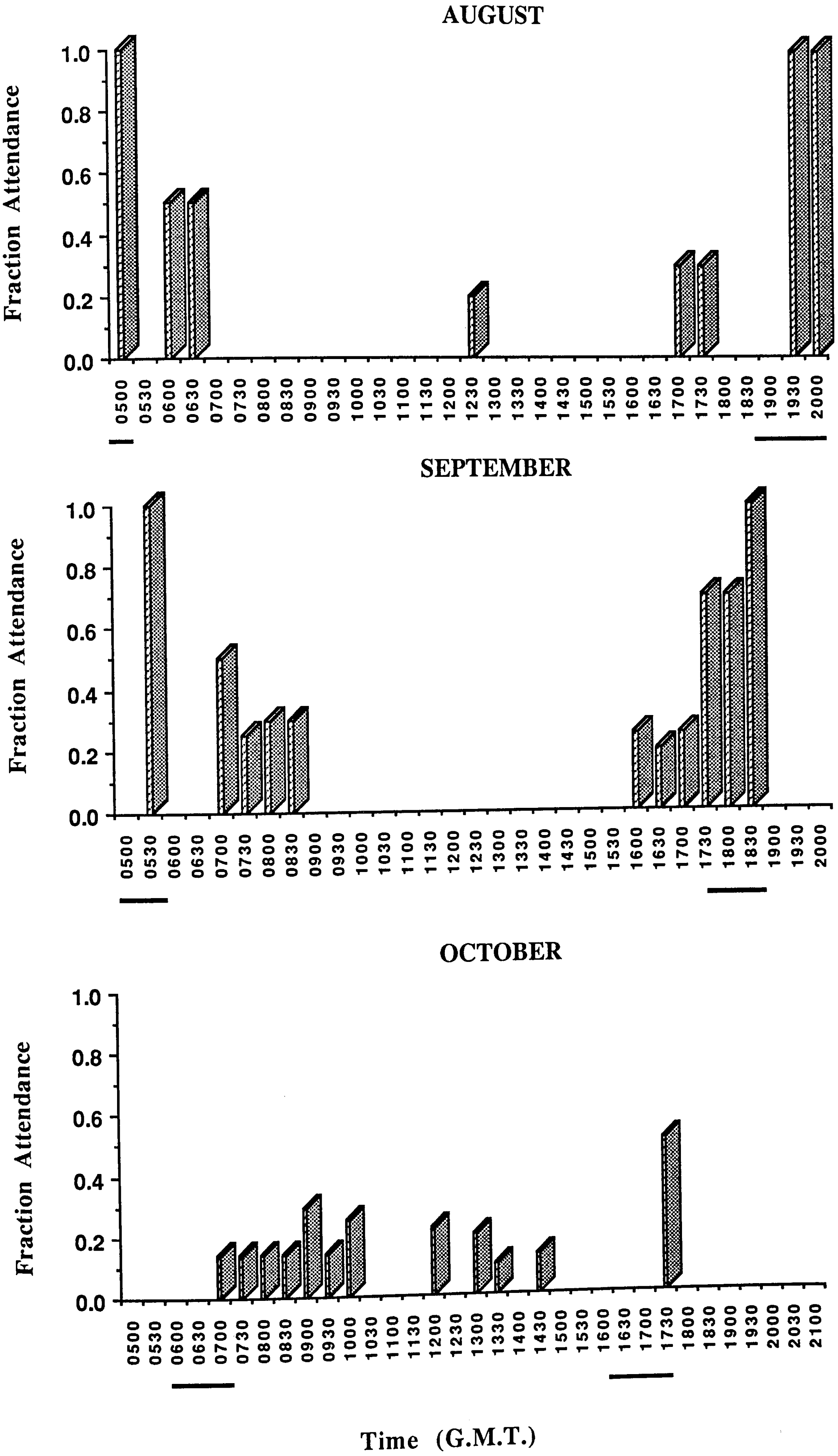
Both these sources of error will underestimate the level of rookery attendance, however I feel the effect of these errors is diminished by the tendency of birds to either attend the rookery in large numbers or not all. The camera was not positioned arbitrarily, but pointed at a perch that is commonly the first used by birds when landing at the rookery. Another reassurance is that frames which record birds as present normally have several (more than 5) birds in frame and so the solitary visitor to the rookery producing a spurious positive result is not a major source of error.

Where necessary, the x-axis has been standardised to Greenwich Mean Time (GMT). The bars below the half-hour blocks indicate the change in sunrise and sunset times during each month at 56N latitude and 4W longitude.

The Pattern of Attendance

In August, attendance is largely confined to the hours around sunrise and sunset. The birds are still using the site as an overnight roost and rarely visit the rookery during the day. The literature reports this pattern of attendance to be typical of that

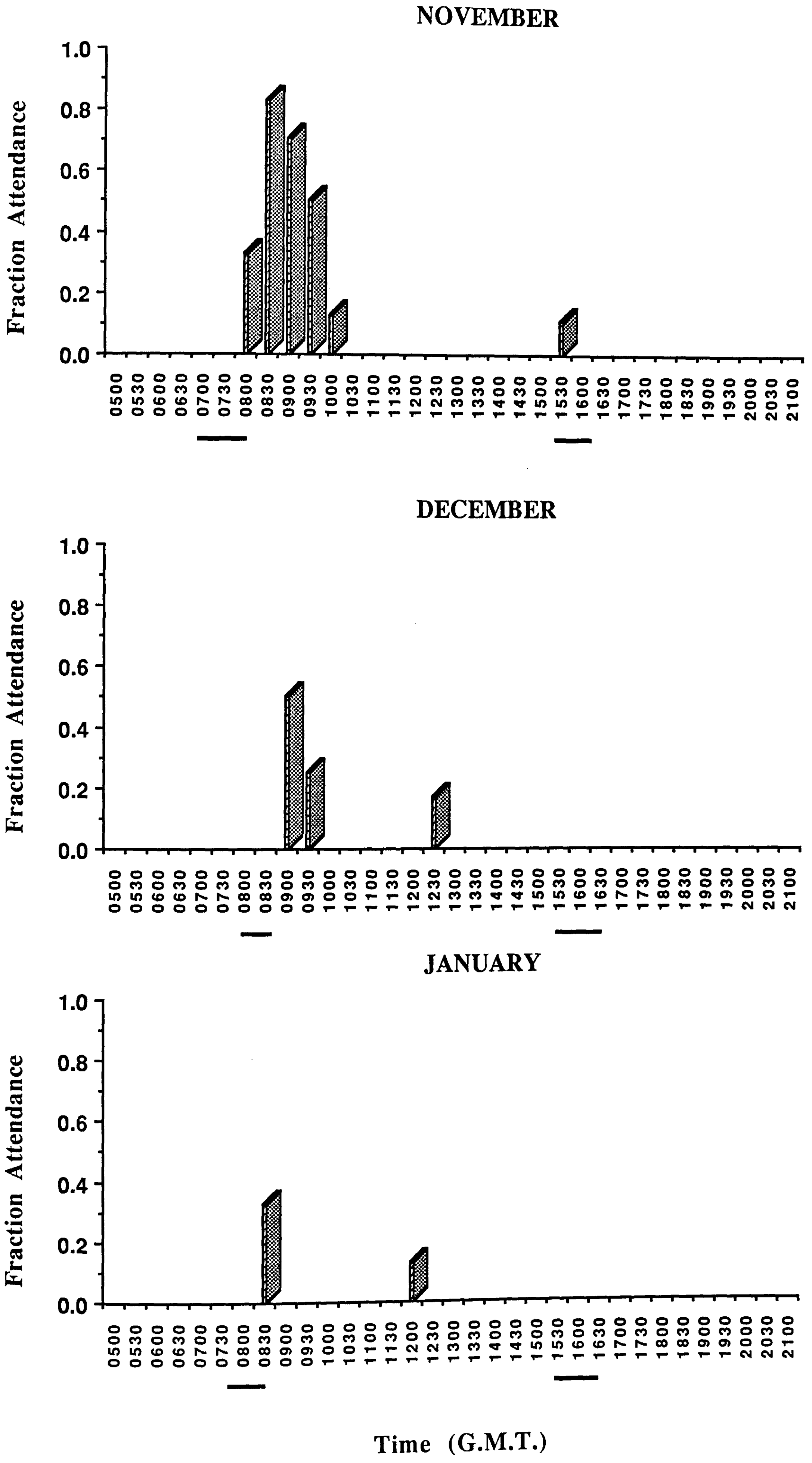
Figure 5.3. The diurnal pattern of rookery attendance between August 1988 and April 1989 as measured using an electronic photographic recorder (see text for details). Daylight hours are shown divided into half-hour blocks along the horizontal axis and the proportion of frames within a time block when birds are present (i.e. fraction attendance) is shown on the vertical axis. The horizontal bars beneath the time intervals represent the change in sunrise and sunset times (calculated for 56N lat. and 4W long.) over the course of the respective month.



AUGUST

SEPTEMBER

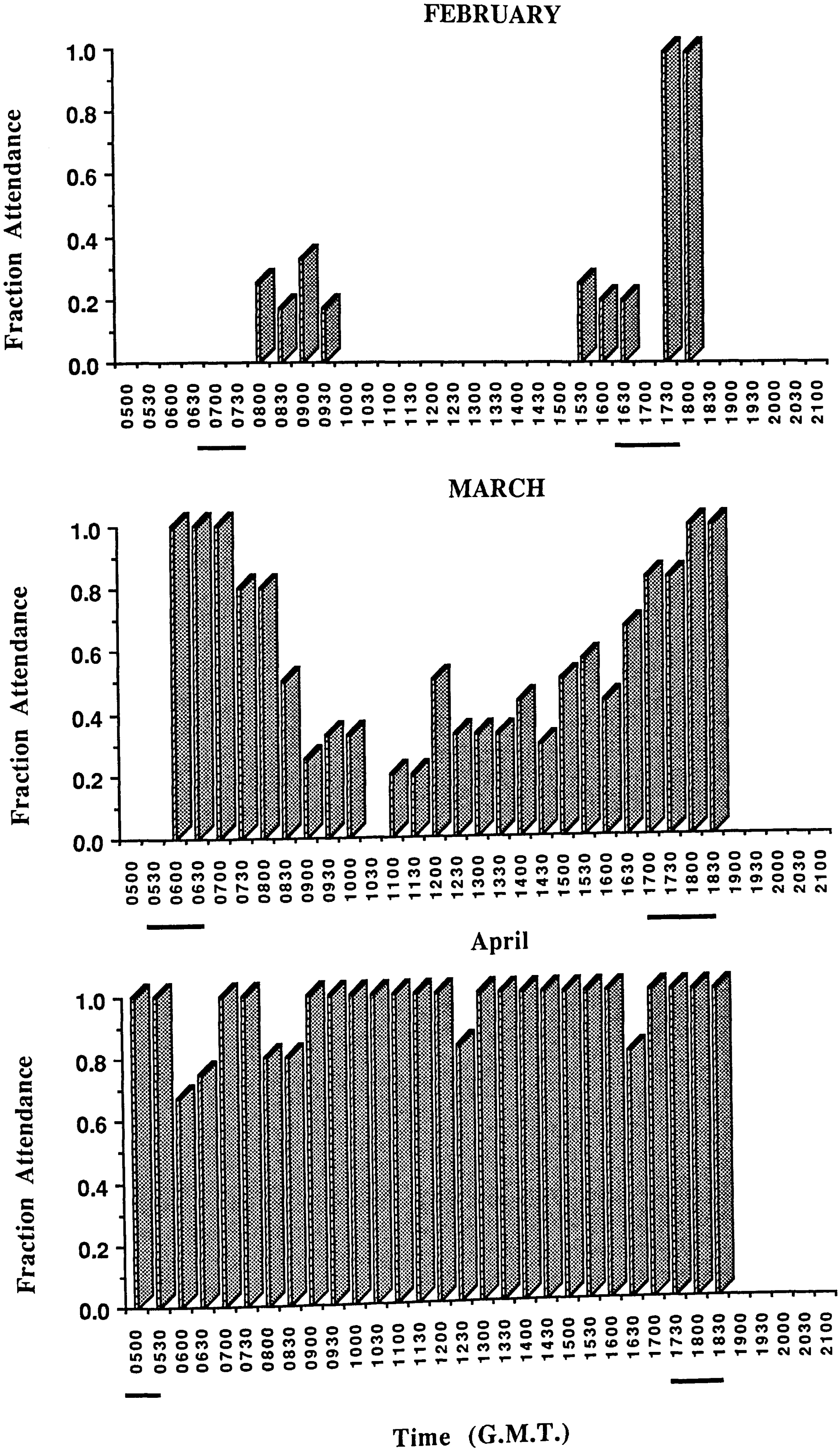
OCTOBER



NOVEMBER

DECEMBER

JANUARY


FEBRUARY
MARCH
April
Fraction Attendance
0.0
0.2
0.4
0.6
0.8
1.0
0500
0530
0600
0630
0700
0730
0800
0830
0900
0930
1000
1030
1100
1130
1200
1230
1300
1330
1400
1430
1500
1530
1600
1630
1700
1730
1800
1830
1900
1930
2000
2030
2100
Time (G.M.T.)

throughout the summer months following the breeding season which ends in late May (Coombs 1961).

A similar pattern emerges for September. It would appear that the birds briefly depart the rookery immediately after sunrise for about an hour. They then return for any length of time between 0.5 - 1.5 hours before finally leaving the rookery until evening. Rooks return at any time up to one and a half hours before dusk, the precise time on each day apparently being under the influence of light intensity (Swingland 1976). It is at this time that a great deal of sexually associated behaviour is apparent.

October, the month of peak autumnal sexual activity, is characterised by a pronounced change in attendance pattern in comparison with the two previous months. The pattern is one of intermittent attendance at a low frequency, throughout the day with a conspicuously high incidence of attendance just before dusk. What is noticeable from the contact sheets produce from negatives in this month and subsequent months until February, is that birds are not present when the shutter fires for the first time at dawn and the last time at dusk. My interpretation of these results is that birds have moved to a communal winter roost and are no longer overnighting at Milton Farm. The low levels of attendance spread out during the morning and early afternoon are, I suggest, indicative of an increased, albeit temporally sporadic attendance at the nest site. This may be for the purpose of prospecting for a nest site for the coming spring, or perhaps, the rookery is the focal point for displaying and attracting a mate. The major point I wish to emphasise, is that there is a definite change in attendance pattern at the rookery during October and this coincides with the period of peak autumn sexual activity.

November is the month when sexual behaviour noticeably declines. The pattern of attendance again differs from any of the previous months, with rooks regularly present during the early and mid-morning (between 0800 and 1030). The absence of birds at dusk confirms that they are no longer roosting at the breeding rookery (an observation also noted by Bain 1982). From observations in the hide made in both 1987 and 1988 (see section 5.2.2), I know that birds enter the rookery at, or just after, sunrise. They do not briefly return to the rookery at dusk as they had done in October perhaps indicating a declining interest in nest sites.

December and January show similar patterns of attendance, with birds visiting the rookery shortly after dawn and an occasionally observed brief return at midday. These months represent the interval between the autumn resurgence of gonadotrophic hormonal activity (September to November) and the active phase (February to April) where gonadotropic hormone levels reach the high concentrations necessary to control full redevelopment of the gonads (Lincoln & Racey 1980). It is important to note that the above months which are associated with low concentrations of sex-related hormones, are also characterised by very low levels of rookery attendance.

The February profile is similar to that of September in that birds visit the rookery at dawn and dusk. The presence of birds at the first exposure after dawn and the last before dusk indicates that the birds are returning to the nesting colony to roost overnight. This is supported by observations made from predawn visits to the hide during this month when it was noted that as February progresses, more and more birds are present in the rookery at daybreak.

March is the month when building begins and attendance is recorded at fairly high levels virtually throughout the day. I suggest that this pattern reflects birds continually coming and going from the rookery in the act of collecting nesting material. The important point is that this pattern of attendance is very different to that of October or November and the level of attendance at the rookery is far higher than for any of the months of winter and autumn. Rooks therefore undertake a major temporal commitment to the nest site in the spring but not in the autumn.

The final histogram of figure 5.3 shows the pattern of attendance in April and is characterised by the virtually constant presence of birds. By the end of this month, most females were incubating their eggs and were therefore tied to the rookery.

5.3.3. Bow-Caw Displays

In section 5.2.3 I outlined the aims of collecting data on the frequency of bow-cawing. A total of 78 hours were spent in the hide during the 1987 and 1988 autumns in an attempt to record the frequency of displays. Of this total, birds were present for just over twelve. Each year's data set is therefore relatively small so the results presented represent the calculations from the amalgamated data.

1) A comparison between autumn and spring display rates.- The calculated display rate (no. displays/bird/min.) for the autumn periods (n=58) was compared with the calculated display rate for spring 1988 (n=179). In addition, a comparison was made on the proportion of individuals displaying in each season (see Appendix 3).

The results show a highly significant difference in the display rate between the two periods ($U = 3421.5$ at $n_1 = 179$, $n_2 = 58$, $p < 0.0001$, Mann Whitney U test) with individuals displaying far more frequently in the autumn than in the spring.* Note that when sample sizes are large ($n_2 > 20$), the U value may be converted to a value of Z (Siegel p.123) and the table of the probability distribution of this test statistic consulted to see if the calculated result is significant at the level of 0.05. The original U value however, is quoted here and in similar Mann-Whitney tests with large sample sizes. This result suggests that the autumn is characterised by a more pressing need for self-advertisement. The observed high frequency of display is predicted if this season serves as either a period of pair-bond formation or nest site selection. The conclusion that birds display more frequently during October and early November does not separate the two hypotheses.

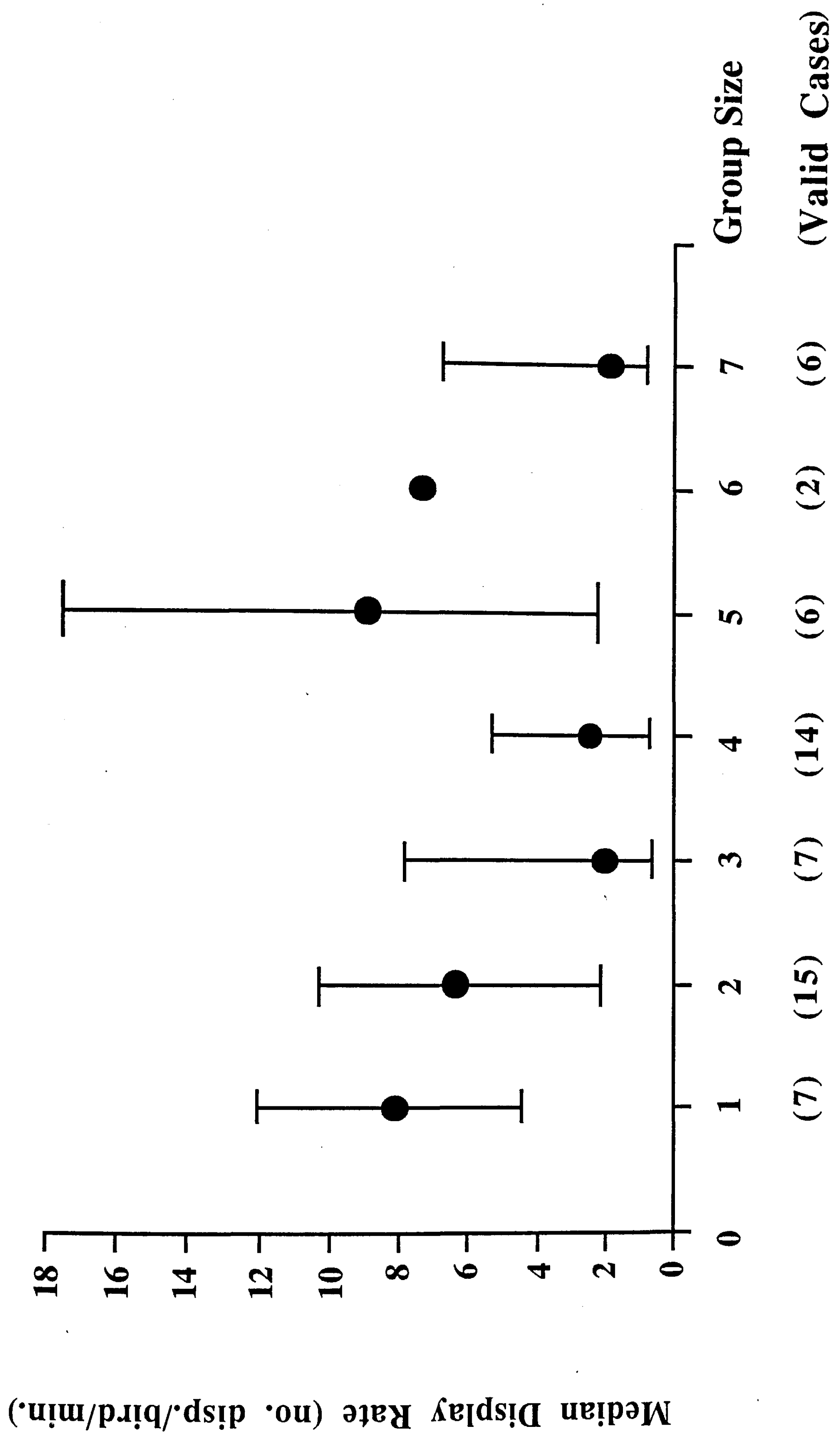
* Median Aut Disp. Rate = 1·88 disp/bird /min

Median Spring Disp. Rate = 0·65 disp. /bird. /min

2) Rate of display of unpaired birds compared to paired birds during the autumn. - Having established the autumn as being a period of self-advertisement, the question is therefore what purpose does bow-cawing fulfil? One of the hypothesised functions is that it serves to attract a mate and establish the pair-bond. If this were true, the expectation is that unpaired birds would display more frequently than paired individuals. If however, the behaviour has an additional function of consolidating an existing pair-bond then one might expect there to be no difference in the display rate between the two classes. Displaying birds were recorded as being obviously paired or unpaired and display rates were calculated for paired and unpaired individuals. The result of a comparison between the two classes in the autumn proved there to be no significant difference in the display rate between them (U= 218.5, P=0.75 Mann-Whitney U test, paired n=16; unpaired n=29). The congruity in display rate between paired and unpaired individuals suggests that bow-cawing is not unique to unpaired birds attempting to attract a partner, but may also be a behaviour shown by paired birds consolidating their pair-bond in the autumn period.

3) The effect of group size on display rate. - By testing for an effect of group size on display rate in the autumn period, I have attempted to examine a) whether solitary birds display at a higher rate than birds in pairs or in a group or b) if the converse is true, and individuals display more frequently when in groups than as solitary individuals. The latter may suggest some inter-pair conflict related to territoriality. Figure 5.4 shows the median display rate against increasing group size. Single and paired individuals, as well as groups of five or six birds were observed to display at relatively high frequency. Testing the data using a Spearman Rank Correlation, showed there to be no relationship between group size and display rate (r_S = - 0.210, n=45, P > 0.05). However, there are several cautions that need to be borne in mind before drawing any firm conclusions from this graph. First of all, as figure 5.4 shows, there is a great deal of variation around the median and this variation is not confined to those group sizes with small numbers of valid cases.

Figure 5.4. Median bow-caw display rate (no.disp./bird/min.) against increasing group size. The error bars indicate the 25% and 75% quartile range around the median.


Median Display Rate (no. disp./bird/min.)
0
2
4
6
8
10
12
14
16
18
0
1
2
3
4
5
6
7
Group Size
(7)
(15)
(7)
(14)
(6)
(2)
(6)
(Valid Cases)

Larger samples are required in all group sizes in order to examine more conclusively for a group effect on display rate. I repeat however, that the initial results suggest there to be no correlation between group size and display rate.

5.3.4. Movements of Marked Birds - Nest Site Fidelity

Low rookery attendance during the autumn meant that some pre-autumn aims were not fulfilled. This was the case with the monitoring of marked individuals within the colony. At the beginning of autumn 1988 I had ringed 80 individuals. In that same season I associated one marked bird with a nest, this being a male with the ring-code R Y/B on nest 3X (see section 4.3.5 for details of the ringing code and 5.2.1 for details of the method of nest labelling). This bird started building on the same nest in the following spring however, the structure was pulled apart on 22/3/89 and the bird disappeared from the vicinity of the hide. For this single example of a bird that consistently used the same nest from autumn to spring, I observed four marked birds that were seen building on nests in spring but had not been observed at the site in the previous autumn. These birds were ringed in spring 1988, the year before they were observed building in the vicinity of the hide in 1989. Five recordings do not constitute evidence at any level other than that of the anecdotal yet they do not support an expensive view which predicts there to be consistent attendance by a pair at a particular nest between the autumn and spring periods.

5.4. Discussion

On the basis of the literature which documented birds manipulating material on the nest during autumn, the initial objective was to assess the extent of autumn building and relate it to the Cheap/Expensive paradigm. The Expensive hypothesis predicts that nests are a valued resource and will merit autumnal maintenance to ensure their persistence to the following breeding season. It follows from this that the individuals which refurbish the nest in the autumn will occupy the same structure in the spring. The Cheap hypothesis states the reverse, that the nest is a low value commodity meriting no special attention in the autumn and is not therefore likely to be attended by the same pair in the following spring.

The major aim of studying the autumn period was to examine which of the above hypotheses was closer to the situation in a natural population. The bulk of the evidence from field studies support the Cheap perspective of nest value. The low levels of rookery attendance in autumn are in sharp contrast with the high levels of early spring and I suggest this to be indicative of a low level of commitment to the nest structure. Low autumnal attendance also reflects an absence of vigilance or aggression related to territoriality. October does however show an anomalous attendance pattern compared to the rest of the autumn and winter. Levels of attendance were recorded through much of the daylight hours (albeit at a low fraction) suggesting that the rookery is performing some function in autumn sexual behaviour, even if this is just as a focal point from which to display. During the autumn there also does not appear to be any refurbishment of the nest, since material was never observed to be brought to and incorporated into, the structure. The marked twig experiment, which was intended to quantify the difference in building effort between the autumn and spring periods, was not successful because markers were often not traced. However, the autumn part of the experiment showed there to be very little change in the height of the outer ring and no new material was apparent in any of the nests with marked twigs.

The pictures taken of nest 5C serve as further evidence of the lack of autumnal building illustrating the absence of fresh twig material added to the structure in this period compared to the spring. Furthermore, if the autumn was a period of refurbishment and building, one would not expect a decrease in nest numbers within the rookery during the autumn months but might instead predict there to be evidence of renovation of existing structures and perhaps some building of new nests. Evidence of nest renovation or construction in the autumn would suggest preparatory building to ensure prompt breeding in the spring. Reference to figure 3.3. shows the change in nest numbers at Milton Farm over the annual cycle. It can be seen that nest numbers continue to fall between September and November. The construction of new nests does not appear to be a feature of autumn behaviour and, as figure 3.6 shows, nests continue to deteriorate during this period. The continued decline in nest numbers and the deterioration of existing structures during the autumn were also features at the four Campsie rookeries (see figures 3.2 and 3.5). These observations do not conform to the idea that the nest is a valuable commodity.

The question remains as to what birds are doing in the observed incidents of them manipulating material in the nest. I suggest that this 'building' is totally gestural as it has no function in refurbishing the nest structure. Evidence for this idea had been described by Lincoln and Racey (1980) who noted birds often carrying pine cones. This is neither food nor nesting material but I suggest, another manifestation of display related to pair formation.

Having refuted autumnal building as being of significant architectural importance, the question is then which of the two remaining adaptive functions of autumn sexuality, pair-bond formation or nest site selection, best accounts for the observed sexual behaviour during the season.

There are many behavioural patterns seen in the autumn consistent with the idea that it is a period of pair-bond formation. For example, the frequency and prevalence of pursuit flights (see Coombs 1978), the food eliciting of females which Richards claims confirms the pair-bond, and on the basis of my own observations, the obvious association of individuals as pairs, both in the field and on the nest. All these indicate there to be some element of pair-bond formation occurring in the autumn however, my data on bow-caw display frequency comparing paired and unpaired birds, showed no difference in display rate. Two reasons may account for this, the first is the question of how accurately I assessed whether a bird was paired or not. An unpaired bird may be paired but simply not accompanied by its mate. Similarly two birds in close proximity need not be a permanent breeding pair. Unless the study is long-term, with most of the population marked and associations known between ringed or tagged individuals, such sources of error must occur. A second reason for there not being a difference in display rate between paired and unpaired birds may be due to the fact that the display fulfils more than one function; namely that bow-cawing may serve to consolidate an existing pair-bond as well as form one. If this is the case, then it would be expected that both paired and unpaired individuals would be observed to display at similar rates.

It is possible that the bow-caw display is not purely for the purpose of attracting or holding onto a mate. Subtle differences in intensity and posture may lead it to perform different functions. However, intuitively supportive of the assertion that autumn pair-bond formation would be a selective advantage, is the fact that the formation of the pair before the start of the actual breeding season may enhance the survival chances of the brood (Feare et al. 1974).

Ian Patterson has suggested that the autumn is used as a period in which unsuccessful pairs from the previous breeding season prospect for new nest sites. His analysis (unpublished) shows that birds that move nest sites, do not in turn do any better than birds which have stayed where they were. I did not have a sufficiently high proportion of my study population ringed to enable me to monitor the movements of large numbers of marked birds. Patterson's theory would suggest that a proportion of the population would be 'prospecting', that is visiting several nests, whilst the remainder would be relatively sedentary, faithful to the successful site of the previous spring. The low incidence of attendance at the Milton rookery does not support the idea of the autumn being a period of prospecting though it is possible that there is not the same selection pressure for nest sites in my study rookery as there was at Ian Patterson's. This study examined for evidence of territoriality by testing for an effect of group size on display rate. The data presented found there to be no correlation between an individual's display frequency and the size of group that it was in. However, as figure 5.4 shows, sample sizes were relatively small which perhaps accounts for the large observed variation about the median. A larger data set is necessary to address more conclusively whether or not group size affects display rate. As a qualitative observation, aggressive encounters were never seen to arise out of territorial disputes in the autumn whereas aggression related to the stealing of nest material and infringement of territory are common in the spring. This suggests that if rooks are prospecting for nest sites in the autumn then it is at least non-competitive.

The question still remains as to why there is a so much greater frequency of bow-caw displaying in the autumn as compared to the spring? There may only be a greater emphasis on display in the autumn because once the business of building and laying has begun in the spring, the requirement to display is negated and hence display rate drops. This issue of changing display rate over time during the spring period is covered in the next chapter in an attempt to explain the difference in display rates between the two periods. What is clear, is that the function of bow-caw displaying is complex. It is possible that the autumn period is one of both nest site selection and pair-bond formation. My results are not detailed or complete enough to dissect the two apart and I suggest that any further study of autumn sexuality in the rook should not simply confine itself to the rookery. Studying the behaviour of birds during feeding and resting outside the rookery will provide an insight into the extent of pair-bond formation or consolidation that occurs in the autumn. Such a programme of study would necessitate a far more concentrated programme of marking than I undertook, and should attempt to mark as many individuals within the colony as possible. If birds are to be recognised and followed whilst feeding in fields, then wing-tagging would be more suitable than colour-ringing as the birds' legs would often be obscured by grass or stubble.

A final attempt to resolve whether bow-cawing is directed towards pair-bond formation or territoriality was undertaken in the spring of 1989 by recording the context in which the display occurred. This is detailed in the following chapter. It is clear from the present study that nests are not refurbished during the autumn period however, further research is necessary in order to distinguish the extent to which this season serves as one of courtship and/or nest site selection.

In summary: The literature reports three proposed adaptive functions to explain the resurgence of sexual behaviour in the autumn (from mid-September to early November), these are; that it is a period of nest refurbishment, that it is a period of pair-bond formation/consolidation, or that it is a period of nest site selection. This study was primarily concerned with establishing the extent to which rooks carry out autumnal nest refurbishment.

In answer to the predictions of the Cheap/Expensive model, it has been shown that autumn is not a period of nest refurbishment. Furthermore, although the month of October shows rooks to be occasionally attendant at the colony during daylight hours, the fraction attendance is very low compared to the spring. Associated with this low attendance is an absence of any vigilant or aggressive behaviour related to territoriality. Results of studies conducted in the autumn therefore support the cheap view of the cost to nest building.

6. NEST BUILDING IN THE SPRING - THE EFFECT OF BUILDING ON REPRODUCTION

6.1. Introduction

6.1.1. The Study Approach and Measurement of Biological Cost

If there is a biological cost to nest building then it may be that the energy expended in nest construction will detract from the parents' capacity for subsequent investment in the eggs and young. Studies conducted in the spring were therefore principally aimed at examining whether observed variation in building behaviour subsequently influenced reproductive success. Generally speaking, if the costs of nest building are low (the viewpoint corresponding to the 'Cheap' hypothesis), then variation in building behaviour will have very little bearing on reproductive performance. Conversely, the 'Expensive' hypothesis predicts that there are features of building behaviour that incur a cost and these differences will correlate to differences in reproductive output. The identification of features of building behaviour that influence fitness will provide a greater understanding of the selective pressures governing both building behaviour and nest design.

During the first year of this study it became apparent that there was variation in several aspects of rook nest building behaviour, most notably differences between pairs in the mode of assimilation of nesting material, in whether old nests were reused or new ones constructed, in the selection of a nest site and in the timing and duration of building itself. These were investigated in greater detail during the subsequent breeding seasons to assess their importance, if any, in the overall cost of nest building. The variability in these features of nest building behaviour can be measured in terms of a reproductive cost which may be manifest as either a) a reduction in reproductive output or b) a delay in the onset of laying resulting in the brood fledging late in the breeding season; the adaptive advantage to early nesting was detailed in section 5.1.1.

The following section elaborates on the features of building studied,examining the manner in which they may influence fitness. The final section in this part of the chapter then states the predictions of the Cheap/Expensive paradigm in relation to the spring.

6.1.2. The Variation in Building Behaviour Under Study

The mode of nest material assimilation. Section 4.3.3 described the method employed in quantifying the assimilation of nesting material. Of particular interest was the conspicuous practice of stealing material from conspecifics within the colony. The questions arising from this observation were i) is the level of stealing constant between pairs and ii) is there an adaptive advantage to its practice?

Two proposed adaptive advantages to stealing are that it reduces the energetic cost of building and/or hastens the onset of laying. These questions will be approached separately in the presentation of results and as I shall shortly describe, this aspect of rook building behaviour prompted a manipulation experiment on a large scale.

Nest reuse. Weeks (1978), working on the Eastern Phoebe, *Sayornis phoebe*, suggested that there was a reduction in mean clutch size in individuals building new nests compared to those reusing old. Such a relationship, if demonstrated in rooks, would clearly support the expensive view of nest building. Week's theory states that reusing an old nest reduces the degree of building effort so conserving energy which is subsequently diverted into increased egg production. It is possible that nest reuse conveys a similar reproductive advantage to rooks but there exists the possibility of an additional adaptive advantage whereby birds refurbishing old nests may be able to breed sooner and thereby increase the post-fledging survival of their brood (see Feare et al. 1974).

Choice of nest site. The influence of nest site on reproduction has been shown by several researchers; be it to protect against predation (Cody 1985, Jackson et al.

1988, Redmond et al. 1982, Simmons & Smith 1985) or the environment (Skeel 1983). There is potentially a third selective pressure which would influence nest site selection, namely the degree of support and anchorage that the chosen site affords the nest. It is possible that a greater degree of building effort is required to secure the nest into some sites than in others. Table 3.2 showed there to be a difference in the extent of nest losses between tree species at the Milton Farm rookery, with a significantly disproportionate number of nests being lost from larch. If there is a high 'cost' to nest building then this supports the idea that choice of nest site may be important in influencing reproduction. Larch is not however the species most commonly used as a nest site at the study rookery, with the vast majority of nests being distributed between sycamore and Scots pine. As I have shown (see section 3.3.2), there is no evidence for a higher rate of nest loss between these two species but it is possible that differences in canopy shape may determine the degree of building effort required to make the nest stable within it. The position of the nest itself may also be important since a broad open canopy such as that of Scots pine may permit easier access to the nest with nesting material than the tighter-knit canopy of sycamores. Ease of access may therefore also reduce the energetic cost of nest building.

In summary, the question is whether canopy morphology influences the amount of time and/or effort required to construct a nest within that tree species so reducing the cost of building. An indicator of such an effect may be a difference in the reproductive output of birds nesting in different tree species.

6.1.3. The Timing and Duration of Nest Building

The timing of nest building may be important in increasing reproductive output because as Feare et al. (1974) showed, there is a period of food shortage in the months of high summer. This is responsible for the high mortality rate recorded in first year birds (Patterson et al. 1988). The selective pressure to breed early and thus permit fledglings a longer growth period before the months of food shortage, should be reflected in building strategies that permit early breeding. The above features of rook building behaviour namely, the mode of material assimilation, nest reuse and choice of nesting site may therefore increase fitness by either conserving energy, permitting a greater investment in egg production or by shortening the duration of building allowing the individual to breed earlier. There is however, an additional point to bear in mind, which is that if building is energetically expensive, a short concentrated burst of building activity may permit the female of the pair to lay early but her reproductive output may be lowered due to the physiological exertion of intense building. A reproductive advantage gained through early nesting may then be lost. Shortening the building period may therefore entail a cost in itself. This effect can be examined by testing for a correlation between the duration of nest building and subsequent reproductive output.

Figure 6.1 summarises the features of building behaviour under study showing the manner in which they may increase fitness.

6.1.4. Predictions of the Cheap and Expensive Hypotheses

One of the advantages of the Cheap/Expensive approach is that it permits the formulation of precise predictions which are then supported or refuted by observation and experimentation. Method of nest material assimilation, nest reuse and choice of nest site are general features of nest building behaviour whose importance in influencing reproductive performance are disputed by the paradigm. The predictions of the Cheap and Expensive hypotheses applicable to these features of rook nest building behaviour are shown below.

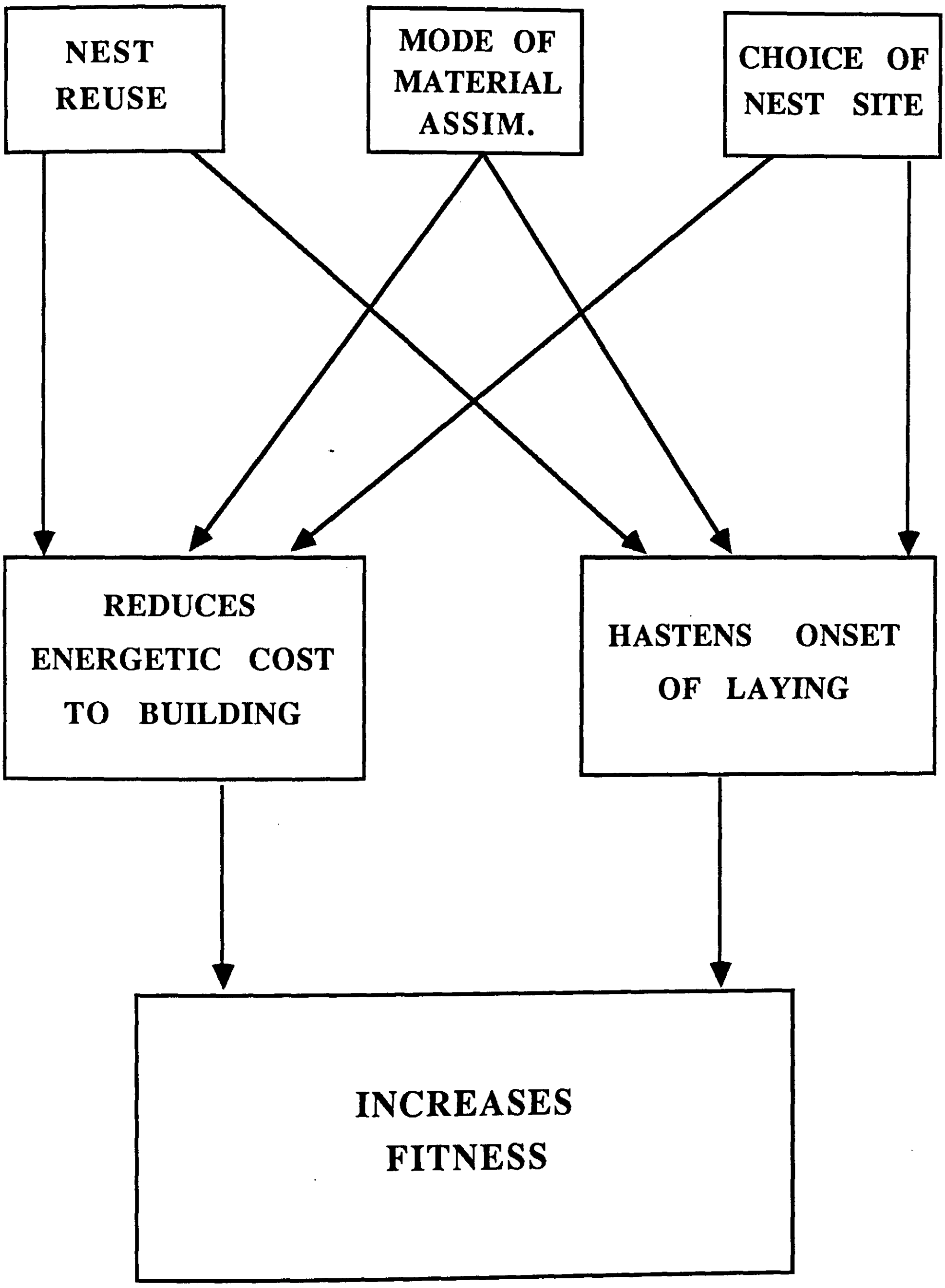
Expensive

a) There is competition for nesting material.

b) Stealing is therefore common and its practice confers a reproductive benefit.

c) There is a high degree of vigilance during building

Figure 6.1. A summary of the features of rook nest building that potentially influence fitness. A reduction in the energetic cost of building and/or a hastening of the onset of laying may both confer a reproductive advantage. In the case of the former, by permitting more energy to be invested in egg production and in the latter, by increasing the post-fledging survival (see Patterson et. al 1988). Nest reuse, mode of material assimilation and choice of nest site may therefore contribute to an increase in fitness by either reducing the energetic cost of building and/or hastening the onset of laying.


NEST REUSE
MODE OF MATERIAL ASSIM.
CHOICE OF NEST SITE
REDUCES ENERGETIC COST TO BUILDING
HASTENS ONSET OF LAYING
INCREASES FITNESS

d) A reproductive penalty is incurred in the construction of a new nest compared to renovating an existing structure.

e) The choice of nest site influences reproductive performance since pairs will choose a site that minimises the building effort required to secure the structure *in situ*. The result in terms of fitness will be a difference in reproductive output between pairs nesting in say for example, different tree species.

Cheap

a) There is an excess of nesting material.

b) Stealing is infrequent.

c) There is low nest vigilance during building.

d) There is no difference in the reproductive output of pairs laying in new nests compared to those laying in old.

e) The choice of nest site has no influence on reproductive performance since the effort required to secure the nest *in situ* is negligible and hence no difference is expected between pairs breeding in different tree species.

The data presented in this chapter is aimed at establishing which predictions best reflect the situation *in vivo*, and addresses specific questions related to nest reuse, differences in the method of nest material assimilation and in the selection of nest site.

6.2 Materials and Methods

6.2.1. The Mode of Nest Material Assimilation

The frequency of 'Collecting', 'Manipulating' and 'Stealing' was recorded for nests in the vicinity of the hide in the 1988 and 1989 spring breeding seasons. By designating a label to each nest (see section 5.2.1), it was possible to sample the frequency of the three strategies practised by the resident pair in the course of their nest building. The frequency of each strategy is then presented as the percentage of the total sum of observations for that nest. Data and subsequent calculations are presented only for those nests with more than 30 observations in attempt to minimise bias due to small sample size.

Further analysis was done in relation to the prevalence of stealing in an attempt to discover the reason for its occurrence and the advantage it confers to its practitioners. This will be detailed in later sections.

6.2.2. The Distinction Between 'New' and 'Old' Nests

In order to examine for an adaptive advantage in the reuse of old nests, it is necessary to define and distinguish new structures from old. A nest is described as 'New' if it was built in the current spring under study, conversely, an 'Old' nest was one that had been present the previous spring and was therefore at least a year old. This distinction was made possible by the mapping of nests described in section 3.2.2. Whenever nests disappeared or appeared, the date as well as the position was noted on the relevant index card. In this manner, 'New' nests were readily distinguishable from 'Old'. Birds nesting in Old nests are referred to as 'Old' nesters and those nesting in new structures, as 'New' nesters.

6.2.3. Recording the Timing and Duration of Building

If the starting date (SD) and finishing date (FD) of nest building are noted for each labelled nest, then the duration is calculated as the number of days between the two dates. The SD is defined as the date on which a bird is first seen carrying nesting material to that nest and was recorded as the day after the 1 March of that year (eg. if building began on 12 March, SD= 12). The FD was defined as the date on which the female of the pair was observed to be constantly in the incubatory position and was also recorded as being the day after the 1 March of that year.

6.2.4. Obtaining and Recording Reproductive Data

Section 4.3.4 described the method for climbing trees to gain access to the nest cup. Nest inspections began once the majority of females nesting in the vicinity of the hide were observed to be incubating. Each accessible nest was visited at least three times in order to record clutch size (CS), hatching success (HS) and fledging success (FS). The first and last dates during which eggs, hatchlings and fledglings (age approx. 3 wks.) were found in the visited nests are outlined below to give an idea of the chronology of climbs.

EGGS - 13 April to 5 May
HATCHLINGS - 22 April to 25 May
FLEDGLINGS - 10 May to 28 May

Further details on the collection of reproductive data, as well as a table of the raw data of the reproductive output of pairs at the Milton Rookery, are given in Appendix 3.

6.2.5. The Rate of Stealing in Relation to the General Level of Building Activity

One of the first questions asked of stealing was, when during the building period was it most prevalent? The rate of stealing was studied in relation to the general level of building activity as part of an investigation into the reason for its practice. For example, the rate of stealing may be high relative to the overall level of building activity only late in the building season when many pairs have collected their nesting material and there is increased competition for the remaining available material amongst late-nesters. Stealing rate is defined as the number of thefts per hour (no. thefts/hr.). This was calculated by multiplying the observed number of thefts for each observation period by 60, and dividing this product by the sample period which is defined as the number of minutes spent observing birds from the hide on that day. For example, say 40 thefts were observed in a sample period of 120 minutes, the theft rate would be 40 x 60 / 120 = 20 thefts/hr.

A similar calculation can be performed to represent the total level of building activity for each day. In this case, total building activity is the sum of the observed frequencies of stealing, collecting and manipulating. Multiplying by 60 and dividing by the sampling period (expressed in minutes) gives the total number of observations per hour (no.obs/hr.) which is defined as the total level of building activity. This is then compared to the observed rate of stealing.

6.2.6. Potential Motives for Stealing Nesting Material

In this section I propose three reasons to account for the rook's habit of stealing nesting material, these reasons and the methods used to test their validity are as follows.

a) Nesting material is a limiting resource and stealing is therefore induced by competition.- To test this, samples were taken of the density of suitable twig nesting material on the floor of the rookery, just prior to, and just after the building period. This density is expressed as the number of twigs/m^2. A significant reduction in the amount of available twig material would suggest that its availability constrained the number of nests that could be built in the colony and there was therefore competition for nesting material. The exact method of quadrat sampling was detailed in section 2.2.3 and will not be repeated here.

b) Stealing material is quicker than collecting.- If there is competition for nesting material, then foraging for it entails a cost. Stealing may reduce this cost if it can be shown that stealing an item of nest material is quicker than collecting it. To test this hypothesis, the time taken to steal an item was compared to the time taken to collect an item. Birds engaged in building were observed from the hide. When an individual left its nest site, a stopwatch count began; the bird was watched to record whether it was stealing material or collecting it from the rookery floor. The count ceased when the same individual returned to the nest site with nesting material having either stolen or collected the item. The time of absence was recorded to the nearest second and categorised as being either a stealing trip or collecting trip. The time taken to steal could then be compared to the time taken to collect an item of nesting material.

c) Stealing is characteristic of New nesters.- Individuals that are constructing entirely new nests (i.e. New nesters) may require more nesting material than Old nesters who have the option of rearranging a previous years' material. New nesters may therefore be under greater pressure to assimilate material and may meet this pressure with a higher incidence of stealing than Old nesters. A comparison was therefore made between the median percentage of material stolen by Old nesters compared to New.

6.2.7. The Study of the Adaptive Function of Stealing Nest Material

In order to examine for an adaptive advantage to stealing, its prevalence was examined in the following contexts.

a) An examination for a difference in the incidence of stealing between 'New' and 'Old' nesters.- Part of a penalty to constructing a new nest may be the increase in the amount of nesting material required. If stealing nesting material does confer a temporal or energetic advantage or indeed, if there is competition for nesting material, then pairs building new nests may steal more frequently than those nesting in old so as to minimise the disadvantage of having to build a new structure.

b) Observed incidence of stealing v's reproductive success.- To test for an effect of stealing on reproductive output, the data was tested for a correlation between the percentage of stolen material brought to the nest and that nest's clutch size, number of chicks hatched and number of chicks fledged. Note that in this analysis, the percentage manipulations are ignored and the percentage of stolen material is calculated from trips undertaken to collect or steal an item.

In addition, the data was analysed to see if stealing conferred its adaptive advantage by shortening the duration of building or permitting nest building to be completed earlier. Furthermore, a direct reproductive advantage to stealing was examined by testing for a positive correlation between observed % stealing and clutch size, number of chicks hatched and number of chicks fledged.

6.2.8. Vigilance at the Nest Site During the Building Season

If the stealing of nesting material confers an advantage to the thieves, then it is likely to incur a penalty to the victims since stolen material and the structural damage done in its removal will need to be replaced and repaired. Following on from the predictions of the 'Expensive' hypothesis, a high incidence of theft may be accompanied by a comparable level of vigilance at the nest site. The level of vigilance will presumably be a trade-off between the pressure to collect nesting material and the need to guard the resource. In the case of rooks, vigilance was recorded as the amount of time spent in attendance at the nest site. Hour-long time samples were taken throughout the building season; during these samples the time (in minutes) was recorded when both birds, one bird and neither bird of the pair were present at the nest. The pattern of nest attendance could be retrospectively related to the nest's proximity to completion by recording the nest's finishing date

(whi or 2 birds in relation to the number of days prior to laying. f 0,1

Further details of the method employed in estimating nest

or 2 are given in Appendix 3.

Furthe[illegible] ilance

are given in Appendix 3.

6.2.9. Twig Removal Experiment - An Attempt to Intensify Competition for Nesting Material in the Spring of 1989.

A large scale manipulation experiment was undertaken prior to the building season of 1989 in an effort to intensify the competition for nesting material and so increase the cost of nest building. On the 5 March, the floor of the rookery was largely cleared of twigs suitable for nest building (i.e. between 10-70 cm.). Approximately 1.5 metric tons of twigs (c.60,000 items) were removed and burnt. It was important to time the rookery clearance so as to minimise the amount of time available for more twigs to fall and become available for building just prior to the onset of building. As the rookery was isolated from any other woodland, twigs on the woodland floor could only have come from trees within the colony. From table 2.1, one can calculate that the average number of twigs in the outer ring of a nest is approximately 524. The removal experiment therefore removed the equivalent of about 115 nests worth of twigs. It was predicted that reducing the amount of locally available twig material would have the following repercussions.

1) There would be an increase in the observed incidence of stealing.
2) The peak number of nests in the colony would be lower than in the previous year.
3) If nest material was harder to obtain, the effort required in nest construction would increase which may cause a reduction in the average reproductive output of pairs in the perturbed year compared to the previous year.
4) The ground experiment conducted in spring 1988 showed there to be preferential selection for twigs in the size category 40.1-50 cms. (see section 2.3.4). If the removal of twig material had the effect of increasing competition, then it was expected that the increased pressure for nesting material would override this preference and birds would no longer discriminate between sizes. A parallel ground experiment to that of 1988 was conducted in 1989 to check for the effect of the rookery clearance on the preferential selection of larger twigs.

Since it is predicted that the removal experiment will influence both building behaviour and reproduction, the presentation of data collected in the springs of 1988 and 1989 is analysed separately. This permits comparisons to be made between years and prevents any effects of the perturbation experiment confusing the results of 1988 so allowing an assessment of the effects of twig removal on the building behaviour and breeding of individuals in 1989.

6.2.10. An Assessment of the Function of the Bow-Caw Display

As noted in the previous chapter, the end of the 1988 autumn season had not resolved the function of this display. Whilst not disputing the conclusion of the previous chapter that bow-cawing may serve several functions, it may be possible to record it prevalence in the proposed context of pair-bond consolidation and territoriality during the spring.

Pairs were often seen displaying to each other or at birds in the immediate vicinity of their nest. These are described as being intra-pair displays (IPD) and extra-pair displays (EPD) respectively. The context of IPDs suggest that the display may be to do with pair-bond consolidation and that of EPDs suggestive of a potential territorial function.

In cases when the subject of the display was ambiguous, as was the case with many single displaying birds, no function was assigned to the sample. A direct comparison could be made to test for a difference in the frequency of IPDs and EPDs in the building period, to discover whether bow-cawing is more commonly observed within a pair, or between a pair and other birds. In addition, the rate of IPDs and EPDs could be recorded in relation to date to examine for a change in rate over time.

6.3 Results

6.3.1. Variation Between Pairs in the Mode of Nest Material Assimilation

Table 6.1 shows the percentage incidence of the three defined building strategies as a percentage of the total building effort. In addition, it details a) the number of trips observed by that pair during building and b) whether the nest was New, i.e. built in the spring under study, or Old.

From the table, it was calculated that the overall observed % Stealing was greater in 1989 than in 1988 (U= 58.5 n_1=16 n_2=13 $p < 0.05$, Mann-Whitney U-test)① but no significant difference was recorded in the observed % Collecting between years (U= 76, n_1=16 n_2=13; $p > 0.05$, Mann-Whitney U-test) or in the % Manipulating (U=

Median 1988 = 21·6%
" 1989 = 35·0%

Table 6.1. A summary of the incidence of the three defined modes of assimilating nest material; collecting (Coll.), manipulating (Manip.), and stealing (Steal), expressed as a percentage of the total building activity observed for a particular nest. The abbreviation 'n' denotes the number of observations from which the percentage of each strategy has been calculated and 'No. of Observed Trips' indicates the number of journeys made by the building pair. This is equal to the sum of the frequencies of journeys to collect and steal material (C+S).

The 'New' category denotes nests that were constructed in the current year whereas 'Old' refers to nests of a previous year.

'Data Uses' refers to the use of this data set in subsequent analysis.

Key to Data Uses:

D = Nest Used in Calculations of Building Duration (see 6.3.3)

R = Nest Monitored to Obtain Reproductive Data (see 6.3.2)

V = Nest Used in Calculations of Vigilance (see 6.3.8)

Year Nest	New/ Old	Mode of Mat. Assim.(%)			n	No. Obs. Trips (C + S)	Data Uses
		Coll.	Manip.	Steal			
1988							
3K	New	19.0	9.5	71.4	42	38	D R V
3C	Old	8.9	37.5	53.6	168	105	D R V
3S	New	36.7	20.0	43.3	6	48	R V
3D	Old	23.7	39.5	36.8	76	46	D R V
3X	New	29.7	37.8	32.4	74	46	D R
7A	Old	27.9	44.2	27.9	233	130	D R V
5A	Old	28.3	49.1	22.6	53	27	D R V
3B	Old	29.7	48.6	21.6	37	19	D R V
1A	Old	43.2	35.1	21.6	37	24	D V
3G	Old	32.3	48.5	19.2	167	86	D R V
3A	Old	33.1	49.4	17.5	154	78	D R V
4B	New	45.2	37.9	16.9	177	110	D
1C	Old	78.9	5.3	15.8	38	36	D V
4D	New	66.7	25.6	7.7	39	29	D
7D	New	45.6	48.5	5.9	68	35	D R V
7C	New	84.6	15.4	0.0	39	33	D R V
1989							
7R	New	12.8	15.4	71.8	39	33	D V
3X	Old	21.4	23.8	54.8	42	32	V
3H	New	19.0	28.6	52.4	42	30	V
3P	New	28.3	28.3	43.3	60	43	V
7C	Old	21.6	35.3	43.1	116	75	D R V
3G	Old	18.1	40.4	41.5	94	56	V
3B	Old	30.7	34.3	35.0	137	90	D V
3R	New	38.8	28.2	33.0	103	74	D R V
3C	Old	10.0	60.0	30.0	40	16	D R V
7B	New	46.6	29.1	24.3	103	73	D R V
5C	New	42.9	34.3	22.9	35	23	V
5A	Old	47.2	33.3	19.4	108	72	D R V
7A	Old	38.7	46.8	14.5	62	33	D R V

84.5, $n_1=16$ $n_2=13$; $p > 0.05$, Mann-Whitney U-test.

Data from this table may also be used to provide evidence in answer to a question posed in the last section, namely the existence of a potential penalty to constructing a new nest induced by the increased requirement for nesting material. Unlike birds nesting in Old nests, New nesters do not have the remains of the previous year's structure to act as a foundation. An increased pressure for nesting material may therefore be manifest by an increase in the observed number of trips to collect nesting material in those birds building new nests. From table 6.1, one can test this prediction. The number of trips for each nest is equal to the % Collecting + % Stealing. A comparison of this summed percentage in the two classes is representative of the percentage of nest building that involved making trips to gather material.

In 1988, no significant difference was found in the percentage number of building trips completed by 'New' nesters compared to 'Old' ($U = 15$ $n_1=9$, $n_2=7$; $p > 0.05$) and in 1989 there was some evidence of 'New' nesters making more trips than 'Old' though this difference was not significant ($U_{1989} = 6.5$ n.s., $n_1=7$ $n_2=6$; $U = 6.0$ at $p=0.05$, Mann-Whitney U test).

In comparing the summed percentages of Collections and Steals, one is also effectively comparing the % Manipulations between classes because this forms the residual percentage of the total observed building behaviour for each nest. The same conclusion as above can therefore be drawn with regard to the % Manipulations between New and Old nesters i.e that there is no significant difference in its incidence between classes in either year.

6.3.2. Does the Duration of Building Affect Reproduction?

Section 6.1.3 introduced the idea that there might be a selective advantage to building strategies that hasten the completion of building and hence the onset of laying, because early nesting may increase post-fledging survival. At that time I also suggested that such intense building may induce a physiological stress that would offset any advantage gained by shortening the building period. If this latter effect exists *in vivo*, one might expect there to be a positive correlation between building duration and reproductive output. In testing for this correlation there is a need to control for an effect of late nesting since late-nesters may have reduced reproductive outputs for reasons unrelated to the energetic stress of building. Some of the alternative explanations for a short building duration and/or a reduced reproductive output in late nesters are outlined below.

a) They are possibly young inexperienced birds that were not in condition to breed or capable of securing a nest site until dominants had done so. Such birds may have low reproductive outputs not because of the stress of building (see Røskaft 1983) but because they are young.

b) Late breeders may also have shorter building durations because they avoid potential disadvantages of building during the period of peak building activity in mid-March. Such disadvantages may be a high incidence of stealing or an intense competition for nesting material.

In order to separate between the effects of the two factors, building duration and finishing date on reproductive performance, multiple regression analysis was used to establish, i) which factor had the greatest influence upon the dependent variable (clutch size, numbers chicks hatched and number of chicks fledged) and ii) if any of the residual variation can be explained by the secondary factor. Results show that in 1988 there was no significant correlation between building duration finishing date and either clutch size, hatching success or fledging success. In 1989, a significant positive correlation was found between clutch size and increased building duration ($r = 0.71$, $p < 0.05$). The residual variation is not explained by finishing date

(Multiple Regression analysis $p > 0.05$). No correlation however, was found between building duration, and either hatching or fledging success. Possible explanations for this result will be discussed in section 6.4.

Having established that finishing date does not effect reproduction in either year, one can present a simple two-way relationship between building duration and reproductive effort measured as clutch size, number chicks hatched and number chicks fledged. This is shown in figure 6.2 for both of the study years.

6.3.3. An Examination Into Whether There is a Reproductive Advantage to Nesting in Old Nests.

The refurbishment of old nests may confer an adaptive advantage in two ways;

i) by reusing existing nesting material these birds may shorten the duration of building and hence laying may commence earlier in the year

or

ii) by reducing the amount of building effort necessary to produce a nest suitable for breeding.

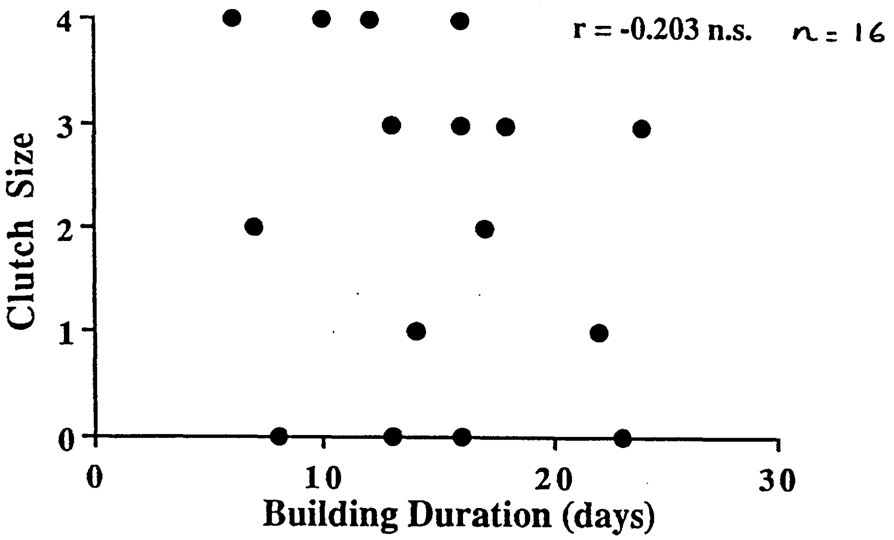
Note that these two advantages are not mutually exclusive.

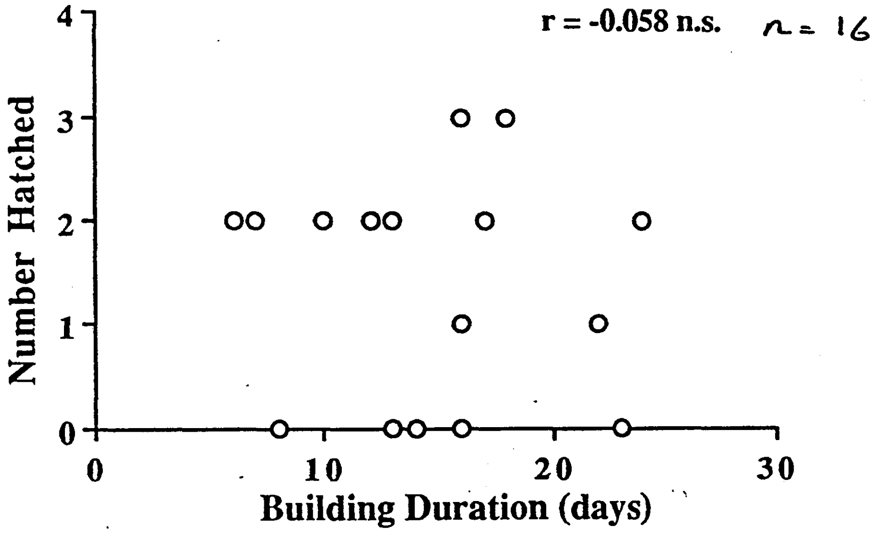
With regard to the first point concerning the effect of nest reuse on the timing and duration of nest building, analysis of the data showed there to be no significant difference in the starting date or finishing date of building between New and Old nesters in either 1988 or 1989. In other words, birds reusing old nests do not start or finish their nest building any earlier in the year than individuals constructing new nests.

Tests for a difference of starting date or finishing date within a class but between years, showed there to be no difference in the timing of building in 1988 and 1989. The only significant difference is found when one looks at the duration of building between Old and New nesters. In both years of the study, New nesters were found

Figure 6.2. The plots and correlations showing the relationship between building duration and clutch size/ number of chicks hatched /number of chicks fledged in 1988.

1988


r = -0.203 n.s.
n = 16
Clutch Size
4
3
2
1
0
0
10
20
30
Building Duration (days)


r = -0.058 n.s.
n = 16
Number Hatched
4
3
2
1
0
0
10
20
30
Building Duration (days)

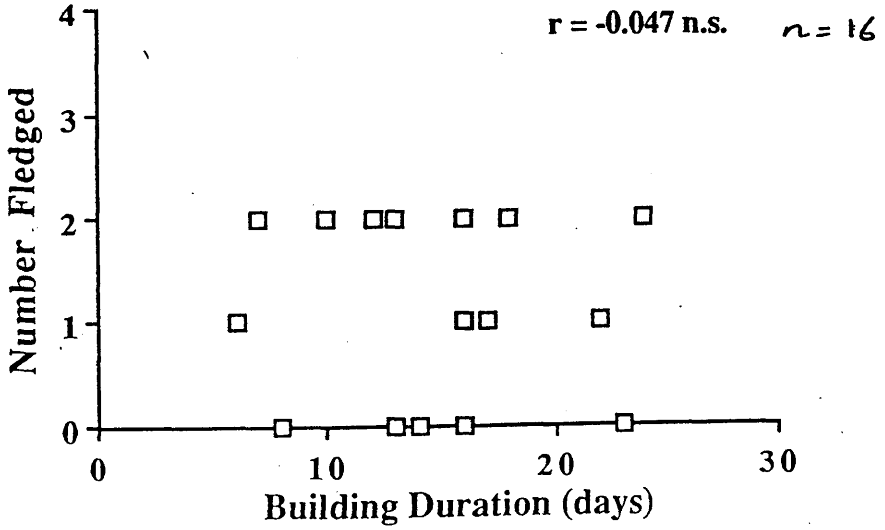
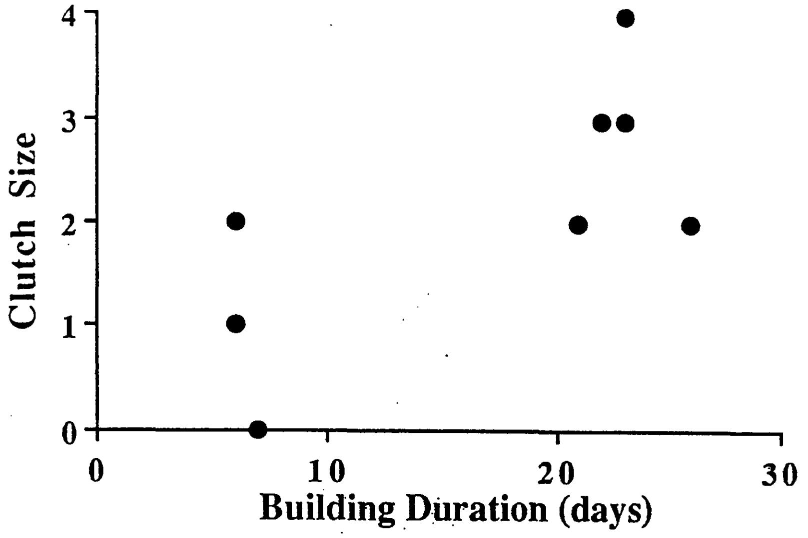
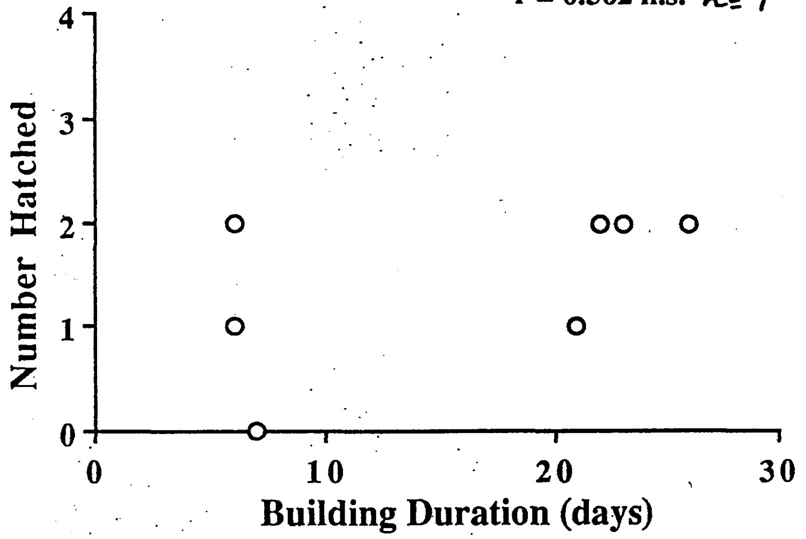

r = -0.047 n.s.
n = 16
Number Fledged
4
3
2
1
0
0
10
20
30
Building Duration (days)

Figure 6.2 (contd.). Plots and correlations of reproductive output v's building duration in 1989. Note the significant positive correlation between clutch size and building duration.

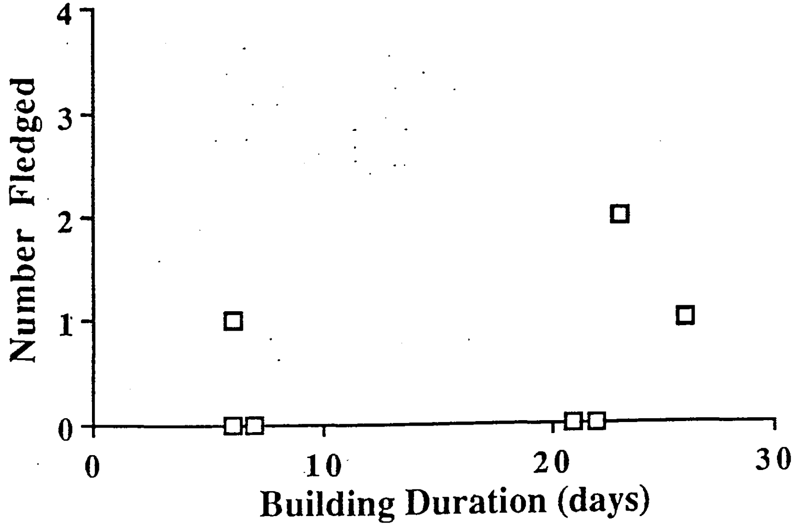
1989



r = 0.710, p<0.10 (2-tailed) n = 8



r = 0.562 n.s. n = 7



r = 0.446 n.s. n = 7

① Median Duration New = 11 days   ② Median Duration New = 7.5 days
" " Old = 17 days   " " Old = 21 days

to have a significantly shorter building duration than Old nesters ($U_{1988} = 10$, $n_1=7$ $n_2=11$; $p < 0.05$ ① : $U_{1989} = 8.5$, $n_1=8$ $n_2=7$; $p < 0.05$ ②, Mann-Whitney U tests). In summary, the timing of building was not observed to differ between years however in both 1988 and 1989, New nesters took significantly less days to construct their nests than Old. Note that this observation is contrary to the view stating that reusing old nests accelerates breeding. These conclusions are summarised in table 6.2.

The second proposed adaptive advantage to reusing a nest is that it may permit an increased reproductive output. Table 6.3 summarises the data on the reproductive performance of 'Old' and 'New' nesters in 1988 and 1989. A comparison was made in the reproductive performance of New nesters and Old nesters a) within the study years, 1988 and 1989 and b) between the study years but within each class. These comparisons were made between the mean clutch sizes, number of chicks hatched and number of chicks fledged using a standard t-test. One of the problems of performing multiple t-tests is that repetition increases the chances of committing a type 1 error, namely rejecting H_0 at $p = 0.05$ when it should not be rejected. All tests have had the critical value of p adjusted using Bonferroni's Multiple Testing Correction. This simply divides the previously designated critical value of p by the number of test being applied to the data. The new value of p, below which H_0 was rejected was therefore set at 0.0125 (0.05/4).

Table 6.4 summarises the results of the multiple tests. The only comparison that was statistically significant was in the mean number of chicks fledged from old nests in 1988 compared to 1989. Reference to table 6.3 shows that significantly more chicks fledged from old nests in 1988 than they did the following year.

6.3.4. The Influence of the Choice of Nest Site on Reproductive Success - A Comparison Between Breeding in Sycamore and Scots Pine

Table 6.5 summarises the data on the reproductive performance of birds nesting in

Table 6.2. A summary of the results of Mann-Whitney U tests on the timing and duration of building in the two classes; 'Old' and 'New' nesters. The former class is defined as those pairs reusing pre-existing structures, the latter as those which build entirely new nests. Table 6.2a compares the starting date, finishing date and building duration in the two classes in 1988 and 1989. Table 6.2b compares the same variables but this time within each class, between years. Note that in both years, building duration was significantly shorter in 'New' nesters than in 'Old'. This is denoted by the asterisked U values.

a) Comparison in the timing and duration of building between 'New' and 'Old' nesters during 1988 and 1989.

1988	Result (U value)
Starting Dates (New v Old)	21.5 ns
Finishing Dates (New v Old)	36.0 ns
Building Duration (New v Old)	10.0 *
1989	
Starting Dates (New v Old)	10.5 ns
Finishing Dates (New v Old)	22.0 ns
Building Duration (New v Old)	8.5 *

b) Summary of the results comparing the timing and duration of building <u>between</u> <u>years</u>.

OLD NESTS '88 v'89	Result (U value)
Starting Dates	33.0 ns
Finishing Dates	34.5 ns
Building Duration	37.5 ns
NEW NESTS '88 v'89	
Starting Dates	22.5 ns
Finishing Dates	23.0 ns
Building Duration	25.0 ns

Key: ns = not significant, * = significant at p = 0.05

Table 6.3. A summary of the data collected in 1988 and 1989 on the reproductive performance of individuals that have bred in ‘New‘ nests compared to those that have bred in ‘Old’. The reproductive variables monitored in both classes were clutch size (C), number of chicks hatched (H) and number of chicks fledged (F).

a)

1988	CN	CO	HN	HO	FN	FO
Sample Size	20	12	20	12	20	12
Mean	2.95	2.92	2.05	1.92	1.80	1.75
Stand. Error	±0.22	±0.26	±0.22	±0.15	±0.23	±0.13

b)

1989	CN	CO	HN	HO	FN	FO
Sample Size	12	20	12	20	12	20
Mean	2.92	2.85	2.00	1.60	1.25	1.10
Stand. Error	±0.29	±0.20	±0.21	±0.20	±0.25	±0.18

Key: CN = Clutch size in New nests
HN = Number of eggs Hatched in New nests
FN = Number of chicks Fledged in New nests

CO = Clutch size in Old nests
HO = Number of eggs Hatched in Old nests
FO = Number of chicks Fledged in Old nests

Table 6.4. A summary of the results of multiple t-tests on the reproductive success of 'New' nesters compared to 'Old' in the two study years (table 6.4a). Reproductive success was recorded in terms of clutch size, number of chicks hatched and number of chicks fledged). Table 6.4b summarises the results of a comparison of the same variables, this time within each class but between years. Note the significant difference in the number of chicks fledging from 'Old' nests when comparing 1988 with 1989.

The significance level at which H0 is rejected was adjusted using Bonferroni's Multiple Testing Correction in order to minimise the likelihood of committing a type 1 error (see text for details).

a) A summary of the results of 2-tailed t-tests examining for a difference in the reproductive output of 'New' and 'Old' nesters in 1988 and 1989.

Comparison - **1988**	Result to 30 d.f.
Clutch Sizes (New v Old)	0.095 ns
Number Hatching (New v Old)	0.428 ns
Number Fledging (New v Old)	0.162 ns
Comparison - **1989**	
Clutch Sizes (New v Old)	0.212 ns
Number Hatching (New v Old)	2.073 ns
Number Fledging (New v Old)	0.305 ns

b) A summary of the results of 2-tailed t-tests comparing the reproductive output of 'New' and 'Old' nesters in the two study seasons.

NEW NESTS'88 v'89	Result to 30 d.f.
Clutch Sizes	0.078 ns
Number Hatching	0.158 ns
Number Fledging	1.490 ns
OLD NESTS'88 v'89	
Clutch Sizes	0.229 ns
Number Hatching	1.410 ns
Number Fledging	3.611 *

Key: ns = not significant, * = significant at p = 0.~~025~~ 0·125 (2-tailed) sycamore and Scots pine in 1988 and 1989. In a similar fashion to before, t-tests were performed to examine for a significant difference in the mean clutch size, number of chicks hatched and number of chicks fledged between the two species. The data was analysed a) within each year but between species and b) within a species, between years. Bonferroni's Multiple Testing Correction was again applied to set the critical value of p at 0.0125.

The results of the comparisons are summarised in table 6.6. The only significant difference was found to be in the number of chicks fledging from Scots pine trees between years. Reference to table 6.5 shows that this difference was due to a reduction in the mean number of chicks that fledged in 1989 compared to the previous year. This finding will be discussed in section 6.4 particularly with regard to the supposed preference for nesting in this tree species which was noted in section 3.3.3.

6.3.5. The Observed Rate of Stealing in Relation to the General Level of Building Activity

Figure 6.3 shows the observed rate of stealing as a percentage of the total rate of building activity in both 1988 and 1989. If a high rate of stealing was apparent late in the building period, then the rate of stealing would comprise a large percentage of the total building activity in late March/early April (i.e c.20+ days after 1 March). This would show a positive correlation between the rate of stealing as a percentage of total building activity and increasing number of days after 1 March. By the same rationale, a high rate of stealing early in the building period would produce a negative correlation between the two variables. As figure 6.3 shows, there is a very low correlation between the two variables in both years (r_{s1988}= - 0.17, 14 d.f.; r_{s1989}= - 0.06, 15 d.f.). This means that the rate of stealing does not change over the building season but rather that there are high levels of stealing on days of high building activity and correspondingly, low levels of stealing on days of low building activity.

Table 6.5 A summary of the data collected in 1988 and 1989 on the reproductive performance of pairs nesting in sycamore (abbreviated to SY) and Scots pine (SP). The variables recorded in each year were clutch size (C), number of chicks hatched (H), and number of chicks fledged (F).

a)

1988	CSY	CSP	HSY	HSP	FSY	FSP
Sample Size	14	18	14	18	14	18
Mean	2.79	3.06	1.86	2.11	1.57	2.06
Stand. Error	±0.28	±0.21	±0.21	±0.21	±0.17	±0.24

b)

1989	CSY	CSP	HSY	HSP	FSY	FSP
Sample Size	10	22	10	22	10	22
Mean	2.60	3.00	1.50	1.86	0.80	1.32
Stand. Error	±0.31	±0.19	±0.22	±0.19	±0.29	±0.15

Key: CSY = Clutch size in Sycamore
HSY = Number of eggs Hatched in Sycamore
FSY = Number of chicks Fledged from Sycamore

CSP = Clutch size in Scots pine
HSP = Number of chicks Hatched in Scots pine
FSP = Number of chicks Fledged in Scots pine

Table 6.6. A summary of the results of multiple t-tests on the reproductive success of pairs breeding in sycamore compared to Scots pine. Table 6.6a summarises the results of comparisons made between the two classes within years and table 6.6b, the results of comparisons made within a class but between years. Note that in 1989, significantly fewer chicks hatched from Sycamore and Scots pine than in the previous year.

Bonferroni's Multiple Testing Correction was again applied to set the critical value of p.

a) A summary of the results of 2-tailed t-tests examining for a difference in the reproductive output of pairs nesting in Sycamore and Scots Pine in 1988 and 1989.

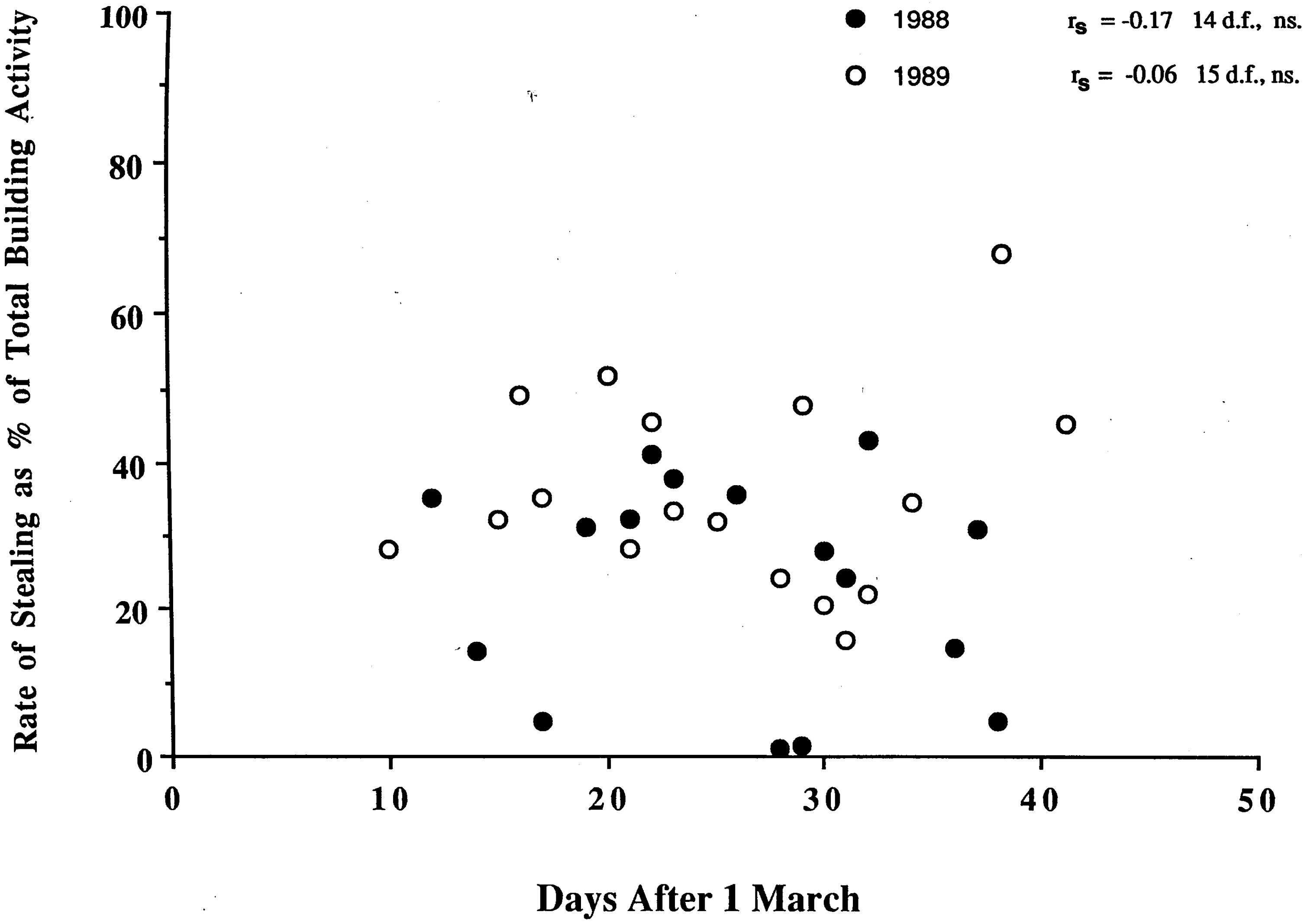
Comparison - 1988	Result to 30 d.f.
Clutch Sizes (Syc.v Scots P.)	0.794 ns
Number Hatching (Syc.v Scots P.)	0.842 ns
Number Fledging (Syc.v Scots P.)	1.573 ns
Comparison - 1989	
Clutch Sizes (Syc.v Scots P.)	1.878 ns
Number Hatching (Syc.v Scots P.)	1.268 ns
Number Fledging (Syc.v Scots P.)	2.072 ns

b) A summary of the results of 2-tailed t-tests comparing the reproductive output within each tree species between years.

SYCAMORE'88 v'89	Result to 22 d.f.
Clutch Sizes	0.41 ns
Number Hatching	1.40 ns
Number Fledging	2.85 **
SCOTS PINE'88 v'89	
Clutch Sizes	0.23 ns
Number Hatching	0.94 ns
Number Fledging	2.95 **

Key: ns = not significant, ** = significant at p = 0.01 (2-tailed)

Figure 6.3. The rate of stealing expressed as a percentage of total building activity, shown in relation to the day after 1 March. The calculated correlation coefficients are low indicating that the rate of stealing is related to the overall level of building activity and not to date.


● 1988
○ 1989
r_s = -0.17 14 d.f., ns.
r_s = -0.06 15 d.f., ns.
Rate of Stealing as % of Total Building Activity
100
80
60
40
20
0
0
10
20
30
40
50
Days After 1 March

6.3.6. Proposed Reasons to Account for Stealing

Section 6.2.6 proposed three possible reasons that would account for the rook's habit of stealing. These were a) because of a competition for nesting material, b) because stealing may be quicker than collecting and c) that it might predominantly be a feature of building behaviour in New nesters as they may be under greater pressure to acquire nesting material.

a) Competition for nesting material.- Table 6.7 summarises the data on quadrat samples taken from the rookery floor before the building season and after the building season. Analysis of the median number of twigs/ m^2 showed there to be no significant difference in twig density in the two periods ($U = 81$, $p > 0.05$, $n_1 14$ $n_2 14$; Mann-Whitney U test). I therefore conclude that the amount of available twig material suitable for nest building is not significantly reduced over the building period and competition for nesting material is not therefore the motive for stealing.

b) Stealing saves time.- The second proposed motive is that the time taken to steal an item is less than the time taken to collect one. Stealing therefore reduces the time invested in building.

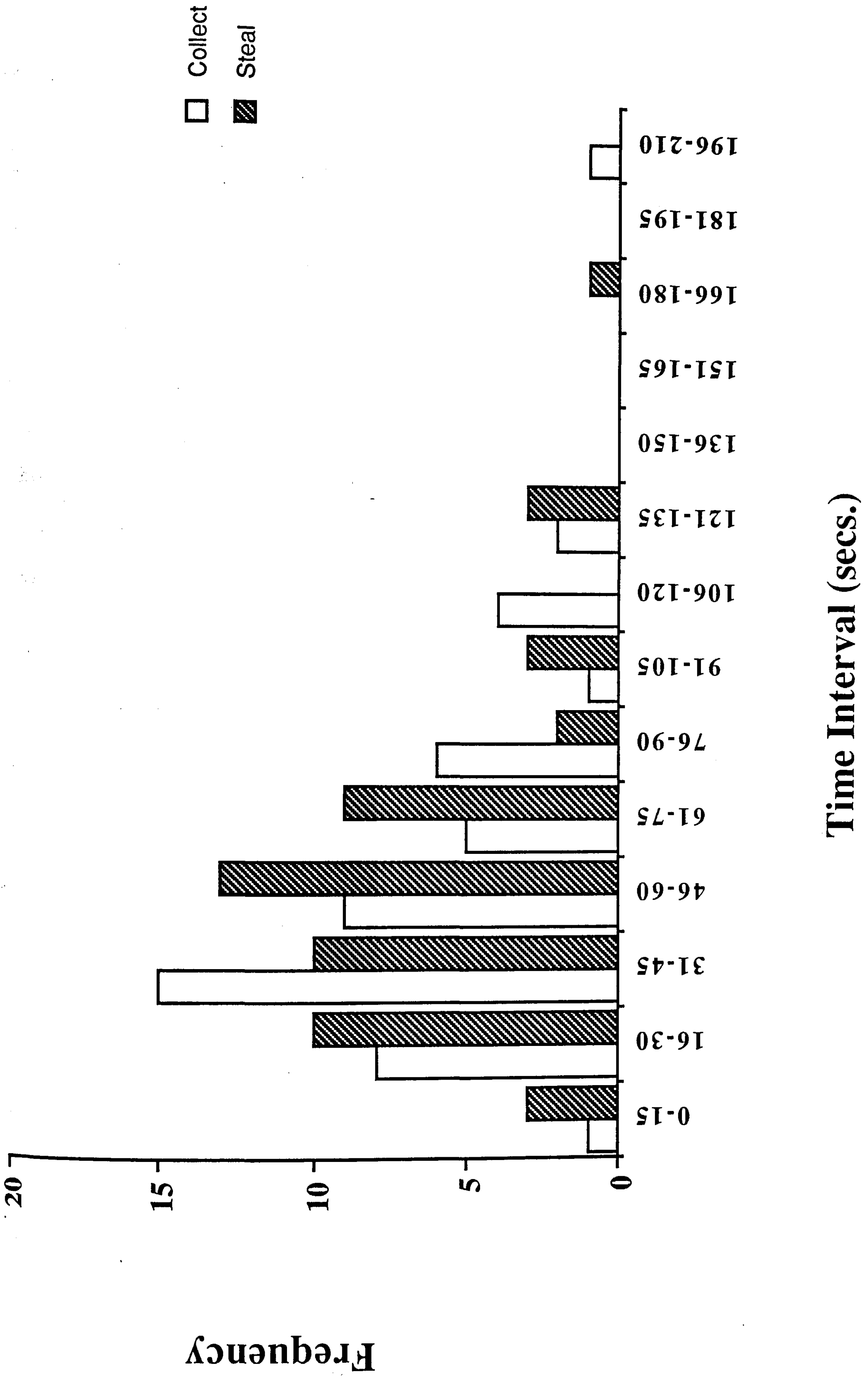
Analysis of data collected on the time taken (measured in secs.) to carry out each strategy showed there to be no significant difference ($z = 0.55$, $p > 0.05$; $n_1=52$ $n_2=53$, Mann-Whitney U test). This conclusion is presented graphically in figure 6.4. Time is divided into fifteen second blocks and is presented on the x-axis with the frequency with which each strategy occurred presented on the y-axis. Were there a difference in the time taken to collect an item as opposed to stealing it, there would not be a substantial overlap in the time distribution of each strategy.

c) Stealing occurs more often in birds having to build a new nest.- To test whether

Table 6.7. A summary of the sampling of twig density (no./m2) on the floor of the rookery at Milton Farm. The mean and median number of twigs/m2 is shown before the building period (samples taken between 26/2 and 5/3/88) and after the building period (samples taken between 5/5 and 20/5/88).

	BEFORE BUILDING	AFTER BUILDING
Number of Quadrats Sampled	14	14
Mean no. Twigs/m^2	59.86	45.43
Standard Error	± 9.94	± 6.66
Median no. Twigs/m^2	61	35
Total no. Twigs Sampled	838	636

Figure 6.4 A comparison of the times taken to collect or steal an item of nesting material. Time is divided into fifteen second intervals along the x-axis and the frequency with which each strategy occurred in each time interval is expressed on the y-axis.


Collect
Steal
Frequency
0
5
10
15
20
Time Interval (secs.)
0-15
16-30
31-45
46-60
61-75
76-90
91-105
106-120
121-135
136-150
151-165
166-180
181-195
196-210

stealing was more prevalent in 'New' nesters compared to Old, a comparison was made between the percentage of stealing observed in the two classes. These data are presented in table 6.1. In the analysis, the category 'Manipulations' is excluded in order to test the level of stealing as a percentage of the actual number of building trips undertaken. No significant difference was found in the percentage of material acquired by stealing between classes in either year (U_{1988}=27, $p > 0.05$; n_1=7 n_2=9: U_{1989} =16, $p > 0.05$; n_1=7 n_2=6, Mann-Whitney U tests).

6.3.7. An Examination of the Reproductive Advantage to Stealing

Two theories were proposed in section 6.2.7 to account for the adaptive function of stealing behaviour. The first was that the strategy conveyed a temporal benefit by shortening the duration of building and /or by advancing the finishing date. The second was that stealing nesting material conserved energy that could be directed into egg production and brood rearing.

With regard to the first proposal, that stealing affects the timing and duration of building, the data gathered in 1988 and 1989 were tested for the existence of a negative correlation between the percentage of trips to the nest with stolen material (observed percentage of stealing) and the finishing date and building duration for that nest. In neither year was there observed to be a significant correlation between observed percentage stealing and finishing date or building duration. The calculated r_s values are shown in table 6.8. I therefore conclude that the stealing of nesting material does not confer a temporal advantage in nest building.

Similarly, when the reproductive data was tested for a correlation between observed percentage stealing and clutch size, number of chicks hatched and number of chicks fledged, no significant correlation was found in either year although there is the suggestion that there was a positive relationship between a high observed percentage of stealing and clutch size in 1989, the season of my twig removal experiment. The results of tests examining for a correlation between stealing and reproduction are

Table 6.8 A summary of the results from 1988 and 1989 testing for a correlation between the observed % stealing and the finishing date and duration of building. In addition, observed % stealing is tested against reproductive output measured in terms of clutch size, number of chicks hatched and number of chicks fledged.

COMPARISON	RESULT (Spearman-Rank Corr. r_s)
1988	
Obs. % Stealing v Finish.Date	0.067 (n=15) ns.
" v Build.Dur	- 0.039 (n=15) ns.
" v Clutch Size	0.282 (n=15) ns.
" v No. Hatched	0.069 (n=15) ns.
" v No. Fledged	0.073 (n=15) ns.
1989	
Obs. % Stealing v Finish.Date	- 0.126 (n=7) ns.
" v Build.Dur	0.144 (n=7) ns.
" v Clutch Size	0.697 (n=7) ns.
" v No. Hatched	0.538 (n=7) ns.
" v No. Fledged	0.089 (n=7) ns.

Critical level of $p = 0.05$

also summarised in table 6.8 and a discussion comparing this relationship between years is included in section 6.4.

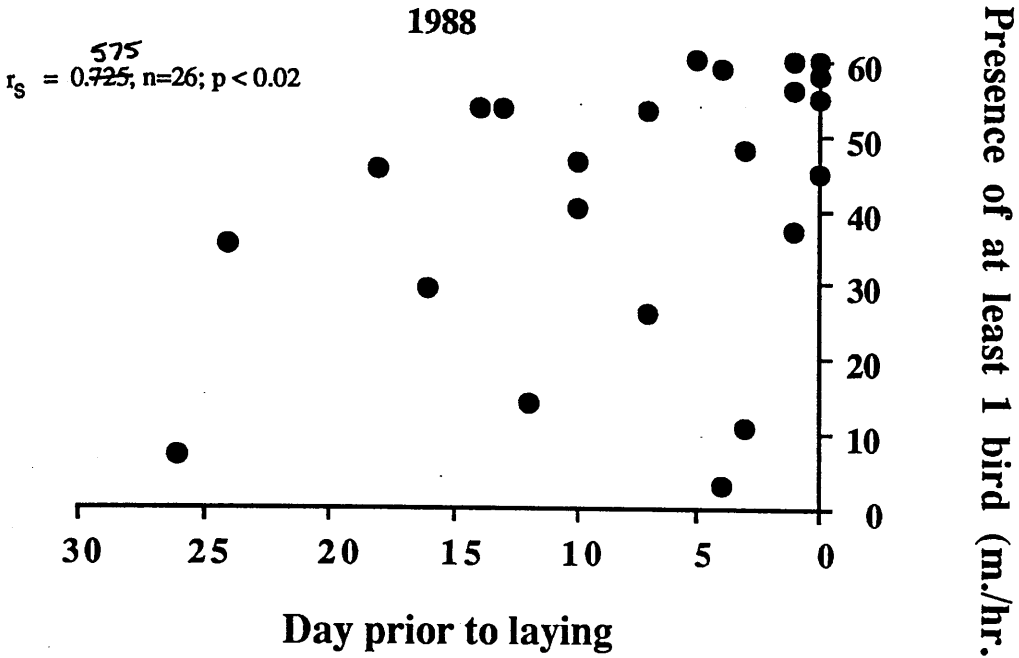
6.3.8 Vigilance at the Nest Site

In a total of 290 hrs. observation in the two study years, stealing was never observed from a nest with at least one of the resident birds present. 'Thieves' caught in the act were attacked and invariably driven away with no nesting material. Resident birds may therefore guard their nest against theft but will be subject to conflicting pressures between guarding and a continuing requirement for nesting material.

The pattern of nest attendance over the building period can be shown by plotting the presence of at least one bird of the pair at the nest site in relation to the day prior to the female being seen constantly in the incubatory position (this approximates to the time of laying). Figure 6.5 shows this relationship for 1988 (top figure) and 1989 (bottom figure). The presence of at least one bird of the pair is presented as minutes/hour on the y-axis and the day prior to the female laying is presented on the x-axis. There is a highly significant positive correlation between the presence of at least one bird and proximity to laying in both years ($r_{s1988}=$ 0.575, n=26; $p < 0.02$, 2-tailed : $r_{s1989}=$ 0.725, n=26; $p < 0.02$, 2-tailed Spearman Rank Correlations).

Since there is a potential conflict between guarding the nest and assimilating material, there may be an allocation of roles within the pair such that one guards while the other collects or steals nesting material. Figure 6.6 shows the amount of time (in minutes per hour) when one or both birds of the resident pair were attendant at the nest in relation to the female's proximity to laying. In the top figure, which shows the data for 1988, there is a highly significant positive correlation between the presence of one bird at the nest site and the day prior to laying ($r_s=$ 0.620, $p < 0.02$, 2-tailed, n = 26). However no correlation is apparent between the presence of both birds of the pair and the day prior to laying ($r_s=$

Figure 6.5. The presence (expressed as m./hr.) of at least one bird of the pair at the nest site in relation to the day prior to laying. Data for 1988 is presented in the top figure and for 1989 on the bottom. A highly significant positive correlation was found between presence of at least one bird at the nest and proximity to laying in both years (Spearman Rank Correlation). See text for details.


1988
r_s = 0.~~725~~575, n=26; p < 0.02
60
50
40
30
20
10
0
30
25
20
15
10
5
0
Day prior to laying
Presence of at least 1 bird (m./hr.)

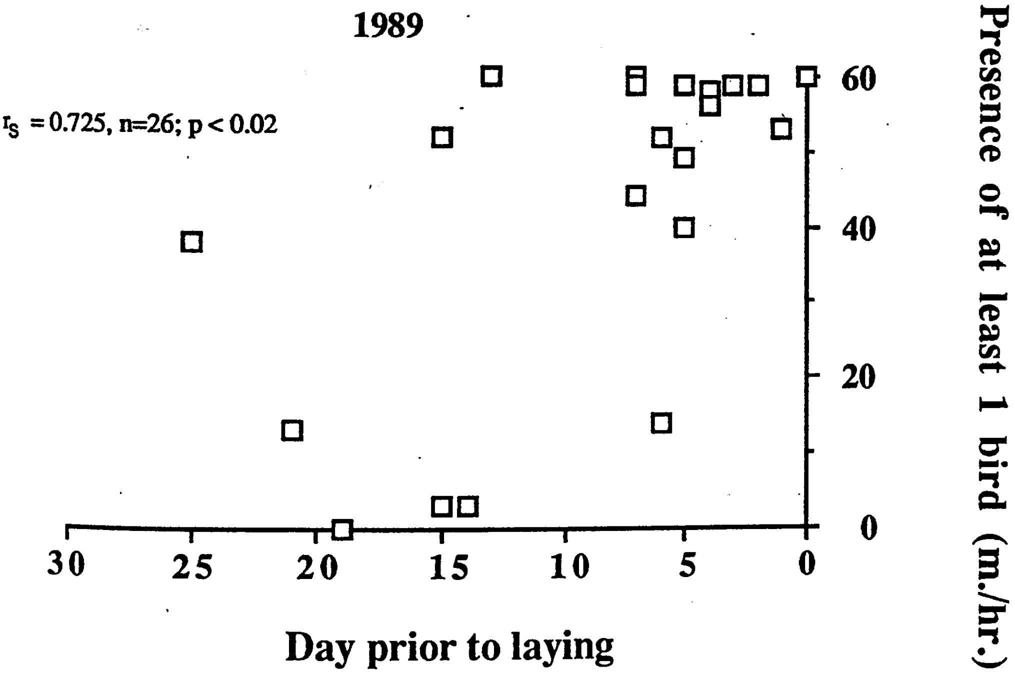
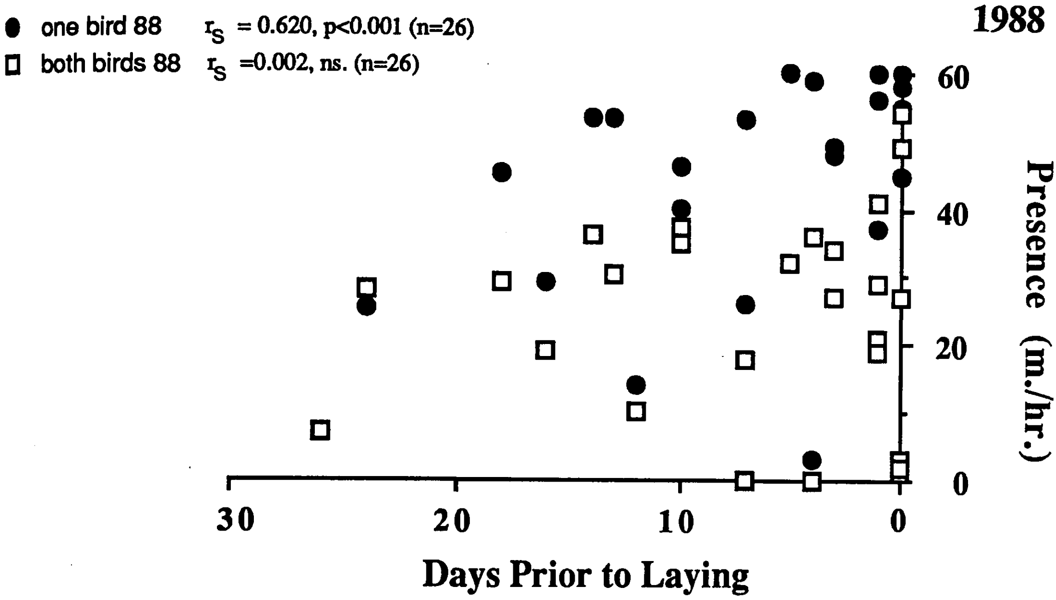
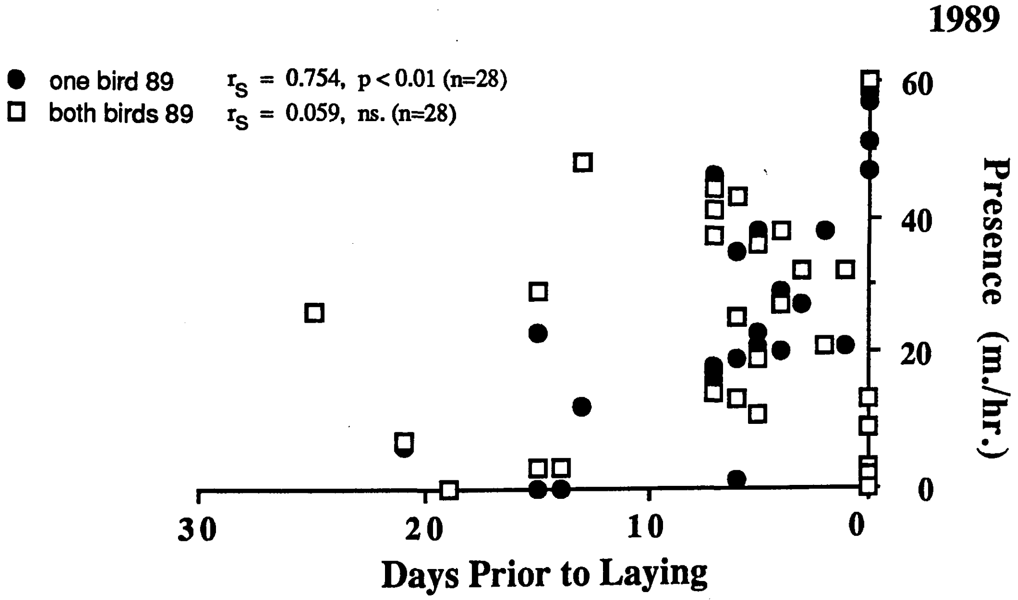

1989
r_s = 0.725, n=26; p < 0.02
60
40
20
0
30
25
20
15
10
5
0
Day prior to laying
Presence of at least 1 bird (m./hr.)

Figure 6.6. The presence of one or both birds (measured in minutes/hour) of a pair at the nest site in relation to the day prior to the female laying. In both 1988 (top figure) and 1989 (bottom figure) there is a highly significant positive correlation between one bird of the pair being present and proximity to laying. However, such a correlation is not apparent for the presence of both birds of the pair.



1988

● one bird 88 r_S = 0.620, $p<0.001$ (n=26)
□ both birds 88 r_S =0.002, ns. (n=26)
Presence (m./hr.)
60
40
20
0
30
20
10
0
Days Prior to Laying



1989

● one bird 89 r_S = 0.754, $p < 0.01$ (n=28)
□ both birds 89 r_S = 0.059, ns. (n=28)
Presence (m./hr.)
60
40
20
0
30
20
10
0
Days Prior to Laying

0.002, n.s., n = 26). The same conclusions were true for 1989 ($r_S = 0.754$, $p < 0.02$, 2-tailed, n = 26 for the presence of one bird and $r_S = 0.059$, n.s., n = 26 for the presence of both birds).

This analysis shows that as egg laying approaches, there is a highly significant increase in the degree of attendance by one bird of the pair but no discernible change in the extent of time in which both birds attend the nest site. A discussion of how this role partitioning relates to the sexes is covered in the discussion section of this chapter.

6.3.9. The Effects of the Twig Removal Experiment

In section 6.2.9, four predictions were made on the effect of the perturbation experiment conducted prior to the building season in 1989.

The first predicted that a reduction in the amount of available twigs would induce a greater competition for nesting material which would be manifest as an increased incidence in stealing. I have shown in section 6.3.1, that the observed level of stealing was significantly higher in the year of the experiment compared to the previous year. The prediction would therefore appear to be substantiated.

Secondly, if the removal of twigs had reduced the availability of nesting material, then it is possible that fewer birds would be able to find sufficient twigs to complete nest building. The result would be a drop in the peak number of nests within the colony. Reference to figure 3.3 which shows the change in nest numbers at Milton Farm over time, reveals that the mid-April peak in nest numbers was in fact higher in 1988 than in 1989; the actual figures being 392 and 359 respectively.

The third prediction made of the experimental year was that twig removal would increase the energetic cost of building and this would result in a lower reproductive output for that season. I have already shown there to be a reduction in the mean number of chicks fledging in subsets of the population in 1989 compared to 1988, namely in birds reusing nests and birds nesting in Scots pine (see tables 6.4 and 6.6 respectively). Table 6.9 summarises the collated reproductive data for the two years of the study. The figures for the mean number of chicks fledged are in bold script because the reduction in the number of fledglings in 1989 is highly significant ($z = 3.01$, 30 d.f.; $p < 0.01$). One can ignore differences in reproduction due to factors such as nest reuse, choice of Scots pine or sycamore as nesting site and incidence of stealing because variation in reproduction between these classes <u>within</u> years has been shown to be not significantly different. What the data does reveal is a year effect with the greatest reduction in fledging rate being recorded in birds reusing nests and nesting in Scots pine. A full discussion of these findings is included in the next section.

The final prediction was that a rerun of the choice experiment, providing birds with twigs in denoted size categories would, unlike in 1988, result in the reduction of any discrimination for twigs on the basis of size because competition for twig material had been intensified.

Table 6.10 summarises the losses from the quadrat in the experimental period which ran from 6/3 - 19/4/89 and the control period from 8/5 - 22/5/89. The results refute the prediction since the disproportionately high loss of twigs in the size category 40-50 cms. is highly significant ($X^2 = 61.66$, $p < 0.01$, 2 d.f.). The conclusion is therefore the same as for 1988, with the disproportionate loss of twigs in the size category 40.1-50 cms. being highly significant. However, a difference was apparent between years in the daily rate of twig loss from the quadrat in all three categories. In 1988 there is no significant correlation between the number of twigs lost per day in any category in relation to the day after the start of the experiment. In other words, the rate of loss of twigs from the quadrat does not vary over the building period. This is not however the case in 1989, where there is a

Table 6.9 A between-year comparison in the reproductive output from all nests monitored in 1988 and 1989. There is a significant reduction in the number of chicks fledged per nest in 1989 (the experimental year). This comparison is indicated by figures in bold script - see text for details.

1988	Clutch Size	No.Chicks Hatched	No.Chicks Fledged
No. Nests	32	32	32
Mean/Nest	2.94	2.00	1.84
Stand. Err.	± 0.17	± 0.15	± 0.15
1989			
No. Nests	32	32	32
Mean/Nest	2.88	1.75	1.16
Stand. Err.	± 0.16	± 0.13	± 0.12

Table 6.10 The number of twigs lost in each size category from the 3x3 m2 quadrat in the experimental period (Period 1 between 6/3/89 and 14/4/89) which coincides with the building period and the control period (Period 2 between 8/5/89 and 22/5/89) when birds have completed building.

Size Category (cm)	Number of Twigs Lost	
	Period 1	Period 2
20 - 30	49	0
30.1 - 40	63	0
40.1 - 50	144	0

highly significant positive correlation between numbers of twigs lost in each size category from within the quadrat and day after the start of the experiment on 9 March.

Figure 6.7 shows the number of twigs lost per day from the quadrat during the course of the experiment in both 1988 and 1989. In the latter year, the indication is that as the building season progressed, the trend was for more twigs to be removed each day. The results therefore indicate that although there was no evidence of a departure from discriminative selection for larger twigs in the experimental year, there was an effect of increased rate of twig loss in all size categories from within the quadrat. The implications of this with regard to the rookery clearance will be discussed at the end of this chapter.

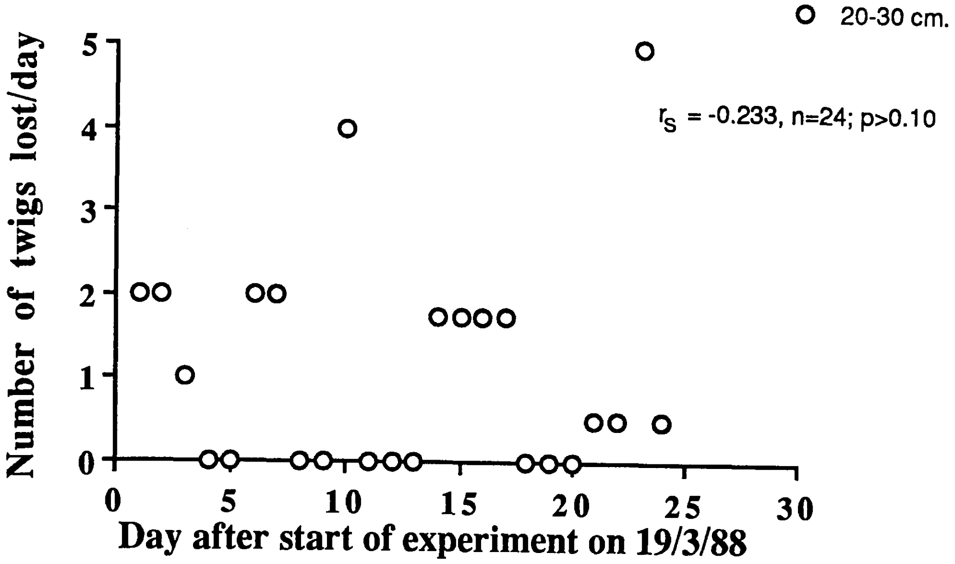
6.3.10. The Timing and Function of the Bow-Caw Display

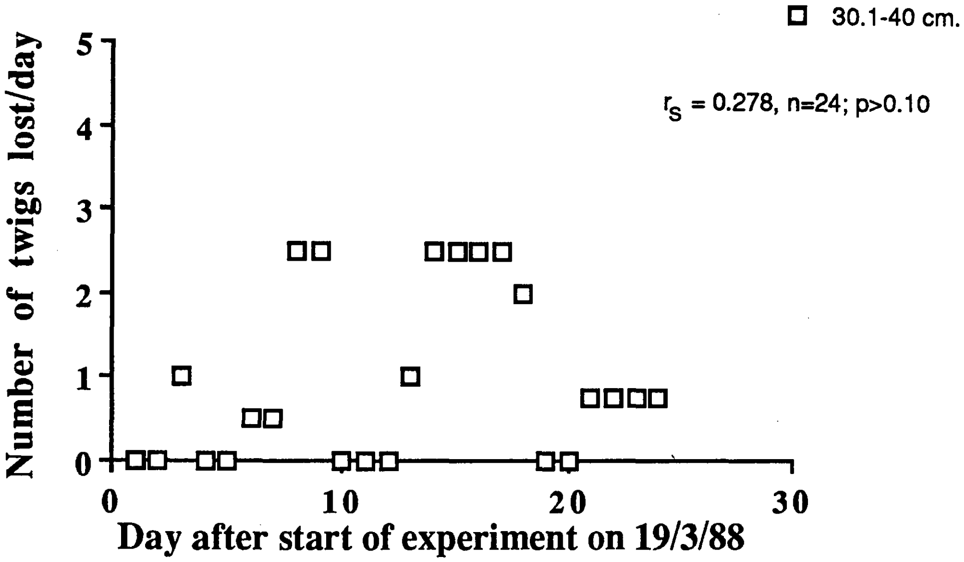
An assessment of the function of bow-cawing is made by studying the context in which it was observed to occur. Extra-pair displays were defined as being those performed by a pair at their nest site, directed at other birds and intra-pair displays were defined as those displays unambiguously directed at the other bird of the pair.

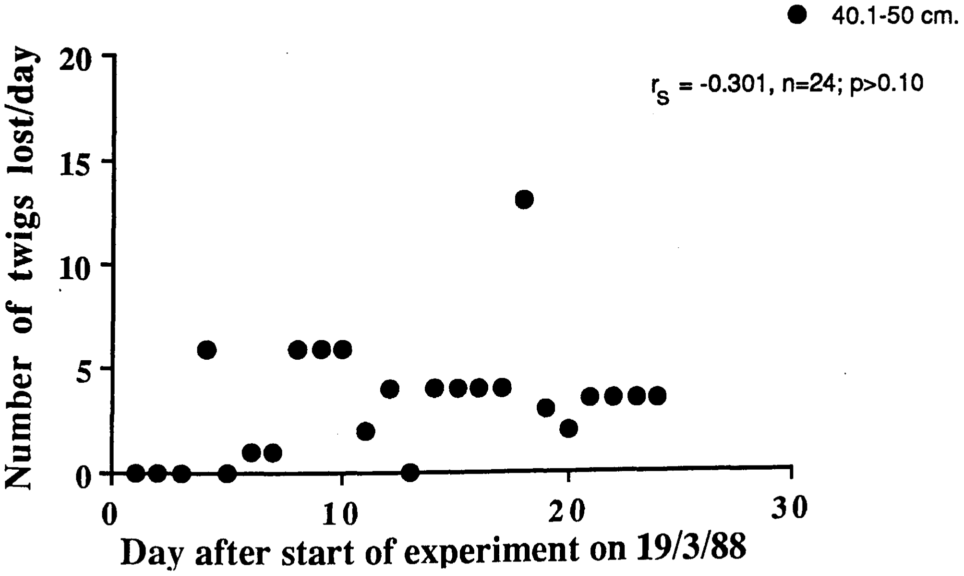
No significant difference was found between the frequency of intra- and extra-pair bow-caw displays observed in the spring period ($U=123$, $n_1=18$ $n_2=18$; $p > 0.05$). If the context of the display reflects the functions of territoriality (Extra-pair displays) and pair-bond consolidation (Intra-pair displays), then the absence of a significant difference in display rate between the two classes supports the idea stated in the last chapter that the display performs more than one function.

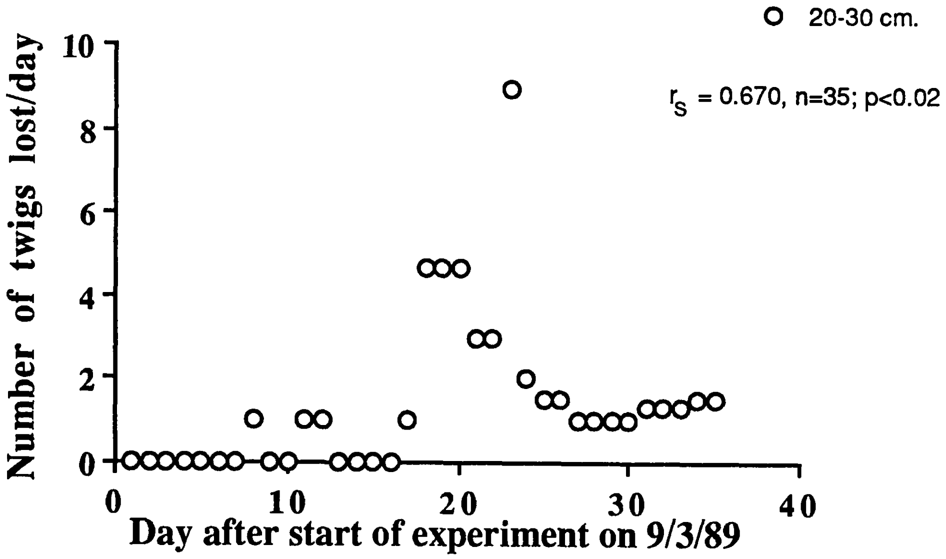
Figure 6.8 shows the plot of display rate against date. A significant negative correlation was found between extra-pair display rate and advancing date and a highly significant negative correlation was found between intra-pair display rate and

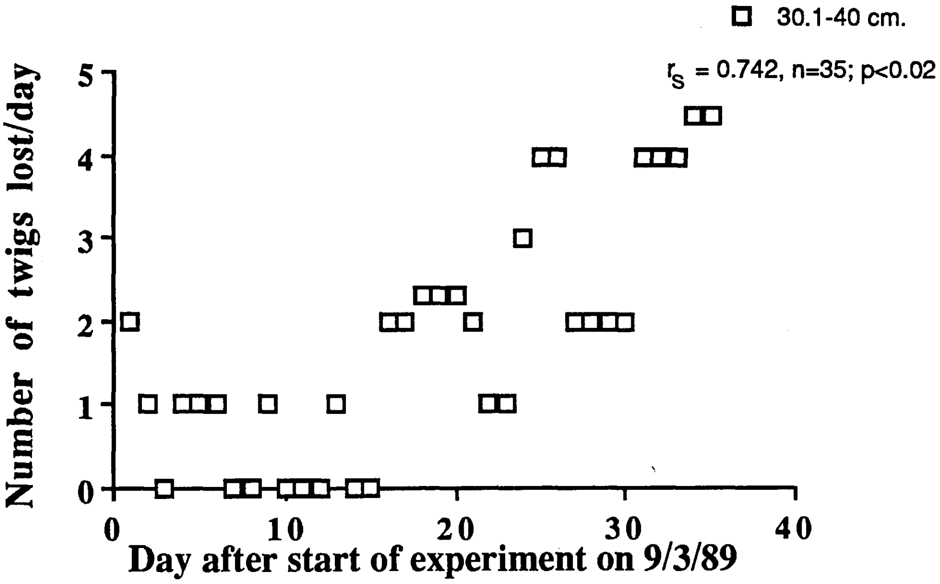
Figure 6.7. Plots of the daily number of twigs lost from each of the twig size categories included in the quadrat; 20-30 cm. (top figure), 30.1-40 cm. (centre figure) and 40.1-50 cm. (bottom figure) against the day after the start of the experiment. The results for 1988 are shown opposite where no correlation was found between daily numbers of twigs lost and date (Spearman Rank Correlation). Overleaf are the results of the identical experiment conducted in 1989. In all three categories a highly significant correlation was found between daily number of twigs lost and date (Spearman Rank Correlation). See text for details.


○ 20-30 cm.
r_S = -0.233, n=24; p>0.10
Number of twigs lost/day
0
1
2
3
4
5
0
5
10
15
20
25
30
Day after start of experiment on 19/3/88


□ 30.1-40 cm.
r_S = 0.278, n=24; p>0.10
Number of twigs lost/day
0
1
2
3
4
5
0
10
20
30
Day after start of experiment on 19/3/88


● 40.1-50 cm.
r_S = -0.301, n=24; p>0.10
Number of twigs lost/day
0
5
10
15
20
0
10
20
30
Day after start of experiment on 19/3/88


○ 20-30 cm.
r_s = 0.670, n=35; p<0.02
Number of twigs lost/day
0
2
4
6
8
10
0
10
20
30
40
Day after start of experiment on 9/3/89


□ 30.1-40 cm.
r_s = 0.742, n=35; p<0.02
Number of twigs lost/day
0
1
2
3
4
5
0
10
20
30
40
Day after start of experiment on 9/3/89

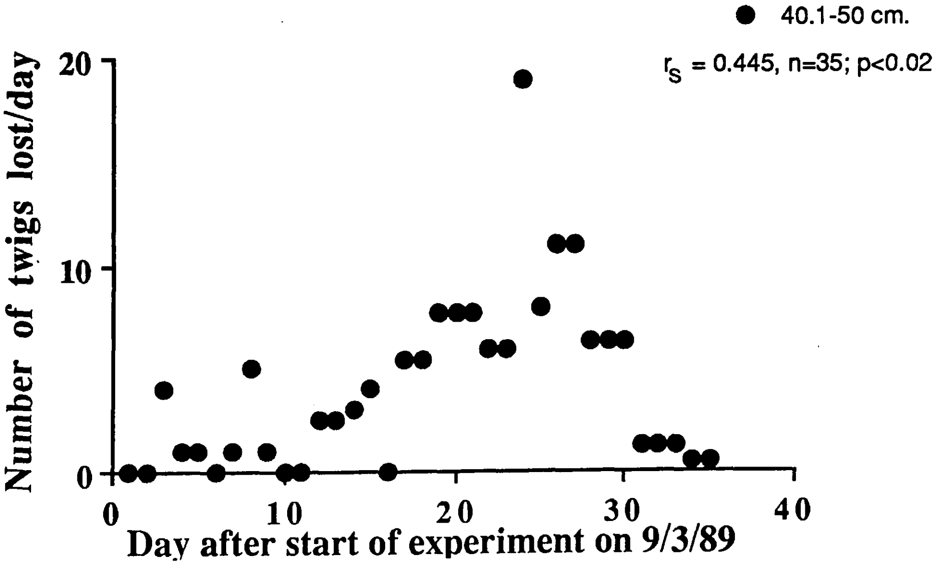
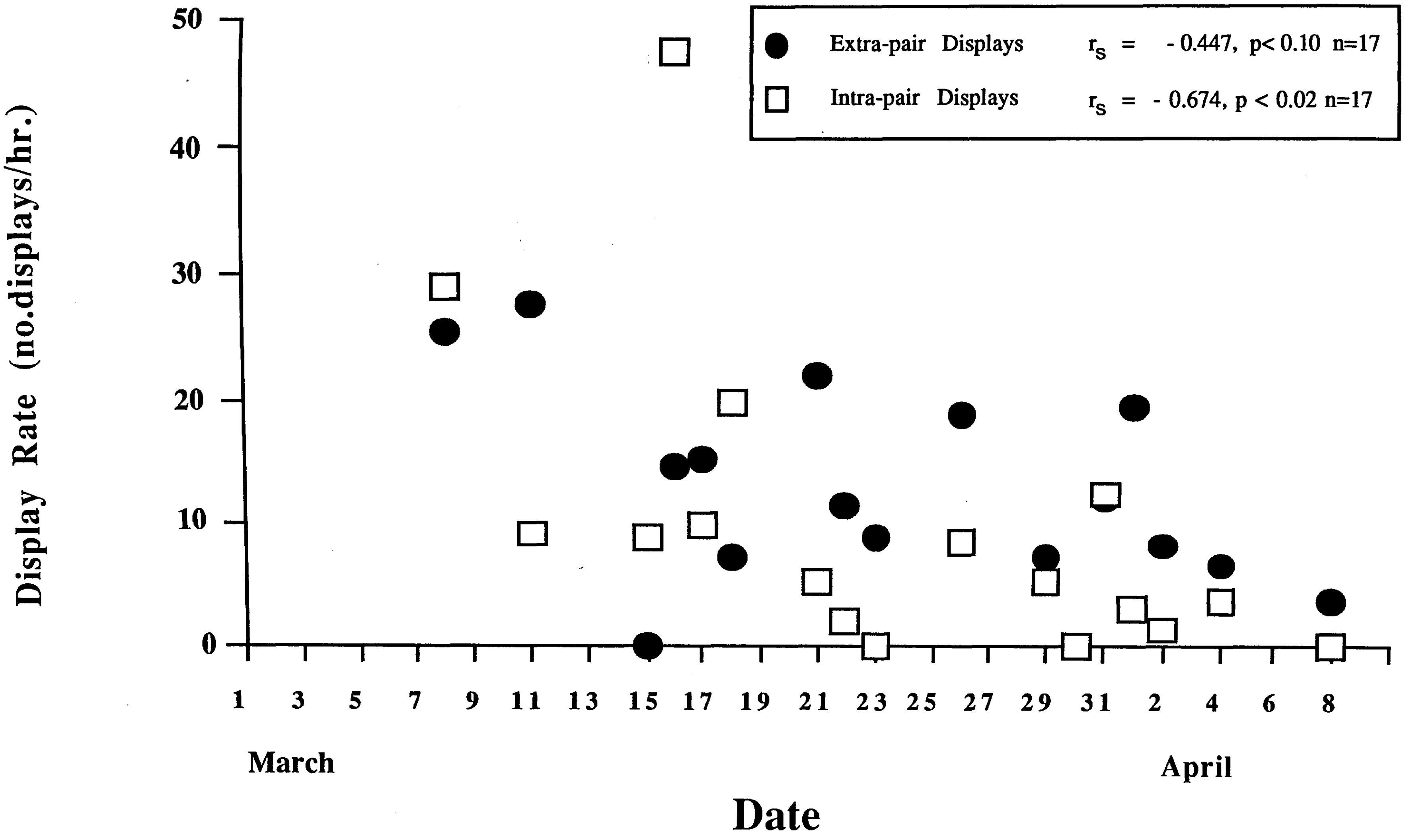

● 40.1-50 cm.
r_s = 0.445, n=35; p<0.02
Number of twigs lost/day
0
10
20
0
10
20
30
40
Day after start of experiment on 9/3/89

Figure 6.8. The rate of Extra-Pair (closed circles) and Intra-Pair (open squares) bow-caw displays shown in relation to date. The last recorded displays were made 5 days before the first female was seen constantly in the incubatory position. The graph show a significant reduction in display rate in relation to advancing date.


● Extra-pair Displays r_S = - 0.447, p< 0.10 n=17
□ Intra-pair Displays r_S = - 0.674, p < 0.02 n=17
Display Rate (no.displays/hr.)
50
40
30
20
10
0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
2
4
6
8
March
April
Date

advancing date. The demonstrated trend is therefore, for display rate to decline as the building season progresses.

6.4 Discussion and Interpretation

The major objective of studies conducted in the spring was to evaluate the biological cost of nest building by correlating variations in building behaviour with reproductive output. An understanding of building strategies which increase fitness will in turn, provide an understanding of the selective pressures governing nest building behaviour.

Three conspicuous features of rook nest building behaviour were studied; the mode of nest material assimilation, the reuse of old nests compared to the construction of new, and the choice of nest site. Variation in behaviour related to these features may be adaptively advantageous if it advances the female's laying date and/or minimises the energetic cost of nest building so permitting a greater investment in egg production and brood rearing.

This discussion is aimed at directing the conclusions from the results of the last section towards answering the predictions of the Cheap and Expensive hypotheses stated in section 6.1.4. An evaluation as to which set of predictions better reflects empirical study will provide an idea of the severity of a reproductive cost incurred by the effort of nest building.

Pairs obviously differ in the degree to which they practise the three defined strategies of assimilating nest material. However, when one looks for a difference in the mode of nest material assimilation between New and Old nesters, it was found that the degree of Collecting, Stealing and Manipulating was not significantly different between the two classes. In addition, New nesters do not have to make more trips for material than Old nesters who already have the platform of a previous year's nest. Moreover, Old nesters do not start or complete nest building earlier in the year than New nesters and are not therefore gaining a temporal advantage. The finding that in both years, New nesters had a significantly shorter building duration than Old nesters is counter-intuitive, since the expectation is that birds refurbishing old structures will capitalise on the presence of old material to reduce their number of building trips and so hasten the completion of building. In 1988, building duration was not observed to influence reproductive output as measured in terms of clutch size, number of chicks hatched or number of chicks fledged. In 1989 however, a significant positive correlation was found between clutch size and building duration. This year was the breeding season of my twig removal experiment and it is possible that one of the effects of reducing the amount of available nesting material was to increase the 'cost' of nest building. Birds building intensively, over a short period, may, I suggest, incur a particularly heavy cost which is manifest as an enforced lowering of the investment in egg production.

Note that there may seem to be an inconsistency in results here; table 6.2 shows that new nests were built quicker than old in both study years. In the light of the above conclusion, one might have expected new nesters to have a reduced clutch size compared to old in 1989. Tables 6.3 and 6.4 show that this is not in fact the case. The significant positive correlation between clutch size and building duration shown for 1989 in figure 6.2 may be caused by the relatively small sample size (n=8). I suggest that more data would be useful in substantiating the trend. If the correlation was still significant in a larger sample size, then the conclusion would indeed appear paradoxical.

To summarise the results, there would appear to be no difference in the degree of building effort between 'New' and 'Old' nest builders, in terms of either mode of material assimilation or the starting or finishing of building. Furthermore, within years, there was found to be no difference in reproductive performance between

Old and New nesters though comparing between years, pairs in old nests fledged fewer chicks in the experimental year (1989).

The question arises as to whether Old nesters are exploiting what is perceived to be the advantages of possessing an old nest. The fact that Old and New nesters were observed to make similar numbers of building journeys suggest that both classes undertake nest construction to the same degree regardless of whether they are starting the nest in a fork of branches or on top of an old nest platform. The continual addition of material to old nests may therefore account for the large discrepancy in nest size that was noted in section 2.3.1. Large nests may not only be caused by the local geometry of the nest site which may dictate that more material is required to make the nest stable, but also by the perennial addition of nesting material which will cause a structure to increase in size over several years. One potential explanation for this overbuilding is that the energetic cost is relatively low to the extent that there is no evidence of a selective pressure upon individuals reusing old nests to reduce their building effort by making use of existing material.

One advantage of nesting colonially is that individuals within the colony benefit from increased nest defence due to the corporate vigilance and aggression of its colony members. Röell & Bossema (1982) have suggested that colonial nesting in rooks benefits individuals in the detection and repulsion of other corvid predators such as the carrion crow, *Corvus corone*, and magpies, *Pica pica*, though this conclusion is debated by P.T. Green (1982a) and Røskaft (1980). Selection of the nest site may not therefore be critical in terms of reducing predation as has been suggested in other species such as the lesser snow goose, *Chen caerulescens caerulescens* (Jackson et al. 1988) and the spruce grouse, *Canachites canadensis* (Redmond et al. 1982). I have suggested that in the case of rooks, where nest defence is unlikely to be a major factor in nest site selection, there may be a preference for sites within the colony on the basis of canopy morphology. Birds should select nest sites that provide maximum support and stability for the nest platform and therefore reduce the amount of material and hence building effort required for its construction.

In the comparison of the reproductive performance of pairs nesting in different tree species (Scots pine and sycamore) one could discount the confounding influences of nest reuse and stealing on reproductive output since this was already shown to be non-existent. In both years of the study, no difference was found in the mean clutch size, mean number of chicks hatched and mean number of chicks fledged from either species. However, a comparison of the reproductive output in both tree species between years showed that in 1989, significantly fewer chicks fledged from Scots pine than they did in 1988. It may be possible that in the experimental year, the removal of twigs from the rookery floor did have the effect of increasing the cost of building and when conditions become more severe, birds nesting at inferior nest sites (i.e. in Scots pine) suffer a reproductive penalty. However, such a hypothesis is contrary to the conclusions drawn from section 3.3.3, which showed Scots pine to contain a significantly higher proportion of nests than would be expected on the basis of the species' prevalence within the rookery. This need not necessarily be interpreted as a preference for nesting in Scots pine if the number of available nesting sites within the tree canopy varied between species. More nests may have been recorded in Scots pine simply because its canopy morphology offered more potential nesting sites. Ideally, in testing for a preferred tree species, one should estimate the proportion of available sites within each, and not just measure preference according to the relative proportion of each tree species in the colony. If it were shown that Scots pine did offer more nesting sites than either sycamore or larch, then the expected number of nests in its canopy would be higher, and a significant difference between the observed and expected numbers of nests in this species may no longer be apparent.

* Alternatively, the observed reduction in the mean number of chicks fledged from

NB.
This paragraph is no longer necessary.

Scots pine in 1989 may be attributable to factors totally unrelated to the inferiority of nest site and hence to the cost of building. Røskaft et al. (1983) has shown there to be an age effect on the reproductive performance of rooks, with younger birds having a lowered reproductive output compared to older more experienced individuals. For example, suppose there was a disproportionate number of young birds nesting in the Scots pine trees sampled in 1989, the result would be a lowered number of chicks fledged in that year. Moreover, Røskaft (1985) has shown that large broods from a previous year may have the effect of reducing the reproductive output of that pair in the following year. The reasons for this are not pertinent to this discussion (though see Røskaft 1987 and George and Ligon 1987) but the fact that there is a year to year influence on reproductive performance means that low numbers of chicks fledged from Scots pine in 1989 may be caused by the large breeding effort of those birds in the previous spring and not by an increase in building effort.

I wish to leave a more detailed discussion of the effects of the twig removal experiment until later when, amongst other issues, I will examine the question of whether it can be regarded as having influenced the reproductive output of individuals. The main point that has emerged from the comparison of reproductive performance in the two major nest-containing tree species is that within years no difference was observed in clutch size, the number of chicks that hatched or the chicks that fledged between them. This suggests that if there is an adaptive advantage to selecting particular nest sites, then it is not based on criteria that can be associated with the nest-containing tree species.

The absence of an effect of nest reuse or selection of nest site on reproductive performance are both conclusions in agreement with predictions of the Cheap perspective. This simple congruence is complicated when one considers the predictions of each hypothesis with regard to the stealing of nest material. To briefly recap, the Cheap hypothesis states that stealing will be an infrequent event;

conversely, the Expensive approach advocates that stealing will be common and furthermore, will confer a reproductive advantage. Despite the fact that its incidence varies between pairs, stealing is a very common and conspicuous feature of rook nest building behaviour which has received surprisingly little attention in the ornithological literature, Ogilvie's paper (1951) being a notable exception.

The practise of stealing nesting material is not unique to rooks and has been reported to occur in penguins (Ainley 1975; Yeates 1975), cormorants (L.Williams 1942), frigatebirds (Nelson 1975), gannets (Nelson 1978), herons (Lowe 1954; Siegfried 1972), some gulls (J.Burger 1974) and swallows (Emlen 1952; Hoogland & Sherman 1976). Apsley Cherry-Garrard who was the assistant biologist on Scott's ill-fated Antarctic expedition in 1911 developed much empathy with the ever-present Adélie penguins. His description of the stealing of pebbles from one another's nests belongs to an era that permitted an ethological indulgence in anthropormorphisms. He writes, " Life is too strenuous for them to have any virtues of brotherly love, good works, charity and benevolence. When they mate the best thief wins: when they nest the best pair of thieves hatch out their eggs." (The Worst Journey in the World 1937). On a more functional level, Cherry-Garrard recognised that by raising the nest on a surround of pebbles, the eggs and chicks were not as vulnerable to floods resulting from thaws. In this conclusion, he preempted the work of Sladen (1958) by a good forty years. My concern was whether Cherry-Garrard's conclusions applied to rooks, was it the best thieves that were at a reproductive advantage?

If the high level of stealing observed is to be regarded as being in agreement with the Expensive hypothesis, then the second part of the prediction which states that its practise will confer a reproductive benefit, is not supported by the data. No correlation was found between an increase in the observed percentage of stealing and increased reproductive output. However it should be noted that the corresponding r_s values for the observed percentage stealing v's clutch size and number of chicks hatched are much higher in 1989, the year of twig removal, than in 1988 (see table 6.8). These correlations are not however, significant.

Stealing did not then manifest its benefit in terms of reproductive output. However, it may still confer a reproductive advantage if it permitted birds to shorten the duration of building and/or hasten the completion of nest building. Tests for a correlation between the observed percentage of stealing and building duration and finishing date were also shown not to be significant so the conclusion is that stealing does not even confer a temporal advantage.

The question remains as to why stealing is so prevalent? I have indicated that it is not provoked by competition for nesting material, as predicted by the Expensive hypothesis, and there was no evidence to suggest that stealing an item took less time than collecting an item. It is therefore true to say that the proposed reasons to account for stealing have not been supported by the data from field studies. Stealing may, under conditions of material shortage, confer a reproductive advantage (as I shall discuss later) however, even in years of plentiful material, being stolen from may incur a penalty. On many occasions I observed the raiding of newly started nests with the result that the precarious structures eventually disintegrated. If this happened regularly, the pair would eventually desert the site, presumably in an attempt to nest elsewhere or even conceivably abandon breeding.

Stealing may therefore be selected for even when there is an abundance of material. If birds are having to compromise time spent in gathering nesting material with being vigilant against thieves, then stealing from other nests may allow birds to meet their requirement for nesting material whilst remaining at canopy level and keeping an eye on their own nest. A similar conclusion is reached by Wittenberger & Hunt (1985), who note that theft of nesting material in birds often occurs under conditions of plentiful building material. The authors share my opinion that stealing may be a compromise between acquiring nesting material and remaining in the vicinity of the nest in order to prevent it being stolen from.

The fact that rooks steal nesting material and potentially suffer a penalty by being stolen from may account for the increased attendance by at least one bird of the pair at the nest site as laying approaches. As figure 6.6 shows, this increased attendance is due to the increasing presence of a single bird with no correlation apparent between the presence of both birds and proximity to laying. Coombs (1981) notes that as laying approaches it is the female who remains at the nest site whilst the male forages for both food and the final pieces of nesting material.

The reason for this increased attendance is unclear; it may be to guard against stealing, and as investment in the nest site grows the resource merits a greater investment manifest in terms of the time spent guarding it. There may be an additional benefit to the female remaining at the nest site when she is close to laying. It is a controversial point, but there is some suggestion that egg production and laying place a physiological stress on the female (see Jones & Ward 1974 and Krementz & Ankney 1986). If laying does stress the female then it might be expected that she will conserve energy when she is gravid and remain in the vicinity of the nest. Increased attendance by the female in relation to proximity to laying is therefore predicted on grounds of both vigilance and energy conservation. My studies do not separate the two. In terms of the Cheap/Expensive paradigm, a high incidence of vigilance during building is predicted by the Expensive approach although a clearer demonstration that this increased attendance was an act of vigilance would be if it could be established that birds who suffered disproportionate losses due to theft also had a reduced reproductive output. I shall suggest a method to resolve this problem in the final chapter.

By the end of the 1988 season, the analysis of results revealed a paradox. Stealing was a prominent features of rook nest building behaviour yet no adaptive advantage could be attributed to its practice. Stealing is not motivated by competition for nesting material since post-building samples of twig density revealed there to still be large numbers of suitable twigs on the rookery floor after the building season. The availability of nesting material is therefore more in accordance with the Cheap hypothesis which predicts it to be in excess. The experimental intervention of removing as much nesting material as possible just prior to the building season was therefore an attempt to increase the cost of building by intensifying competition for nesting material.

In section 6.2.9, I predicted the effects of the twig removal experiment on a) the incidence of stealing, b) the peak in nest numbers within the colony, c) the reproductive output of colony members and d) the preference for certain types of twig material. The major problem with drawing conclusions from the results of differences in these studies between years is that there is no control against which to compare proposed effects of the perturbation experiment. Recorded effects cannot be definitely attributed to twig removal since they may simply reflect a year to year variation. However, examination of even the circumstantial evidence may support or refute the argument that the experiment conducted in the spring of 1989 altered the behaviour and reproductive output of the colony.

Though the incidence of stealing significantly increased in 1989, there is no way of measuring what the level of stealing would have been if the removal of twigs from the rookery floor had not occurred. The peak numbers of nests in the colony in the experimental year was also below the peak of the previous year, a drop of approximately 9%. One can compare this change to the year to year change in peak nest numbers at the four Campsie rookeries. In each year between 1987 and 1989 an increase was noted in the peak numbers of nests in each colony and this increase varied between 23.5 % (Craigend 1987-88) and 2% (Craigend 1988-89) (refer to figure 3.2 for trend). It would appear then that Milton Farm was the only rookery monitored that suffered a drop in peak nest numbers, all the other rookeries showed a small percentage increase in each year. Although the situation at Milton is anomalous, the same warning needs to be voiced as was noted for the increase in the incidence of stealing; was the drop in peak nest numbers at Milton Farm due to the effects of twig removal or was it just a natural fluctuation?

The third prediction was that by removing twigs, the cost of building would increase and correspondingly less energy could be invested in reproduction. Breeding performance would therefore be lower in 1989 than in the previous year. As I mentioned in section 6.3.2, in the year of the experiment, short building durations were associated with a reduction in clutch size. I have suggested this may be indicative of a cost to building though it could be a result of a small sample. Table 6.9 summarised the collated results of the reproductive performance of sampled nests in 1988 and 1989. It shows a significant reduction in the mean number of chicks fledged per nest in the experimental year but no significant difference in clutch size or hatching rates between years. It is possible that birds suffered an increased cost in building and though the pair managed to incubate and hatch the brood, rearing efficiency was reduced with the result that fewer chicks fledged. Note too, that when 1989 is compared to 1988, there was a far greater positive correlation between increasing observed percentage stealing and clutch size and number of chicks hatched (see table 6.8). Though this result is not significant, it is possible that stealing may have benefited birds in their egg laying and hatching however, it does not explain why this advantage should be lost by the time it came to fledging. As the table shows, the correlation between observed percentage stealing and number of chicks fledged is similar for 1988 and 1989.

The rerun of the ground experiment in 1989 was essentially a check on the effects of twig removal, the rationale being that a reduction in the availability of twig material would negate the preferential selection for large twigs that had been demonstrated in 1988. The results did not support this prediction as the frequency of twigs between 40.1-50 cms. lost from the quadrat in 1989 was significantly higher than the two smaller size categories, just as it had been in 1988. A highly significant positive correlation was observed between the day after the start of the experiment and the rate of twig loss (expressed as the number of twigs lost per day) in 1989, though not in 1988. This suggests that the twigs supplied in the quadrat were being utilised more readily in the experimental year than in the previous year.

With hindsight, it may have been possible to assess the effects of twig removal by a more direct method than rerunning the ground experiment. Twig density could have been estimated (in terms of number per m^2) after the breeding season of 1989, just as had been done in 1988. A comparison would then have been possible between post-building twig density in both years to test the prediction that twig removal had caused a shortage of nesting material. If this were true, then one would predict that the post-building twig density would be significantly lower in 1989 than in 1988.

The absence of a control to the twig removal experiment prevents the formation of definitive conclusions as to its influence on building behaviour and reproduction. The circumstantial evidence however, certainly suggests that it may have had some effect. In the experimental year, stealing was more prevalent, peak nest numbers were down, the number of chicks fledged per nest was lower and more twigs were removed from the quadrat. It may be possible that under conditions of extreme competition for nesting material, stealing may benefit individuals by a) ensuring they acquire enough material to construct a nest and breed or b) by reducing the energetic cost of nest construction. In general however, I do not believe that rooks suffer from a severe shortage of nesting material such that the high prevalence of stealing is explained by competition. I have proposed that the selective pressure behind its practice may be the result of a compromise between the gathering of nest material and vigilance.

No difference was apparent in the context in which bow-caw displays were observed to occur indicating that the proposed functions of the display namely territoriality and pair-bond consolidation may be equally important during the building season. The significant negative correlation between display rate and advancing date is relevant to the comparison made between display rate during the building period in the spring and that of the autumn. In section 5.4 I suggested that the recorded difference in display rate between the two periods may be due to the fact that spring displays culminate in building and breeding with the result that rate will decline as individuals become involved with these other activities.

Although I have only recorded Extra-pair and Intra-pair displays, the indication is that display rate drops as building progresses and this seasonal decline in the spring may explain the difference in seasonal display rate noted in section 5.3.3.

In summary: The study of the effects of building as a cost to reproductive output reveal that variation in mode of nest material assimilation, nest reuse and choice of nest location have very little influence on reproductive output. Such findings overwhelmingly support the Cheap perspective of the cost to nest building in the rook. Stealing and high levels of attendance at the nest site are the only anomalies to a wholehearted adoption of the Cheap approach although attendance may be explained by the fact that the female is conserving energy for egg production rather than being vigilant. It is possible that the twig removal experiment of 1989 did have some effect on the building behaviour and reproductive output of the colony though, in the absence of a control it is not possible to be entirely certain that this was the result of an induced increase to the cost of nest building.

The rate of bow-caw displays within a pair, and between a pair and other individuals, was shown to decline over the building period and this may explain the difference in display rate between autumn and spring. The frequency of display in relation to context did not however differ over this period and evidence suggests that bow-cawing fulfils more than one function.

7. GENERAL DISCUSSION

7.1. Introduction

Nest building, like other forms of parental care in birds, is presumed to incur a cost to the parent (O'Connor 1984). Natural selection should favour those individuals that balance the trade-off between building effort and nest quality so as to maximise their reproductive success. This study has focused on the problem of assessing the biological cost of nest building in birds since nest structure and building behaviour play a vital role in the breeding effort of many species (see section 1.1.4). It is precisely because nest building is such a conspicuous feature of avian breeding biology, that studies of the costs of building may contribute information to the much broader debate regarding the cost of reproduction in birds.

This study has used the rook as a model system measuring the cost of nest building largely in terms of the time invested in the nest site (both during and outside the breeding season), as well as the effect of variation in nest building behaviour on individual fitness.

The initial premise of this project was that nests were a valuable commodity to the breeding bird. The large size of the structures and reports that rooks used them perennially (Coombs 1978) and refurbished them in the autumn (Brown 1928, Coombs 1960), suggested the structures to be in some sense 'costly'.

The examination of this premise and the general assessment of this cost was made using the Cheap/Expensive model. This paradigm permitted the formulation of testable predictions derived from the two alternative perspectives thereby permitting conclusions to be drawn as to the cost of nest building in the rook.

This discussion begins by reviewing the empirical evidence of this study in order to determine whether the initial premise was substantiated. It continues by considering whether the rook was a good model system before making suggestions for further work on this species. Potential methods of measuring the cost of building in other species are then proposed. Section 7.6 focuses on whether or not the conclusions of this study should be considered applicable to avian nest construction in general and finally, I shall discuss how the costs of nest building may relate to other facets of reproduction such as egg laying, incubation and brood rearing, in order to evaluate whether nest construction is a significant component in the reproductive costs of birds.

7.2. A Review of the Evidence in the Evaluation of the Biological Cost to Nest Building in the Rook

The principle aim of chapter two was to describe the structure of rooks' nests and examine for variation in design, physical parameters and the types of building materials used . In devising a method to quantify nest structure, the aim was to provide the basic information upon which to test for; a) the preference for certain types of building materials, b) establish the major site of material collection and c) correlate differences in nest structure with differences in reproductive performance. The conclusion was that all structures are built to a similar plan consisting of a roughly-circular base of twigs around which an outer wall is constructed. The resulting central depression is then lined with insulatory material and forms the nest cup.

There is considerable variability in nest size however, particularly in outer ring circumference, dry weight and number of twigs used. This could occur for three reasons; i) the practice of birds to use their nests over more than one breeding season means that there is an accumulation of nesting material at the nest site, ii) some sites require more material to secure the structure in its position in the tree (this may largely be due to the shape of the crotch in which the nest is sited) or iii) birds actually over-build because it is an activity that incurs no cost and the tendency to overbuild is not selected against.

The quadrat sampling of the twig flora on the rookery floor revealed a close relationship between the species of twigs on the ground and those used in nest construction. This supported the qualitative observation that a large portion of building material was collected from the rookery floor. Sampling the rookery floor also served to provide information on the availability of twigs for use in nest building. In addition, Multiway Frequency Analysis was used to show that the incidence of larger twigs (>30 cm.), larch twigs and forked twigs, was significantly higher than would be predicted by their availability. I suggest that this is indicative of a preference for twigs possessing these features. It was also shown that size rather than species or degree of branching was the most important criterion in the selection of twig material by the bird. This conclusion was supported by the twig removal experiment which showed that twigs in the largest size category (40.1 -50 cm.) were removed significantly more frequently than those in the two smaller size categories.

Chapter three contained the first predictions of the Cheap/Expensive model, which were made in relation to the pattern of change in nest numbers within a rookery over the annual cycle. At all five rookeries studied, the number of nests within the colony showed a continual decline outside the breeding season. Moreover, nests were not refurbished at any point of the year other than during the building period in the spring. During this period, the number of nests within the colony often increased by over 100%. Both these observations are in agreement with the cheap perspective which predicted that a nest, as a low value commodity, did not merit refurbishment throughout the year and thus breeding birds would readily replace a lost nest in the spring.

It was also noted that the proportion of nests lost from the rookery varied between colonies. This was attributed to the fact that some sites, in particular the colony at Lernock, were more exposed with the result that nests were more likely to be blown out of their trees. It was also suggested that some tree species may offer more secure nesting sites than others and would therefore be less likely to lose their nests in a storm. The species composition of the trees in the rookery may therefore influence the extent of nest losses that occur within it. The differential loss of nests from certain tree species was demonstrated at Milton Farm with a significantly greater proportion being lost from larch than expected by chance. This observation was attributed to the fact that the upper canopy of a larch is comprised of rather fine branches which would not provide the same stability and security for nest attachment as the wider, more thickly-branched crotches found in Scots pine and sycamore. Furthermore, data were collected which showed that nests were built far more frequently in Scots pine than would be expected if nest frequency was proportional to the species' incidence in the rookery.

These conclusions stating that birds avoid building in some tree species and preferentially build in others that offer greater stability, may be interpreted as supporting an expensive view of nest building since they indicate that birds are attempting to build nests that last. Nest persistence however, need not be interpreted as a long-term saving to offset annual building costs. Instead, there may be a far more severe short-term penalty incurred in building an unstable nest in that if it does not last the breeding season, the clutch or chicks (and possibly the season's breeding effort) is lost. The cost of building a nest in an insecure place is not then the investment required to rebuild but the potential loss of offspring.

The general conclusions of this chapter, ie. the high rate of nest loss outside the breeding season, the absence of any nest refurbishment and the high level of building undertaken each spring indicate a low cost to building.

Chapter five dealt with the subject of the resurgence of autumn sexual behaviour. The principle objective of this part of the study was to establish the extent of building reported to occur in the autumn. Extensive construction or refurbishment would be indicative of the nest being an expensive commodity meriting an energetic and temporal investment midway between breeding seasons in order to increase the chances of it persisting until the following spring.

There was no evidence to suggest birds undertook any building of architectural significance during this season. The conclusions of chapter three which showed that nests continued to be lost and structures continue to deteriorate between September and November, suggested an absence of nest building activity. During the autumn period, birds were never seen to gather material and incorporate it into the nest structure and the initial results from the marked twig experiment showed there to be no addition of nesting material. This conclusion was supported by photographic evidence which illustrated the absence of building over the autumn period.

The level of time spent at the nest site was estimated by sampling rookery attendance over the autumn period using a photographic time-lapse technique. The low levels of rookery attendance between September and November indicate a low temporal investment to the nest site during the autumn which is a further conclusion supporting the cheap perspective of building. The attendance pattern in October (which is the middle of the period of sexual resurgence) is anomalous in that the birds deviate from their normal dawn and dusk visits. I suggest that the almost constant, albeit low-level of attendance during daylight hours may indicate that the rookery is a focus for some sexually-related activity such as displays orientated toward courtship or the establishment of a territory.

Having rejected nest refurbishment as an adaptive function of autumn sexuality, an attempt was made to resolve whether the primary function of the autumn season was one of the alternatives proposed by the literature, namely to form and/or consolidate the pair bond or to prospect for nest sites. Analysis of the frequency of the bow-caw display revealed there to be no difference in the display rate between unpaired and paired birds during the autumn period suggesting that the display was not one primarily performed by single birds searching for a mate. Similarly, no correlation was found between group size and display rate, refuting the hypothesis that proximity to neighbours might prompt displays functioning to establish nest sites and territory. In addition, it was pointed out that low levels of attendance at the rookery are not supportive of the view that the autumn is a period in which birds prospect for nest sites. Further information regarding the function of autumn sexual behaviour may be obtained through recording the behaviour of marked birds over several years; their associations with other individuals and with particular nest sites. I shall return to this point in section 7.4.

As was the case with the data relating to chapter three, studies on autumn building behaviour entirely supported the predictions of the Cheap hypothesis. The absence of any building activity and the low temporal investment in the nest site during the autumn period again suggested the nest to be a relatively inexpensive commodity.

The final approach to assessing the biological cost of nest construction was to study the effects of variation in building behaviour on the reproductive performance of breeding rooks in the spring. This was the primary objective presented in chapter six. The major behavioural features studied were the potential advantages in reusing old nests (old nesters) over constructing new ones (new nesters), the choice of nesting site as reflected in the choice of tree species in which to build and inter-pair differences in the mode of material assimilation. An adaptive advantage to any of these building strategies could be shown if they permitted the individual to a) breed and so fledge their young earlier (Feare et al. 1974) or b) increase its reproductive output as measured by a larger clutch size, more chicks hatched or more chicks fledged.

Old nesters were not observed to differ in their mode of material assimilation compared to new nesters and the latter were not observed to make more journeys to collect building material in order to compensate for the lack of a previous year's nest which might have acted as a base. In addition, old nesters did not gain a perceptible temporal advantage through nest reuse since there was no difference in the starting and finishing dates of building between the two classes. In both 1988 and 1989, new nesters had shorter building durations than old. In 1988 this was found to have no effect on reproductive output (as measured in terms of clutch size, number of chicks hatched and number of chicks fledged), however, in 1989, a significant positive correlation was found between clutch size and building duration. A possible explanation for this correlation is that birds with short building durations incurred a reproductive penalty due to their intensive building effort. I suggest that this increased building effort was induced by the twig removal experiment carried out in that year and that in pairs which built rapidly under conditions of twig shortage, the observed reduction in clutch size is explained by the female of the pair subsequently lacking the reserves to invest in egg production. However, it must be noted that the sample size is small (n = 8, fig. 6.2) and one cannot discount that one or two extreme values may cause a spurious correlation. In summary, the data shows that old nesters were not benefiting in terms of a temporal or direct reproductive advantage through refurbishing a previous year's nest; a conclusion that again supports a low cost to building.

A comparison was also made in the reproductive performance of pairs nesting in sycamore compared to those nesting in Scots pine. Within years, there was no difference in reproductive output between the two classes however, the mean number of chicks fledged in both species was lower in 1989 than in 1988 and significantly so for those birds nesting in Scots pine. This conclusion seems contrary in the light of the conclusion of section 3.3.3 which stated that there was a preference for nesting in Scots pine. However, as was explained in the discussion section of that chapter, the high incidence of nests in Scots pine was based on the proportional occurrence of the species within the rookery. It was noted that the number of individual trees of each species does not necessarily reflect the number of available nesting sites within them. If Scots pine holds more nests per canopy than other species, then the expected number of birds nesting within it would be high and no suggestion of a preference need be implicated. In terms of the Cheap/Expensive model, the data showed there to be no difference in the breeding performance of pairs nesting in the two main nest-containing tree species within years. This conclusion also supports the prediction of the Cheap hypothesis.

The theft of nesting material is a highly conspicuous feature of rook nest building behaviour meriting special consideration not only because the adaptive function of its practice remains unclear, but also because its prevalence represents an anomaly in what has been till now, an uncontested adoption of the cheap view of nest construction. In both 1988 and 1989, no correlation was found between the observed % stealing and either finishing date or building duration. This indicates that birds that stole often were not gaining a temporal advantage by completing building earlier or quicker. Similarly in 1988, no correlation was found between observed percentage stealing and reproductive output. In 1989 however, a substantial increase was seen in the correlation coefficients of observed % stealing v's clutch size and no. hatched. (see table 6.8). Though these coefficients are not statistically significant they are noticeably higher in the year of my twig removal experiment than in the previous year. This may be indicative of an advantage to stealing under conditions of a shortage of nesting material whereby the energy conserved by stealing rather than searching for a limited resource, may well be manifest as an increased reproductive output.

The question still remains as to why stealing is so prevalent even under conditions of excess nesting material such as in 1988? I have suggested that stealing may permit an individual to both keep guard over its nest and still assimilate nesting material, a conclusion also reached by Wittenberger & Hunt (1985) in other colonial nesting species where stealing has been observed . Stealing may therefore be a compromise between vigilance and the assimilation of nest material. I shall return to a methods for assessing the penalties of being stolen from in a later section though the existence of a penalty as a result of being stolen from is supported by my personal observations on nests suffering heavy losses from thieves. The result was that the resident birds abandoned the nest site presumably moving elsewhere or even failing to breed. The highly significant increase in attendance by at least one bird of the pair over the course of the building period, suggests this may be vigilance against thieves. Alternatively, since this increased attendance is normally by the female, it is possible that by staying close to the nest prior to laying, the gravid bird is conserving energy. These proposed advantages to increased attendance are not necessarily exclusive.

One of the major objectives of the twig removal experiment in 1989 was to intensify the competition for nesting material and so perhaps show an adaptive function to stealing. The experimental year did show an increase in the incidence of stealing over the previous year. Furthermore, the incidence of stealing was shown to be positively correlated to clutch size and number of chicks hatched though not significantly so. Another of the predicted effects of twig removal was that it would lower the peak in nest numbers in the colony compared to the previous year. This prediction was substantiated. Finally it was predicted that increased competition for nesting material would break down the preference for large-sized twigs in the ground quadrat experiment. This was not shown to be the case although more twigs were removed from the quadrat in 1989 than in 1988 which may be a result of twig shortage.

On balance, it would appear that the twig removal experiment did have an effect, if not wholly substantiating all the initial predictions. I mentioned in section 6.4, when discussing the results of the experiment, that there was no simultaneous 'control' to the twig removal experiment and that the observed effects may just be due to a year to year variation. This is not to say however, that the experiment lacked a control entirely. Results from 1989 were compared to the previous year which can be regarded as the control year. It is of course, valid to say that there is likely to be a year to year variation in the level of stealing, peak nest numbers and reproductive output. Nevertheless, the experiment was conducted in the same rookery in both years eliminating environmental differences associated with location, differences such as proximity to feeding sites and the composition of tree species in the rookery. Such factors may affect the building and reproductive behaviour of the birds perhaps to the same or to a greater degree than would be apparent in normal annual variation. In any manipulation of a wild population it would be impossible to fulfil the experimental ideal which would require two identical rookeries, one experimental and one control, so that the building and breeding performance of birds could be studied simultaneously. I propose that geographical variability between colonies may influence building and breeding to a substantial degree and therefore, manipulation experiments such as the one described are best carried out on the same colony over separate years recognising that observed trends may in part, be due to year to year variation.

The great majority of the experimental evidence of this study has supported the cheap view of the cost to nest building in the rook which is contrary to the initial premise of this study. In the light of this general conclusion, one must examine whether the rook was a good model system or whether the technical difficulties involved in studying its nest building behaviour as well as features of its breeding biology, obscured an objective evaluation of the cost of nest construction.

7.3. Was the Rook a Good Model System?

Technical and Logistical Problem

Field-based studies occupy a very important role in ornithological and ethological study (eg. Cullen 1957, Tinbergen 1972) though they often present technical and empirical difficulties through the inability to control the animal's environment. In section 1.2.3 I mentioned some features of rook biology that made it a suitable study species. Undoubtedly the major disadvantage of studying its nest building behaviour is the inaccessibility of the structures themselves. Having said this, the tower and hide system described in section 4.3.2 used to observe and record building behaviour was, I believe, successful. Elevated hides have been used to observe rooks in studies prior to this one (Swingland 1977; Røskaft 1981, 1983b) and such a technique is commonly used in ornithological research (eg. Strahl 1988 or Nadkarni 1988). The tower and hide were constructed in time for colony members to adjust to its presence before the 1987 building and breeding season and it did not perceptibly perturb the colony inhabitants during the reproductive seasons studied. However, the necessity for a stable structure meant that it had to be relatively permanent. One is therefore limited to studying those birds that nest in the immediate vicinity of the hide with the consequence that only a small subset of the breeding population is studied. If the aim is to correlate building effort with subsequent reproductive effort then nest failure or the abandoning of proximal nest structures can diminish sample sizes.

The problem of disturbance and nest desertion also arises in the gathering of reproductive data which, in the case of this study, meant climbing trees to obtain a record of clutch sizes, the number of chicks hatched and the number of chicks fledged. In practise, this involved a 4-6 week period of intensive climbing between mid-April and the end of May. The habit of rooks of nesting in close proximity to each other and the fact that neighbouring birds may not be breeding in synchrony means that regular visits to a nest to check the eggs or brood might cause a neighbouring pair to desert if the female is not close to laying and is not so strongly tied to the nest site as is a gravid or incubating bird. It was noted that in both 1988 and 1989, what looked to be completed nest structures in monitored trees were deserted. It is a possibility that this may have been caused by experimenter disturbance though past studies have obtained reproductive data by climbing the nest-containing trees (eg. Røskaft 1983a and see Steenhof 1987). This is however, a labour-intensive and time-consuming way of obtaining data and sample sizes are often limited by the number of trees which are possible to climb (a problem also recognised by Røskaft-see above). In recording the study colony's reproductive performance, one is presented with a limited time period in which to collect the required information whilst minimising disturbance to the birds at a sensitive period of their reproductive season. The most efficient way to maximise information collection whilst minimising disturbance is for a team of climbers to check the nests simultaneously. All ascendable trees could therefore be monitored quickly and the birds allowed to return to their nest before the eggs or hatchlings chilled. The assistance of two other climbers greatly facilitated the monitoring of reproductive performance by the birds in 1989 but the body of data is still constrained by manpower.

Another factor which limited the information obtainable from the observational set up was the lack of marked individuals in the vicinity of the hide. Again the techniques of colour-ringing and wing-tagging to distinguish individuals has been a successful technique in ornithological studies (e.g. Patterson & Grace 1984, Wolf et al. 1990). This study attempted to ring the birds nesting by the hide in order to establish a) the extent of nest site fidelity, b) study the role of the sexes in nest construction and c) provide information on the function of autumn sexual behaviour. In order to maximise the chances of trapping these specific individuals, traps were sited beneath the hide and when returns from this site diminished, traps were set close to the structure in the field adjacent to the rookery. Although over one hundred birds were ringed, only one marked bird was associated with a nest by the autumn of 1988, and only four ringed individuals nested in the vicinity of the hide in the spring of 1989. It is clear that a far larger and more intensive ringing programme would have been required for this 'shotgun' method of ringing to have paid dividends. The problem is compounded by the fact that mortalities, immigrations and emigrations will cause there to be regular changes in the individuals nesting in the colony (Richardson et al. 1979). As Green (1981) indicated, rooks are only caught in significant numbers between mid-March and June, these months coincide with the building and nesting period which meant that the trapping programme had to be carried out simultaneously to the study of building behaviour and recording reproductive data. The emptying of traps and processing of birds in the immediate vicinity of the rookery was another source of disturbance to the colony and it was always necessary to allow the birds to resettle before their behaviour could be recorded. In order to effect the intensive ringing programme necessary to ring an entire colony, one would require perhaps ten or more traps located in and around the rookery. The effective processing of trapped birds would then require a team of people to ensure the efficient processing of trapped birds and thus minimise disturbance to the colony.

Only with information gathered from marked individuals could any conclusions be drawn on some of the predictions of the Cheap/Expensive model. For example, on the extent of nest site fidelity between autumn and spring which may in turn, be an important line of evidence in resolving the function of autumn sexuality by establishing the degree to which a pair nest in the same structure from one breeding season to the next.

For much of this study, the approach has been largely observational. This was necessary since accounts of rook nest building were to date qualitative or anecdotal. Whilst objective observation plays a very valid and important part in ethological studies, (see chapter 1 in Martin & Bateson 1986) I feel that conclusions based on observations should, where possible, be supported by experiment. At the end of the 1988 breeding season, a function to the stealing of nest material remained unclear. In the absence of an infinite period in which to observe whether this conclusion was generally applicable or relevant only to that year, it was decided to attempt to manipulate the system by removing as many twigs from the rookery floor as possible. The results of this experiment suggested that there may be a benefit to stealing in all but good or average years. Despite its empirical limitations, the point I wish to make is that without attempting some form of experimental intervention, possible functions of stealing may take longer or may never come to light using observational techniques alone. I shall expand on the potential for manipulative experiments along with suggestions for further work on nest building in rooks in a later section.

Biological Problems

In evaluating the suitability of the rook as a model species for studying building behaviour, one must also look at the bird's breeding biology in relation to the timespan of the study and recognise the limitations of conclusions based on short-term studies in relation to the adaptive behaviour of a relatively long-lived species. The benefits of long-term studies as the most accurate measure of fitness are stated by Newton (1989).

A reproductive cost to nest building, if there is one, may be clouded by the fact that there are a multitude of factors which determine the reproductive output of an adult rook. Disparity in output between colony members may be due to differences in the age and experience of individuals (Crawford 1977, De Steven 1978, Harvey et al. 1979, Røskaft 1983a). This is normally attributed to differences in the egg-laying ability of young female birds, the reduced efficiency of brooding by young females, lower egg fertilisation by young pairs and most commonly, a difference in the provisioning ability of young parents. Observed differences in rearing ability need not be only age-related; it is quite possible that there will be inter-individual differences in the incubating, brooding and rearing efficiency of birds of equal age and these may mask any advantages or penalties induced by nest building. In addition, there is some evidence that laying date and clutch size may be inherited (van Noordwijk et al. 1980) or as Callum & Coulson's (1988) study on kittiwakes has shown, that some birds are simply better 'quality' individuals that not only live longer but have higher annual reproductive rates. Though this does not mean that one should discount a potential effect of building, it does suggest there to be genetic differences in the reproductive output of individuals for which no adaptation in building behaviour can compensate.

If indeed correlations between building behaviour and reproductive output are going to be confounded by the types of inter-individual differences mentioned above, then I suggest there to be a greater necessity for marking members of the study colony in order to follow the reproductive performance of known birds in both normal and experimental years. In this manner, the age and past breeding record of the builders can be considered in the final analysis.

A second potential reason why this study may not have shown building to incur a reproductive cost may be due to the fact that reproductive success as measured in the reproductive output of one or two seasons, may not be a true indicator of a bird's fitness. Lack (1948, 1954) first proposed that birds should lay the number of eggs which will result in the largest number of surviving young from that year's breeding effort. However Lack's basic hypothesis is modified in the light of Williams' point (1966) which states that as many birds breed over several years, the meaningful measure of reproductive success is the number of young reared over a lifetime and not within a single season (see also Horn & Rubenstein 1984). Reproductive output must therefore also account for adult survival and longetivity. Røskaft (1985) experimentally enlarged broods and showed that parents of artificially enlarged brood reduced their reproductive output compared to a control group in the following year. His conclusion was that rooks adjust their reproductive performance in the light of previous experience so as to prolong their reproductive lifespan and hence the total number of young reared within it. The point is that any benefits attributable to variability in building behaviour to long-lived birds such as rooks may be long-term and not manifest in a three year study. The ideal would be to initiate a long-term study with the intention of marking the entire study colony. Under such circumstances one could assess; a) the variability in reproductive performance in relation to parent age, b) the effect of previous breeding on current reproduction and c) potential long-term benefits to variations in nest building behaviour.

The third, final and most important consideration in assessing the suitability of rooks as a model system is one only realised with the benefit of hindsight. Rooks build platform nests containing a central insulated cup in which to incubate and rear the brood. Such a design is only one of the many employed by birds to perform the functions of protecting the eggs and young (I shall discuss some of the other designs later). In chapter 2, I showed that there is variation in nest size and in the choice of materials used (however size may not be a true measure of building effort as the nest may have been built up over several years). More importantly,I noted that there is a conservatism to nest design by which I mean that all nests are constructed to the same plan of a twig platform and a central cup. Future studies, examining for architecturally-related differences in fitness between individuals, might be better undertaken on species which show marked variation in features of their nest design or alternatively, nest under conditions where some form of experimental manipulation of the nest structure is more practicable. The following section suggests areas of rook building and breeding behaviour that require further study and section 7.5 then discusses the potential for studying the cost of nest building in other bird species.

7.4. Suggestions for Further Work on Rooks

In chapters 2,3 and 5, I have briefly mentioned areas that merit further investigation. At this point it would be useful to collate and reiterate those suggestions in the light of the overall conclusion of this study.

In chapter three, I described a method to distinguish new nests from old by mapping nest-containing trees in the rookery. In chapter six, I compared the reproductive performance of birds in these two classes to test whether the cost of building a new nest reduced reproductive output thereby suggesting an increased building effort compared to birds reusing old nests. The results showed there to be no significant difference between the two classes. However, it would be possible to make a more refined assessment of whether the amount of material used in nest construction (which can be taken as a measure of the degree of building effort) does directly influence reproduction. This could be achieved by identifying new nests at the start of the building season and the reproductive output (measured as clutch size, number of chicks hatched and number of chicks fledged) of the resident pair could be monitored during the spring. I suggest clutch size to be the key measure of reproductive performance since subsequent hatching and fledging rates will be influenced by factors other than building effort, namely climate and food availability during the rearing phase. Immediately after the last chick fledged, the nest could be removed and analysed in the laboratory to have its constituent materials quantified. It would then be possible to test for a relationship between the reproductive performance of its constructors and the amount of building effort involved in its construction (measured perhaps in terms of its total dry weight or the number of twigs used). If the general conclusion of this study is true, and building incurs a low energetic cost, nests that varied in size would not significantly vary in reproductive output.

The fluctuation in nest numbers was shown in chapter three, to be similar in all colonies studied. The proportion of nests lost during the year varied greatly between colonies. For example, Lernock and Low Gartocharran suffered far greater losses than Old Manse. I mentioned in the same chapter, that climatic factors such as exposure to wind, may explain differences in the extent of nest losses between colonies. Monthly patterns of nest losses could therefore be related to climatic factors such as sampled recording of air speed at canopy level. It would then be possible to test whether there was a relationship between months recorded to have had particularly high winds and the timing of nest losses.

Differential nest losses could be related to reproductive costs by making a comparison in the average reproductive outputs from a colony that underwent a high degree of rebuilding in the spring (eg. Lernock) with a colony that loses relatively few nests (eg. Old Manse).

Studies at Milton Farm on autumn nest building, proved conclusively that this season did not involve any nest refurbishment or the construction of new nests. The fact that nest numbers continued to decline in the autumn months at the rookeries monitored in the Campsies, suggest that the Milton colony is not atypical and that autumn nest building is not a feature of rook behaviour.

In rejecting nest refurbishment as a potential adaptive explanation for autumn sexuality, greater consideration must be paid to the alternative hypotheses, namely that it is a period of nest site selection , pair-bond formation or pair-bond consolidation. The time spent in the rookery during the autumn period (as measured using the time-lapse photography technique) may then represent a temporal cost devoted to either courtship or nest site prospecting during the season.

I have suggested that an intense wing-tagging programme would enable birds from a breeding colony to be followed outside the rookery. Social interaction and pair-bond related behaviour could then be studied throughout the year and in particular in the months leading up to and through the autumn. Moreover, the questions of prospecting for nest sites and nest site fidelity could be answered more conclusively if the time and resources were available to wing-tag the greater proportion of a study colony and hence monitor the movements of individual birds within it.

As I mentioned in section 7.2, increased attendance at the nest site as building progresses may be a result of increasing vigilance in response to the theft of nesting material since, as I have mentioned earlier, theft only ever takes place in the absence of the resident pair. This hypothesis would be strengthened if it could be established that there was a penalty to being stolen from. It is possible to sample the number of trips a pair make to acquire building material (see table 6.1) and therefore simultaneously sample the number of thefts from the structure. I suggest one could then calculate a trips/thefts index (simply the number of building trips divided by the number of thefts from the same nest). A high index number would indicate a nest that suffered relatively small losses relative to the amount of material assimilated, and a low number (or even fraction) would indicate a nest that suffered a relatively high loss of material due to theft. This index figure could be correlated to the timing or duration of building as well as the reproductive performance of the resident pair, to test whether a low index figure was associated with a late or protracted building period or even a lowered reproductive output. If such a relationship were established, it would suggest a penalty to being stolen from and therefore a selective pressure to guard the nest.

In section 7.1, with regard to discussing potential reasons why building costs have not been shown to influence fitness, I mentioned Williams' theory which stated that an individual's reproductive output should be measured over a lifetime. For a feature of building biology to confer a reproductive advantage within a season, its effect would have to be quite dramatic (I will return to this point later with regard to Weeks' and den Baeyen's papers). The observed variation in rook nest building behaviour (ie. in the reuse of existing structures or in the variable incidence of stealing) may confer no selective advantage but equally incur no cost.

If the greater proportion of the study colony were marked, it should be possible to monitor the reproductive output of individuals over several years, if not their lifetime. By simultaneously studying their building behaviour, one may reveal more subtle, long-term benefits to traits such as stealing or reusing old nests. Variation in reproductive output due to age and climatic factors within any one year could then be incorporated into an evaluation of total lifetime reproductive output.

As I mentioned in the previous section, much of this study has relied on observational data since little or no quantitative information was available on rook nest building behaviour prior to this study. On the basis of observations made in the breeding seasons of 1987 and 1988, it was possible to study the cost of nest building using a more experimental or manipulative approach in 1989. I have reviewed the effects of the twig removal experiment indicating that there is some evidence to suggest that it did intensify competition for nesting material (as shown by an increase in the incidence of stealing) and possibly effect reproductive output (ie. the lowered fledging rate in the experimental year). An experimental approach may provide more information on areas such as; i) the cost of building, ii) the penalty incurred by being stolen from, iii) the temporal compromise made by an individual between feeding and building and iv) a more detailed investigation into the selection of nesting materials. The major problem with perturbation experiments conducted on wild populations is one I have mentioned earlier, namely that of disturbance. An experimenter must attempt to assess whether his or her actions may disrupt the birds to the point where they abandon their breeding attempt or worse, the colony. However, intervention experiments need not necessarily cause disturbance as for example, in this study, where the large-scale removal of twigs from the rookery floor at Milton farm in 1989 was carried out with minimal disturbance to the colony as human presence was restricted to a time when birds were not present. Below, I shall briefly outline some manipulative approaches that may provide useful information on the four issues mentioned above.

i) The cost of building. - I have already mentioned that the observed differences between 1988 and 1989 (see section 6.4) may have been due to increased competition for nest material or simply an annual variation. The degree of year to year variation may be established by running a second 'control' season in the year subsequent to the manipulated one. For example, if this study had an additional year, one could sample the number of twigs on the rookery floor prior to spring to establish whether the density of twig material was of a comparable level to 1988. If it were, this would be indicative that twig availability was similar to the year prior to the experiment and that the system had 'recovered'. One could then collect information on variables such as incidence of stealing, peak nest numbers, reproductive output etc., and examine whether the recorded data was similar to 1988. This second unperturbed year may help to establish the degree of annual variation in the parameters under study and hence support or refute the claim that changes in 1989 were a result of twig removal.

The size of the Milton rookery meant that it was only practical to clear it of twigs once. At a smaller colony it may be possible to continue to clear the rookery floor of twigs throughout the building period at regular intervals so ensuring a continued shortage of nest material. The results obtained from this experimental year could be compared to another in which no perturbation of the system was undertaken. One problem in studying a rookery small enough to clear of twigs regularly, is that the study population is smaller which may have the effect of limiting sample sizes.

Another perturbation experiment that would be practically feasible in a small rookery, is to systematically remove all, or a large proportion, of the nests in the colony, outside the breeding season. All colony members would then have to build anew in the spring and a cost to building may tested by comparing the reproductive output of individuals in that year with their output from a previous year. This experiment would be operating a habitat control but not of course, a temporal one (see section 7.2 on twig removal experiment). If one then allied this information to a comparison of reproductive output between differing colonies in the same year (e.g. Lernock and Milton), the effect of extensive rebuilding on reproductive output would have been studied under conditions where both temporal and habitat variation had been controlled. Ideally birds would be marked so that matched samples of reproductive output could be made.

ii) The penalty of being stolen from. - If it were possible to reach nests daily without undue disturbance (for example, if one could study a colony nesting in relatively small trees), it would be possible to regularly remove twigs from the nest structure and retard a pair's progress. This could be done to varying degrees throughout the colony, perhaps removing five twigs from some, ten from others etc. and then test for the effect of removal on building duration, finishing date and reproductive output. By establishing the penalty to being stolen from, one may provide evidence in support of the hypothesis that the increasing attendance at the nest site noted in section 6.3.8, is an act of vigilance against thieves.

iii) An assessment of the temporal compromise between building and feeding. - An assessment of the cost of building might be made by studying the extent to which birds compromise maintenance activities such as feeding, with the those related to nest construction. Though a precise evaluation of an individual's daily activity budget is a complex undertaking, an idea of the degree to which the separate activities of building and feeding impose a conflict on a bird's activities may be provided quite simply, by supplying the colony with an excess of food. The provisioning of adult birds with food has been shown to accelerate laying date in kestrels, *Falco tinnunculus* (Meijer et al 1988) and great tits, *Parus major* (Kallander 1974). By alleviating the need to search for food, one might predict that individuals would significantly shorten their building duration in order to commence laying earlier since early breeding is advantageous (see section 6.1.3). If food provisioning did advance reproduction compared to normal years, then this would suggest that a) there is a pressure to build nests early and b) this aim is compromised by the need for maintenance activities such as feeding.

iv) A preference in the selection of building materials. - Rooks will build nests in captivity (Richards 1976), so affording the opportunity for a more rigorous investigation into preferences for certain types of twig material by precisely controlling availability. Though I have shown there to be a preference for larger twigs (see section 2.3.4), there is still the potential for studying preferences on the basis of twig species or degree of branching. The advantage of working on captive individuals is that the only source of nesting material could be that provided by the experimenter hence the availability of twigs of differing characteristics can be more precisely controlled than in a field experiment where individuals have access to other sources.

7.5. Studying the Cost of Nest Building in Other Bird Species.

This study has focused on measuring a cost to nest building principally by examining for an effect of variations in building behaviour on reproductive output. This approach may be equally well applied to other bird species. As I mentioned in the last section, a possible reason why no such cost was apparent may be because rooks' nests are essentially monomorphic in design and despite the apparent variation in nest size, building is a relatively cheap activity with little effect on fitness. This does not mean however, that the approach of correlating variation in nest design with differential reproductive output would not be a valid one for other species which show a marked di- or polymorphism in their nest design, since the construction of one design may be more energetically costly than another so effecting reproductive performance.

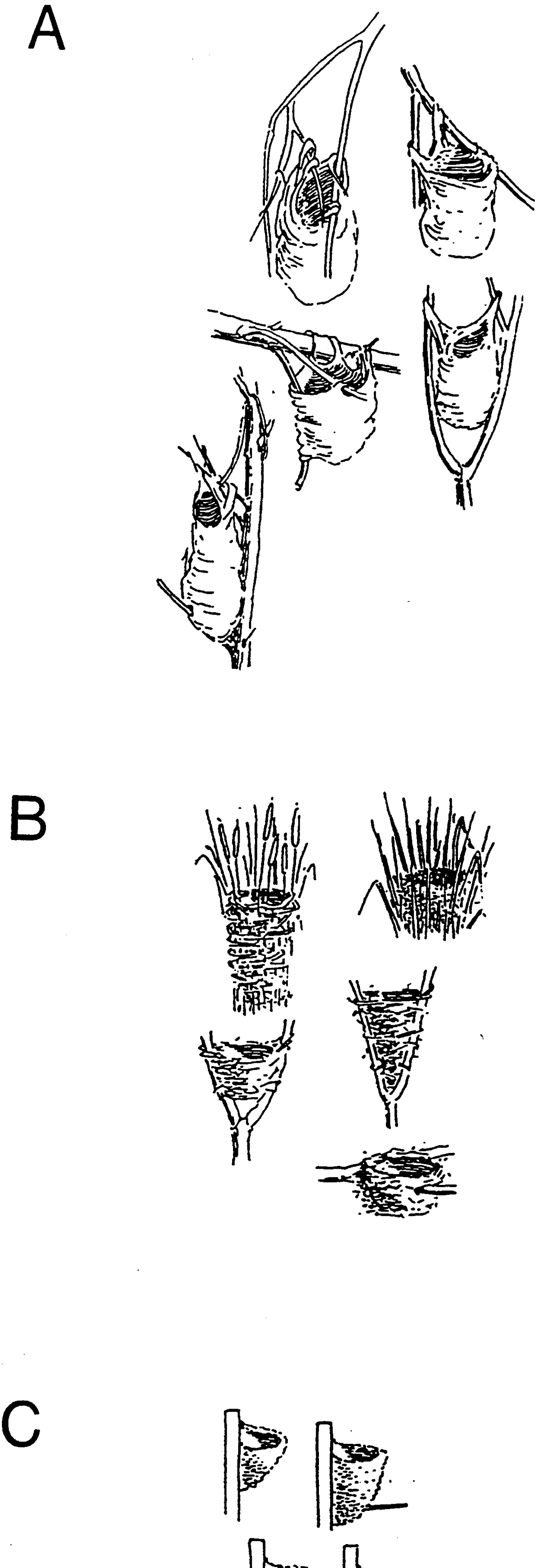
Two studies, which have been mentioned before, by den Baeyens (1981) and Weeks (1978) have suggested a reproductive cost related to nest design. In the former study, den Baeyens showed that magpies, *P. pica*, build either domed or undomed nests and that predation of eggs and chicks by Carrion crows, *C. corone*, was reduced in covered structures. In the two types of nest, the additional design feature of a roofing is obviously a selective advantage but the question arise as to why don't all magpies build roofed nests? Is it because doming the nest is in some manner costly? Birkhead (pers. comm.) has recorded a difference in the incidence of domed nests between populations and has noted that domed structures are more frequently built by older, well-established birds than by young or late-breeding individuals. It may be therefore, that time and/or experience and not building effort account for why some birds build inferior, open nests.

Weeks, studying the Eastern phoebe, *S.phoebe*, showed clutch sizes to be consistently higher in nests supported from beneath (what he called statant nests) compared to adherant nests and concluded that this was due to the greater energetic demand required to build the latter. A similar question arises as was posed for the magpies, ie. why do some birds apparently build inferior nests? Weeks concludes that birds may build adherant nests when support and a suitable location for statant nests are no longer available. Furthermore, in the two years of his study, he noted consistently higher clutch sizes in birds reusing old nests compared to those building new. However, it should be noted that although these observed trends were apparent in both years, the increased clutch size of statant over adherant nesters and old over new nesters were not statistically significant.

There are several other species known build their nests to more than one design including; the Baltimore oriole, *Icterus galbula*, the red-winged blackbird, *Agelaius phoeniceus*, the barn swallow, *Hirundo rustica*, the red-eyed and yellow-throated vireos, *Vireo olivaceus* and *V. gilvus* and the blue-gray gnatcatcher, *Polioptila* *caerulea* (some of these variants are shown in figure 7.1). Nickell (1958) notes that these variations in nest design are largely differences due to the siting and method of attachment of the structure. No mention is made of whether the observed variations are due to a limitation on optimum nest sites or whether they represent different ways of building on the same type of site. Similarly, no data is presented on the comparative reproductive performance of individuals breeding in the different designs. As figure 7.1 shows, the Eastern phoebe is among the species Nickell quotes as exhibiting more than one kind of engineering design. Weeks' data suggests that variation in engineering design may affect reproduction. Species such as those named above, which have been described as exhibiting some form of constructive variation would be suitable for studying the cost of nest building since one may examine whether the variation in nest design correlates to differences in reproductive output.

Although nest reuse has been implicated as being a selective advantage to Eastern phoebes, this was not shown to be the case for rooks. Nevertheless, there exists a great deal of potential for further studies on colonial species that both reuse old nests as well as build new ones (for example in many storks, raptors and swallows). If it were shown, as Weeks suggests, that there is a reproductive advantage to nest reusers, the implication is that there is a cost to nest construction. Colonial species that commonly reuse old structures and may therefore be suitable study animals include the cliff swallow, *Hirundo pyrrhonota* (Emlen 1954) and the barn swallow, *Hirundo rustica* (Shields 1984). However, it should be noted that in deciding whether or not to reuse an old nest, the individual will often have to take into account other costs besides the potential benefits of not having to build. I have already quoted the elegant study by Brown & Brown (1986) who demonstrated that parent birds may elect to construct a new nest if an old nest proved to be heavily infested with the swallow bug, *Oeciacus vicarius* which was shown to lower nestling survivorship. The fact that adult birds tolerate infestation at all, is suggestive of a cost to nest construction though the virulence of the ectoparasite will largely dictate the level of

Figure 7.1 The variants in nest design exhibited by three bird species; the Baltimore Oriole, *Icterus galbula* (A), the Red-Winged Blackbird, *Agelaius phoeniceus* (B) and the Eastern Phoebe, *Sayornis phoebe* (C). Adapted from Nickell 1958.


A
B
C

parasitisation the adult birds are likely to tolerate. The point is that the decision to reuse a nest must be the result of an assessment of the benefits against the costs, one of which will be the cost of nest construction. I am however, pre-empting a future discussion on the need to consider balancing selection pressures when evaluating the cost of nest construction.

A reproductive cost to building need not only be studied in wild populations since there exists the potential for experimental studies on captive birds in flight aviaries. The reproductive cost of nest building may be apparent by studying two captive populations maintained under standard environmental conditions. One population is supplied with the raw materials normally utilised in nest construction whilst the other is given no nesting material but is supplied with nest boxes that are ready to receive a clutch thereby negating the requirement for individuals to build. A suitable study species should be a small passerine (to minimise spatial requirements), known to build substantial nest structures yet be adaptable enough to breed readily in ready-made nests which could be provided. Consultation with the many commercial aviary handbooks (e.g. Rutgers 1964 or Koepff 1984), would provide information on potential study species. Several weaverbird and finch species seem suitable such as the bronze manakin, *Lonchura cucullata*, the red-cheeked cordon-bleu, *Uraegnithus bengalus*, or the Napolean weaver, *Euplectes afra afara*, since these species reportedly build and breed readily in captivity.

If such breeding populations could be established, then it should be possible to test for reproductive differences, for example in egg production, between builders and non-builders. As many of these birds produce several clutches a year, data should be readily obtainable since one is not limited to a breeding season. Furthermore, such a system provides the potential for manipulative experiments to increase the time and effort involved in construction. It would be feasible to devise an experimental set-up whereby birds had to complete a measurable amount of work in order to obtain nesting material. Such operant conditioning has been used by Roper (1973) who rewarded naive female white mice with paper for nest building conditional upon their pressing a 'pigeon key' set in a recess of their cage. Under such a system it would be possible to alter the amount of work required of the experimental animal to assimilate nest material by simply increasing or decreasing the number of key presses necessary for the operant behaviour to be reinforced. Alternative means of manipulating the amount of work necessary to complete nest building may be undertaken by providing birds with less suitable nesting materials or even by removing partly-built nests, forcing birds to rebuild. Such intervention may increase the cost of construction until a reproductive difference is apparent between the manipulated builders and those birds that were provided with nests.

As well as studying reproductive costs in terms of a penalty to egg production, the potential also exists to make direct estimates of the energy involved in construction. Collias (1986) estimated the cost of nest construction in the village weaverbird, *Ploceus cucullatus*, to be approximately 37.8 kcal. This calculation is based on the observation that a 40g male village weaverbird flew a total of 325 kilometres to gather the material required for nest construction. The estimate of energy expenditure is then based on the calorific cost of flight in the budgerigar, *Melopsittacus undulatus*, which was calculated to be 2.9 kcal per kilogramme per kilometre (Tucker 1970). Collias' estimate however, a) assumes the calorific cost of flight in the weaverbird to be equitable to that of the budgerigar and b) does not account for the effort expended in actually manipulating and incorporating the material into the nest structure which may be considerable. Furthermore, as a 'stand alone' figure, Collias' estimate does not tell us whether 2.9 kcal per kilogramme per kilometre represents a great or small burden upon the bird's total energy budget. The energetic cost of nest construction must be related to some standard measure of energy expenditure if the relative cost is to be assessed. Such a comparative measure of energetic cost may be made by estimating the energy expenditure during nest building and comparing it to the bird's Basal Metabolic Rate (BMR).

An alternative way of approaching the question of the cost to nest building is to ask how costly a component is nest construction in the overall costs of reproduction in birds? Despite the great amount of research focusing on the reproductive costs of avian breeding, as far as I know, not a single study has attempted to assess the costs of construction in the context of overall reproductive costs. This may be approached by studying the influence of variations in building behaviour or nest structure on reproductive performance (as was done in this study), by measuring the decline in parental body condition during breeding or by directly estimating the energy expended during nest construction. The last of these may be achieved using doubly-labelled water techniques as described below. The subject of the relative cost of nest building as part of the overall cost of avian reproduction is one I shall return to in the last section of this discussion.

The use of doubly-labelled 'heavy' water (D_2O^{18}) to calculate daily energy expenditure (DEE) during nest building, provides a means to measure accurately the energetic cost of building. The technique involves the labelling of body water via an injection of D_2O^{18}. After equilibrium, the oxygen-18 isotope is lost either as respiratory carbon dioxide or body water. The loss as water is measured independently by measuring the decline in the hydrogen label. These turnover rates are used to determine the rate of CO_2 production which is normally expressed as the Average Daily Metabolic Rate (ADMR) before being converted to a figure representing the DEE. A detailed account of the utilisation of doubly-labelled water techniques to measure energy expenditure is provided by Lifson & McClintock (1966). Tatner & Bryant (1988) have recently reviewed the application of the technique to the study of measuring energy expenditure in free-living birds. They begin by indicating some of the assumptions of the technique namely:

a) That body water volume is constant.

b) The rate of water flux and carbon dioxide production are constant.

c) That the isotope only labels body water and carbon dioxide.

d) That the isotope only leaves the body as body water and carbon dioxide.

e) The isotopic enrichments in water and carbon dioxide leaving the body are the same as in the body water (ie. that there is minimal isotopic fractionation which is the tendency of one isotope of an atom (normally the lighter), to be preferentially selected over another in the transition from liquid to gas phase. This may cause the residue liquid to become enriched with the heavier isotope).

f) Water or carbon dioxide do not enter the animal across the skin or lung surfaces.

The authors conclude that the assumptions are relatively minor such that any one of the above factors will not significantly influence calculated energy expenditures.

Where estimates of DEE using heavily-labelled water have been compared to those made using time-activity-laboratory methods (Mugaas & King 1981), results have shown a reasonable congruence (Bryant et al. 1984; Williams & Nagy 1984; Williams 1985). The great advantage in using HWL techniques is that estimates of DEE can be made on birds in the wild (see Bryant and Westerterp 1983; Bryant et al. 1984; Bryant & Tatner 1988, Davis et al. 1989). The study by Bryant & Tatner estimates the energy expenditure of the dipper, *Cinclus cinclus*, throughout the annual cycle. Naturally this includes the reproductive period and estimates of DEE are provided for both males and females during incubation, territory defence by the male, rearing of nestlings and even moult. Regrettably the data does not extend to a measure of DEE during the construction of their globe-shape nests, built from moss, grass and sedge. An estimate of the DEE during nest construction could then be compared to estimates of DEE in other stages of the reproductive cycle (eg. laying, incubating, mate/nest site guarding and brood provisioning) in order to gain an impression of the relative energetic cost of nest building compared to other activities related to reproduction.

Heavy water labelling techniques therefore provide the potential to evaluate the energetic expenditure of nest building in relation to other reproductive and maintenance activities. However, they also provide a method to compare the relative energetic costs of nest building between species. Bryant et al. (1984) suggest that interspecific comparisons of energy expenditure can be made by using the ratio of DEE/Basal Metabolic Rate (BMR). I suggest that this idea may be applied to interspecific studies of the energetic cost to nest building by comparing their DEE/BMR ratios during the nest building phase.

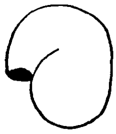
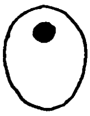
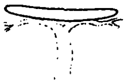
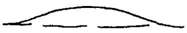
Measuring energy expenditure represents one way of quantifying the cost of reproduction in birds and may even be a means to measure the inter-specific costs of nest construction. In the penultimate section of this discussion I wish to argue that the cheap view of nest building concluded from this study on the rook should not be considered generally applicable to avian nest building since there is such a diversity in nest location, design, and of the availability and utilisation of building materials within the class. A meaningful evaluation of the cost of nest building can only be made by assessing the cost in relation to the bird's overall reproductive biology. One must ask if there is a cost to reproduction, then where does it occur? In brood provisioning, in egg production , incubating, or even earlier, in nest building?

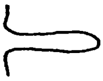
7.6. Should the Proposed Low Cost to Nest Building in Rooks Apply to Avian Nest Building in General?

Nest Variability

Birds' nests exhibit great variation in their positioning, their size, their shape, their mode of attachment and in the materials of which they are made. The platform nest built by a rook has been shown by this study to be a relatively cheap artefact however, this represents only one design adapted to meeting the functional requirements of a nest (see section 1.1.4). There is no reason to presuppose that the cheap perspective should apply to nests that differ in not only basic architecture, but in position, size and the type of materials used in construction. Figure 7.2 is a

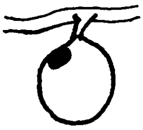
Figure 7.2. A classification of birds' nests emphasising differences in shape (column 1) and mode of attachment (column 2). Examples of each type of nest and the source are also quoted.

NEST SHAPE	TYPE OF ATTACHMENT (Refer to Key)	EXAMPLES	REFERENCE
RETORT 	3	Cliff Swallow Hirundo pyrrhonata	Harrison (1978)
	4	Cassin's Malimbe Malimbus cassini	Collias & Collias (1964)
DOMED 	1	Cape Penduline Tit Anthoscopus minutus	Skead (1959)
	3	Rock Nuthatch Sitta neumayer	Goodfellow (1977)
	4	Thick-billed Weaver Amblyospiza albifrons	Collias & Collias (1964)
	5	Magpie Pica pica	Coombs (1978)
	6	Flappet Lark Mirafra rufocinnamomea	Goodfellow (1977)
CUP 	1	Hermit Hummingbird Phaethornis preterei	Skutch (1973)
	2	Red-eyed Vireo Vireo olivaceus	Herrick (1911)
	3	Cave Swiftlet Collocalia fuciphaga	Medway (1960)
	4	Reed Warbler Acrocephalus scirpaceus	Goodfellow (1977)
	5	Blue-grey gnatcatcher Polioptila caerulea	Nickell (1958)
PLATFORM 	5	White Stork Ciconia ciconia	Haverschmidt (1949)
	6	Magpie goose Anseranas semipalmata	Davies (1962)
MOUND 	5	Hammerkop Scopus umbretta	Liversidge (1963)
	6	Mallee-fowl Leipoa ocellata	Frith (1962)
SCRAPE 	6	Sooty Tern Sterna fuscata	Howell & Bartholomew (1962)

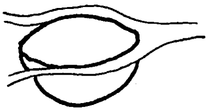
NEST SHAPE	TYPE OF ATTACHMENT (Refer to Key)	EXAMPLES	REFERENCE
BURROW (In Banks)	-	Common Kingfisher Alcedo atthis	Coward (1950)
BURROW (In Ground) 	-	D'Arnaud's Barbet Trachyphonus darnaudii	Goodfellow (1977)

Key to Types of Attachment

1 = TOP

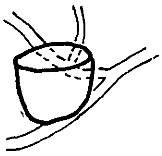


2 = TOP LIP

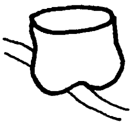


3 = VERTICALLY ADHERED

4 = MULTIPLE ATTACHMENTS



5 = BOTTOM (Cross-Section)



6 = BOTTOM SUBSTRATE

classification of birds' nests with the emphasis on variation in shape and mode of attachment. Note that these are just two characteristics of a nest and one could equally well base a classification on features such as location, material or mode of construction and an exhaustive taxonomy should account for these variables. The purpose of the figure however, is to illustrate the diversity of structures used by birds using only the two characteristics of shape and mode of attachment so emphasising that such variation in structure may well entail different costs of construction.

As an example, the time and energy spent constructing a shallow scrape on the ground as a receptacle for the eggs (eg. in the Egyptian plover, *Pluvionus aegyptus*, Howell 1979 or the common tern, *Sterna hirundo*, Harrison 1979) is likely to be considerably less than that involved in building the suspended hammock of vegetation which is the typical nest design of the vireos (Herrick 1911). For the plover and tern, the major cost might well be in locating a suitable nest site; vireos must not only do this but must also collect suitable nesting material, attach it to the chosen site and then build the suspended basket which will eventually hold their clutch.

Such variety in nest building strategies require first that the cost of building must be related to the individual's overall reproductive biology and only then, by expressing nest building costs in relation to the bird's overall reproductive budget, can one begin to generalise on the cost of various building strategies such as, the construction of a hanging nest compared to a cup nest, or a burrow nest to an adherent mud nest. It is also important to note that in the assessment of the component cost of building in the bird's overall reproductive costs, one must not only look at the energy, time or risk invested in construction, but also at the return on this investment.

Cost v's Cost Effectiveness

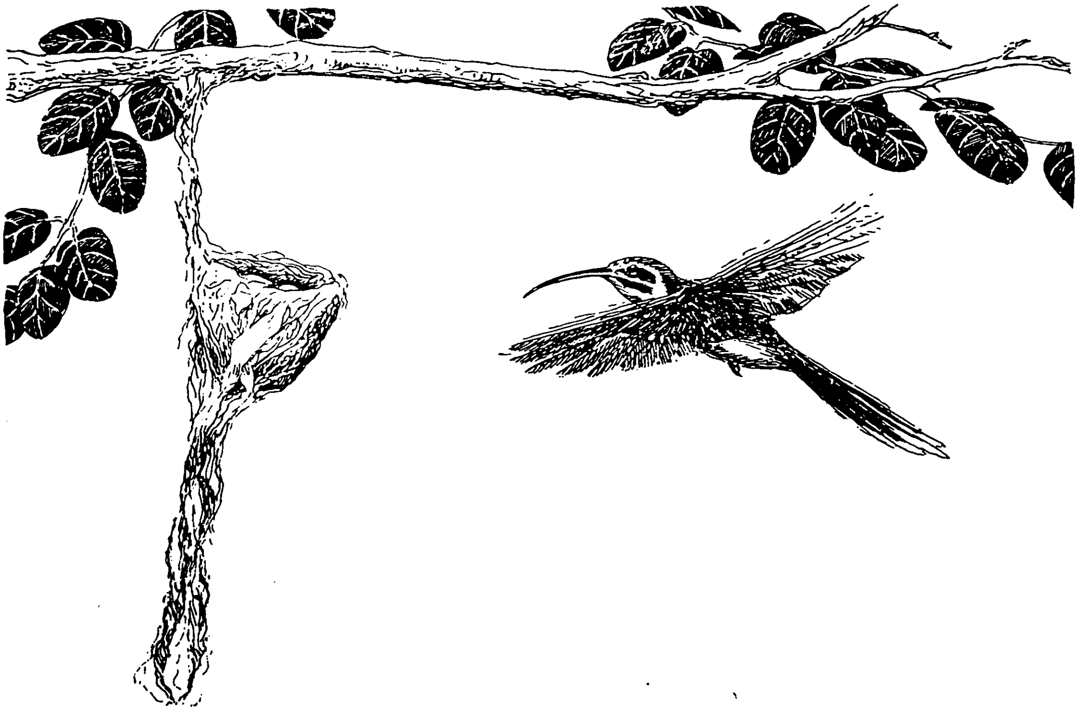
I have stated that rooks build their nests to a single common plan though the amount of constituent material and hence size, varies. Variability in nest size has also been documented for the shag, *Phalacrocorax aristotelis* (Snow 1960), the black-necked grebe, *Podiceps nigricollis* (Bochenski 1961) and the wood-pigeon, *Columba palumbus* (Møller 1982). Of these studies, only that by Snow has correlated variation in nest design with reproductive output and the data shows a positive correlation between increasing nest size and number of young. This would appear to be supportive of the cheap view of nest building advocated for rooks, since in the shag, the construction of bigger nests has not apparently incurred a reproductive cost. Snow's data however raises an important consideration in the relationship between building effort (be it interpreted as size or structural complexity) and cost. It may be that increasing nest size in the shag positively correlates to increasing number of young because a larger base raises the impending clutch off the ground which is a damp and cold surface; this may benefit both egg and chick development and hence enhance reproduction. The key point is that if there is an energetic penalty incurred by building larger basal platforms, then this may be outweighed by the benefits of the feature, namely offering better insulation and protection to the brood. The reason some birds build smaller nests may be due to the fact that these birds lack the reserves, experience or materials to build larger nests. The resulting structure is therefore the optimum under the prevailing circumstances. The idea that nest structure is optimal may explain why species such as those quoted by Nickell build several different types of nests. Polymorphism in nest design may reflect environmentally-dependent optima which may determine nest size, nest shape or even mode of attachment.

This example serves to illustrate that increased building costs may be a necessity to ensure a high reproductive return and that the complex structures seen in groups such as the weaverbirds and icterids may be a necessity to ensure that the structure fulfils its functional requirements be it part of courtship, the protection of the brood from predation or the regulation of nest temperature for optimal egg and chick development. The converse to this argument is that bird species may build low cost structures such as the afore-mentioned shallow scrapes (eg. the horned lark, *Eremophila alpestris*) or simple platforms (eg. the turtle dove, *Streptopelia turtur*) because the benefits to building a larger or more complex structure are minimal.

The developing picture is therefore one that suggests that the cost of construction should be gauged relative to the requirements of the artefact. Kern and Van Riper III (1984) studied variations in the nests of the Hawaiian honeycreeper, *Hemignathus virens virens*, showing that nests in wet, mild climates were situated so as to be sheltered from rain and built to facilitate drainage, not maximise insulation. Nests of individuals nesting at higher, drier but colder altitudes, were positioned so as to maximise exposure to solar radiation and possessed greater insulation than those nests from warmer, lower and wetter altitudes. Their paper makes no mention of the comparative reproductive performance in the two types of nest but the positioning and greater insulation of higher altitude nests are presumably design features adapted to maximise insulation. These characteristics have evolved because any additional cost to such construction features compared with the design of lower altitude nests, is outweighed by the reproductive benefit.

A similar argument can be stated for the Planalto hermit hummingbird, *Phaethornis pretrei*, of Venezuela, which builds a nest suspended by a cable of silk from an overhanging support (Goodfellow 1977). The nest is counter-balanced by another strand of silk impregnated with bits of clay or pebbles in order to prevent the cup from tilting away from its single point of attachment (see figure 7.3). Such a design necessitates the female to be continually on the wing during construction. Moreover, though spider silk may be a good building material because of its great tensile strength (Denny 1976) it may be difficult to obtain in the quantities necessary and is therefore an expensive material to build with. Though this nest may be extremely costly to build, costly in terms of energy and costly in terms of the time involved in

Figure 7.3 The nest of the Planalto hermit hummingbird, *Phaethornis pretrei*. The cup nest is suspended from its overhanging support by a cable of spider silk. A second thread impregnated with pebbles and clay hangs below the structure to counterbalance the cup, preventing it tilting away from its point of attachment. Adapted from Goodfellow 1977.



construction, it still may be cost effective because the female has built a nest that maximises the security of her brood and hence her own reproductive output. Any compromise in location and/or building materials may make the nest more accessible to predators with the result that parental investment in both nest construction and the brood would be lost. An individual may therefore have to build a costly nest just to breed at all.

A final example of a potentially costly feature of nest design is provided by the African penduline tit, *Anthoscopus caroli*, which builds a collapsible nest entrance separate from a more conspicuous entrance that leads into a blind-ending chamber. Skutch (1976) suggests that this is an adaptation to fooling predators. The actual cost to incorporating this design feature may be great or small however, its existence leads one to assume that it has evolved as a design feature of the nest because the benefits bestowed in terms of enhanced brood protection outweigh the cost of additional construction.

In summary, the cost of nest building may well vary between species due to differences in features such as shape, mode of attachment and utilisation of materials. However, one can gain an appreciation of the cost of nest construction by determining the relative cost of nest building in relation to other reproductive costs. In this manner it would be possible to establish the importance of this behaviour in the context of the individual's total reproductive effort. As costs to reproduction have been implicated in moulding life history strategies (Nur 1988), one can surmise that in species where nest construction fulfils the major part of an individual's reproductive investment, then nest construction may be a very important influence in the bird's reproductive and life history strategy. It is this point that is the central issue of the final section.

7.7. Nest Building as a Cost of Reproduction and its Influence on Avian Breeding Biology

The cost of reproduction is often regarded has having an important influence on the evolution of life history strategies (Stearns 1976). However, the relevant literature reveals there to be considerable debate as to the relative cost of the various components of the reproductive cycle particularly in the cost of egg production, incubation and brood provisioning. King (1973), in his essay on the energetics of reproduction in birds calculated that egg production entails a relatively great energetic investment, estimated as being 20-30% above daily energy requirements in a sample of galliforms, 50-70% in anseriforms and the rather lesser figure of between 13-16% in small passeriforms such as the house wren, *Troglodytes aedon* or the white-crowned sparrow, *Zonotrichia leucophrys.* This distinction of a difference in the cost of egg production between altrical and precocial species is supported by a later study by Krementz & Ankney (1986). Differences in the cost of egg production are also apparent when these costs are measured in terms of effect on parental body condition. Houston et al. (1983) concluded that egg production makes heavy demands on the protein reserves of the Lesser black-backed gull, *Larus fuscus,* whilst Murphy (1986) showed that though egg quality is correlated to female body condition in the Eastern kingbird, *Tyrannus tyrannus,* the process by no means drains the resources of the individual and clutch size is independent of body condition.

The general pattern that precocial species invest more energy in egg production than altrical species is explained by the fact that the young of the former undergo a far greater degree of development in the egg and are capable of moving and feeding independently soon after hatching. In terms of reproductive energy budgets, it could be argued that more energy is devoted to egg production because the parent is not subsequently required to provision the brood and can therefore invest more in its eggs. It would therefore appear to be the case that differing breeding strategies apportion differing relative costs to the various stages of the reproductive cycle. For example, in the Megapodes, the great amount of time and effort spent tending the mounds may reflect the fact that the costs of incubation are diverted into the costs of mound building.

Incubation, like egg production, is also the subject of some controversy with regard to its 'cost'. In his paper quoted above, King concluded that the energetic burden for incubation was minimal in the house wren, *Troglodytes aedon*, herring gull, *Larus argentatus* and the zebra finch, *Poephila guttata*, since the metabolic heat of the bird at rest can supply a large fraction of the heat required for incubation. This conclusion is debated for the latter species by Vleck (1981), who found that the VO_2 of incubating zebra finches averaged 20% higher than birds sitting on empty nests at the same temperature and she interpreted this increased metabolic rate as the energetic cost of incubation.

Many studies indicate that body condition at the start of incubation influences hatching success (eg. in turkeys, *Meleagris gallopavo*, Porter et al. 1983; ruffed grouse, *Bonassa umbellus*, Beckerton & Middleton 1982; ptarmigan, *Lagopus mutus*, Moss & Watson 1984). In contrast to these precocial species, many altrical birds have the female provisioned by the male during incubation (eg. the snow bunting, *Plectrophenax nivalis*, Lyon & Montgomerie 1983, the pied flycatcher, *Ficedula hypoleuca*, Lifjeld & Slagsvold as well as the rook). In such species, the cost of incubating in terms of net loss in body condition, is presumably greatly reduced for the female though an associated increased reproductive cost may be borne by the male who must increase his foraging to provision his mate.

The severity of incubation costs, and which sex it is borne by is therefore influenced by the species' mating system (ie. whether it is monogamous, polygamous, polyandrous or promiscuous). In addition, as Martin (1987) suggests, relative incubation costs will depend on the species reproductive strategy since birds with precocial young do not need to use energy to feed the brood and may deplete their energy reserves to a far greater extent during egg production and incubation than would altrical species.

Many studies have sought to establish the parental cost of chickrearing by attempting to correlate some index of reproductive effort with a potential costs (as I have done in this study) or by manipulating clutch size and measuring a cost-related response. Again, the evidence is mixed, the studies by Smith (1981) and De Steven (1980) show no effect of increased brood size on adult survival and Alerstam and Hogstedt (1984) argue that adult mortality is not clutch size dependent since if a parent 'over-invests' and dies, the brood die with it and the trait is maladaptive. Clutch size is therefore adapted to meet with what Drent & Daan (1980) termed an 'energetic ceiling' for sustained parental performance. Experimentally enlarging clutch sizes only reveals a cost because it artificially exceeds the amount of parental effort the birds would normally put in. Though this is a valid criticism, there are many studies which show a cost to the parent in response to increasing reproductive effort in unmanipulated systems. This cost may be manifest either in terms of increased weight loss (Hussel 1972, Bryant 1979, Westerterp et al. 1982) or reduced survival (Dow & Fredga 1984, Tinbergen et al. 1985). It may be that like the costs of egg production and incubation, the costs of brood provisioning vary across species. Tuomi et al. (1983) make an important point in proposing that such costs might be relative to the abundance or limitations of resources and therefore the costs of reproduction will be affected by the bird's environment.

What must be emphasised is that in talking about the costs of the various stages of reproduction, one must be aware of the fact that all stages are inter-related. For example, depletion of energy reserves in egg production might limit the reserves for incubation and hence lower reproductive rate. Such an effect has been used to explain the fact that hatching success has decreased with increasing clutch size in the yellow warbler, *Dendroica petechia* (Goossen & Healy 1982) and the savannah sparrow, *Passerculus sandwichensis* (Dixon 1978). It is for this reason that we approach reproductive costs in terms of energy budgets accounting for both resource availability (income) as well as the reproductive costs (expenditure). From this balance one can ask what portion of that budget is allocated to the various stages of the cycle. The first point that I wish to advocate, is that nest building is a very important stage in the reproductive cycle of many birds. The design, as I have argued, is finely adapted to meeting its functional requirements. For this reason we must consider the component cost of nest building in our assessment of the reproductive budget of a species. The second point is that factors such as mating system, environmental effects (eg. food availability) and whether a species is altrical or precocial, influence the relative cost that the various stages of reproduction incur upon the bird. I suggest that the cost of nest building in avian reproduction will be no different. In some species it will be negligible whilst in others quite considerable. Moreover, the cost of building may be shared by both sexes - most commonly in monogamous species such as many corvids and tits, or incurred specifically by one eg. by males in the polygamous weaverbirds and some wrens, and by females in the bowerbirds and vireos. In polygamous species, where the male contributes no further parental care beyond building and attracting the mate to the nest, his entire parental investment is devoted to courtship and nest building.

That such activities entail a cost to polygamous males has been demonstrated by Jones & Ward (1976) who found a decline in pectoral muscle weight and body fat in male red-billed queleas, *Quelea quelea*, during the building phase. The general conclusion from their study was that body condition is the proximate factor controlling the onset and cessation of breeding. In females this means the individual must have the reserves for egg production whilst in males it is presumably that he must have the body reserves to complete construction. The cost of nest building may therefore be an important influence in regulating this species' breeding, controlling not only the timing of reproduction but also the success of the individual's breeding effort since poor condition males may build fewer nests, or structures less attractive to mates.

It is possible that male body condition may constrain nest building ability and hence the fitness of other polygamous multiple nest builders such as the European wren, *Troglodytes troglodytes* (Garson 1980), the long-billed marsh wren, *Telmatodytes palustris* (Verner & Engelsen 1970) or the village weaverbird, *Ploceus cucullatus* (Collias & Collias 1970). The question that needs to be researched for such species, is whether or not male fitness is related to his ability to meet the costs of nest construction? If it is, then nest building and its associated costs must surely be having a major influence on the species' life history.

It is clear that the significance of nest construction on bird breeding biology is greatly under-researched. Much of this discussion has been devoted to suggestions that would further our understanding of the costs of nest building since this neglected factor is likely to have a major influence on avian life history strategies. Though initial studies may address the cost of construction in a particular species, the ultimate aim must be to draw broader conclusions and examine for generality in nesting behaviour between species with similar biologies. Lack's (1968) publication, 'Ecological Adaptations for Breeding in Birds' set the precedent, adopting the comparative approach in studying adaptive breeding strategies at the level of the subfamily. In the book, he set out 'ecological groupings' which include the Passeriforms, other land nidicolous species, cursorial nidifugous land birds, wading and littoral birds, freshwater aquatic and marine aquatic species. The rationale was to establish if features of breeding such as nesting dispersion, mating system, clutch size, incubation and fledging period are similar within these ecological groups. Homogeneity, Lack argued, was indicative of an adaptive breeding strategy within a particular environment. The great contribution of his comparative approach however, was to impose a sense of order upon the diverse breeding strategies of birds showing for example, the positive correlation between clutch size and growth rate and the association between nesting system and habitat (species with inaccessible nest sites can afford to nest colonially and be conspicuous because their locale reduces predator pressure). The order that Lack brings to avian reproductive strategies provides a basis for field experiments aimed at studying adaptations of breeding biology. By his own admission, the significance of the detailed structure of the nest receives little attention because it was a component of reproduction that had been little studied.

Over twenty years on, the situation has not substantially changed, nevertheless, if the importance of nest building in bird breeding biology is to be understood, then we must ultimately adopt a comparative approach. For example, is there a difference in the relative cost of nest construction between nidicolous and nidifugous species as has been proposed for the cost of egg production? If so, then which strategy is likely to incur the heavier cost, is it the case that nidicolous species invest more in nest building because the structure must hold and protect the growing chicks? Alternatively, do nidifugous species, who do not have to invest in brood provisioning, therefore allocate a greater portion of their reproductive budget to nest building? One might also ask whether the relative cost of building is greater in environments where the brood is likely to be subject to greater predator and adverse climatic pressure? If this is proven to be the case, it leads one to ask what affect this high cost of construction will have on other aspects of the bird's breeding biology, such as clutch size or its mating system? I suggest that in order to answer such questions one must begin by adopting the approach of this study, investigating the influence of nest construction on reproductive output and so contributing to the understanding of avian life history strategies.

A Summary of the Morphometric Measurements Taken from Adult Rooks Trapped at Milton Farm Between March and June 1987-89.

Introduction

As detailed in section 4.3.5, the primary reason for colour ringing rooks was to associate marked individuals with nests in the immediate vicinity of the hide in order to a) establish the extent of nest site fidelity and b) study sex-related differences in building behaviour. When possible, trapped birds were weighed and had their head and bill and maximum wing lengths measured (see 4.3.5 for details).

Results and Discussion

A total of 103 birds were ringed; of these, 25 were fledglings and 78 adults. Data collected from fledglings are not included in the results presented since the variables measured will change markedly over a short period of time during what is a rapid growth period. Of the 78 adults ringed, it was not always possible to take the intended measurements since birds were not weighed if wet. On two occasions, heavy rain merited the decision to simply ring and release individuals without taking any measurements as their feathers were rapidly becoming waterlogged rendering them susceptible to chilling.

Table 1 is a summary of the morphometric data on birds trapped at Milton Farm showing the mean weight, head and bill length and maximum wing length of marked individuals. Two of the measured variables, weight and max. wing length are common to those taken by Green (1981). Though Green segregates his data according to sex, the range for each of the two variables is similar in both studies.

Table 2 summarises the calculated Pearson Correlation Coefficients for pairwise comparisons between the three variables recorded. Although all three comparisons show a statistically significant positive correlation, the coefficient of determination

Table 1. The mean weight, head and bill and maximum wing length of adult birds trapped at the Milton Farm rookery between March and June 1987-89.

Measure	Mean	S.E.	n	Range	C
Weight (g)	417.3	± 5.8	62	335-530	0.11
Head & Bill Length (mm)	100	± 0.05	64	91-109	0.04
Maximum Wing Length (mm)	310	± 0.15	62	288-335	0.04

C = Coefficient of variation

Table 2. A summary of calculated Pearson Correlation Coefficients (r) comparing; Weight v's Maximum Wing length, Weight v's Head and Bill length and Head and Bill length v's Maximum Wing length. Although all correlations are statistically significant, the low value of the coefficient of determination (r2) in each comparison indicates that relatively little of the variation in one variable is explained by variation in the other.

Comparison	n	r	Signif.	r^2
Weight v's Max.Wing Length	48	0.551	**	0.30
Weight v's Head & Bill Length	48	0.323	*	0.10
Head & Bill v's Max.Wing Length	62	0.412	**	0.17

KEY: * = $p < 0.05$; ** = $p < 0.01$

(r^2) is relatively low for each indicating that relatively little of the variation noted in one variable can be attributed to variation in the other. I therefore suggest that though statistically significant, correlations between weight and max. wing length, weight and head and bill length and head and bill length and max. wing length, are not strong. Weight is especially variable since it will be influenced for example by the time of the bird's last feed. As all traps were heavily baited, birds entering the trap early are likely to have fed heavily and more recently than birds that entered the trap shortly before it was emptied.

Sexing trapped birds. - In species where there is a sex related size difference (as with rooks - see Green's paper quoted above), differences in body measurements can be used to determine the sex of individuals. This can be achieved by using discriminant function analysis (Green 1982b) or by plotting measurements of the variable against cumulative frequency on arithmetic probability paper (Coulson et al. 1983). Discriminant function analysis requires a subset of the data to be of known sex in order to calculate the discriminant value of each variable. In the present study, the sex of only 8 birds was known (5 female and 3 male) which is not sufficient to calculate discriminant values.

Sex discrimination using arithmetic probability paper depends on bimodal data being divided into two normal distributions. The resulting probability plot is sigmoid with the point of inflexion corresponding to the variable's discriminating value. Measurements of birds trapped at Milton Farm were used to plot cumulative percentage against head and bill length and maximum wing length on arithmetic probability paper. The resulting curve was not sufficiently sigmoidal to identify a point of inflexion. This technique did not then discern any bimodality in the data, hence it was not possible to sex the trapped birds.

A Simple Electronic Timing Device for Triggering Time-lapse Cameras and its Use in the Instantaneous Time Sampling of Rookery Attendance

Time sampling provides a method of condensing information permitting the simultaneous recording of several different behaviour patterns, or the recording of a single behaviour pattern over a protracted period. In addition it can be used to quantify behaviour patterns whose duration varies (Martin & Bateson 1986). Time sampling can prove difficult in long-term studies where the subject may be elusive or inaccessible. Under such circumstances, time-lapse photography has proved a useful method of collecting data (Mudge et al. 1987), since it minimizes disturbance to the subject and the apparatus can be set to monitor at precise sample points in time over a greater period than might be possible manually.

In this paper we describe a design for an electronic camera controller, capable of sampling at precise, regular intervals ranging from 1 s up to 12 h. It therefore provides a suitable means for long-term photographic monitoring that is both cheap (approximately £125.00 including the camera) and suitable for use in the field.

The camera controller takes advantage of the availability of cheap, portable, yet very precise, digital laboratory timer-clocks. These all have an internal sounder which is activated at the end of the selected period. In the present design, the driving voltage for the sounder is used to trigger the controller, though the sounder itself is not disconnected. This opens the camera shutter if it is daylight and simultaneously restarts the timer on a repetition of the same period. To allow this automatic repetition the timer chosen must be capable of being restarted on the same count-down period by simply pressing the Start button twice. In the described design, the timer was obtained from Whatman Labsales (Maidstone, Kent, U.K.) but an alternative make would suffice provided it fulfilled the above criterion.

The electronic circuit (Fig. 1) of the controller is fairly simple and consumes little power. It is constructed on a printed circuit board which can be made available to interested research workers. In use, the time period is set up on the timer, the Start button is pressed and switch S1 is closed to activate the camera controller. At the end of the timer countdown period, the sounder triggers two monostable pulse generators contained within a CMOS integrated circuit (IC1a, b). IC1b generates a 2·5-s pulse to switch on TR1 and cause a solenoid connected to A, B to press the camera shutter release. A miniature 12-V thrust action solenoid is used with a coil power of 3·0 W delivering 50 gf from a 4-mm stroke. This can occur only in daylight, since in the dark a photosensor (LDR)

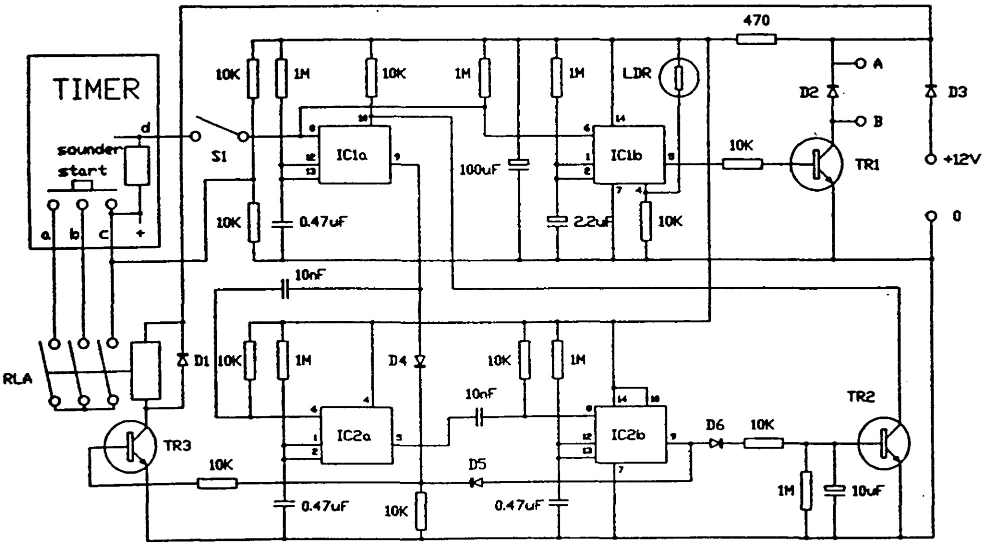


Figure 1. Circuit diagram of the camera timer. IC1, IC2 are 7556 CMOS timer integrated circuits, the transistors are all Darlington transistors (BCX38B) and all the diodes are 1N4148 except D3 which are 1N4001. The light-dependant resistor (LDR, an ORP12) is connected by a shorting jack socket so that the circuit can be tested when it is disconnected. See the text for circuit description.

allows IC1b to be held in the reset state, preventing generation of the solenoid driver pulse.

The remainder of the circuit simply emulates a user by electrically pressing the Start button twice. IC1a produces a 0·5-s pulse to turn on transistor TR3 via D4, closing the relay (RLA) which is connected to the three contacts of the timer Start button. It also initiates a delay pulse of 0·5 s generated by IC2a, the end of which triggers IC2b to produce a 0·5-s pulse which closes RLA again via D5 and TR3. Since each pressing of the Start button activates the sounder in the timer, it is necessary to use a crude monostable pulse generator consisting of TR2 and the components connected to its base to reset IC1a and prevent its repeated triggering. The solenoid driver pulse generated by IC1b lasts long enough to render the monostable pulse generator immune to retriggering by the sounder. The total reset to restart time for the timer is 1·0 s and should be added to the delay time preselected on the timer.

The camera used is a 35 mm Olympus AF1 compact, which is particularly suitable since it has automatic film wind-on and exposure facilities. It is mounted on a tripod fitted with an aluminium bracket carrying the solenoid which presses the shutter release button. Since it is a weatherproof model, no additional protective measures are necessary to use it in the field.

In the present study the camera controller is being used to provide a photographic record of the attendance pattern of rooks, *Corvus frugilegus* L., at a rookery during daylight hours throughout the year. The requirement for data collection over a long period makes an automatic technique essential. This record is used to monitor changes in attendance pattern at the rookery over the annual cycle. Of particular interest is the pattern of attendance during the autumn (September–November). This period marks a resurgence in sexual behaviour in the rook, and rookery attendance is used to examine one potential adaptive function of this autumn sexuality, namely nest-site selection. High levels of attendance are indicative of a temporal commitment to the nest site midway between breeding seasons.

The apparatus is sited in a hide providing a view across a section of the rookery at canopy level. Seven nest sites are monitored and the rooks can be distinguished from about 15 m away. To record the attendance of rooks, the timer is set to release the shutter at half-hour intervals. A large-figure liquid crystal digital clock suspended in the field of view provides a precise record of the time of the exposure. This rather crude system of verification might be avoided by using a more expensive camera model equipped with a data-back, thereby rendering the clock superfluous. A 36-exposure film allows monitoring of the rookery for between 30 and 72 h depending on seasonal changes in daylength. Once exposed, the film is developed and printed as a contact sheet, and each frame examined for the presence of rooks.

The camera controller is also being used to monitor the frequency of appearance of scavenging birds at a sheep carcass in the field over much longer periods. For this a Bauer C500XLM stop-frame 8 mm cine camera is being used enclosed with the controller within a splashproof box. Since this camera has a remote input, a solenoid is unnecessary. The remote jack is connected to B and OV and diode D2 is removed.

In addition to the two applications described here, the controller could easily be adapted to operating other recorders, dispensers or feeders with a relay attached to A, B. The described apparatus' simplicity, cheapness and adaptability make it an extremely useful alternative to commercial apparatus.

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Additional Information on Methodology and Sampling Procedures.

Chapter 2

Section 2.2.1 - Study Site

Note that accessibility was the main criterion in deciding which nests were to be removed for analysis. The nests removed were not a random sample since no attempt was made to take very large nests which could not be physically loosened from their site intact.

A second consideration was to avoid removing nests used to record building behaviour in the spring, as this might have the effect of reducing the number of nests visible from the hide which were used to record behavioural data in the spring. Note also that in table 2.1, nests 6 and 8 were structures from which behavioural data had been collected in the previous building season.

Chapter 4

Section 4.3.3 - The Assimilation of Nesting Material

Section 5.2.1 outlines the method used in distinguishing individual nests visible from any one porthole within the hide. The technique used in acquiring data on the mode of material assimilation was to observe birds already present at nests through one of the hide portholes, and record every incidence of the three defined strategies; collecting, stealing, manipulating for all of the visible nests, simultaneously.

Note that this method of focal nest sampling was biased toward birds that were already building, in order that the amount of information obtained during the building season was maximised. Hence, the decision to terminate observations from one porthole and begin observations from another would often be determined by a decline in building activity visible from the former porthole and an increase in building activity at nests visible from another.

Chapter 5

Section 5.2.3 - Bow Caw Displays (Methodology)

Typically sample duration varied between 1 - 86 seconds in the autumn (Median = 40.5 secs.) and 2 - 98 seconds in the spring (median = 39.0 secs.).
Group size varied between 1 and 7 with an observed maximum of 5 birds displaying during a sample period within a group. Occasions where no birds in a group were observed displaying in a sample duration were also included in analyses.

Section 5.3.3 - Bow Caw Displays (Results - A Comparison of the Proportion of Individuals Displaying in Autumn and Spring)

In the light of the conclusion that there is a difference in the display rate of individuals in the autumn and spring seasons (see section 5.3.3), an additional Chi-square analysis reveals there to be no significant difference in the proportion of individuals displaying in each season ($X_2 = 3.68$ at 1 d.f.; ns, Yates' correction applied). The conclusion of section 5.3.3 which states that there is an increase display rate (expressed as no.disp/bird/min.) in the autumn, is therefore not affected.

Chapter 6

Section 6.2.4 - Obtaining and Recording Reproductive Data

It should be noted that the reproductive data analysed in this chapter is not exclusively from nests in the vicinity in the hide. Nests used for both behavioural and reproductive data are indicated in table 6.1. In order to maximise the sample size however, all accessible nests within the colony were monitored since all nests within the colony had been categorised as being 'New' or 'Old' (see section 6.2.2) or as having been built in Scots Pine or Sycamore.

The raw reproductive data for the 1988 and 1989 breeding seasons is shown in Table 1.

Table 1. Reproductive data collected from nests at the Milton Farm rookery in 1988 and 1989.

Key:

Tree Sp. = Nest Containing Tree Species

CS = Clutch Size

HS = Hatching Success

FS = Fledging Success

1988					1989				
Nest No.	Tree Sp.	CS	HS	FS	Nest No.	Tree Sp.	CS	HS	FS
11A	SP	3	2	2	11A	SP	3	2	2
11B	SP	2	2	2	50B	SY	2	1	0
50A	SY	3	2	2	50C	"	3	2	0
50B	"	4	3	2	50R	"	2	2	0
50C	"	2	2	2	50J	"	1	1	1
50D	"	4	2	2	53A	"	4	1	0
50R	"	3	3	2	59A	"	1	0	0
50X	"	2	2	2	67A	"	2	0	0
52A	"	3	1	1	67C	"	3	2	2
52B	"	3	2	2	67D	"	4	2	2
52C	"	2	1	0	67F	"	3	2	2
67A	"	3	2	2	68A	"	2	2	1
67B	"	2	1	0	69A	SP	2	2	2
67C	"	3	2	2	69B	"	2	2	2
67D	"	4	2	2	76A	"	4	3	1
67E	"	1	1	1	76C	"	3	2	1
76A	SP	3	2	2	76E	"	4	1	1
76B	"	3	2	2	76G	"	3	1	1
76C	"	4	2	2	76H	"	3	2	1
76D	"	4	2	2	76K	"	3	2	1
76E	"	3	2	2	76N	"	4	3	1
76F	"	4	3	3	76P	"	3	3	0
76H	"	2	2	2	77A	"	4	3	3
76L	"	3	3	2	77B	"	2	1	1
76P	"	3	2	2	78A	"	3	3	2
76R	"	4	2	2	78B	"	2	1	1
79A	"	2	2	2	78C	"	4	1	1
79B	"	3	1	1	79A	"	3	1	1
90A	"	3	2	2	79B	"	2	1	1
90B	"	4	2	2	90A	"	3	2	2
95A	"	3	3	3	90B	"	4	2	2
95B	"	2	2	2	95A	"	4	3	2

Section 6.2.8 - Vigilance at the Nest Site During the Building Season

Note that data on the vigilance of nest owners at their nest site was collected from birds nesting in proximity to the hide. The sample is therefore a subset of the data set used to record the frequency of modes of material assimilation and those nests used in vigilance sampling are indicated in table 6.1.

The sample is again biased towards birds which were attendant at their nest site at the beginning of the sample. As was previously stated, this bias is accepted in order to maximise the information gathered as to the level of vigilance during the building period.

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