Reproductive strategies of cotton-top tamarins

by

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A breeding female cotton-top tamarin, Elsa

Abstract

The reproductive strategies of cotton-top tamarins (*Saguinus oedipus*) were investigated over a 2.5-year period in a captive breeding colony. Groups ranged in size from two to 14. The care of 21 infant tamarins was investigated over the first 12 weeks of life. Infants in larger families received more care than those in smaller families; singleton infants were carried more than twins. Parents provided more care than older siblings (helpers); older helpers provided more care than younger helpers. Individual contributions to care, particularly of fathers, declined as group size increased. There was evidence that tamarins competed to carry infants, and that some individuals attempted to restrict carrying by others.

Tamarins carrying infants spent significantly less time feeding, foraging and moving than they did when not carrying, due partly to a decrease in general mobility, and partly to an increase in the time they spent concealed, presumably to avoid predation.

The behaviour of five breeding pairs was observed for approximately 12 weeks before and 12 weeks after birth. During lactation, breeding females increased their feeding and foraging times to levels up to twice as high as those seen in pregnancy. There was evidence that breeding females attempted to encourage males to stay nearby to help with infant care by increasing grooming, and proceptive and receptive behaviour, shortly before parturition. However, females were most attractive to males during the first weeks postpartum. Males mounted females significantly more often when carrying infants, suggesting that they might be using infants as part of a courtship strategy.

Observations of a polyandrous group showed that the female had no preferred sexual partner. All three males in the group mated with her, and did not interfere in one another's copulations. A daughter in another group became pregnant and gave birth to a stillborn infant. There was no evidence of aggression between her and her parents.

The possible benefits to be gained from a communal rearing system by both breeding and helping tamarins are discussed, and some predictions put forward to guide further research.

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General Introduction

The reproductive strategies of any species involve making choices amongst many options: with whom an individual should mate; when and how much it should invest in relationships with others; how it should rear its offspring to maximise the chance that they will survive to breed themselves. The small New World primates known as marmosets and tamarins (Callitrichidae) are particularly interesting in this respect as they exhibit a variety of mating patterns, together with a remarkable degree of involvement by fathers, siblings and others, as well as mothers, in the care of offspring. Among the many strategies available for maximising reproductive success, systems in which individuals care for offspring that are not their own pose a particular challenge to understanding as at first sight they appear to involve behaviour that is costly to the donor while being beneficial to the recipient (Emlen & Vehrencamp 1985), where costs and benefits are defined in terms of their contribution to an individual's inclusive fitness (Hamilton 1964; Trivers 1971; Wilson 1975). Recently, ideas developed from the study of similar systems in both birds and mammals have been applied to the callitrichids in an attempt to understand the complexities of their social organisation. In this introductory chapter I first provide a brief overview of the most important features of these communal systems of care and discuss some difficulties with terminology, and then go on to consider marmosets and tamarins themselves in more detail.

Background and definitions

Situations in which individuals other than the two genetic parents provide care in the rearing of young have been called *cooperative breeding* (Emlen 1984; Emlen & Vehrencamp 1985), or *communal breeding* (Brown 1987). Although Emlen's terminology has been widely adopted, Brown (1987) has argued that since the term "cooperative" has previously been used to describe a particular form of interaction in which both individuals benefit in terms of fitness (Hamilton 1964), it should not be used as a description of relationships in which the fitness costs and benefits are not known. "Helping" behaviour could be either altruistic or cooperative in Hamilton's (1964) scheme, and thus descriptive terms such as "communal" are preferable.

However, the term "communal breeding" also has disadvantages. The social and reproductive life of a group involves several systems, which need to be distinguished. As Wickler & Seibt (1983) have pointed out, "social system" and "mating system" are often confused; furthermore, there are important differences between *producing* offspring and *caring* for them. For example, at least four different types of definition have been used in the past for monogamy (Wickler & Seibt 1983; Dewsbury 1987), based on (a) mating exclusivity; (b) an association between a male and a female; (c) parental behaviour involving both a male and a female; or (d) the contribution of gametes to the next generation. I would argue that three different components of a species' reproductive strategy need to be considered: *mating system* (i.e. who copulates with whom); *breeding system* (i.e. who actually contributes genes to the next generation); and *rearing system* (i.e. who cares for offspring). Clearly, successful reproduction must include rearing offspring to maturity, not merely producing them. (A *social system* may also be distinct from all of these: for example, as Kleiman (1980, 1981) has pointed out, species that are monogamous in mating and breeding vary considerably in the size of the social unit they form and the length of time for which it persists.)

These systems are of course interrelated. Nevertheless, distinctions are necessary, because no one system maps exactly on to the others, and thus participation in one cannot be inferred from participation in another. The fact that an individual mates does not necessarily imply that it breeds (e.g. if mate-guarding or some other mechanism ensures that it does not mate at the time of conception) or cares for infants; breeding involves mating but not necessarily infant care (e.g. fathers' contribution to infant care may decrease considerably as group size increases); and care need not have involved prior breeding or mating (e.g. adult offspring may care for younger siblings, as in species with "helpers at the nest"). For example, in callitrichids, as in dwarf mongooses (Rasa 1973) and some other species, it seems sensible to separate mating from breeding given that subordinate individuals, particularly females, may mate but not breed as a result of fertility suppression (Abbott 1984). The groove-billed anis (*Crotophaga sulcirostris*) studied by Vehrencamp (1977) provide an interesting example of the distinction between a mating or breeding system, and a rearing system. Nesting groups in this species consist of 1-4 monogamous pairs, and all the adult females lay eggs. All males and females then help to incubate the eggs and feed the nestlings. The only cross-system inference that can confidently be made, then, is that a breeding individual must also have mated. Consequently, use of terms such as "communal breeding", which imply that parentage of offspring is shared amongst several individuals, should not be used to refer to monogamous breeding pairs who have non-breeding helpers. Whether one or more than one member of each sex breeds, what all these systems *do* have in common is the involvement of some individuals in rearing young that are not theirs, and I will therefore use the term "communal rearing".

"Helping" behaviour has been of interest since it was first described in several bird species by Skutch (1935, 1961), and its existence has now been reported in a range of taxa, including 200-300 birds (about 2.5% of the known species) and more than 120 mammalian species (Riedman 1982; Emlen 1982*a*, 1984; Brown 1987). Several comprehensive reviews covering specific taxonomic groups are available (e.g. birds: Koenig & Pitelka 1981, Emlen & Vehrencamp 1985, Brown 1987; mongooses: Rood 1986; canids: Macdonald 1983, Moehlman 1986; fish: Taborsky & Limberger 1981), and I will therefore make no attempt at a complete listing of the species which have adopted communal rearing.

Two main types of communal rearing can be distinguished:

(1) Species in which a single pair breeds, while additional caretakers, or *helpers*, contribute physically but not genetically. A helper can therefore be defined as "an individual that performs parent-like behaviour toward young that are not generally their own offspring" (Brown 1987, p. 300). Helpers are also known as *auxiliaries* or *alloparents* (Wilson 1975; Riedman 1982; Emlen 1984). These species have been called *helpers at the nest/den* (Emlen 1984), or *singular breeders* (Brown 1987), i.e. only a single pair breeds, but non-parents help

with rearing. Brown's terminology will be used here.

The dwarf mongoose, *Helogale parvula*, is an example of this type (Rood 1983, 1986, 1990; Rasa 1987). Dwarf mongooses live in multi-male, multi-female packs. Breeding, however, appears to be limited to a single dominant pair (usually the oldest members of the pack): although subordinates may mate, the dominant male monopolises the breeding female when she is in oestrus, and there is evidence that even if subordinate females conceive they may not produce surviving young. Packs include both young born into the group and immigrants, although the relatedness of immigrants to the resident mongooses is not usually known. All pack members help to guard, feed, transport and groom the offspring of the breeding female, with the main helpers being immigrants and natal mongooses. Subordinate females may even lactate and suckle the young despite not having been seen to be pregnant. All group members also help in scanning for predators, and aiding trapped or injured individuals.

Similarly, in the green woodhoopoe, *Phoeniculus purpureus* (Ligon & Ligon 1982, 1983), there is only one breeding pair, although a flock may have up to 16 members. Helpers are usually, but not invariably, siblings or older offspring of one or both of the breeding pair, and provide a large proportion of the nestlings' food.

(2) Systems in which the parentage as well as the rearing of the offspring is shared by more than two breeders. These species have been termed (confusingly) *communal breeders* by Emlen (1984) and *plural breeders* by Brown (1987). Again, Brown's terminology will be used here. For example, the banded mongoose, *Mungos mungo* (Rood 1974, 1986) lives in packs averaging about 15 members. Several females breed synchronously, and the young are suckled indiscriminately by any female. All group members contribute to the communal care of the offspring, grooming, guarding, transporting and playing with the infants. Adult males guard infants most frequently, while lactating females never do so.

There is no simple dichotomy between these two basic forms, and some species may exhibit elements of both types. Groups of the acorn woodpecker, *Melanerpes formicivorus*, for example, contain both multiple breeders and non-breeding helpers independently and often simultaneously (Stacey 1979; Stacey & Koenig 1984; Koenig *et al*. 1984). Mate-sharing ("cooperative polygynandry"; Koenig *et al*. 1984) is common amongst breeders, and there is no evidence of exclusive male-female pairs: all adults participate in every stage of reproduction - mating, breeding and rearing - and do not interfere in copulations by others. Observations of egg-laying confirm that more than one female in a group may breed, while there is also evidence from genetic analyses that more than one male may father offspring (Joste *et al*. 1985). Breeders may be related or unrelated, but helpers are usually group offspring from previous years - young woodpeckers may remain in their natal groups for up to five years. The entire group tends a single nest, in addition to maintaining and defending the group's food store. Immigrants may join groups, but if they do so *after* the eggs have been laid, they do not contribute to the care of the nestlings.

Helping and competition

Helping behaviour in these systems may take several forms. In most species, care of the young is a prominent feature. This may include feeding and transporting them, and guarding them while other group members are foraging. Other types of helping have also been described, including aiding sick individuals (e.g. Rasa 1983), defence of territories or resources and acquisition of food (e.g. Stacey & Koenig 1984), and vigilance and anti-predator behaviour (e.g. Rasa 1986).

Despite the prominence of helping behaviour, however, competition may also be in evidence. In species in which breeding is confined to a single pair, subordinates or adult offspring may be prevented from breeding via behavioural or physiological mechanisms (e.g. wolves, *Canis lupus*: Zimen 1976, Packard *et al*. 1986; dwarf mongooses: Rasa 1973; red foxes, *Vulpes vulpes*: Macdonald 1980).

Competition between breeders has also been observed in plural breeding species. For example, in both acorn woodpeckers (Mumme *et al*. 1983) and groove-billed anis

(Vehrencamp 1977) females remove one another's eggs from the nest, the result being that the clutch is biased in favour of the last female to lay. This occurs even when the females involved are sisters, where one would expect apparent cooperation to be most likely (Mumme *et al.* 1983). Losses and gains in inclusive fitness can be subdivided into two components (Brown & Brown 1981; Brown 1987): *direct* fitness (i.e. effects on the individual itself and its descendent kin), and *indirect* fitness (effects on *non*-descendent kin). For female anis and acorn woodpeckers, the benefits in terms of direct fitness to be gained from removing their relatives' eggs are presumably sufficient to offset the loss in indirect fitness.

Characteristics of communal rearing

Communally rearing species are very diverse in group size, mating system, and the age and sex of helpers (Brown 1987). However, there are some general features which apply to most species. Auxiliaries or helpers are generally younger than breeders, and are often older offspring of the breeding individuals (Emlen & Vehrencamp 1985). Many species are non-migratory permanent residents of their territories (Brown 1978, 1987). Perhaps the most general common features of such systems are that they are restricted to taxa in which parental care is well-developed, and in which some fraction of the population has difficulty in reaching breeding status (Brown 1983).

Several attempts have been made to link the occurrence of these systems with particular demographic and ecological factors. The demographic correlates of communal rearing are similar to those of K-selection (Brown 1987), and include delayed breeding (fertility suppression), a lower reproductive rate and an increased survival rate, diminished dispersal (i.e. fewer individuals disperse, and they do not travel as far), little migration (with most groups remaining permanently resident on group territories), and density-dependent mortality. However, it has proved more difficult to find ecological correlates. Although Brown (1987) has suggested that one of the characteristics associated with helping and plural breeding was a stable, predictable habitat, Emlen (1982*a*) and Riedman (1982) have pointed out that such species also occur in situations where the habitat is harsh, fluctuating and highly unpredictable.

Theoretical issues

The study of these systems has focussed on finding answers to three main questions (Emlen 1984; Brown 1987):

(1) Breeders may suffer if they have to share their territory and its resources with others, who may eventually compete with them for ownership of the territory. Inexperienced helpers may even cause the loss of offspring. Why then do breeders allow other individuals (i.e. helpers) to stay in their group and/or on their territory?

(2) Assuming that the opportunity for dispersing and breeding elsewhere exists, the option of helping is not advantageous to all parties concerned unless the *per capita* reproductive rate is higher than if helping does not occur (Koenig & Pitelka 1981). Why then do helpers elect to remain on another's territory (either their parents', or that of some other individual), rather than adopting the alternative strategy of dispersing and breeding independently? This can be subdivided into two issues (Brown 1987): (i) why is dispersal delayed?; and (ii) why is breeding delayed?

(3) Given that they stay, why should helpers engage in such a costly activity as helping to care for another's offspring?

Helping behaviour is likely to have multiple origins (Brown 1987), and thus there are several possible answers to each of these questions.

Benefits to breeders. Breeders may gain various benefits from allowing other individuals to remain on their territory, such as decreased susceptibility to predation, improved foraging efficiency, and so on. However, the existence of benefits to breeders would be most convincingly demonstrated if it could be shown that their reproductive success was increased by the presence of helpers. This has been investigated in two ways. First, several workers have looked for correlations between offspring survival and the number of helpers available. Moehlman (1979), for example, found that pup survival in silver-backed jackals (*Canis* *mesomelas*) was positively correlated with the number of helpers in a pack. However, correlational analyses suffer from an important limitation (Emlen 1984): it is possible that a third factor, such as territory quality, may also influence survival. This has been controlled for in experiments which match groups for habitat quality and then remove helpers from selected groups. This has been done by Brown *et al.* (1982) in a population of grey-crowned babblers (*Pomatostomus temporalis*). All but one helper were removed from nine experimental groups; control groups had 6-8 helpers. The results showed that control groups raised three times as many offspring as groups who had lost the majority of their helpers.

Studies such as these demonstrate that breeders can benefit from retaining helpers via increased survival of young. However, not all studies have reported the same result: for example, Leonard *et al.* (1989) found that the removal of helpers in moorhens (*Gallinula chloropus*) had little effect on breeding success. Breeders may therefore benefit in some other way. Brown *et al.* (1978) found that the presence of helpers in grey-crowned babblers did not result in an increase in the amount of food provided for the nestlings, but because food provisioning was divided amongst more adults, each adult made fewer foraging trips. The energetic costs to the breeders of rearing a given clutch or litter may therefore be reduced; they may therefore be more likely to survive and produce greater numbers of offspring in the future, thus increasing their lifetime reproductive success. Support for this comes from a study by Stallcup & Woolfenden (1978), who presented evidence that in groups of Florida scrub jays (*Aphelocoma coerulescens*), those breeders who had helpers lived longer and produced more young.

Finally, as long as the breeders' *offspring* benefit from the arrangement, it is not necessary for helpers to increase the survival of the breeders themselves, or of their siblings, since the breeders' direct fitness will still be increased (Brown 1987).

Benefits to helpers. Several hypotheses have been proposed in an attempt to explain why dispersal is not the favoured option for helpers. Koenig & Pitelka (1981) have put forward a hypothesis of *habitat-forced cooperative breeding*. They suggest that in a stable environment in which suitable habitat is restricted and marginal habitats are scarce, surplus individuals are unable to disperse to unoccupied habitat and are therefore "forced" to remain on the natal territory. This hypothesis has been extended to variable environments by Emlen (1982*a*) with the *ecological constraints theory*. This theory postulates that for one of several possible reasons, the costs of staying on the natal territory and helping are less than the costs of dispersing and attempting to breed independently. Staying might occur if dispersal was particularly risky, perhaps because of high levels of predation; if there were few territories available on which to breed because of habitat saturation; if there were few members of the opposite sex to mate with, if, for example, the population sex ratio was biased; or if successful reproduction was simply too difficult, especially for an inexperienced individual in an unpredictable environment.

As yet there have been only a few tests of this theory. In acorn woodpeckers, lack of suitable territories seemed to be the important factor (Emlen 1984): the percentage of yearlings staying with their natal groups was higher when the number of territories becoming vacant each year decreased. In the area where white-fronted bee-eaters (*Merops bullockoides*) have been studied by Emlen (1982*a*, 1984), rainfall was erratic and thus the quality of the available habitat varied from year to year. The percentage of the population helping increased as rainfall decreased.

It may therefore be advantageous in some circumstances for young animals to opt for remaining on their natal territory instead of leaving. This does not explain, however, why they help to rear offspring that are not their own (Emlen 1982*b*). There are several possible reasons why they might do so (summarised by Emlen & Vehrencamp 1985, and Emlen & Wrege 1989): (1) they may gain a survivorship advantage, either due to the increased group size resulting from the production of more young, or because they can take advantage of the safety and familiarity of their natal territory; (2) they gain experience in parental skills which may be important for success when they go on to breed themselves; (3) parents may manipulate their offspring into helping in return for allowing them to stay on their territory; (4) helping may assist the development of liaisons which could be important in the future (e.g. to increase status; recruit helpers of their own for the future or to increase the chance of taking over a territory; form a bond with a member of the opposite sex; or expand the group's territory and eventually "bud off" a territory of their own); and (5) helpers who are related to the breeders may gain from inclusive fitness, either by reducing the workload of the breeders, and thus increase the probability that the breeders will survive and reproduce in the future, or by increasing the survival of the recipient young.

These hypotheses are not mutually exclusive, but it is possible to make specific and separable predictions based on each. For example, a recent study by Emlen & Wrege (1989) found that the best explanation for helping behaviour in white-fronted bee-eaters was the large indirect fitness benefit they accrued by increasing the number of their younger siblings that fledged; other explanations, such as gaining experience in parental care or improving their own survival, were not adequate to explain the maintenance of a helping strategy.

Communal rearing in the Callitrichidae

This general framework has recently been applied to marmosets and tamarins. In the past, primates have been largely ignored in the literature devoted to communal rearing: one of the major reviews (Emlen 1984) does not mention them at all. Yet it has been recognised for some time that, at least in the laboratory, callitrichid fathers, older offspring and occasionally unrelated individuals make considerable contributions to infant care (e.g. Epple 1975*a*), and thus resemble species of birds with "helpers at the nest". Until recently, little was known of the behaviour and social organisation of marmosets and tamarins in the wild, but over the last ten years or so, the traditional view of callitrichids as monogamous and intolerant of unrelated conspecifics (e.g. Epple 1975*a*) has been challenged by data from long-term field studies (more than one year; Dawson 1976, 1978; Neyman 1978, 1980; Rylands 1985; Terborgh & Goldizen 1985; Goldizen 1987*a*). These have suggested that in addition to the presence of non-breeding helpers, some callitrichid groups may also show elements of plural breeding, in that breeding is not confined to a single monogamous pair in each group. In the following sections I give a brief overview of callitrichid biology and behaviour, describe helping behaviour in callitrichids and compare their parental behaviour with that of other primates, discuss some problems that have arisen in interpreting the available data, and finally review the evidence for non-monogamous mating and breeding in some detail.

Marmosets and tamarins: taxonomy and distribution

The Callitrichidae are a family of New World monkeys that includes all but two or three of the smallest living primates (Hershkovitz 1977). Until recently, the major taxonomic works covering the whole callitrichid family were those of Hershkovitz (1977) and Mittermeier & Coimbra-Filho (1981). A revision has now been published (Mittermeier *et al.* 1988) which takes account of data that have become available over the past ten years, and it is followed in this thesis. Mittermeier *et al.* (1988) recognise 25 species of callitrichid in four genera (table 1.1). In accordance with this classification, the Goeldi's monkey, *Callimico goeldii*, is not considered a member of this family; although it shares several of the features of callitrichids, it also has some characteristics that more closely resemble those of the cebids, and has been placed in a separate family of its own, the Callimiconidae (Hershkovitz 1977; Mittermeier & Coimbra-Filho 1981).

Marmosets and tamarins are distributed through the tropical and sub-tropical wooded areas of Central and South America (Hershkovitz 1977), from about 9°N (Panama and south-east Costa Rica) to about 24°S (Brazil and Bolivia). The two marmoset genera (*Callithrix* and *Cebuella*), like the two genera of tamarins (*Saguinus* and *Leontopithecus*), are not sympatric. *Callithrix* and *Saguinus* are also normally allopatric, although there are two areas of Brazil where they may be found together (de Vivo 1985; S. Ferrari, pers. comm.): *Callithrix argentata* and *Saguinus midas* are sympatric in the Cametá region of Pará, and *Callithrix emiliae* may be sympatric with *Saguinus fuscicollis* in Rondônia. *Cebuella*, on the other hand, is sympatric with *Saguinus* in several areas, while *Callithrix kuhli* has been found together with *Leontopithecus chrysomelas* (Stevenson & Rylands 1988).

The characteristic features of callitrichids are described in detail by Hershkovitz (1977) and Sussman & Kinzey (1984). They include the production of multiple offspring, usually twins; chimerism resulting from the development of anastomoses of the placental circulation

TABLE 1.1. Species of Callitrichidae (after Mittermeier et al. 1988)

Scientific name	*Common name*
Cebuella pygmaea	pygmy marmoset
Callithrix argentata	silvery marmoset
Callithrix aurita	buffy marmoset
*Callithrix emiliae**	
Callithrix flaviceps	buffy-headed marmoset
Callithrix geoffroyi	Geoffroy's marmoset
Callithrix humeralifer	tassel-eared marmoset
Callithrix jacchus	common marmoset
Callithrix kuhli	Wied's black tufted-ear marmoset
Callithrix penicillata	black-pencilled marmoset
Saguinus bicolor	pied tamarin
Saguinus fuscicollis	saddle-back tamarin
Saguinus geoffroyi	Geoffroy's tamarin
Saguinus imperator	emperor tamarin
Saguinus inustus	mottled-face tamarin
Saguinus labiatus	red-bellied tamarin
Saguinus leucopus	white-handed tamarin
Saguinus midas	red-handed tamarin
Saguinus mystax	moustached tamarin
Saguinus nigricollis	black-mantled tamarin
Saguinus oedipus	cotton-top tamarin
Saguinus tripartitus†	
Leontopithecus rosalia	golden lion tamarin
Leontopithecus chrysomelas	golden-headed lion tamarin
Leontopithecus chrysopygus	golden-rumped lion tamarin

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* Recently reclassified as separate species (de Vivo 1985; Mittermeier et al. 1988); no common name.

† Recently reclassified as separate species (Thorington 1988; Mittermeier et al. 1988); no common name.

between developing foetuses, which leads to the interchange of cells (Wislocki 1932); widely-spaced axillary nipples that allow twin infants to be fed simultaneously; little if any sexual dimorphism in size and colouration; claw-like nails on all digits except the hallux; a three-cusped upper molar morphology; and the lack of a third molar in both maxilla and mandible. The two genera of marmosets are distinguished from the tamarins on the basis of their dentition: marmosets have dentition that is specialised for gouging holes in trees to obtain exudates (e.g. Lacher *et al.* 1981, 1984), with small lower canines and narrow elongate incisors, while tamarins have well-developed recurved lower canines and incisors that are shorter than the canines. *Cebuella* is the smallest callitrichid species (and indeed the smallest anthropoid primate), weighing about 100-120g; the largest are the *Leontopithecus* species, weighing up to 700g.

Ecology of marmosets and tamarins

The ecology and population characteristics of wild marmosets and tamarins are reviewed by Sussman & Kinzey (1984), Goldizen (1987*b*), Soini (1988), Stevenson & Rylands (1988), Snowdon & Soini (1988), Kleiman *et al.* (1988), and Ferrari & Lopes Ferrari (1989). The following summary is based largely on their work.

Callitrichids may use a variety of habitat types, but are frequently found in secondary forest and edge habitats. For example, Mittermeier *et al.* (1978) reported in a study of Surinam primates that *Saguinus midas* was the only species to be found more often in edge than non-edge habitats. Goldizen (1987*b*) suggests that this apparent preference for edge habitats may result from reduced competition from larger primates in such areas, rather than from a callitrichid preference for secondary forest *per se*: callitrichids have frequently been studied in secondary forests near human populations where the larger primates are more heavily hunted.

All callitrichids are diurnal and arboreal, and their diet incorporates a range of foods, including insects, small vertebrates, fruit, plant exudates and nectar. Tamarins appear to include more fruit in their diet than marmosets, but all callitrichids show a tendency to concentrate on one favoured plant species at a time (Sussman & Kinzey 1984; Terborgh &

Stern 1987).

Both marmosets and tamarins include a large proportion of insects (especially orthopterans) in their diet. Several species of *Callithrix* take advantage of the disturbance of forest litter arthropod fauna caused by army ants, *Eciton burchelli* and *Labidus praedetor* (Rylands *et al.* 1989). The importance of animal matter in the callitrichid diet may account for the relatively large distances that they cover while foraging (Ferrari & Lopes Ferrari 1989).

Unlike tamarins, marmosets have specialised dentition which enables them to feed on plant exudates. Under certain circumstances tamarins may also be able to exploit gum (e.g. Garber 1980, 1984; Peres 1989), and Garber (1984) has suggested that at least in the diet of *Saguinus geoffroyi*, exudates may provide an important source of nutrients, particularly calcium. However, other *Saguinus* species utilise exudates to a much smaller extent (e.g. *S. fuscicollis* and *S. imperator*: Terborgh 1983). The ability of marmosets to exploit gum means that scarce periods have less serious consequences for them than for tamarins, since the availability of exudates tends to be less seasonal than that of other plant resources (Ferrari & Lopes Ferrari 1989; Peres 1989). Marmosets are often able to produce two litters of infants a year; tamarins, on the other hand, typically have a single annual birth peak. The lower reproductive capacity of tamarins may be caused by the scarcity of fruit and insects in the dry season: for example, saddle-back tamarins in Peru are forced to turn to nectar during the four-month dry season, spending 75% of their time feeding on it in a two-month period (Terborgh & Stern 1987). Garber (1988) also found that sympatric *S. fuscicollis* and *S. mystax* fed on nectar 22-31% of the time in the dry season. The nectar season seems to form an annual bottle-neck in which saddle-back tamarins lose about 5% of their body weight, and consequently they are apparently unable to carry the extra energetic costs of reproduction. As a result, they breed seasonally, with lactation and weaning occurring when there is plenty of food (Goldizen *et al.* 1988).

Territoriality has been reported in some species, but not in others. Although two of the best studied tamarin species, *Saguinus oedipus* and *S. fuscicollis*, do appear to be territorial (Neyman 1978, 1980; Terborgh & Stern 1987), *S. geoffroyi* may be territorial only in some areas (Dawson 1976, 1978). Tamarin territories (or home ranges) are often more than 30 hectares in size. Marmosets, in contrast, have smaller ranges, typically less than 20 hectares (Ferrari & Lopes Ferrari 1989), and these may not be defended as territories (e.g. *Callithrix flaviceps*: Ferrari 1988). *Cebuella* is territorial, but has particularly small territories (less than 0.5 hectares; Soini 1982, 1988), and appears to be unique in its habit of switching territories every few months or years (Soini 1982, 1988).

The area used by a callitrichid group often contains a mix of habitat types. Although generally seen in the middle to lower canopy, marmosets and tamarins will also move high in the canopy, and use the ground on occasion. This tendency to use a variety of habitat zones and substrates is considered by Sussman & Kinzey (1984) to be a hallmark of callitrichid ecology. For example, saddle-back tamarin territories apparently need to contain a mixture of habitat types containing sufficient numbers of each of the plant species that form the animals' year-round diet (Terborgh & Stern 1987). These include the *Combretum* vine, on which saddle-backs place a heavy reliance for nectar in the dry season. This may explain why tamarin territory sizes are larger than would be expected on the basis of their body size.

The range sizes of marmosets may also be dependent on the distribution of particular plant resources: in their case, gum-producing trees. For example, Scanlon *et al*. (1989) found that the core areas of the home ranges of *Callithrix jacchus* groups contained a higher density of gum-producing species, and suggested that each group may need access to a certain minimum number of these trees at a minimum density. Thus, reliance on particular resources appears to have a major influence on the ranging behaviour of both marmosets and tamarins - territorial or range boundaries remain remarkably fixed over time despite changes in the size and composition of the groups occupying them (Terborgh & Stern 1987; Scanlon *et al*. 1989).

A particularly interesting feature of tamarin ecology is their tendency to form mixed-species associations. Those so far described all involve *S. fuscicollis* joining with a sympatric *Saguinus* species. Mixed-species groups occupy and defend joint territories (Goldizen 1987*b*; Buchanan-Smith 1989). Exactly how the two species avoid feeding competition is not known, but they may use different foraging techniques, utilise resources and forest strata differently, and have different locomotor patterns (Terborgh 1983). The benefits of mixed-species associations are also not well understood (Goldizen 1987*b*), but may include improved predator detection, or more efficient use of resources (Terborgh 1983).

Parental care in callitrichids and other primates

Parental investment can be defined as investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the expense of the parent's ability to invest in other offspring (Trivers 1972). In communally rearing species, behaviour resembling parental investment may also be performed by non-parents. Potentially, behaviours such as territorial defence or anti-predator behaviour could be seen as "parental care" since they are likely to improve an offspring's access to resources and its survival. However, allocation of carrying or food to one offspring means that it cannot be given to another; behaviour such as territorial defence, on the other hand, can be beneficial to several offspring simultaneously. Therefore, following Whitten (1987), I include as "care" only those types of behaviour involving interactions between caretakers and infants, such as carrying and feeding; behaviour not directed specifically towards infants is excluded.

Parental behaviour in primates has received a great deal of attention. In the majority of primate species, care is primarily the responsibility of the infant's mother (Altmann 1986; Higley & Suomi 1986). There are exceptions to this, notably in monogamous species in which the male may make a considerable contribution to care either once the infant has left early infancy (e.g. siamang, *Symphalangus syndactylus*: Gittins & Raemaekers 1980), or immediately the infant is born, for example in the New World genera *Aotus* and *Callicebus* (Wright 1984). However, although both paternal and alloparental care occur in other species, callitrichids appear to be unique amongst primates in the extent to which all group members - not only fathers, but also older siblings and other individuals - contribute to the rearing of young.

The extensive contributions to infant care made by callitrichid males lie at one extreme of a continuum of male-infant interactions in primates. Among mammals, paternal care occurs particularly often in carnivores, perissodactyls, and primates (Kleiman & Malcolm 1981) - 30-40% of the genera in each order exhibit some form of paternal care, compared to 9-10% of mammalian genera as a whole. Male-infant interactions in primates cover a whole range of behaviour, from aggression (and sometimes infanticide) and exploitation, through indifference and tolerance, to affiliation, and finally the intensive male care seen in monogamous New World monkeys, in which the father performs all parental duties except suckling as much as, or more than, the mother (Mitchell 1969; Mitchell & Brandt 1972; Hrdy 1976; Snowdon & Suomi 1982; Whitten 1987). In some circumstances, males may use infants to regulate their relationships with others. This is rather different from male care, which resembles maternal behaviour. For example, in the Barbary macaque, *Macaca sylvana* (Deag & Crook 1971; Deag 1980), subordinate males "present" infants to higher-ranking individuals. This appears to result in reduced aggression and increased affiliation between males, and has been termed "agonistic buffering". Similar behaviour in chacma baboons (*Papio ursinus*), on the other hand, has been interpreted as an attempt by likely fathers to protect their infants from potentially infanticidal males (Busse & Hamilton 1981).

Parental or parent-like behaviour by non-parents, usually females (alloparenting or "aunting") also occurs in many primates, but is much more extensive in some species than in others (Nicolson 1987). For example, amongst Old World monkeys, the handling of infants by non-mothers is much more common in colobines than in cercopithecines (McKenna 1979, 1987), although vervets (e.g. Lee 1989) and Barbary macaques (Deag and Crook 1971; Deag 1980; Small 1990) are notable exceptions to this. In addition, only colobines living in one-male groups appear to show aunting behaviour (Kohda 1985). In New World monkeys, allomothering occurs in *Saimiri*, and in the monogamous genera: *Aotus*, *Callicebus*, and the callitrichids (Kohda 1985). Reviews of allomothering behaviour (Hrdy 1976; Quiatt 1979; Nicolson 1987) have indicated several possible functions, including mothering practice, enhanced status for the allomother, freedom for the mother to forage unencumbered by an infant, increased independence for the infant and the establishment of bonds that might lead to adoption if the mother dies, and kin benefits. These are not mutually exclusive, and any one or more may apply in a given case (Quiatt 1987).

Helpers in marmosets and tamarins

The occurrence of helping by non-breeding older offspring and possibly other relatives or non-relatives is now well-documented both in captive marmosets and tamarins and, more recently, in wild populations. Much of this material will be considered in detail in chapters 3 and 4. Here, I will briefly describe the findings of field studies that support the existence of helping in callitrichids.

Observations of infant care in several species in the wild have confirmed that most, if not all, group members contribute (*Cebuella*: Soini 1988; *Callithrix flaviceps*: Ferrari 1987*a*, *b*; *C. humeralifer*: Rylands 1985; *C. jacchus*: Scanlon *et al.* 1987, Stevenson & Rylands 1988; Alonso & Langguth 1989; *Saguinus fuscicollis*: Goldizen & Terborgh 1986, Goldizen 1987*a*, 1989; *S. geoffroyi*: Lindsay 1979; *S. mystax*: Garber 1986, Ruth 1987; *S. oedipus*: Savage *et al.* 1989*a*). Adult males are often reported to carry more than any other individuals (Garber 1986; Goldizen & Terborgh 1986; Goldizen 1987*a*). However, although Goldizen (1987*a*) found that the two males in a potentially polyandrous group of saddle-back tamarins split carrying duties approximately equally, male callitrichids do not always carry at high levels: Alonso & Langguth (1989) found that while one of the two adult males in a group of common marmosets carried more than the mother, the other did not, while in Rylands' (1985) study group of *C. humeralifer*, one of the three adult males consistently carried far less than the other two over observations of three litters. Group size and composition are likely to affect the relative amounts of carrying done by males and females: Garber (1986) found that a reduction in the number of males in a moustached tamarin group from four to two led to an increase in the proportion of carrying done by females, in particular the contribution made by a non-breeding female. Similar factors might affect carrying by immature individuals: several studies report that juveniles carry very little compared to older group members (Rylands 1985; Goldizen & Terborgh 1986; Alonso & Langguth 1989), but Goldizen & Terborgh (1986) found that juveniles in one saddle-back tamarin group increased their share of infant carrying considerably after three adult males had emigrated.

Plural breeding in marmosets and tamarins

Several authors have recently begun to suggest that rather than a strictly monogamous mating system, callitrichids may instead have flexible systems of mating. Terborgh & Goldizen (1985) have rightly pointed out that there has been little evidence from field studies that could either confirm or reject the assumption of monogamy in callitrichids. However, is there yet sufficient evidence to accurately redefine callitrichid mating and breeding systems?

Perhaps because the traditional ideas of monogamy have promoted a large body of research, it would be premature to dismiss them completely, and several problems have emerged in the use of different terms which have not been so apparent in studies of other communally rearing species. Authors proposing new approaches to the classification of callitrichid reproduction and social behaviour have unfortunately not been consistent in their application of terms and concepts, and have not always exercised sufficient care in interpreting often scanty field data.

Studies of callitrichids have fallen prey to the confusion between mating, breeding and rearing systems discussed earlier. However, a second set of problems has emerged in attempting to classify the *mating* systems of callitrichids. For this, useful definitions of terms like "monogamy" are needed. Mating systems can be defined according to the number of individuals of each sex involved (Brown 1987):

Monogamy	Mating between one male and one female
Polygyny	Mating between one male and more than one female
Polyandry	Mating between one female and more than one male
Polygynandry	Mating between more than one male and more than one female

In all the above, there are behavioural restrictions on whom an individual mates with (Brown 1987); typically, mating is confined to members of a group, and extra-group copulations are unusual. They can therefore be distinguished from a fifth type of mating system, *promiscuity*, in which an individual may mate with any other individual available.

There are, however, problems in applying these definitions: for example, McGrew (1986) used similar definitions, but specified that mating relationships should be "stable". But what constitutes "stable"? For example, in the case of monogamy, different authors have proposed different time scales over which a relationship must persist, e.g. Wittenberger & Tilson (1980) adopted the criterion that each pairing relationship should persist for at least 20-25% of the breeding season, while Kleiman (1977) suggested that the concept implied that the mated pair remained together for all of one or more breeding seasons, with the male remaining with the female during the rearing of offspring.

How exclusive any mating relationship should be is a further question. As far as monogamy is concerned, although some authors (e.g. Epple 1978*a*) have proposed that occasionally non-monogamous mating does not negate the presence of monogamy, others (e.g. Sussman & Garber 1987) will not accept any deviations in a "monogamous' system - and presumably to be meaningful in terms of breeding, mating exclusivity is imperative, even if only at the time of impregnation. Perhaps one must distinguish different "degrees" of monogamy based on the duration and exclusivity of the relationship (Wickler & Seibt 1983), for example serial versus lifetime monogamy.

A further problem appears in trying to apply definitions to populations rather than to groups. Variation in mating systems frequently occurs both between and within populations (Brown 1987; Dewsbury 1987). Brown (1987), in a comprehensive review, notes several species of communally rearing bird in which a variety of mating systems have been recorded. Dietz & Kleiman (pers. comm.) point out that deciding whether to describe a population as, for example, monogamous therefore depends on the method used. Finding a case of a non-monogamous group ("single-case exclusion") has been used to justify calling callitrichids non-monogamous, but it is unhelpful since some groups are strictly monogamous, and therefore no other single classification can be ascribed to the population either. For example, Terborgh & Goldizen (1985) described groups of apparently polyandrous, polygynous and monogamous saddle-back tamarins in their study population.

Kleiman (1977) has pointed out that the concept of monogamy implies mating exclusivity, but considered that several other features could indicate the presence of monogamy even if mating exclusivity could not be positively confirmed. These diagnostic features include the continual close proximity of an adult pair, mating preferences, and the absence of unrelated conspecifics. Previous authors working with callitrichids have taken the presence or absence of Kleiman's (1977) suggested features of monogamy as indicative of the mating system practised by their study groups. Two quotations from recent publications illustrate how the data have been used in this way:

> "Mortality ... group size and composition, the relationship between the number of adult helpers and infant survivorship, frequency of migrations, and the fact that only a single adult female in each group produces young, indicate that theories other than monogamy are needed to explain mating patterns in *S. mystax*." (Garber *et al.* 1984, p. 24).
>
> "... callitrichids are not monogamous by any of these criteria [stable mated pair, absence of unrelated conspecifics, and only one breeding adult of each sex]." (Sussman & Garber 1987, p. 82).

The following section will therefore review these data and consider to what extent they can be taken as evidence for plural breeding systems in callitrichids. Note that, for instance, a group in which the female mates with more than one male will be referred to as a "polyandrous group"; this is purely for convenience and does not imply anything about the group's rearing or social system.

Regrettably, most of the available data on the Callitrichidae come from only a few of the 25 species. Moreover, in captive studies groups are usually maintained as monogamous pairs, and few field studies longer than a few months have been published, though more are in progress. Nevertheless, at least some data on group sizes are available for many callitrichid species (table 1.2; see also Goldizen 1987*b*; Sussman & Garber 1987; Soini 1988; Snowdon &

TABLE 1.2. Group sizes of wild marmosets and tamarins. Only sources for which sample sizes of at least four groups were used are given, unless a source was the only one available for the species. Values are means for total group size, except where stated.

Species	*N*	*Range*	*Mean*	*Reference*
Cebuella pygmaea	80	2-9	5.0	Soini (1988)*
Callithrix argentata	2	5-6	5.5	Freese *et al.* (1982)
C. a. melanura	4	5-14	9.5	Stallings & Mittermeier (1983)
C. aurita	4	5-8	-	Muskin (1984)
C. flaviceps	8	5-16	9.8	Ferrari & Lopes Ferrari (1989)
C. humeralifer	4	4-13	10.0	Rylands (1981)
	5	1-9	5.0	Ayres & Milton (1981)†
C. jacchus	6	4-13	-	Stevenson & Rylands (1988)
	12	3-13	8.6	Hubrecht (1984)
	5	6-14	9.6	Scanlon *et al.* (1988)††
C. kuhli	8	5-9	6.6	Stevenson & Rylands (1988)
C. penicillata	2	4-5	4.5	Fonseca & Lacher (1984)
Saguinus fuscicollis	13	2-7	4.7	Yoneda (1984*a,b*)
	21	1-7	4.1	Moynihan (1976)
	11	3-14	5.4	Ramirez (1984)
	7	2-10	-	Goldizen &Terborgh (1986)
	11	4-12	7.1	Glander *et al.* (1984)
	16	2-9	5.0	Freese *et al.* (1982)
	?	2-10	6.0	Soini (1987*a*)*
	15	2-9	6.5	Buchanan-Smith (1989)
S. geoffroyi	28	1-9	3.4	Moynihan (1970)
	21	1-8	5.2	Lindsay (1979)
	71	1-14	6.9	Dawson (1978)
S. imperator	4	1-3	2.5	Freese *et al.* (1982)
	-	2-10	4.0	Terborgh (1983)
S. labiatus	10	2-7	4.2	Yoneda (1981, 1984*a*)
	7	1-13	5.7	Freese *et al.* (1982)
	12	5-10	6.3	Buchanan-Smith (1989)
S. midas	8	2-6	3.4	Thorington (1968)
S. mystax	16	2-8	5.9	Glander *et al.* (1984)
	9	2-9	5.0	Ramirez (1984)
	18	3-8	5.2	Garber *et al.* (1984)
S. nigricollis	10	4-8	6.3	Izawa (1978)
	10	4-12	6.2	Moynihan (1976)
S. oedipus	6	1-13	-	Neyman (1978)
Leontopithecus rosalia	30	2-11	6.1	Dietz & Kleiman (1986)
L. chrysomelas	3	5-8	6.7	Rylands (1982, cited in Kleiman *et al.* 1988)

† Minimum group sizes.
†† Mean calculated from values given in table 1, p. 298.
* Modal number of independently moving individuals.

Soini 1988; Stevenson & Rylands 1988; Kleiman *et al.* 1988). Most callitrichids live in groups of between three and 13 members, with an average of usually about five to seven. Ferrari & Lopes Ferrari (1989) have suggested that marmosets tend to live in larger groups than tamarins. However, the figures are consistent in most cases with an adult pair plus one or more sets of offspring. Since offspring could remain in their natal group for several years (e.g. Goldizen & Terborgh (1989) found that saddle-back tamarins typically did not emigrate until they were more than two years old), even large groups could fit this nuclear family pattern (McGrew 1986). As marmosets may be more likely to have two litters a year than tamarins, larger group sizes would be expected. However, other interpretations than nuclear families are also possible, and these demographic data are thus of little use in determining mating systems.

Far fewer data are available on the age-sex compositions of individual callitrichid groups than for group sizes; data on adult numbers are summarised in table 1.3. The figures here represent total adults; breeding adults may form only a proportion of the total (e.g. Dawson & Dukelow 1976), but in general it is not known which adults are breeding, particularly in the case of males. Most of the species for which data are available have more than two adults per group: on average about three, and ranging from two to eight. Marmoset groups tend to have slightly more adults than tamarin groups, but the difference is not striking. *Cebuella* groups may have fewer adults than other callitrichids, but have more immature individuals (Soini 1988).

In addition, there seems to be a slight trend towards more adult males than females. This point can be tackled slightly differently by looking at the proportion of groups in specific populations with certain adult sex ratios: equal numbers of males and females, more males than females, or more females than males. This is summarised in table 1.4. (Single-sex groups have been excluded as they are not potentially reproductive.) Again there is a slight trend in favour of a preponderance of males, though most samples have examples of all three types. However, this trend does appear to be more marked for tamarins than marmosets: Goldizen & Terborgh (1989) reported that seven of nine field studies of *Saguinus* found more males than females in the population. Snowdon & Soini (1988) suggest that such biases may reflect a

TABLE 1.3. Number of adults in wild callitrichid groups.

Species	*N*	*Total adults*		*Adult males*		*Adult females*		*Reference*
		Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*	
Cebuella pygmaea	20	2-3	2.8	1-3	1.4	1-2	1.4	Soini (1988)
Callithrix humeralifer	4	3-7	5	2-3	2.5	1-4	2.5	Rylands (1981)
Callithrix jacchus	3	3-5	3.7	2-3	2.3	1-2	1.3	Hubrecht (1984)
Callithrix jacchus	5	2-8	-	1-3	-	1-6	-	Scanlon *et al.* (1988)
Callithrix penicillata	2	3-4	3.5	-	-	-	-	Fonseca & Lacher (1984)
Saguinus fuscicollis	-	-	-	-	2.0	-	1.1	Goldizen (1987*b*)
Saguinus geoffroyi	5	-	4.5	-	2.4	-	2.1	Dawson (1978)
Saguinus geoffroyi	3	2-5	3.3	1-2	1.3	1-3	2.0	Lindsay (1979)
Saguinus labiatus	2	4-5	4.5	2-3	2.5	1-2	1.5	Buchanan-Smith (1989)
Saguinus mystax	5	1-4	2.8	0-2	1.4	1-2	1.4	Ramirez (1984)
Saguinus mystax	22	2-5	3.6	1-3	2.1	1-3	1.9	Garber *et al.* (1984)
Saguinus nigricollis	10	2-4	2.6	1-2	1.3	1-2	1.3	Izawa (1978)
Saguinus oedipus	5	3-6	4.4	2-4	2.8	1-3	1.6	Neyman (1980)
Leontopithecus rosalia	8	3-5	4.1	1-2	1.9	1-3	2.3	Kleiman *et al.* (1986)
Callithrix overall		2-8	4.4	1-3	2.4	1-6	1.9	
Saguinus overall		1-6	3.7	0-4	2.0	1-3	1.6	

TABLE 1.4. Adult sex ratios in potentially reproductive wild callitrichid groups.

Species	*N*	*M=F*	*M>F*	*M<F*	*Reference*
Cebuella pygmaea	20	11	5	4	Soini (1988)
Callithrix humeralifer	4	2	1	1	Rylands (1981)
Callithrix jacchus	3	0	3	0	Hubrecht (1984)
Callithrix jacchus (a) (b)	5 3	2 1	1 0	2 2	Scanlon *et al.* (1988) (two captures)
Saguinus fuscicollis	7	17%	62%	6%	Goldizen & Terborgh (1986) (% of group months)
Saguinus geoffroyi	3	1	0	2	Lindsay (1979)
Saguinus labiatus	2	0	2	0	Buchanan-Smith (1989)
Saguinus mystax	4	1	2	1	Ramirez (1984)
Saguinus mystax	18	6	7	5	Garber *et al.* (1984)
Saguinus nigricollis	10	6	2	2	Izawa (1978)
Saguinus oedipus	5	1	4	0	Neyman (1980)
Leontopithecus rosalia	8	3	1	4	Kleiman *et al.* (1986)
Callithrix overall	15	5	5	5	
Saguinus overall*	42	15	17	10	

*excluding *S. fuscicollis* as data are not directly comparable.

tendency for females to leave their natal groups earlier, and/or spend more time as transients (see also McGrew & McLuckie 1986). A sample of 93 *Cebuella* (Soini 1988) produced a 1:1 ratio. Only one study has analysed sex ratios for a large population: Garber *et al.* (1984) found that a moustached tamarin (*Saguinus mystax*) population had an overall adult sex ratio that was significantly biased towards males (1.2 : 1; n = 1938 individuals); however, this population was translocated, and the possibility of differential capture rates or mortality in captivity cannot be discounted.

Sex ratios, group composition, and the presence of "extra" adults in callitrichid groups have all been seen as indications of at least potential non-monogamy (Dawson 1978; Garber *et al.* 1984; Goldizen & Terborgh 1986; Goldizen 1987*b*). However, group composition data and adult sex ratios are not sufficient bases for inferring mating systems, for the following reason. As Kleiman (1980, 1981) has pointed out, the size and composition of the social units that monogamous species form may vary despite sharing the criterion of mating exclusivity. Males and females may be essentially solitary, they may live together with only dependent offspring, or older offspring may remain with them into adulthood. It is also possible for unrelated conspecifics to live in a monogamous group while retaining non-breeding status. A group with more adults than a breeding pair may simply be a nuclear family with adult offspring, or an extended family with other relatives. If the adult sex ratio is uneven this may represent a bias in dispersal of offspring, as has been suggested for cotton-top tamarins, *Saguinus oedipus* (Neyman 1978, 1980; McGrew & McLuckie 1986). Dawson's (1976, 1978) data for Geoffroy's tamarins, *Saguinus geoffroyi*, suggested that at least one adult male remained in each group throughout the study, providing evidence for a stable core of one breeding female and one resident male, with dependent offspring. Other "transient" individuals were younger than the breeding pair.

Infant care by adult males, sometimes seen as indirect evidence for polyandry (Rylands 1985; Alonso & Langguth 1989), is also of little use in determining mating systems, as it confuses mating with rearing. Although Epple (1972), in a study of trios of two males and one female in captive saddle-back tamarins (*Saguinus fuscicollis*), did find that males who had a closer sexual and social relationship with the female also tended to carry infants more, many other captive studies have demonstrated that substantial contributions to infant care may be made by older offspring (e.g. Cleveland & Snowdon 1984; McGrew 1988) and even unrelated non-breeding individuals (e.g. Box 1977; Vogt *et al.* 1978).

The final type of evidence not based directly on observation of mating and breeding comes from inter-group movements, which are summarised in table 1.5. Two points have been made by previous authors about these data. First, apparently high levels of such movements have often been taken as evidence that adults in a group are likely to be unrelated (e.g. Garber *et al.* 1984; Sussman & Kinzey 1984), or at least not older offspring born into the group (Goldizen 1988) and therefore that Kleiman's (1977) criterion for monogamy of the absence of unrelated conspecifics is violated. Second, it has been suggested that tamarin groups are less stable than marmoset groups (Ferrari & Lopes Ferrari 1989). However, several important points are often overlooked.

Populations for which high levels of migration have been claimed include Dawson's (1978) study population of Geoffroy's tamarins, Scanlon *et al.*'s (1988) common marmoset (*Callithrix jacchus*) groups, and Neyman's (1980) population of cotton-top tamarins. In contrast, Terborgh & Goldizen (1985) stated that births predominated over immigration as a source of recruitment in *Saguinus fuscicollis*. Soini (1987*a*) reported that sub-adults and adults in the same species left and entered troops, but were often known to have left the same troop not long before. The breeding core of the group, a dominant male and female, remained stable. Garber *et al.* (1984) stated that there was evidence of frequent migration in their groups of *Saguinus mystax*, but saw only one case (a disappearance) during their own two-month study. Furthermore, this was a translocated population, and most movement had apparently occurred in the year between the translocation and the start of observations. There are also questions about how much care was taken to trap, keep and release whole groups together, rather than mix previously unfamiliar monkeys (C. Snowdon, pers. comm.). It is notable that another study of the same species (Ramirez 1984; Norconk, cited in Ramirez 1984) failed to find similarly high levels of migration: no movements were seen in 28 months. Alonso & Langguth

TABLE 1.5. Inter-group movements in wild callitrichids. Frequencies of known migrations only, except where stated.

Species	*Details*	*Study length*	*Frequency/group-year*	*Reference*
Cebuella pygmaea	Young adults repeatedly left and rejoined troops.	17mths	-	Soini (1982, 1988)
Callithrix flaviceps	Study group remained stable for 1yr, then 1 male & 3 females left. Formed new group with others from neighbouring group.	15mths	3.20	Ferrari (1987*b*)
Callithrix humeralifer	An adult female immigrated into an established group one month after a sub-adult female disappeared.	17mths	0.71†-1.42*	Rylands (1981, 1985)
Callithrix jacchus	Two immigrations into established groups.	5.5mths	0.83	Hubrecht (1984, 1985)
Callithrix jacchus	50% turnover in group membership in 6 months. Particularly low recapture rate for adult males.	9mths	-	Scanlon *et al.* (1988)
Saguinus fuscicollis	27 transfers: 18 males, 9 females. Births predominated over transfers as source of recruitment. Known ages at migration 1.3-4.3 yrs (most > 2yrs). 44% moved to adjacent territory.	84mths	0.55†-1.16*	Terborgh & Goldizen (1985), Goldizen & Terborgh (1986, 1989)
Saguinus fuscicollis	Sub-adults/adults left, entered and rejoined troops.	4yrs	-	Soini (1987*a*)
Saguinus geoffroyi	41 immigrations/emigrations, most often immatures. Often reentered original group or moved to neighbouring group.	17mths	5.79	Dawson (1976, 1978)
Saguinus geoffroyi	"High frequency" of intergroup transfer.	~8yrs	-	Rasmussen (1989)
Saguinus labiatus	One immigration (adult male).	5mths	1.20	Buchanan-Smith (1989)
Saguinus nigricollis	3 immigrations: 2 adult males, one juvenile female.	7mths	0.86†-2.57*	Izawa (1978)
Saguinus oedipus	9 immigrations, 8 emigrations, 7 transfers. 30/31 transients were adults; 3 parous females.	55mths	1.45	Neyman (1978)
Saguinus oedipus	2 transfers, 1 immigration (1 juv. & 1 s-ad. male, 1 juv. fem.)	24mths	1.00	Savage *et al.* (1989*a*)
Leontopithecus rosalia	38/126 marked individuals seen in more than one group.	~2yrs	0.85-1.70††	Dietz & Kleiman (pers. comm.)
Leontopithecus rosalia	Unspecified no. of emigrations, precipitated by aggression.	2yrs	-	Baker (1987)

* including disappearances; † excluding disappearances; †† study period not given for each individual group: minimum and maximum possible values given

(1989) reported no known migrations in 13 months in a group of *C. jacchus*. Ferrari & Lopes Ferrari (1989) have suggested that an unusually high population density may account for the instability of common marmoset groups found by Scanlon *et al.* (1988). A recent study of cotton-top tamarins (Savage *et al.* 1989*a*) noted that groups appeared to be much more stable over time than those described by Neyman (1978, 1980).

In an attempt to obtain a more accurate picture of the level of inter-group movements in callitrichids, wherever possible I used the published data to calculate estimates of the frequency of movements into and out of groups. The lengths of observation for each group in a given study were summed to give a value for the number of "group-years" of observation. The total number of movements reported was then divided by the number of group-years to give the frequency per group-year. This figure gives an estimate of how many individuals an average group could expect to gain or lose by migration (as opposed to births or deaths) each year. I encountered several problems in making these calculations: not all studies clearly distinguished between disappearances and known emigrations; some studies counted emigration and subsequent immigration by a single individual as two separate events, others as a single event (a transfer); and lastly, precise study durations for each group were often not given. In addition, the fact that most studies were not continued over a long period means that whether the observations made were typical of the population is not known.

The values obtained (see table 1.5) can therefore be considered only crude estimates. Nevertheless, some interesting points emerge. First, the only tamarin species for which known migrations occurred with striking frequency is *Saguinus geoffroyi* (Dawson 1976, 1978) - movements occurred up to five times more often than in other tamarins, which all produced similar values. In particular, it is notable that Neyman's (1978, 1980) cotton-tops did not in fact transfer particularly often, despite the impression given by both Neyman and others that they did. Since most tamarin species appear able to rear twins each year (e.g. infant survival to one year in cotton-top tamarins was 75%; Neyman 1980), about this number of individuals would be expected to leave a group each year and perhaps form a new one, simply to maintain group size at an appropriate limit.

Furthermore, in contrast to Ferrari & Lopes Ferrari's (1989) interpretation, there was little difference between marmosets and tamarins overall; indeed, despite Ferrari's (1987*b*) assertion that his group of *Callithrix flaviceps* was very stable, on this basis it showed much higher levels of movement than most tamarins. The same appears to be true of Scanlon *et al.*'s (1988) population of *C. jacchus*. The total number of movements between groups may not be the best measure of group stability since emigrants often leave with other group members rather than alone. For example, Neyman (1980) found that single transients were less common than groups in her cotton-top tamarin population. In between such events, groups may remain stable for relatively long periods. Ferrari's (1987*b*) group of *C. flaviceps* remained stable for over a year, but four individuals then left in a short period, either to join another established group, or to form a new one. In most studies, such information is lacking, and consequently, it is premature to suggest that generic differences exist in group stability.

Another important consideration is that, while Dawson's (1978) study is often cited as evidence that supernumerary adults are often unrelated, many of his observations concerned individuals reentering their original group, and emigrations to neighbouring groups were the most common. In addition, many of his migrants were immature and therefore not, at least initially, potential breeders in the groups into which they moved. Pygmy marmosets (*Cebuella pygmaea*; Soini 1982) and saddle-back tamarins (Soini 1987*a*) were also often seen to leave and then rejoin groups. Soini (1987*a*) observed that in seven cases where one or more tamarins were seen joining a group, the behaviour of the residents clearly indicated that the newcomers were not strangers to them. Transients may therefore be individuals who are searching for breeding openings, making forays out of the natal family until they are successful. Thus migrants may be more, rather than less, likely to be related to members of their "new" group. Indeed, a recent captive study has suggested that both cotton-top tamarins and common marmosets are less aggressive to monkeys they have previously lived with than to strangers (Harrison & Tardif 1988), although there is some evidence from a field study of another species (*L. rosalia*) that once individuals have been forced to leave they are not permitted to reenter their original group (Baker 1987). In most cases we know nothing of the degree of relatedness of individuals in wild callitrichid groups, and I would argue that inter-group movements cannot be reliably used to assess likely degrees of relatedness.

Finally, even if some individuals in a group *are* unrelated, they may not all be involved in mating and breeding. Vogt *et al.* (1978) and Box (1977) each described cases of young captive callitrichid males who were housed with unrelated families. Each male helped care for two sets of infants before being attacked. Similarly, unrelated individuals in wild groups could be acting as helpers, perhaps with the aim of recruiting future helpers for themselves, or of taking over breeding positions.

No callitrichid species has yet been found to show a significant difference in migration by one sex rather than the other, although the transient cotton-top tamarins in Neyman's (1980) study population tended to be female, as opposed to a slight bias towards males in established groups. Scanlon *et al.* (1988), on the other hand, found that there was a particularly high turnover rate for males in groups of *Callithrix jacchus*. Goldizen & Terborgh (1989) found that male *S. fuscicollis* immigrated significantly more than females, but there were no sex differences in the overall frequency of dispersal, or in disappearances.

The crucial evidence for plural breeding in callitrichids comes from observations of mating and breeding. Unfortunately, different criteria have been used for assessing polyandry and polygyny. Evidence for breeding by more than one female is usually based on easily observable criteria (e.g. the number of infants in a group, lactation, pregnancy, nipple length, etc.). However, it is often not possible to tell whether parous females are simultaneously breeding. Obtaining evidence for mating or breeding by more than one male is even more problematical, and usually depends on seeing copulations. Direct observations of mating, however, are relatively few. For polyandry, the criterion is observations of mating by more than one male with the same female at approximately the same time. Though this demonstrates sexual activity that is closely spaced in time, it does not allow the assignment of paternity, as it is usually not known if the observed mating could have resulted in conception. Therefore a polyandrous *mating* system cannot be distinguished from a *breeding* system in which more than one male contributes gametes. In all analyses it is important to distinguish simultaneous from consecutive breeding by more than one individual of each sex.

Bearing all this in mind, what exactly do we know about callitrichids? Table 1.6 summarises the evidence for plural breeding in wild callitrichids. In only two species, *Callithrix humeralifer* (Rylands 1985) and *S. fuscicollis* (Terborgh & Goldizen 1985; Goldizen 1987*a*) has mating by more than one male in a group been seen. The type of group most commonly observed by Terborgh & Goldizen (1985) they called "cooperative polyandry". In most cases no evidence was available as to whether or not mating by these males could have resulted in conception, although Goldizen (1987*a*) and Terborgh & Goldizen (1985) saw cases of two males mating in the mating season. Goldizen (1987*a*, 1989) saw two males mate many times with the breeding female; they also had quite similar relationships with her. However, Terborgh & Goldizen (1985) also saw "consortships" in three cases, in which one male attempted to sequester a female. Rylands reported only that all three males in a group copulated with the breeding female on the same day. Work on captive callitrichids (e.g. Rothe 1975) has suggested that although subordinates may mate, they may be harassed by the dominant male when the breeding female is in oestrus, the only time when mating can result in conception. Soini (1988) also noticed that although a subordinate male in a wild group of *Cebuella* attempted to mate during the breeding female's oestrus, he was always thwarted by aggression from the dominant male. Breeding (as opposed to mating) by multiple males in wild callitrichid groups is thus not yet proven. Moreover, the existence or extent of polyandrous mating in the majority of species in unknown. Despite this, authors such as Terborgh (1986) have categorised all callitrichids as polyandrous with little qualification.

For females, there is very little evidence of successful and simultaneous breeding by more than one individual in a group. For several species, observations of only one set of infants or juveniles at a time suggest that only one female per group is breeding (*Cebuella pygmaea*: Soini 1982; *Saguinus geoffroyi*: Dawson 1978; Dawson & Dukelow 1976; *S. mystax*: Garber *et al.* 1984; *S. nigricollis*: Izawa 1978; *S. oedipus*: Neyman 1980). Rylands' (1985) group of *Callithrix humeralifer* showed successive but not simultaneous breeding by two females (there

TABLE 1.6. *Non-monogamous mating and breeding in wild callitrichids.*

Species	*Males*	*Females*	*Reference*
Callithrix humeralifer	3 adult males mated with the breeding female on the same day.	One group had two breeding females, but consecutively, not simultaneously.	Rylands (1985)
Callithrix jacchus	-	A 10-15 month old non-breeding female mated with one or more males in a neighbouring group.	Hubrecht (1985)
Callithrix jacchus	-	1/5 groups had 1 lactating female when first captured; at second capture, the first female was not lactating, a second was, and a third had swollen breasts.	Scanlon *et al.* (1988)
Saguinus fuscicollis	In 4/5 cases, both males in a 2-male group In 3 groups, males mated evenly during mating season. Some evidence for "consortships" in three cases.	(1) A mother and daughter both became pregnant, but daughter's infants never seen. (2) A group contained 2 parous females and 2 sets of infants less than 6 months apart.	Terborgh & Goldizen (1985), Goldizen & Terborgh (1986), Goldizen (1987*a*)
Saguinus mystax	-	A group contained 2 females who gave birth within a month, but 1 litter died.	Ramirez (1984, and cited in Sussman & Garber 1987)
Saguinus oedipus	-	One group had two pregnant females, but only one (who was not original breeding female) produced viable offspring.	Savage *et al.* (1989*a*)
Leontopithecus rosalia	-	5/30 groups contained 2 females who had reproduced.	Dietz & Kleiman (pers. comm.)
Leontopithecus rosalia	-	Two females successfully reared infants in the same group.	A. Baker (cited in French *et al.* 1989)

was an interval of five months between litters, suggesting that the second female became pregnant after the first had given birth for the final time), although both females remained resident throughout. Despite Kinzey's (1986) assertion that *C. jacchus* females known not to be the breeding female have been observed copulating, Hubrecht's (1984) observations of common marmosets, to which Kinzey is presumably referring, concerned a single non-breeding and probably immature 10-15 month old female. This female mated with one or more males from a neighbouring group; whether she became pregnant or left her group was not known. Hubrecht himself suggested that this may have been a prelude to group formation rather than a deviation from a monogamous mating system. In Dietz & Kleiman's (pers. comm.) population of golden lion tamarins (*Leontopithecus rosalia*), five of 30 groups contained more than one female who had bred, but there was no evidence that they did so simultaneously. Changes in breeding female, as in Rylands' (1985) group, or migration of parous females, as in Neyman's (1980) cotton-tops, could easily explain this. However, cases of simultaneous breeding have occurred in wild saddle-back and moustached tamarins (Goldizen 1987*a*; Ramirez 1984, and cited in Garber *et al*. 1984), but only one set of infants ever survived.

More difficult to interpret is Terborgh & Goldizen's (1985) observation of a group of saddle-back tamarins with two parous females and two sets of juveniles less than six months apart in age. Immigration by one of the females may explain this, or the case could represent a transition between breeding females. In addition, while only one litter per year was usual in this population, births did occur throughout the year, and females in some tamarin populations have been seen to give birth twice a year (e.g. *S. fuscicollis* and *S. mystax*; Garber and Norconk, both cited in Garber & Teaford 1986; *S. fuscicollis*, Soini 1987*a*). Given a gestation period of about five months in saddle-back tamarins (Gengozian *et al*. 1974) one female could have produced both sets of infants. Terborgh and Goldizen did not report whether or not the infants' age difference was less than the gestation period. However, since births are highly seasonal in this population (Goldizen *et al*. 1988), and the shortest known inter-birth interval in the population was nine months (A. Goldizen, pers. comm.), the latter explanation is probably the least likely. It remains possible, however, in the absence of any further data. Scanlon *et al.* (1988) suggest similar explanations for their observation that more than one female may have been breeding in a group of *C. jacchus*. When first captured, this group had one breeding female, as indicated by lactation. However, when trapped again six months later this female was apparently not breeding, whereas a second was lactating, and a third had swollen mammary glands, though no milk was expressed. At the time of the second capture there were also three infants (i.e. less than five months old) of similar age in the group. Pregnancy, however, was not detected in any of the females. Only one confirmed report of successful polygyny in the wild exists: A. Baker (cited in French *et al.* 1989) saw two *L. rosalia* females produce living offspring in each breeding season.

Many captive studies have shown that more than one breeding female per group is unlikely; the dominant female suppresses ovulation in the subordinates, and frequently evicts them from the group (Epple 1975*a*; Abbott 1978, 1984). In groups of unrelated adult *C. jacchus*, a pairbond forms between the dominant male and female; although copulations are not confined to the dominant pair, they frequently disrupt copulations by subordinates. Aggression by the dominant female to subordinate females, and interference by the dominant male in the copulations of the others, may be more frequent when the dominant female is in oestrus (Rothe 1975; Abbott 1978, 1984). In three of four two-male/one-female trios of saddle-back tamarins studied by Epple (1972), the female mated far more with one male than the other. In two trios, the males actively competed for the female when she was in oestrus, but with no overt aggression. Two dominance reversals between males in trios were seen, with associated changes in the social interactions of the males with the females, so females may switch mates. Kleiman (1978*b*) conducted a similar investigation of trios of *L. rosalia*, and in all groups, one male showed higher levels of sexual behaviour than the other.

In summary, there are few data from either captive or field studies that prove either a non-monogamous mating system or a monogamous one in any population. Furthermore, there is little evidence that any of the groups studied had a plural breeding system. What sort of evidence is needed? Any criterion should include the existence of one or more of the following features:

(1) Copulations by two or more resident adult males in a group, which would indicate a non-monogamous mating system. In the wild it is hard to assess whether or not all males are equally likely to have fathered any resulting offspring, unless ejaculation and sperm production can be recorded. When one male monopolises a female around the estimated time of conception and is therefore the only male likely to father offspring, the breeding system may still involve only one male.

(2) Overlapping production of surviving offspring by two or more resident females. For the present, I define "overlapping" as overlap in pregnancy. A situation in which one female was lactating (but not pregnant) while another was pregnant would not be classed as overlapping by this definition.

Thus, the following types of observation should not be considered conclusive evidence of a non-monogamous mating system or of plural breeding, though they may be suggestive:

(1) Two or more adult females breeding consecutively but not concurrently in a group. When two or more females become pregnant or give birth, but only one successfully rears offspring, this might qualify as plural breeding, but if only one set of infants can be reared then this is questionable.

(2) Extra-group mating by young natal adults, which may be precursors to the formation of new groups, particularly if there is no evidence of resulting pregnancy (which suggests fertility suppression).

It is clear from the above discussion that there are many unresolved questions concerning callitrichid social organisation. Detailed studies of each component of the reproductive strategies of marmosets and tamarins are required. This study therefore focussed on one tamarin species in an attempt to address some of these issues.

The cotton-top tamarin

Taxonomy

The subject of this study was the cotton-top tamarin, which belongs to the *Saguinus* *oedipus* group of bare-faced tamarins described by Hershkovitz (1966, 1977). The other two members of this group are the Panamanian or Geoffroy's tamarin, and the white-footed or silvery brown bare-face tamarin (*Saguinus leucopus*). The group comprise the most northerly callitrichids, and are geographically isolated from the other *Saguinus* species (Skinner 1986). The cotton-top and the white-footed tamarin are confined to Colombia, while Geoffroy's tamarin extends from Colombia into Panama and possibly Costa Rica (Hershkovitz 1977; Wolfheim 1983; see fig. 1.1), although its occurrence in Costa Rica is not yet confirmed (Skinner 1986). The three populations do not appear to be sympatric at any point, although a recent survey in Colombia (INDERENA 1988) suggested that cotton-tops and Geoffroy's tamarins may be parapatric (i.e. found in adjoining areas), or even sympatric, in one region. Whether there is any intergradation between the two forms in this area remains to be confirmed.

The relationships of the three members of the *Saguinus oedipus* group to one another have been the subject of some debate. Most authorities (e.g. Hershkovitz 1977; Wolfheim 1983; Natori & Hanihara 1988) acknowledge the white-footed tamarin to be less closely related to the other two. However, while several authors (e.g. Wolfheim 1983; Sussman & Garber 1987) follow Hershkovitz (1966, 1977) in classifying the cotton-top and Geoffroy's tamarin as sub-species of *S. oedipus* (*S.o. oedipus* and *S. o. geoffroyi* respectively), Mittermeier & Coimbra-Filho (1981) consider them to be separate species (*S. oedipus* and *S. geoffroyi*), on the grounds that there is as yet no evidence of intergradation between the two populations. This has led to some confusion: for example, Goldizen (1988, p. 36) refers to both *oedipus* and *geoffroyi* as "cotton-top tamarins".

Recently, analyses of morphological characteristics in *Saguinus* species have been used to tackle these issues, and have provided support for the view that *oedipus* and *geoffroyi* should be considered separate species. Hanihara & Natori (1987) used multivariate techniques to analyse dental measurements in several species of *Saguinus*, and found that while *oedipus* and *geoffroyi* were indeed closer to each other than either was to *S. leucopus*, the distance between *oedipus* and *geoffroyi* was greater than that separating other *Saguinus* pairs classified as

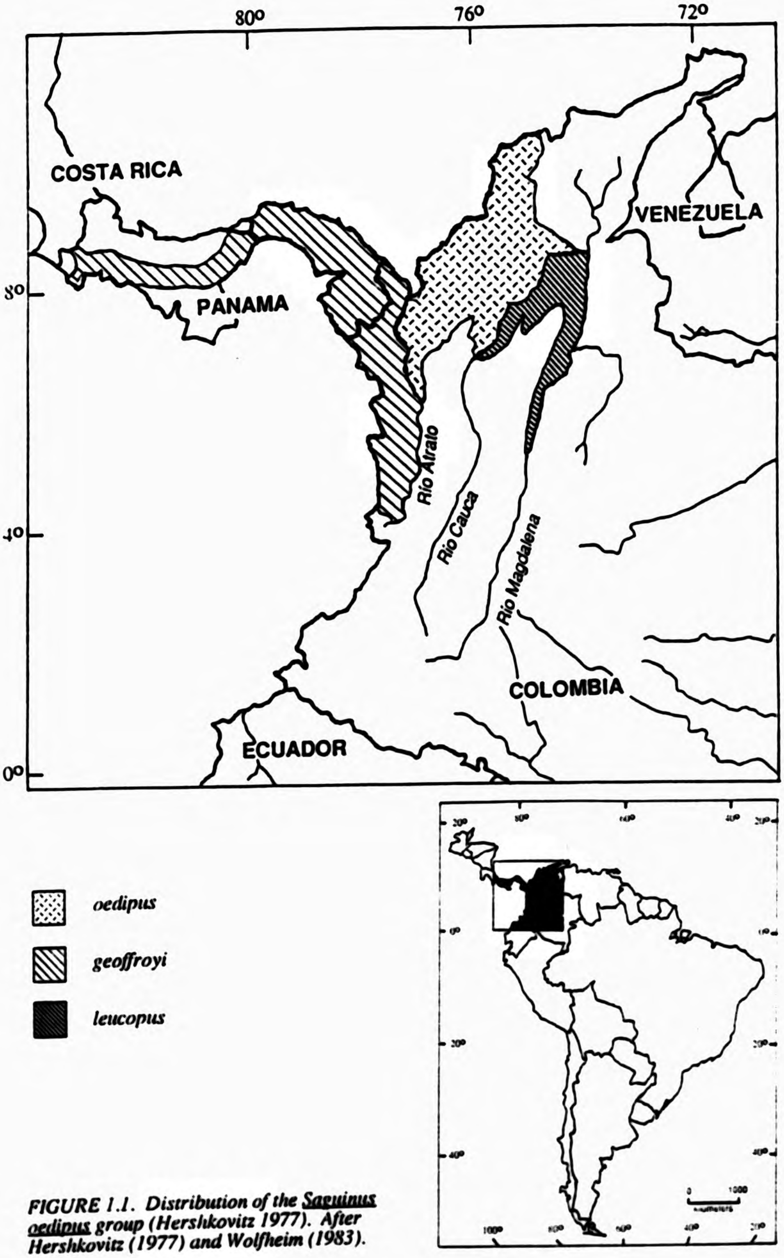


FIGURE 1.1. Distribution of the Saguinus oedipus group (Hershkovitz 1977). After Hershkovitz (1977) and Wolfheim (1983).

separate species. A similar approach was applied by Natori & Hanihara (1988) to cranial measurements, and again, a difference between *oedipus* and *geoffroyi* was found that was as great as that between pairs recognised as different species, and greater than that between other pairs classed as sub-species. Skinner (1986) found that wild adult male *geoffroyi* were significantly heavier than male *oedipus*; further analysis of 17 morphological characters showed that *geoffroyi* was in fact more similar to *leucopus* than to *oedipus*.

A comparison of the field data provided by Neyman (1978, 1980) for cotton-tops and by Dawson (1976, 1978) and Rasmussen (1989) for Geoffroy's tamarin also reveals several major behavioural differences between the two: Geoffroy's tamarins are not territorial, at least under some conditions, whereas cotton-tops are; ranges are larger and there is considerably more range overlap in Geoffroy's tamarins; and while cotton-tops frequently rear twins, Geoffroy's tamarins commonly only rear a single infant from multiple litters. In accordance with this, the cotton-top tamarin and Geoffroy's tamarin are considered separate species throughout this thesis.

Distribution in the wild and conservation status

The cotton-top tamarin is confined to north-western Colombia. Hershkovitz (1977) and Wolfheim (1983) describe it as occurring between the Río Atrato and the Río Cauca-Magdalena (see fig. 1.1), at altitudes ranging from near sea-level to almost 1500m. It is listed as an endangered species in the IUCN Red Data Book, on the Protected Species List of the Colombian government, and in Appendix 1 of CITES (Mittermeier *et al.* 1978; Cerquera 1985). The species has been heavily exploited for the pet trade and biomedical research, and much of its original habitat has been effectively destroyed (Hernandez-Camacho & Cooper 1976). As a result, the cotton-top has been protected by law in Colombia since 1969. A resolution by INDERENA (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente) in 1973 stopped export of primates from Colombia, although legal export of cotton-top tamarins for scientific use continued until 1974 (Neyman 1978). Neyman (1978) estimated that over much of the cotton-top's range, particularly in the north, the forest had been reduced to isolated patches, with as much as 70% of its original range cleared for agriculture by

1966. The southern quarter of the species' range contains about 80% of the remaining populations (Mittermeier *et al.* 1978), with cotton-tops possibly protected in the Paramillo National Park (460,000 hectares) in the Department of Cordoba, and in Los Colorados Sanctuary (1,000 hectares) further north in the Department of Magdalena (Hernandez-Camacho & Defler 1985). Unfortunately, the Paramillo Park is the site for two planned dams, which would cause the loss of about a quarter of the cotton-top's remaining range (Cerquera 1985). This project has, however, been suspended because of lack of funds (Savage *et al.* 1989*a*). Cotton-top tamarins are now considered by the Colombian authorities to be in imminent danger (INDERENA 1988). Nevertheless, although the outlook appears bleak, a recent study (Tardif *et al.* 1989*b*) found that cotton-top tamarins in one forest fragment showed a surprisingly high degree of genetic diversity: 13 feral tamarins had eight polymorphic loci (23%), compared to a captive sample from the US with only two (7%). In addition, a conservation education programme has recently been started in Colombia (Savage *et al.* 1989*b*).

In captivity, the cotton-top tamarin has become fairly well established (Tardif 1985; Tardif & Colley 1988), partly as a result of its use as a model in some biomedical research projects. In particular, its susceptibility to colon cancer, apparently unique among those callitrichid species commonly maintained in captivity (e.g. Clapp *et al.* 1985), has made it a prominent research species. It also appears to be a unique model for Epstein-Barr virus-induced lympho-proliferative diseases (Tardif 1985). Breeding the species in captivity has met with mixed success in the past, with some colonies reporting high degrees of infant mortality from abortion, stillbirth and parental rejection of infants (e.g. Carroll 1983; Evans 1983*a*; Kilborn *et al.* 1983; Kirkwood *et al.* 1983; Tardif *et al.* 1984*b*; Scullion 1987). More recently, though, the situation has improved, particularly in those colonies which adopt policies designed to reduce stress, improve the captive environment, and allow young tamarins sufficient experience with infant siblings to develop competent parental skills, and also maintain groups of similar size and composition to those in the wild (Tardif *et al.* 1984*b*, 1986*b*; Clapp & Tardif 1985; Kirkwood *et al.* 1985; Snowdon *et al.* 1985; Price & McGrew, in press *a*). The captive population is now fairly large (estimated at 1000-1300 individuals), about 30% of which are in zoos, and the remainder in research colonies (Tardif 1985). Both British Isles and

International Studbooks have been initiated (Colley 1989; Tardif & Colley 1988).

Previous research

As yet, only one field study of the cotton-top tamarin has been published (Neyman 1978, 1980), although another study is currently in progress (Savage *et al.* 1989*a*). Neyman's study produced data on feeding, ranging, and group size and composition, but little information on social behaviour. Her essentially isolated study population inhabited very dry tropical forest, with low rainfall occurring in a highly seasonal pattern. The tamarins fed on a variety of foods, ranging from fruits, leaves, stems and nectar to insects and, occasionally, small vertebrates. Vegetative parts formed a minor proportion of the diet, and were most important in the dry season when fruit was less available. The cotton-tops foraged and fed in all strata of the forest, including the ground, although most food trees were middle-canopy species. Established groups ranged in size from three to 13 individuals. Home range sizes of three groups were 7.8, 10 and 10 hectares, giving density estimates of 0.3-1.8 tamarins per hectare. Overlap with the home ranges of neighbouring groups was 20, 25 and 43% respectively. Home range boundaries appeared to be stable, and inter-group encounters, which were usually agonistic, occurred in the overlap areas. Adult males were the most obvious participants in these encounters. The tamarins visited most of their range in the course of a few days, although usage tended to be concentrated in certain areas of the range. Daily path length for one group was estimated at 1.6±0.15 km/day. Apart from established groups, transient individuals were seen who were not attached to established groups. Such transients were almost always adults. All groups contained several adults, though there were usually more adult males than females. Only one set of infants at a time was seen in any group. Seventeen litters of infants were observed, of which 13 (76%) were twins, and the remainder singletons. Infant survival to one year was 75%. About three-quarters of births occurred in the first six months of the year, although births did take place in most months. Five estimated interbirth intervals ranged from about six to 20 months, but there was only one birth per year in most groups (mean interbirth interval was 11.8 months, n = 5).

Some preliminary data are now available from Savage *et al.*'s (1989*a*) study. Three study groups ranged in size from three to nine individuals over a two-year period. Three immigrations and emigrations occurred, but groups appeared more stable over time than those described by Neyman. Nevertheless, new members appeared to be integrated into groups without the high levels of aggression seen in experimental introductions in captivity. Territorial encounters were relatively infrequent compared to Neyman's results, and varied in nature according to which of the three groups were involved. Encounters between two groups were clearly territorial, and females scent-marked primarily during these meetings. However, the third group had no aggressive encounters with either of the others. Savage *et al.* therefore speculate that this group may be a temporary or permanent aggregation of offspring from the two main groups.

Data on ecology revealed that the tamarins covered more of their home range on a daily basis in the dry season. Levels of social interaction were lower than those observed in captivity, but time spent foraging was greater. Four sets of twins whose development was observed became independent at about the same rate as in captivity, and all group members shared in their care.

The most interesting data to emerge from Savage *et al.*'s study concerns the relatedness of group members, which was determined on the basis of shared loci. In one group there was evidence that there had been a change of breeding female: the female seen to give birth in the first year of the study was not the mother of the other group members. Furthermore, in the second year of the study, this female as well as another became pregnant; however, only the second female delivered viable offspring. In a second group, one juvenile had a genetic pattern that was different from that of the other members of the group, but the same as that of individuals in another group.

Several aspects of the biology and behaviour of the cotton-top tamarin have now been studied fairly intensively in the laboratory. The gestation period averages 184 days, a month longer than that reported for any other species, and a postpartum oestrus occurs two to four weeks after parturition (Ziegler *et al.* 1987*a*). In common with other callitrichid species, there is no lactational anoestrus (French 1983; Ziegler *et al.* 1987*a*), but there is some evidence for seasonal breeding (Brand 1980). The length of the oestrus cycle is about 23 days (Brand 1981*b*, 1984; French *et al.* 1983), but few correlations between sociosexual behaviour and any point in the cycle have been found (French 1982; Brand & Martin 1983; Brand 1984). Most colonies report a predominance of twin litters, though up to 25% of births may be triplets (Kirkwood *et al.* 1985; Tardif *et al.* 1986*a*; Price & McGrew, in press *a*).

Groups of cotton-top tamarins in captivity are typically maintained as monogamous breeding pairs and their offspring. Pair bond formation in monogamous groups and changes in pair relationships with time have been described by Savage *et al.* (1988). Little attention, on the other hand, has been paid to the possibility of alternative mating systems. A recent study, however (Price & McGrew, in press *b*) suggested that polyandry may sometimes be a stable option, although polygyny appeared unlikely to be viable in the long-term. Captive studies have found that normally only one female in a group breeds (e.g. Hampton *et al.* 1966). The fertility of additional females, whether her daughters or unrelated subordinates, is suppressed and they do not ovulate or show ovarian cyclicity (French *et al.* 1984; Savage *et al.* 1988). If the mother in a family dies, the eldest daughter begins cycling and suppresses the fertility of her younger sisters (Heistermann *et al.* 1989). Scent-marking has been implicated in this suppression (Savage *et al.* 1988), and it has been demonstrated that cotton-top tamarins can distinguish marks from different classes of individuals (Belcher *et al.* 1988; Epple *et al.* 1988). Scent-marking has also been shown to increase following a female's removal from her natal family and pairing with a male (Tardif 1983; French *et al.* 1984). However, young female tamarins still show hormonal indications of puberty at 15-17 months (Ziegler *et al.* 1987*b*), although there is some evidence that they mature later if they remain in their natal families (Tardif 1984).

Aspects of infant care and development are described by Cleveland & Snowdon (1984), French & Cleveland (1984), Feistner (1985), Feistner & Chamove (1986) and Tardif *et al.* (1986*b*). Fathers and older offspring typically help extensively in rearing infants, although parental contributions to care, particularly that of the father, decline as group size increases

(McGrew 1988). Although no sex differences in infant behaviour have been found (Cleveland & Snowdon 1984; French & Cleveland 1984), recent data from the Stirling colony suggest that some sex differences in social behaviour may exist in older offspring, with females more likely to show interest in dispersal opportunities (McGrew & McLuckie 1986), and males more likely to initiate social interactions with other family members (McGrew, in press; K. Moore, unpublished data). These differences may parallel the slight trend found by Neyman (1978, 1980) towards a preponderance of males in established groups, in contrast with the transient population in which females were more common. Sexual dimorphism has also been found in the behaviour of breeding adults. It is well-established that breeding females scent-mark at considerably higher frequencies than males (Wolters 1978; French & Cleveland 1984; S. Evans, pers. comm.), and the degree of sexual dimorphism in scent-marking behaviour appears to be unusual among callitrichids (French & Cleveland 1984). In addition, males appear to be more aggressive when faced with intruders, whereas females respond with increased rates of scent-marking (French & Snowdon 1981). Moore *et al.* (submitted for publication) also found that breeding females tended to be more interested in looking at neighbouring groups. There are also differences in the type of inter-group vocalisations used by the two sexes (McConnell & Snowdon 1986).

Although in marmosets it is possible to assign ranks to individual family members indicating their relative status (e.g. Sutcliffe & Poole 1984*b*), in cotton-top tamarins detecting any dominance hierarchy is considerably more difficult. Conventional methods based on agonistic or approach/retreat interactions are not applicable to cotton-tops (Wolters 1978), and aggression and submissive behaviour are rare (personal observation). Relative status may well be important to the reproductive strategies of cotton-top tamarins, but remains to be studied in detail.

Aims of the study

Despite the fact that much of the evidence is so far inconclusive, assistance with infant care, whether from a pair's older offspring or from additional breeding adults, appears to be important for successful reproduction in callitrichids. The above review has indicated several areas where further research is needed. However, while there is fairly extensive data on infant care in several callitrichid species in captivity, and some from the wild, much previous work has been done on captive groups in which, for research or husbandry purposes, offspring are at the age of approximately two years, when their family has about eight members. Furthermore, surprisingly few studies have directly addressed the questions of how callitrichid mating and rearing systems benefit the individuals concerned, and what costs they might entail. In general, only superficial analyses of how much each family member contributes to infant care have been carried out, and none has considered in detail the advantages and disadvantages of such investment to each individual - investment which may involve considerable energy expenditure and reduced access to important resources such as food. The Stirling colony of cotton-top tamarins, with its wide range of group sizes and compositions, including groups both with and without adult offspring, was ideal for a study of the important factors affecting their reproductive strategies. The aim of this research was therefore to investigate these strategies in some detail, focussing on the following areas:

(1) how helpers help: the distribution of care within cotton-top tamarins and how it is affected by the presence of helpers.

(2) how the pattern of care is influenced by competition and control between family members.

(3) the costs of infant care.

(4) the strategies adopted by monogamously-mated male and female tamarins.

(5) a preliminary investigation of alternative mating systems.

Chapter 2

Materials and Methods

Subjects

Details of groups

The subjects for this study were drawn from 12 groups of cotton-top tamarins housed in the Primate Unit of the Department of Psychology at the University of Stirling. The colony was obtained from the Department of Zoology, University College of Wales, Aberystwyth in May 1982. Initially it consisted of four breeding pairs, and grew to a maximum of ten groups at any one time, with new breeding adults being either offspring of the original pairs, or brought in from other colonies to reduce inbreeding. The members of two of the original breeding pairs were wild caught, but were legally imported before the UK ratifed CITES (the Convention on International Trade in Endangered Species) in 1976. All other animals were captive born.

Ten groups consisted of a monogamous breeding pair and up to 14 of their offspring; the other two (Pixie and Shoshone) were formed from an adult male and some of his offspring, and an unrelated female introduced to replace the male's original mate. Group sizes during the study ranged from two to 16. As far as possible, tamarins were only removed from their families if involved in severe aggression, or occasionally if families in the smaller cages became overcrowded. Sometimes, however, adult offspring were removed if a new breeding adult was needed for another group.

Further details of the breeding groups are given elsewhere (Evans 1983*a*; Price & McGrew, in press *a*). Details of changes in the composition of each group during the study period (January 1987 - August 1989) are presented in Appendix A. More information on the specific individuals involved in each phase of the study is given in the appropriate chapters.

The reproductive characteristics of the cotton-top tamarin groups at Stirling were comparable in most respects with recent descriptions of other successful colonies (e.g. Snowdon *et al.* 1985), and are described in detail by Price & McGrew (in press *a*). Briefly, there was a mild degree of seasonality in breeding, particularly for females giving birth to their first four litters, with a birth peak in the spring months, as in other colonies housed under natural lighting conditions (Brand 1980; Kirkwood *et al.* 1985). Interbirth intervals were typically six to seven months (median = 206 days). Mean litter size surviving to adulthood was 1.5. Although all our captive-born breeding females had had considerable experience with infant siblings (typically two to three litters) before being paired, infant survival increased with parity. This can be attributed to two interacting factors: a decrease in the average litter size born, and an increase in the number of infants surviving from each litter. Even if infants died, signs of rejection such as injury were not usually apparent. About three quarters of the litters born were twins, with most of the remainder triplets. Only two singleton births occurred. None of the females ever succeeded in rearing triplets, but no hand-rearing or supplemental feeding was attempted. In almost all observed cases, parental care was competent from the moment of birth onwards (Price, in press *b*).

In general, the tamarins remained in excellent health throughout the study. Three adult deaths occurred during the study period. A male (Tim) died of *Klebsiella pneumoniae* infection following removal from his group for bullying younger siblings. A young adult male (Kansas), one of three males in a polyandrous group, died after a fight with his older brother despite treatment for post-traumatic shock. Further details of this case are given in chapter 7. Finally, a breeding female (Sioux) died four weeks after giving birth to her thirteenth litter. Four days after parturition she began to have severe diarrhoea, and both infants died within a week of birth, apparently of starvation. Charcoal was given in an attempt to ease the diarrhoea and prevent dehydration, but Sioux collapsed and died soon after despite the administration of antibiotics and electrolyte solution. Post-mortem examination revealed no obvious cause of death, and an analysis of a section of colon by F. Scullion at Bristol University showed only mild colitis. The only other deaths in the colony were of infants under the age of three weeks.

Age classifications

Two main approaches to assigning age classes in cotton-top tamarins have been used in the past. Cleveland & Snowdon (1984), in a captive study, used categories based on interbirth intervals (infant: 0-7 months; juvenile: 7-14 months; sub-adult: 14-21 months; adult: >21 months). This classification scheme has since been adopted in other studies (e.g. McGrew & McLuckie 1986). However, since interbirth intervals in Stirling are often less than seven months (Price & McGrew, in press *a*; see figure 2.1), the use of this classification would have led to some young tamarins experiencing the birth of the following litter being classed as infants, while others were classed as juveniles.

Neyman (1978, 1980), in her field study, used tooth wear characteristics to estimate age. On the basis of this, she described six age classes (juveniles: J1 and J2, up to one year; sub-adults: A1, 1-2 years; adults: A2, A3 and A4, more than 2 years). She also estimated that minimum adult weight was reached at about 18 months, and average adult weight at 2 years or more. Glassman (1982, cited in Richter 1984) found that the last closure of the long bone epiphyses occurred at about two years old. In addition, Kirkwood *et al*. (1985) found that female cotton-top tamarins only bred successfully after the age of about 29 months, suggesting a first successful conception at a little under two years, in spite of evidence that puberty occurs at around 15-17 months (Ziegler *et al*. 1987*b*). Tamarins in the Stirling colony reached adult weight (average approximately 550g) at 18-24 months (figure 2.2). The following age classification system was therefore adopted:

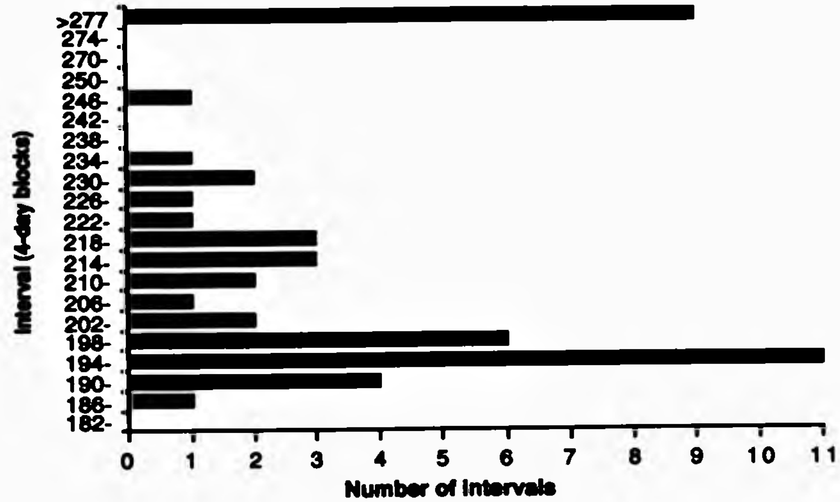


FIGURE 2.1. Interbirth intervals in the Stirling colony from 1/6/82 to 30/10/88.

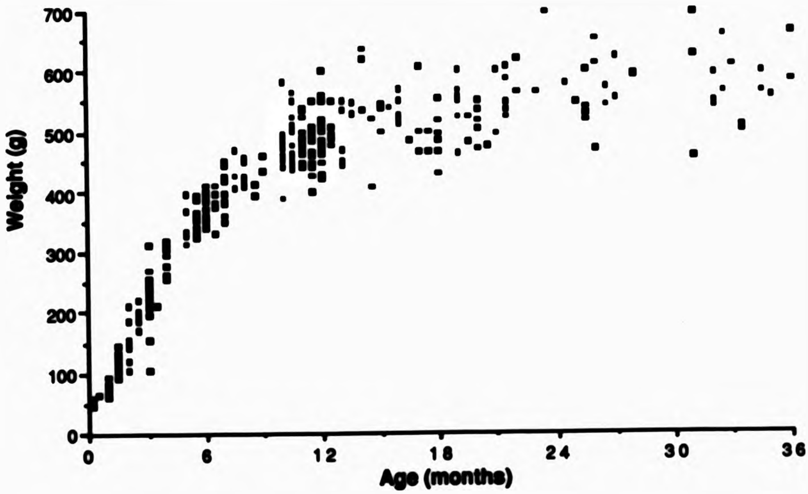


FIGURE 2.2. Weights of cotton-top tamarins born in the Stirling colony between 1/6/82 and 31/12/88. Each point represents one of 350 weight records obtained on an opportunistic basis from 80 different individuals. Each individual contributed between one and ten records.

Infant	birth - 12 weeks
Juvenile	13 weeks - 1 year
Sub-adult	1-2 years
Adult	>2 years

Husbandry

Housing

Conversion of the Primate Unit, originally designed for macaques (Chamove 1981) is described by Evans (1984). Entry to the unit was restricted. The aim of this was to reduce stress to the tamarins; however, the frequent presence of familiar people, and occasional unfamiliar visitors and undergraduate students, provided stimulation. The colony was used for undergraduate teaching purposes, and for research by undergraduates, postgraduates, and members of staff. All research was non-invasive.

The four largest groups were each housed in a separate room (average dimensions 2.91m high x 3.45m wide x 3.54m deep; mean volume 35.3m^3). Until June 1989, the smaller groups were housed in a single large colony room in either one or two cage units (type I colony cages; each unit measuring 1.97m high x 1.19m wide x 1.68m deep). In June 1989, these cages were removed and replaced by eight cage units (type II colony cages) built to fit the space available. Each unit measured 2.5m high x 1.5m wide x 1.5m deep, and groups were housed in either one or two units. Throughout the study, groups housed in the colony room had regular access to four large outdoor areas (mean volume 29.3m^3) in good weather. Large groups housed in separate rooms had more intermittent access to the outdoor areas. Groups were maintained in visual isolation, but could hear and probably also smell each other. Semi-transparent flexible ducting 15cm in diameter (Crystaflex; Flexible Ducting Limited, Milngavie, Glasgow) was used to connect different areas of the monkeys' living quarters together, and allowed us to move groups to new housing easily (for example, when a group was moved to a larger room as it increased in size). The tamarins were thoroughly habituated to this apparatus and would readily travel distances of 30m to new areas. The various types of housing are illustrated in plate 2.1.

All rooms had large skylights which permitted natural light to enter at all times. Additional lighting was provided by fluorescent strip lights. Until December 1987 these were on a 12 hour light/dark cycle running from 0700 to 1900 and operated by automatic time switches. After that, seasonal changes were made four times a year to mimic changes in day length in the cotton-top's natural habitat in north-west Colombia (spring and autumn: 0700-1900; summer: 0645-1930; winter: 0715-1845). Temperature in the indoor areas was maintained between 20 and 25 °C by a hot air duct system, and by additional heaters in each room when required, and humidity was kept at 40-60% by humidifiers. Extractor fans in each room changed the air 12-25 times an hour during working hours (0845-1715 on weekdays, and approximately 0900-1100 at weekends). All living areas were furnished with a variety of natural branches, wooden perches, platforms, toys and swings, screens of rope and curtain material, and mesh for climbing, and fresh leafy branches were placed in each cage at regular intervals. Each group was provided with one to three nest boxes. Further details of furnishings are given by McKenzie *et al.* (1986). Indoor housing was furnished with a layer of woodchips (2-4cm deep) covering the entire floor. Plants were grown in the outdoor areas, and from time to time the tamarins were given various devices designed to enrich their environment (Chamove *et al.*, unpublished data). Type I colony cages were cleaned weekly, type II cages fortnightly, and rooms once every eight weeks. Outside areas were hosed weekly and cleaned thoroughly once every eight weeks. All personnel wore lab coats and paper masks, and disinfectant foot baths were placed outside each animal room. Animals were caught up only if they required medical treatment, or when they were marked for identification purposes.

Diet

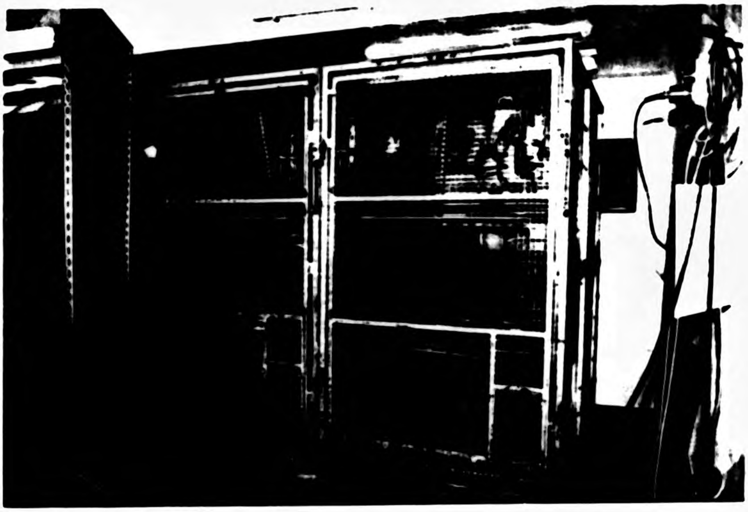
The tamarins were fed a mixed diet of commercially prepared foods and fresh food. On

PLATE 2.1

Housing for cotton-top tamarins in the Stirling colony.

- *(a) Type I colony cage*
- *(b) Room*
- *(c) Type II colony cage*
- *(d) Outside area*
- *(e) Three tamarins using ducting to move from a type I colony cage (right) to an outside area*

a



b

c

d

e

weekdays, three meals were provided daily. Each morning dry chow, soaked chow with condensed milk or powdered milk, and peanuts in their shells were given, together with one or two of the following: marmoset jelly; milk mix or porridge mix with rosehip syrup; hard boiled eggs; peas and beans. Vitamin supplements were given weekly (D_3, approx. 1000 IU per animal; multivitamins; B_2). A small quantity of milk was given daily, and water was available *ad lib*. At midday a mixture of chopped fresh fruit was given with a small amount of fruit-flavoured yoghurt, and in the late afternoon a small quantity of chopped apple was provided. All fresh fruit was soaked in disinfectant before being fed to the monkeys. The weekend routine was similar, except that the apple and fruit salad were combined in one meal in the late morning. From August 1988 onwards, the food for larger groups was split between two sets of dishes. This made the feeding routine more interesting for the monkeys, and also reduced competition at the feeding sites, ensuring that any individuals who were being harassed by other family members were given a chance to feed.

Marking procedures

For identification purposes, tamarins over the age of 12 months were fitted with loose-fitting light chain necklaces holding coloured discs; infants and juveniles were marked on their crests with picric acid, a yellow dye. In the case of juveniles, sub-adults and adults, the tamarin to be marked was caught using a hand net, removed to a treatment room, and dyed or fitted with a disc. The opportunity was taken to weigh the monkey and check it for any superficial problems. It was then returned to its family immediately, usually no more than ten minutes after being captured.

Since infants were not independent when first marked, the procedure was slightly different. Infants were first marked when they were 4-7 days old, and, in the case of a triplet litter, after the third infant had died. Infants were caught together with their carrier, but were removed from the carrier for sexing, weighing, and marking with picric acid. Whenever possible an infant was given back to the adult carrying it before being returned to the rest of the group. Some carriers, however, refused to take infants back, and in these cases the infant was placed either in a small carrying box or into a nestbox, from where the family would retrieve it. One infant died when being returned in this way when the parents and three adult sons in a large family all attempted to pick it up at the same time. The infant was badly injured in the process, and although removed immediately, it was extremely weak and had to be euthanased. After this, the procedure was modified so that only one or two reliable adults were present when an infant was returned. All other infants were marked without mishap, though minor bites from carriers trying to dump infants were sometimes inflicted as the carrier and infant were being removed from the net after being caught. One infant received permanent facial damage as a result. Most infants observed during the study were marked in this way, although towards the end of the study, alternatives to this procedure were explored that did not require the removal of infants from carriers (see Halloren *et al.* 1989). This involved accustoming adults to a swab saturated with dye; when the infants were born, carriers were tempted over with a piece of a favourite food, and the infant's head was then marked using the swab.

Data collection

Ecological validity

A captive study had several advantages over field studies: in the monogamous groups of tamarins maintained here, the details of genetic relationships between individuals were generally known. A larger number of groups and subjects could be studied in depth than is feasible in most field studies, and since subjects were unlikely to be out of view for long periods, detailed information on the behaviour of individuals could be obtained relatively easily. There were, however, several disadvantages as well: access to potential mates was artificially controlled, young tamarins could not leave their groups voluntarily, families had little opportunity to engage in encounters with neighbours, there were no predators, and because food was readily available they needed to spend much less time in searching for and processing food. However, as the main research emphasis in the colony was on the social behaviour and reproductive strategies of cotton-top tamarins, the priority was to maintain groups of similar size and composition to those in the wild, as far as is possible in a captive environment. Neyman (1980) found that no parous female in her study population appeared to be less than five years old. In the wild, therefore, young tamarins may stay with their natal family (or perhaps even with other groups) for several years before beginning to breed, and thus experience the birth and rearing of several sets of infants. The large amount of space and the complex, semi-naturalistic environment we were able to provide for our tamarins allowed us to maintain larger groups than many other colonies can, and thus to keep offspring in their natal families well into adulthood, as long as six years in some cases. A comparison of several parameters with Neyman's (1978, 1980) field study of the cotton-top tamarin is given in table 2.1. Group sizes and number of adults of each sex and the reproductive characteristics of our groups were comparable to those in the wild. Since few data are available on the mating patterns of cotton-tops in the wild, we could not assess whether our usually monogamous breeding pairs and their offspring were typical of wild groups.

I was also encouraged by the fact that despite the major differences between the wild and the captive environment, the Stirling tamarins still retained several features of wild groups, including intolerance of unrelated conspecifics (personal observation), and an apparent sex difference in dispersal tendencies (McGrew & McLuckie 1986), with some associated sex differences in social relationships (K. Moore, unpublished data; McGrew, in press). In addition, our husbandry practices encouraged the tamarins to forage in the woodchips on the floor for items of food that they had dropped, and they often spent considerable periods of time doing so.

Ethogram

No complete ethogram for the cotton-top tamarin has yet been published, but several aspects of their behaviour have been described by previous authors (infant care and development: Cleveland & Snowdon 1984, Tardif *et al.* 1986*b*; food-sharing: Feistner 1985, Feistner & Chamove 1986; scent-marking and inter-group behaviour: French & Snowdon

TABLE 2.1. Comparative data on group characteristics and reproduction from the Stirling colony and the wild.

		Stirling[1]	*Wild*[2]
Group size:	mean	6.88	5.67
	range	2-11	3-13
No. adult males:	mean	2.25	2.67
	range	1-4	2-4
No. adult females:	mean	1.88	1.50
	range	1-4	1-4
Total no. adults:	mean	4.13	4.33
	range	2-7	3-6
Infants per litter surviving to 1 year:	mean	1.52	1.67
Birth peak		Jan-July	Jan-July

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1. From Price & McGrew (in press *a*); data for October 1988; n = 8 groups
2. From Neyman (1980), fig. 16, pp. 60-61; data for August 1975; n = 6 groups

1981, French & Cleveland 1984; vocalisations: Cleveland & Snowdon 1982; sexual behaviour: Brand & Martin 1983, Brand 1984, Savage *et al.* 1988). Wherever possible, the terminology used in previous studies was adopted. In order to select and describe categories of behaviour appropriate for the planned research, pilot observations were made of eight infants and their families. A brief description of the behavioural categories recorded during the study is given here. Terms in bold type indicate names of categories recorded. Lists of the types of behaviour recorded in each phase of the research, and information on recording methods for each category, are given in the relevant chapters.

(a) Infant care

Carrying was scored if an infant was clinging to a carrier with at least two limbs, and its weight was supported by the carrier. To be recorded as carrying, contact had to be maintained for at least 10 seconds. An infant who was not being carried was said to be **off**.

Transfers referred to successful or unsuccessful attempts to move an infant from one carrier to another, from a carrier to the substrate, or from the substrate to a carrier. A **completed transfer** occurred when an infant, carrier or taker successfully effected such a move. An **attempted transfer** occurred when a carrier, potential taker or infant tried to effect a transfer, but failed. The behaviour of carrier, taker and infant, and intervention by third parties, was recorded for all transfers. Further details are given in chapter 4.

Since the nipples are axillary rather than pectoral, it was not possible to tell if an infant was actually on the nipple or not. **Suckling** was therefore scored if an infant's head was in the axillary position, and it was not moving its head around (which would have indicated it was still searching for the nipple). Who initiated and terminated suckling bouts was recorded if it could be seen. Infants terminated suckling by moving dorsally, and initiated suckling by moving ventrally and rooting for the nipple. Mothers initiated bouts by pulling the infant round with her hands, and terminated bouts either by pushing at the infant or biting it gently, or by giving a trill vocalisation (Type C trill, Cleveland & Snowdon 1982). The infant almost invariably stopped feeding voluntarily within two minutes of the mother giving the vocalisation.

Food-sharing behaviour was split into various types. **Begging** was recorded if an infant approached a possessor of food, vocalised and attempted to take the food. If the possessor allowed the infant to take the food (= shared; Feistner 1985), a **successful beg** was recorded; if the possessor denied it (= refused; Feistner 1985), by running away, cuffing the infant or dropping the food, an **unsuccessful beg** was recorded. **Offering** occurred when a possessor of food held out the item and vocalised (Type D chirp, Cleveland & Snowdon 1982), and an infant approached and took the food. **Food stealing**, when one individual obtained food despite resistance by the possessor, was also observed occasionally. Infants were not seen to steal as an older animal could always prevent them from taking food.

(b) Social behaviour

Allogrooming consisted of parting the groomée's fur with the hands and using the mouth to remove particles. A specialised form of grooming, anal cleaning (licking the anogenital area), was performed by adults to infants. Other sorts of affiliative behaviour were classed together as **affection**. This descriptive term included sniffing and nuzzling (when an individual put its face close to or in contact with the face or body of another monkey), touching with the hand, and licking. **Anogenital sniffing** was recorded separately.

Aggression took several forms, ranging from mild chastisement (cuffing with the hand, pulling the hair on the crown, and lunging towards another animal) through biting, to attacks and fighting, which often resulted in superficial wounds. The latter occurred only rarely; records of aggression in this thesis refer to the milder forms except where stated to the contrary. Recipients of aggression often responded by giving squawking vocalisations (Cleveland & Snowdon 1982).

In **face-pressing**, two tamarins pressed their faces together, usually with mouths open and often accompanied by loud screaming vocalisations. Its function is unclear, though it may be related to status.

Social play consisted of play chasing and wrestling, and was easily distinguishable from aggression on the basis of the accompanying vocalisations and the context.

Scent-marking in the cotton-top tamarin occurs in several forms, which may have different functions. **Anogenital marking** involves rubbing the anogenital area from side to side or along the substrate. **Suprapubic marking** involves dragging the area above the genital region along the substrate with the legs splayed. Suprapubic marking was extremely rare in this study. Breeding females would often anogenital mark other members of their families (**allomark**; referred to as **partner mark** if marking the mate), and also frequently showed **genital rubbing** (rubbing the genital area with the hand) in association with scent-marking. They did not obviously use the "scented" hand to mark after genital rubbing.

(c) Sexual behaviour

Several categories of mounting were seen. **Full mounts** were scored if mounting by the male (grasping the female round the waist and leaning his weight on her) was accompanied by pelvic thrusting. Previous authors have attempted to determine ejaculation in one of two ways. Savage *et al.* (1988) defined an ejaculatory mount as one in which the male groomed his genitals after dismounting. However, they gave no justification for this, and it is not clear whether it is a reliable criterion. Brand (1984) used the occurrence of one or two deeper thrusts after the usual series of rapid thrusts; however, I was not confident of my ability to detect these. Therefore no attempt was made to assess whether or not ejaculation had occurred. **Partial mounts** were mounts without thrusting. **Attempted mounts** were scored if the male moved behind the female and placed his hands on her flanks, but did not actually mount.

The female's response to mounts (**accept** or **reject**) was also recorded. Female presenting was not seen (c.f. Brand 1984). Breeding females occasionally mounted their mates (**female mount**).

Males often gave a trill vocalisation (**male trill**; not described by Cleveland & Snowdon 1982) immediately before or during mounting, and both the male and the female often showed **head-shaking** and **tongue-flicking** in sexual contexts. Head-shaking and tongue-flicking were considered to be soliciting (see also Brand 1984; Widowski *et al.*, in press). Since forms of both head-shaking and tongue-flicking were also seen in other contexts, including face pressing, aggressive threats, play, and interactions with infants, they were classed as sexual only if they occurred when the male and female were near one another (within 20cm), and if no other context was applicable.

(d) Spatial relationships

An individual was said to be **solitary** if it was more than 20cm (approximately the body length of a seated tamarin) from any other monkey. The identities of any individuals **near** the subject (i.e. within 20cm) or in **contact** with it, were recorded. Movement to within 20cm of another monkey was classified as **approach** if the approaching individual stayed within 20cm for at least three seconds; movement away from another monkey to a distance of more than 20cm for at least three seconds was classified as **leave**.

(e) Non-social behaviour

A tamarin was **sitting** if it was not locomoting, feeding, or foraging, and also not engaged in social behaviour such as grooming. Therefore, clinging and hanging were also classified as sitting. No account was taken of the animal's spatial relationships with others (i.e. a sitting tamarin could be in contact with others, or not). **Locomotion** involved movement resulting in the spatial displacement of the animal's body by at least 15cm (to exclude changes of position during resting periods). Behaviour related to feeding included visually **scanning** the ground for food that had been dropped, and manually **searching** for food in woodchips, etc. Although these two categories were recorded separately, searching occurred very rarely, and so for analysis they were combined into one category, **foraging.** Similarly, **feeding** included both consuming food or water (**eat/drink**), and **holding** food in the hand, which occurred only occasionally without simultaneous eating. Two forms of self-grooming were recorded: **scratching** and **autogrooming**.

Observation procedure

Groups were confined to their indoor housing for observation. All observations were made with the observer seated one to two metres from the front of the cage, in full view of the tamarins. Unnecessary movement and noise were avoided. The monkeys were fully habituated to this procedure, usually ignoring the observer after a minute or two, and appeared to display a full range of behaviour while being watched. However, it was not known whether they in fact behaved in the same way when they were not being observed; for example, Caine (1990) has reported that red-chested tamarins (*Saguinus labiatus*) changed their behaviour when retiring to their nest boxes in the evenings if an observer was present.

Time intervals were indicated by a tone emitted by an electronic metronome. The tone was audible to the monkeys, but they did not respond to it in any way (for example, by giving a startle response, or by looking in the direction of the sound), and their behaviour appeared to be unaffected by it.

Data collection methods

Most data were collected on checksheets. Audio and video recording were used in some circumstances, for example in pilot studies where actual frequencies and durations of a range of behaviours were desired, in intra-observer reliability tests, and occasionally when changes in behaviour occurred very rapidly. In general, however, I felt that the time required to transcribe data from tapes did not justify the extra detail that could be obtained. Checksheets provided an extremely flexible method of collecting data which could easily be modified to suit the requirements of each phase of the study.

Sampling and recording methods

The aims of the study required the collection of data on a range of behaviour. The high activity levels of the monkeys, their characteristically rapid changes of behaviour, and the short bouts in which most types of behaviour occurred made collecting actual frequencies or durations impracticable for all but a relatively few behavioural categories. It was therefore necessary to adopt a sampling strategy. Two decisions had to be made: first, whether to sample from one individual at a time (*focal animal sampling*), or to collect data from the whole group (*group sampling*) (Altmann 1974; Martin & Bateson 1986); and second, what sort of recording techniques would be appropriate for investigating the particular categories of behaviour I was interested in.

For all but the simplest and most obvious behavioural categories, collecting data from more than one individual at a time would not have been feasible, particularly in the larger families housed in rooms, and therefore only infant carrying was scored using a group scan technique. For all other categories of behaviour, a focal animal sampling technique, whereby the behaviour of a given individual was recorded for a specified period of time, was used throughout this study. Though this method has limitations in situations where individual subjects are difficult to follow for extended periods, in the captive environment the tamarins were rarely out of view. Focal sampling provided a detailed picture of the behaviour of individuals that could not have been obtained by other methods.

There are several methods of scoring behaviour (Altmann 1974). Actual frequencies (*all occurrences*) or durations of the behaviour of interest can be collected; behaviour can be scored as occurring or not occurring at a specific point in time (*point* or *instantaneous sampling*); or behaviour can be scored if it occurs during a specified time interval (*one-zero* or *partial interval* *sampling*). All these methods have been used in the study of primate behaviour in the past. However, each has different properties, and the choice of which to employ depends on several factors, including the nature of the behaviour under investigation, the type of information required, and ease of use. One-zero sampling in particular is a controversial technique. In the 1970s, its use was heavily criticised by several authors (Altmann 1974; Dunbar 1976; Kraemer 1979), largely on the grounds that it does not provide accurate estimates of either true frequency or duration: since the occurrence of a behaviour is scored once and only once in an interval regardless of how frequently it actually occurred or how long it lasted, the method systematically overestimates duration and underestimates frequency (Suen & Ary 1984, 1986). However, more recently its use has received support from other authors (Rhine & Flanigon 1978; Rhine & Linville 1980; Rhine & Ender 1983; Smith 1985; Martin & Bateson 1986), who have pointed out that there is no reason to assume that either actual frequency or actual duration are necessarily valid measures of behaviour (i.e. true indices of the phenomenon of interest, Rhine & Linville 1980; Smith 1985). Since one-zero scores are excellent predictors of a combination of frequency and duration (e.g. Rhine & Ender 1983) they can be seen as just as appropriate as these other measures for sampling behaviour.

Two major types of data were to be collected in the study: information on social relationships between individuals, and information on the time spent by particular individuals in certain activities - carrying infants, feeding, moving, and so on. One-zero sampling has been shown by others (Box & Pook 1974; Evans 1981; Carroll 1985) to be a particularly useful method for investigating the behaviour of callitrichids, since their repertoire consists of many behaviours that occur rapidly and frequently, and are of short duration. I therefore chose this method to study social relationships, since it was not feasible to record frequencies and durations of all behaviours, particularly in large families; and also because, particularly in juveniles and infants, interactions often occurred in very brief and widely spaced bouts. For a few behavioural categories that occurred in short, discrete and easily recognisable bouts, it proved possible to record actual frequencies.

However, one-zero sampling can only provide accurate estimates of time spent in various activities under certain restricted circumstances (Suen & Ary 1984, 1986). For data on social relationships this was not a problem as the information required was to be used to compare the relative strengths of the interactions between individuals, and this method would enable me to catch very brief events. For time budgets, on the other hand, accurate estimates of true duration were desirable. Although Carroll (1985) has suggested that one-zero sampling gives a better indication of activity levels in callitrichids and related species as they tend to move in short bursts, and therefore they may be stationary at the moment of sampling, in his study of the Goeldi's monkey (*Callimico goeldii*) this method of sampling activity produced scores of up to 75% of intervals active (i.e. locomoting), clearly a considerable deviation from any likely value of actual duration. It was not feasible to record actual durations, so for aspects of the study where I wished to have a more accurate picture of how individuals spent their time, instantaneous sampling seemed to be a more appropriate technique. However, instantaneous sampling had previously been shown to be inefficient for recording some aspects of callitrichid behaviour such as scent-marking (Box & Pook 1974; Evans 1981). It therefore seemed advisable to assess the accuracy of this method, and choose an appropriate sampling interval.

Selection of sampling interval

To facilitate data collection and comparison of results, I decided to select a standard sampling interval for use throughout the study. To determine an appropriate sampling interval that would provide accurate estimates of actual duration using instantaneous sampling, a pilot study was conducted.

The behaviour of 13 monkeys in four families was investigated (see table 2.2). Focal subjects were each observed for two hours, split into eight 15-minute sessions over an 11-14 day period. Data were initially collected by dictating a continuous record of the individual's behaviour on to audio tape. The recordings were then transcribed to obtain actual frequencies

TABLE 2.2. Details of subjects observed in pilot study of instantaneous sampling.

Name	*Age class*	*Sex*	*Period of data collection*
Genevieve	Breeding adult	Female	3/11/86 - 13/11/86
Reading	Breeding adult	Male	4/11/86 - 14/11/86
Alpha	Adult	Female	4/11/86 - 14/11/86
Beta	Juvenile	Female	4/11/86 - 14/11/86
Blocker	Juvenile	Male	4/11/86 - 14/11/86
Pixie	Breeding adult	Female	24/11/86 - 6/12/86
Bilbo	Breeding adult	Male	24/11/86 - 6/12/86
Gloria	Sub-adult	Female	24/11/86 - 6/12/86
Graham	Sub-adult	Male	24/11/86 - 6/12/86
Delaware	Breeding adult	Female	29/11/86 - 12/12/86
Arnold	Breeding adult	Male	29/11/86 - 12/12/86
Erica	Breeding adult	Female	29/11/86 - 12/12/86
London	Breeding adult	Male	29/11/86 - 12/12/86

and durations (to the nearest second) of five categories of behaviour: *stationary* (sit or scan), *locomote*, *eat/drink*, *allogroom*, and *social play*. Behaviour not falling readily into any of these categories was classified as "other", and was not included in subsequent analysis.

Suen & Ary (1984, 1986) provide a method for determining an appropriate sampling interval for various sampling techniques. For instantaneous sampling, their criterion is that the interval should be shorter than both the shortest bout length and the shortest interval between bouts. From the pilot study it was clear that this would produce impracticably short interval lengths. As an example, the data from the pilot study for the category "locomote" are presented in table 2.3. From the transcripts, total duration and frequency of bouts were extracted, and from these mean bout lengths were calculated. Similarly, mean durations of intervals between bouts were obtained from the total amount of time between bouts of locomotion, and the frequency of inter-bout intervals. Bout lengths of one second were very frequent (56.9% of all bouts recorded, n=2561/4498), leading to a required interval length of less than one second.

It was therefore necessary to determine an appropriate interval length empirically. The method used was that suggested by Martin & Bateson (1986). The transcribed data were transferred to time-ruled checksheets and used to calculate the number of intervals at which each behaviour would have occurred if instantaneous sampling had been used. The intervals analysed were 5, 10, 15, 30 and 60 seconds. From this, estimates of time spent in each category of behaviour were obtained for each subject at each interval, by multiplying the number of intervals by the interval length. Percentage deviations from the actual durations were then calculated, and from these the mean deviation for each category at each interval was obtained (table 2.4). A mean deviation of less than 10% from the actual value was arbitrarily considered an acceptable estimate. Figure 2.3 shows the proportion of behavioural categories which met this criterion at each interval. Five, 10 and 15 second intervals proved equally good at estimating durations, but 30 and 60 second intervals were less good. Following the advice of Martin & Bateson (1986), the longest interval that produced a reasonably accurate measure,

TABLE 2.3. Data from the pilot study for the category "locomote". Total time spent in locomotion (Dur.), number of bouts recorded (Freq.), mean bout length (M.B.L.), and mean interval between bouts (M.B.I.) were obtained from tape transcripts of two hours observation for each of 13 subjects. All times are in seconds.

Subject	Dur.	Freq.	M.B.L.	M.B.I.	Frequency of bouts of given duration 1 sec	2 secs	3 secs	4 secs	5 secs	>5 secs
Bilbo	320	188	1.70	24.89	105	52	22	7	1	1
Pixie	563	327	1.72	15.86	173	102	28	17	5	2
Gloria	1026	592	1.73	8.93	341	158	53	16	11	13
Graham	1039	638	1.63	8.48	371	175	63	23	4	2
Delaware	449	252	1.74	16.71	147	64	26	10	7	4
Arnold	678	484	1.40	9.98	368	59	38	14	3	2
Erica	175	139	1.26	20.67	109	25	3	2	0	0
London	319	227	1.41	22.32	167	41	9	4	6	0
Genevieve	533	219	2.43	22.18	95	59	22	14	7	22
Reading	547	353	1.55	18.33	229	83	24	11	2	4
Alpha	649	298	2.18	18.47	144	83	42	14	7	10
Beta	1036	428	2.42	13.12	175	109	69	25	19	31
Blocker	1020	347	2.94	12.45	137	96	43	21	16	34
Totals	8354	4492	1.86	14.27	2561	1106	442	178	88	125

TABLE 2.4. Accuracy of estimates of actual durations obtained using instantaneous sampling at five different sampling intervals, for five behavioural categories (expressed as mean percentage deviations from the actual durations).

	Sampling interval (seconds)				
Behavioural category	*5*	*10*	*15*	*30*	*60*
Stationary	+1.17	+1.23	+1.82	+3.74	+2.91
Locomote	-3.07	-8.33	-1.71	-5.70	-15.12
Eat/drink	+3.11	+2.26	+2.25	+2.99	+5.94
Allogroom	+1.93	+6.66	+4.57	+23.98	+24.48
Social play	-1.04	-3.23	+6.72	-15.24	-12.24

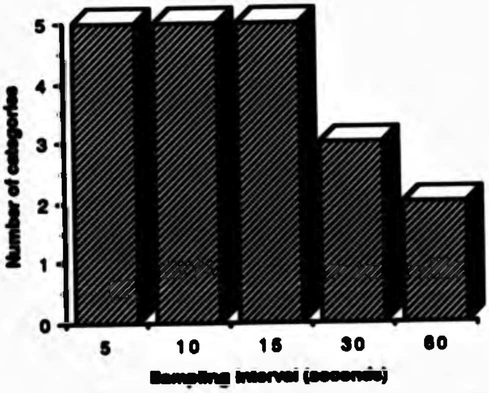


FIGURE 2.3. The number of behavioural categories (out of a maximum of five) for which accurate estimates of actual durations were obtained using instantaneous sampling at each of five different sampling intervals. An accurate estimate was defined as one which deviated by a mean of less than 10% from the actual duration.

in this case 15 seconds, was selected as the standard sampling interval, and was used throughout the study.

Controlling for variability in behaviour

Pilot studies on both adults and infants indicated that the behaviour of the tamarins could vary considerably from one observation session to the next. This problem can be particularly important when relatively rare events (such as sexual behaviour) are of interest. One method of coping with this variability is to collect multiple observations per subject for each time period of interest, and use mean values per session as the basic units of analysis (Thiemann & Kraemer 1984; Tartabini & Simpson 1986). Since much of the present study was concerned with changes in behaviour over time, most data were to be analysed on a weekly basis. I therefore decided to collect 2-2.5 hours of data per subject each week, split into 15 or 30-minute sessions, depending on the phase of the study. As far as possible, focal subjects, whether adults or infants, were observed once, or at most twice, per day. Sessions on the same day were separated by at least half an hour to maintain the independence of the samples. Weekly mean values for each behaviour were then calculated and used for subsequent analysis.

A further problem in scheduling observations is that patterns of social interaction may vary according to the predominant activity of the group (Harcourt 1978). For example, Simpson (cited in Harcourt 1978) found that patterns of interaction between rhesus monkey mothers and their infants varied in relation to the infants' activity periods. From pilot studies it was clear that the tamarins varied their activity patterns during the day. Periods of feeding and play were interspersed with rest periods when huddling and allogrooming were common. These apparent daily cycles were not, however, entirely predictable. It was therefore difficult to control for this problem in an entirely satisfactory manner, but in an attempt to deal with it each week's observations on a given individual were spread evenly over the day between 1000 and 1800. I hoped this would minimise the problem of diurnal variation in activity and any attendant variation in social interactions. Between 0900 and 1000 the animals were checked by technical staff, the previous day's feeding dishes were removed, and the first meal of the day given out. As food dishes were not present at this time, conditions were different from the rest of the day. Most observations did not therefore start before 1000. Except where feeding behaviour was of primary interest (for example, in studies of food-sharing behaviour), observations were also avoided within ten minutes of feeding times: it was impossible to sample every subject every week at feeding times, so they were avoided altogether. By 1800 the monkeys were beginning to settle down for the night, though the time at which this occurred varied from group to group, with some groups remaining active up to 1845. Groups with young infants often retired earlier than usual, so observations on infants were generally not made after 1730.

Reliability tests

Caro *et al.* (1979) and Martin & Bateson (1986) point out that in any study, checks of the reliability of the recording methods used are useful. In order to check this for my own data collection techniques, tests of inter-observer and intra-observer reliability were conducted.

(a) Inter-observer reliability. Two assessments of inter-observer reliability were made, one for adults and one for infants. Each used a different second observer (adults: AH; infants: KM). Both other observers had had experience of observing tamarins, but neither was engaged on research on cotton-tops at the time of the tests. No observer with similar experience to myself was available, and it was not possible to train one to an equivalent standard. However, four practice sessions were conducted with both other observers to enable them to familiarise themselves with the behavioural categories and recording techniques.

The behaviour of nine adult tamarins (four males and five females) was observed simultaneously by myself and AH under the same conditions as data were to be collected, i.e. 15-minute samples, taken at various times of day, using the standard checksheet. One male was observed twice (in sessions several weeks apart and with two different mates), giving a total of ten test sessions. Similarly, the infant care behaviour directed to four infant tamarins (a set of male-female twins and two singletons, one male and one female) was recorded on standard checksheets by myself and KM, each for 30-minute periods at different times of day. Since the behaviour of infants and their caretakers alters as they develop (for example, there are changes in the duration and frequency of carrying bouts), each litter was observed at a different age to ensure that reliability was maintained despite age-related variation in behaviour.

Caro *et al.* (1979) and Martin & Bateson (1986) recommend that the measures of reliability used should reflect the purpose for which the behaviour is recorded. Three measures of reliability were used here, depending on the method used for recording a particular behaviour and the information required. The formulae used follow Caro *et al.* (1979). For individual behaviour, i.e. instantaneous samples of activity, and records of the frequency of occurrence of brief events such as scent-marking, the formula A/(A+D) was used, where A is the lower of the scores obtained by the two observers for a given behavioural category, and D the difference between the two scores. As the ability of the recording methods to distinguish between different individuals, or the same individual at different times, was also important in this study, a Spearman correlation (r_s) between the scores of the two observers was calculated for behaviours for which sufficient data were available, using each test session as one data point.

For social interactions and spatial relationships with other group members, where the identity of the other individuals involved and the direction of the interaction were also important, agreements and disagreements on each occurrence were scored, and reliability calculated using the formula A/(A+D), where A is the number of agreements, and D the number of disagreements. An observation was only recorded as an agreement if the direction of the interaction and the identity of all the other tamarins involved were scored identically; otherwise it was classed as a disagreement.

The scores of each observer were calculated for each behaviour and for each test session separately, and coefficients of reliability were calculated. Mean coefficients of reliability were then obtained for each behavioural category. As some categories of behaviour (face-pressing, sexual behaviour, aggression and affection) did not occur during the tests, their reliability could not be assessed. A mean reliability score of greater than 0.7 was considered acceptable.

The results of the tests are presented in tables 2.5*a* and 2.5*b* (adults) and 2.6*a* and 2.6*b* (infants). Full details of the results for individual sessions are given in Appendix B. Reliability on measures of infant care was acceptable for all behaviours, although spatial relationships were less reliable than carrying. This is probably because young infants tend to be surrounded by several older monkeys as they explore their environment, making complete agreement on which individuals are in contact with the infant and which are near it difficult to obtain. As far as adults are concerned, reliability for activity sampling was acceptable in most sessions. Although reliability was lower for less frequently occurring activities, even for these categories very high correlations between the scores of the two observers were obtained. For some other behaviours, notably approaches and leaves, reliability appeared to decrease as the frequency of occurrence increased, and did not reach acceptable levels in several cases. Caro *et al.* (1979) have also noted that frequency of occurrence can affect reliability both if events are rare, and if they occur at very high rates. In this study, the fact that the second observer was not completely familiar with the checksheet meant that she was likely to miss uncommon behaviours of short duration, and also be unable to record accurately all occurrences of very frequent behaviours. For example, a negative correlation was obtained for both approaches and leaves between reliability and the frequency with which I scored the behaviour, though this was not statistically significant (for both approach and leave, Spearman rank order correlation coefficients $r_s = -0.55$, $n = 10$, d.f. $= 8$, $0.05 < p < 0.1$).

The lack of agreement for some behaviours was of sufficient concern for me to reassess the situation. As there was no way of training a second observer to a sufficiently high level of

TABLE 2.5a. Mean frequencies obtained by two observers (EP and AH) for nine behavioural categories over ten adult observation sessions, and the mean coefficients of reliability (r)[1] per session.

	Behavioural category								
	Sit	*Move*	*Feed*	*Forage*	*Groom*	*Other*	*Scratch*	*Scent mark*	*Genital rub*
Mean freq. (EP)	45.0	2.1	7.1	4.5	0.6	0.5	5.1	2.2	1.7
Mean freq. (AH)	44.0	2.1	7.0	4.6	0.4	0.4	4.1	1.8	0.8
Mean r	**0.93**	**0.74**	**0.91**	**0.79**	**0.33**	**0.67**	**0.73**	**0.74**	**0.43**
r_s[2]	0.97	0.79	0.99	0.95	-	-	0.92	-	-

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained by the two observers, and D = the difference between the two scores.
2. r_s = Spearman rank order correlation coefficient. All values give $p < 0.01$, n=10, d.f.=8.

TABLE 2.5b. Mean number of agreements (A) and disagreements (D) obtained by two observers for six behavioural categories over ten adult observation sessions, and the mean coefficients of reliability (r)[1] per session.

	Behavioural category					
	Overall activity	*Spatial relationship*	*Approach*	*Leave*	*Groom*	*Affection*
Mean no. A	53.5	53.3	11.5	11.0	0.8	0
Mean no. D	6.5	6.7	6.7	7.1	0.3	0.5
Mean r	**0.90**	**0.89**	**0.68**	**0.66**	**0.58**	**0**

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

TABLE 2.6a. Mean frequencies obtained by two observers (EP and KM) for five behavioural categories over four infant observation sessions, and the mean coefficients of reliability (r)[1] *per session.*

	Behavioural category				
	Number of carry bouts (focal inf)	*Number of carry bouts (other inf)*	*Number of bouts off (focal inf)*	*Number of bouts off (other inf)*	*Number of bouts suckle (focal inf)*
Mean freq. (EP)	3.5	1.5	1.75	1.0	0.75
Mean freq. (KM)	3.5	1.5	1.75	1.0	0.75
Mean r	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained by the two observers, and D = the difference between the two scores.

TABLE 2.6b. Mean number of agreements (A) and disagreements (D) obtained by two observers for five behavioural categories over four infant observation sessions, and the mean coefficients of reliability (r)[1] *per session.*

	Behavioural category				
	Carrier of focal infant	*Carrier of other infant*	*Suckle*	*Spatial relations (if infant off)*	*Food-sharing*
Mean no. A	119.0	118.5	13.3	51.0	2.0
Mean no. D	1.0	1.5	0	19.5	0.8
Mean r	**0.99**	**0.99**	**1.00**	**0.72**	**0.73**

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

proficiency, I decided to conduct intra-observer reliability tests.

(b) Intra-observer reliability. These tests were conducted both in an attempt to resolve the problems encountered in the inter-observer reliability checks, and to ensure that I was consistent over time in my recording of behaviour (the problem of "observer drift" described by Martin & Bateson (1986)). The behaviour of eight adult tamarins (four males and four females) was recorded on video tape, in 15-minute sessions, at various times of day. The video tapes were transcribed on to the standard checksheets the following day in the same way as for live observations, and then again eight months later. Coefficients of reliability between the two sets of scores were calculated as before.

The results are presented in tables 2.7*a* and 2.7*b*. Details of individual tests are given in appendix B. Intra-observer reliability was high for all categories. This confirmed that I was consistent in my recording of behaviour over time, and also that continuing to use the categories for which inter-observer reliability was less good was justified.

Analysis of data

Most data were analysed on a weekly or fortnightly basis. Mean scores per session per week or fortnight, as appropriate, were calculated for each category of interest and used in subsequent analysis. Such means were considered independent samples for statistical purposes.

Infants in the same litter cannot always be considered independent subjects (Abbey & Howard 1973). Spearman rank order correlation coefficients were therefore calculated for each behavioural category of interest. If the scores for twins proved to be significantly positively correlated on this basis, litter means were calculated and used for further analysis, except when differences between infants in the same litter were of interest (for example, in the investigation of sex differences).

TABLE 2.7a. Mean frequencies obtained by the same observer (EP) for nine behavioural categories in repeated viewings (sessions 1 and 2) of eight adult observation sessions, and the mean coefficients of reliability (r)[1] *per session.*

	Behavioural category								
	Sit	*Move*	*Feed*	*Forage*	*Groom*	*Other*	*Scratch*	*Scent mark*	*Genital rub*
Mean freq. session 1	41.9	4.3	6.8	5.8	0.9	0.6	7.4	1.6	1.9
Mean freq. session 2	41.6	4.6	7.1	5.1	0.9	0.6	7.4	1.5	2.0
Mean r	**0.98**	**0.90**	**0.94**	**0.92**	**1.00**	**1.00**	**0.93**	**0.94**	**0.86**
r_s[2]	0.96	0.96	0.99	0.98	-	-	0.99	-	-

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained in the two sessions, and D = the difference between the two scores.
2. r_s = Spearman rank order correlation coefficient. All values give $p < 0.001$, n = 8, d.f. = 6.

TABLE 2.7b. Mean number of agreements (A) and disagreements (D) obtained by the same observer (EP) for six behavioural categories in repeated viewings of eight adult observation sessions, and the mean coefficients of reliability (r)[1] *per session.*

	Behavioural category					
	Overall activity	*Spatial relationship*	*Approach*	*Leave*	*Groom*	*Affection*
Mean no. A	58.0	57.1	10.1	10.3	2.5	0.4
Mean no. D	2.0	2.9	1.8	1.8	0.3	0.5
Mean r	**0.97**	**0.95**	**0.88**	**0.88**	**0.93**	**0.75**

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

The use of statistical tests followed Siegel (1956) and Sokal & Rohlf (1981). The small sample sizes used in most sections of the study meant that where possible non-parametric statistical tests were generally used, unless there was no equivalent to the appropriate parametric test available. If parametric tests were required, the data were inspected to determine whether or not they met the assumptions required for the use of parametric statistics. To test for deviations from a normal distribution, the Kolmogorov-Smirnov goodness-of-fit test, which is especially appropriate for small sample sizes (Sokal & Rohlf 1981) was used.

Data were analysed on a DEC VAX 11-780 computer, using the statistical packages SPSS^X (SPSS Inc. 1986) and BMDP (Dixon *et al*. 1988).

Chapter 3

Infant care in captive groups of cotton-top tamarins

Introduction

Infant care has now been studied in a range of callitrichid species in captivity, and some information is also available from wild populations. Although captive studies are relatively numerous, with rare exceptions (e.g. Cleveland & Snowdon 1984; Feistner 1985; McGrew 1988) they have been conducted on small groups with no adult offspring, and are thus unlikely to accurately represent the situation in the wild. There was therefore a need for a detailed study of infant care in groups of tamarins similar in size and composition to those found in field studies.

Previous studies of marmosets and tamarins, and of other species with communal rearing, suggested several possible hypotheses that could be tested. These fall into two main groups: first, the benefits to be gained from dividing care among a number of individuals; and second, the factors influencing the amount of care provided by a given individual.

Benefits of additional helpers

Effects on amount of care received by infants

If infants can benefit from additional care (e.g. by being less exposed to predation; obtaining more food; etc.) such that their chances of survival are improved, then it would be of benefit to each family member to provide as much care as possible. However, Locke-Haydon & Chalmers (1983) have suggested that there may be a maximum amount of care that caretakers are prepared to give. Infants in larger groups should thus receive more care than those in smaller groups, and Garber *et al.* (1984) have presented data suggesting that there is indeed a positive correlation between infant survival and group size in wild moustached tamarins (*Saguinus mystax*). Thus I predicted that infants in large groups would receive more care than those in smaller groups.

Effects on parental contributions

Rylands (1985) has suggested that the dominant male and the breeding female in a callitrichid group benefit by sharing infant care with helpers. In support of this, Ingram (1977, 1978*a*) found that as group size increased in families of *Callithrix jacchus*, mothers tended to concentrate increasingly on their infants' essential food requirements, leaving carrying to others; and McGrew (1988) found that the contributions of both parents to infant care in *Saguinus oedipus* declined as group size increased. I therefore expected group size to have several effects on the contributions that parents made to infant care. First, both mothers and fathers were expected to do less as the number of available helpers increased. Second, as mothers were freed from carrying duties by helpers, I predicted that those mothers in larger groups would spend a greater percentage of their carrying time actually suckling infants. Finally, if mothers in larger groups were required to do less carrying, they might have more energy available for milk production. I therefore expected that infants in larger families would be suckled more.

Distributing the load

One of the major benefits of helpers is likely to be that each individual in a large group needs to perform less care than those in smaller groups, thus spreading the load and reducing the costs to a given individual (e.g. Feistner 1985). Thus I predicted that there would be a negative correlation between family size and the mean amount of care (carrying infants or sharing food with them) done by each member of the group. Twin infants in smaller groups would also be expected to spend less time on the same carrier than those in bigger groups.

Factors governing the amount of care invested by a given individual

Chalmers & Locke-Haydon (1985) have pointed out that it is important to investigate the mechanisms by which the duties of infant care are distributed among the breeders and the available helpers. Important factors are likely to be (a) the particular characteristics of the individual concerned; (b) the size and composition of the group; and (c) the size and composition of the litter.

Effects of individual characteristics

Factors that might be important in determining the extent to which a given individual invests in infants include its *age*, its *sex*, and its *position* in the group (i.e. whether it is a parent/breeder or a non-breeding helper).

Age, as well as prior experience with infants and social rank, has been found to have considerable effects on the amount of care invested by an individual, with older, more experienced, or higher-ranking individuals carrying infants more. Bucher & Anzenberger (1980) found that carrying time in *Callithrix jacchus* was positively correlated with both age and rank position. Epple (1975*b*) also speculated that social rank would influence carrying, although she presented no supporting data. Juveniles in several species have been reported to carry relatively little (e.g. Epple 1975*b*; Box 1975*b*, 1977; Ingram 1977, 1978*a*; Welker *et al.* 1981; Goldizen & Terborgh 1986; Tardif *et al.* 1986*b*). Presumably, as Ingram (1977, 1978*a*) suggests, this is firstly because they have no previous experience and need to acquire the necessary skills before becoming proficient; and secondly, they are smaller and less able to bear the load of an infant. They may also be in competition with their new-born siblings for the care that they themselves are accustomed to receiving. Therefore I predicted an effect of age on contributions to infant care, with older siblings doing more than younger ones.

Sex may have an effect on the contributions made by both parents and offspring. Lactation imposes a burden on the mother in addition to carrying infants, and this may mean that she can afford to invest less care in infants than her mate or older offspring in other ways (for example, sharing food with them, or carrying them when not suckling). Sex might also affect the contributions of older offspring. The role of males, both fathers and siblings, in infant care has been emphasised in several studies of tamarins (e.g. Vogt *et al.* 1978; Cleveland & Snowdon 1984; McGrew 1987). McGrew & McLuckie (1986) hypothesised that investment in infants by siblings could be seen as "payment" extracted by parents for "allowing" older offspring to remain on their territory. A similar hypothesis has been proposed for birds by Gaston (1978). As McGrew & McLuckie (1986) had presented data suggesting that older sons might be more likely than daughters to stay and inherit their natal territory instead of dispersing, they predicted that eldest sons should invest most in infants. McGrew (1987) reported that more carrying was done by sons than daughters in captive cotton-top tamarins, but did not analyse the data according to the age of the helpers. However, there are also reasons why daughters might be expected to invest in infants. Experience with infant siblings is of considerable importance to later successful reproduction in callitrichids (e.g. Epple 1975*b*, 1978*b*; Hoage 1978; Ingram 1978*b*; Tardif *et al.* 1984*a*), and appears to be particularly crucial for females. If, as McGrew & McLuckie (1986) suggest, daughters leave their natal families at a younger age than sons, they would be expected to try and gain as much experience as possible before emigrating; however, few previous studies have investigated sex differences in care by siblings in relation to age. I therefore predicted an interaction between age and sex in care by siblings, with older sons carrying more than daughters of similar age, but younger daughters carrying more than younger sons.

Finally, whether an individual is a *parent/breeder* or a non-breeding *helper* may affect its contributions. Mumme & de Queiroz (1985) have suggested that since non-breeding helpers do not realise a direct reproductive reward, they must profit less than breeders from any contribution to cooperative behaviour, and that helpers should therefore contribute less than breeders. In several studies of other species, breeders have indeed been reported to contribute more than helpers to behaviour such as care and feeding of offspring and resource defence (e.g. coyotes, *Canis latrans*: Bekoff & Wells 1982; acorn woodpeckers, *Melanerpes formicivorus*: Mumme & de Queiroz 1985; purple gallinules, *Porphyrula martinica*: Hunter 1987). However, in other species, at least some categories of helper may contribute as much or more than breeders (e.g. dwarf mongooses, *Helogale parvula*: Rood 1978; Florida scrub jays, *Aphelocoma c. coerulescens*: Stallcup & Woolfenden 1978; stripe-backed wrens, *Campylorhynchus nuchalis*: Rabenold 1985). No specific predictions were therefore made about the relative contributions to care of parents versus helpers in cotton-top tamarins.

Effects of group size

As well as the overall effect of group size on the mean contribution made to infant care by each group member, there may also be differential effects on investment by particular classes of individual. For example, although in early studies (e.g. Epple 1967, 1975*b*) fathers were often described as the primary carriers, this view has since been challenged by a number of authors (e.g. Box 1977; Wolters 1978; Hoage 1982; McGrew 1988; Wamboldt *et al.* 1988). However, paternal contributions are highly variable. One factor that might explain these rather confusing results is group size. McGrew (1988) has suggested that while fathers could in principle provide no care at all if there are sufficient numbers of other helpers available to take over, mothers must invest a certain minimum amount as only they can provide food for infants until they are weaned. Changes with group size in the amount invested were therefore predicted to be greater for fathers than for mothers, with the father's contribution decreasing not only absolutely as group size increased, but also relative to the mother's contribution.

Carrying by siblings might also be expected to be related to group size: for example, in families with adult offspring present, juveniles might carry only rarely. However, in a family in which only juveniles are present, they might do more.

Effects of size and composition of litter

Litter size might be expected to affect investment as singletons may be less energetically expensive to care for than twins. This might lead to greater tolerance on the part of caretakers, and therefore singletons might become independent later than individual twins (e.g. Buchanan-Smith 1984).

The sex of the infants might also affect the amount of care they receive, and whom they receive it from. Hoage (1978) found that parents in *Leontopithecus rosalia* preferentially carried infants of the same sex. Another possibility is that if polyandry is a possible mating system for males, males might invest more in male infants in order to develop strong bonds and thus make it more likely that they will be able to recruit them as potential "partners" or helpers for the future. There seems to be no reason why females should preferentially invest in one sex rather than the other.

This part of the study was therefore designed to investigate these predictions in cotton-top tamarins. Locke-Haydon (1984*a*, p.806) has defined care as "any activity which benefits the infant at some cost (of time and the opportunity to engage in other activities) to the caregivers". However, differences might exist in the pattern of investment according to the measure used: different types of care are likely to involve different degrees of cost and benefit to caretakers, depending on the nature of the activity concerned and on the individual involved. Play, for example, might be beneficial to juveniles as well as to infants. Three measures of investment were adopted for the purposes of this study: carrying, suckling (obviously confined to the mother), and food-sharing. These categories were chosen as they were almost exclusively confined to caretaker-infant relationships, in contrast to activities such as play or allogrooming which are a feature of most social relationships; collecting data on various different measures also provided the opportunity to compare different types of care.

Infants were observed from birth until the age of 12 weeks. This period was chosen as it covered most of the major changes in infant care: food-sharing reaches a peak at 12 weeks but then declines (Feistner 1985), while carrying and suckling are rare after this age (Cleveland & Snowdon 1984; Gerlach 1986).

The aim of this chapter is therefore to describe three main aspects of infant care in cotton-top tamarins: (1) the benefits of extra assistance, both in terms of the amount of care available to infants, and the reduction in the costs of care to individual caretakers; (2) the factors governing the amount of care invested in infants by a given individual; and (3) any differences in the pattern of care according to the measure of infant care used.

Methods

Subjects and housing

The subjects of this study were 21 cotton-top tamarin infants (seven sets of twins and seven singletons) born into eight captive families ranging in size from two to 12 individuals, excluding the infants themselves (see table 3.1). Nine of the infants were male, and 12 female. Two of the seven twin litters were originally triplets; in each case one infant died within the first five days. Five of the seven singleton infants were also born into multiple litters. However, as all these infants lost their litter-mates before the age of 10 days, they were classed as singletons. All focal infants survive to the present.

Litters 1-3, 7, 10 and 14 lived with their families in one or two type I colony cages; the remaining groups were housed in separate rooms. Further details of housing and husbandry are given in chapter 2.

Infants were caught up between the ages of four and seven days (and following the death of one infant in the case of triplet litters) to be sexed, weighed and marked using the method described in chapter 2. One infant in each set was marked with a yellow dye on the head; twin infants were remarked once during the observation period if necessary. Six of seven yellow-marked infants were redyed between the ages of four and 11 weeks, and three of the unmarked infants were also caught to verify their sexes, but no infant was caught up more than twice during the observation period. Generally, the first infant to be caught was dyed; although attempts were made to ensure that infants were marked randomly with respect to sex, in practice more male infants than females were dyed. However, there was no evidence that marking had any effect on behaviour (personal observation) or on physical development and survival (Halloren *et al.* 1989). Data collected before the infants were individually identifiable were not used in analyses of differences due to infant sex.

Behavioural categories and recording methods

The large size of several families meant that it was not feasible to conduct focal samples on individual caretakers. The infants themselves were therefore followed, and all care given to

TABLE 3.1. Details of the infants observed and their families.

	Litter no.	Family	Infant	Sex[1]	Dye mark[2]	Date of birth	Group size[3]	Older offspring present at birth[4] Juveniles	Sub-adults	Adults	Comments
Twins	1	Hopi	Cameron Ceilidhe	M F	Y P	5/2/87	5	2F	1M	-	-
	2	Delaware	Alan Alda	M F	Y P	18/3/87	2	-	-	-	-
	4	Sioux	James Jessie	M F	Y P	4/4/87	6	1M,1F	1M	1M	Triplet (F) died 9/4/87
	5	Roxanne	Vincent Vanne	M F	P Y	18/5/87	12	1M,1F	2M,1F	4M,1F	Triplet (F) died 20/5/87
	8	Genevieve	Electra Ela	F F	Y P	26/1/88	7	-	2M,2F	1F	-
	9	Elsa	Zeus Zoe	M F	Y P	6/2/88	8 (11)	1F	1M	3M,1F	3 other adult male offspring evicted in week 2; they did not carry the infants
	12	Elsa	Austin Allegro	M F	Y P	18/8/88	9	1M,1F	1M,1F	2M,1F	-
Singletons	3	Pixie	Hanna	F	-	23/3/87	4	-	1M,1F	-	Twin (M) died 24/3/87 (rejected)
	6	Elsa	Yolanda	F	Y	27/7/87	10	1M	2M	4M,1F	Twin (F) died 30/7/87 (after marking)
	7	Erica	Brendan	M	-	6/10/87	2	-	-	-	-
	10	Erica	Conal	M	P	20/5/88	3	1M	-	-	Twin (F) died 31/5/88 (pneumonia)
	11	Roxanne	Xenia	F	-	8/7/88	9	2M	2M,2F	1M	-
	13	Genevieve	Fiona	F	P	18/11/88	9	2F	1M,1F	1M,2F	Triplet (F) died during breech birth; triplet (F) died 24/11/88 (pneumonia)
	14	Hopi	Ewan	M	P	25/11/88	6	2F	1M,1F	-	Twin (M) died 2/12/88 (pneumonia)

1. M : male; F : female
2. Y : yellow mark; P : no mark; - : not removed for marking
3. Group sizes excluding infants
4. Juvenile : ≤ 12 months; Sub-adult : 13-24 months; Adult : > 24 months

them by other group members was recorded. This method also allowed the effects of infant variables to be investigated in detail. Focal infants were observed for 1.5-2.5 hours each per week (mean = 2.4 hours, n = 252 infant-weeks) divided into 30-minute observation sessions. Each week's sessions were spread evenly between 1000 and 1730. In order to obtain data on food-sharing comparable to that of Feistner (1985), one session per week for each infant was scheduled at the midday fruit feed.

All data were collected on checksheets divided into 15-second intervals. The identities of the *carriers* of both the focal infant and, in the case of twin litters, the other infant, were recorded using instantaneous sampling. A tamarin was given a score of 1 if carrying one infant at a 15-second point, and a score of 2 if it was carrying both infants. Thus there was a maximum possible total per 30 minutes of 240 for twin litters and 120 for singletons. If an infant was not being carried, it was scored as *off*. *Suckling* (focal infant only) was also scored using instantaneous sampling. Mothers nursing infants were given separate scores for both carrying and suckling. All occurrences of food-sharing involving the focal infant were recorded; the identity of the possessor of the food, the behaviour of the infant and the possessor, and the outcome of the episode were recorded. Food-sharing episodes from the infant's point of view were classified as *successful beg*, *unsuccessful beg*, or *offer*. For definitions of these terms, see chapter 2. The possessor's response to a successful infant beg was correspondingly termed *positive* (i.e. the infant received the food), and to an unsuccessful beg, *resist* (i.e. the infant did not receive the food). Data were also collected on infant transfers; for details, see chapter 4. Additional data collected on social relationships of infants will be presented elsewhere.

Analysis of data

As the number of samples per litter varied slightly from week to week, it was not possible to use simple total scores to compare the time that infants spent off, the time mothers spent suckling, or the contributions made by different family members to carrying. Weekly mean values per 30 minutes of time off, carrying or suckling were therefore calculated for each infant, litter or caretaker as appropriate, and used for analysis. The weekly mean carrying scores per 30-minute session for each caretaker were summed to give an index of his or her overall contribution to infant carrying (*carrying index*). Similar methods were used to obtain an overall index of the time that infants spent off carriers (*index of time off*), and an overall index of the time they were suckled (*suckling index*).

Total scores for food-sharing were taken from each week's lunchtime sample. The total frequencies of successful begs, unsuccessful begs and offers were found for each infant, and from these scores the following were calculated: total number of items received, percentage of items received that were offers, and begging success (number of successful begs/total number of successful and unsuccessful begs).

Three direct measures of food-sharing were obtained for each caretaker, using totals from each litter: number of positive responses to begging attempts by infants, number of times the caretaker resisted a begging attempt by an infant, and number of offers made to infants. From these, three other measures were calculated: total items shared (number of items shared in response to begging plus number of offers), offers as a percentage of total shared, and the proportion of positive responses to begging by infants (number of successful begs by infants/total number of successful and unsuccessful begs).

Five of the eight families contributed data from more than one litter: two (one twin litter and one singleton each) in the case of Roxanne's, Hopi's, Genevieve's and Erica's groups, and three (two sets of twins and one singleton) in the case of Elsa's group. As each litter was born into a group of unique composition, the infants were considered to be independent subjects (see also Cleveland & Snowdon 1984). However, the data obtained were not strictly independent for caretakers who were present for the rearing of more than one litter. For analyses where group composition, age of caretakers, etc. were not important, means per individual caretaker over all litters were therefore calculated and used. However, if other factors were important, it was necessary to treat the contributions made by the same individual to the different litters as separate scores, since the age class of helpers frequently changed from one litter to the next (e.g. a juvenile helper for one litter would be a sub-adult when the next litter was born); position in family may also have changed if other group members had been removed; and group size and composition would also have altered. Altogether, 62 different individuals acted as caretakers (eight sets of parents, 19 daughters and 27 sons). Eighteen of these 62 took care of two litters each, and six of them, three litters each. The effective sample size for some analyses was therefore 92. This approach has been used in previous studies (e.g. Cleveland & Snowdon 1984).

Infants were described in terms of their sex and status (singleton or twin). To assess whether co-twins could be considered as independent subjects in a given analysis, Spearman rank order correlation coefficients using each infant's total scores (n = 7 pairs of twins) were used to investigate whether co-twins' scores were significantly correlated. If they were, litter means were calculated and used in further analyses; if they were not, each infant was treated as an independent subject.

Caretakers were described in terms of their sex, age class (adult, sub-adult or juvenile; see chapter 2), and position in family (parent or offspring). For some analyses, age in months when the infants were born was used instead of age class. In the case of siblings, the original intention was also to investigate the effect on care of their "sibling rank". This was a number indicating the position of siblings in the family in relation to one another. Due to the difficulty of assessing rank on the basis of agonistic interactions (see chapter 1), sibling ranks were assigned on the basis of relative age: the eldest sibling was given the rank of 1, and so on; twins were given the mean of the two relevant ranks. This is similar to the concept of "seniority" used by Moore *et al.* (submitted for publication). The wide age range of offspring in the study meant that siblings with a rank of 1, for example, had actual ages varying from six months to six years. However, rank and actual age proved to be significantly negatively correlated (Spearman correlation coefficient, $r_s = -0.659$, $n = 64$, $p = 0.00$). I therefore decided that analysis of rank would add little to analyses based on age.

In order to investigate the effects of these various factors on contributions to infant care, parametric statistical techniques were desirable as these would allow the analysis of interactions as well as main effects of several variables at once. The data were inspected to establish whether they met the assumptions necessary for the application of parametric tests. If deviations were suspected, Kolmogorov-Smirnov goodness-of-fit tests were used to test for normality. If the data did not meet the requirements, or if parametric techniques were not needed, non-parametric techniques were used.

Where group size was predicted to be an important variable, data analyses using analysis of variance (ANOVA) were repeated controlling for group size by including it as a covariate in analyses of covariance (ANCOVA). This was done in order to investigate whether or not controlling for group size affected the conclusions drawn. If the covariate had a significant effect, and/or controlling for group size substantially altered the effects of other factors, then the results of both forms of analysis are reported for comparison. If not, only the results of the ANOVA are given. ANOVAs for behaviour of caretakers were of the form sex (two levels) x age class (four levels) x litter size (two levels).

Statistical analyses also were conducted to investigate whether any class of caretaker showed preferences for investing in infants of one sex rather than the other when a choice was available (i.e. in mixed-sex twin pairs). Two of the six heterosexual twin litters were from the same family (Elsa's), and seven caretakers (the parents, three sons and two daughters) were present in the group for both litters. Their total scores for the two litters were therefore averaged so that each individual contributed only one pair of data points to the analysis.

All statistically significant results are reported. However, for clarity, in most cases non-significant results are not given here. Complete results can be found in appendix C.

Results

Infant carrying

Development of infant independence: effects of group size, litter size and sex of infant

Infants were rarely seen off carriers before the age of five weeks; thereafter, time off increased rapidly, until at 12 weeks infants were off for 88% of their time on average (fig.

3.1). Infants were normally carried dorsally, except when being suckled (see plate 3.1).

The mean number of 15-second intervals per 30-minute observation session spent *off* by each infant each week was calculated and then summed to give an index of total time off. A two-way ANOVA was applied to the resulting indices to look for effects of sex and status on time off. There was no significant main effect of sex, and no interaction between sex and status (sex: $F_{(1,17)} = 2.54$, $p = 0.13$; sex x status: $F_{(1,17)} = 0.95$, $p = 0.34$). However, there was a significant main effect of status: singleton infants spent less time off than twin infants ($F_{(1,17)} = 4.81$, $p = 0.04$). Controlling for group size using an ANCOVA did not significantly affect these results (sex: $F_{(1,16)} = 0.67$, $p = 0.425$; status: $F_{(1,16)} = 8.82$, $p = 0.009$; sex x status: $F_{(1,16)} = 0.02$, $p = 0.880$), although the effect of group size was significant ($F_{(1,16)} = 6.39$, $p = 0.022$).

To test whether there was a correlation between group size and the index of time spent off, a partial correlation, controlling for status, was applied to the data. There was a significant negative correlation between group size and time off (fig. 3.2), demonstrating that infants in larger families were carried more than those in smaller families ($r = -0.60$, d.f. = 18, $p = 0.005$).

However, one possible source of error was treating twins as independent subjects. A Spearman rank order correlation coefficient demonstrated that the total time co-twins spent off was significantly correlated ($r_s = 0.96$, $n = 7$, $p < 0.05$). Because of this, and as there were no sex differences, mean indices were calculated for twin litters and the analyses were repeated. An ANOVA of the effect of status on time off again showed a strong trend for twins to spend more time off than singletons, but with the reduced sample size this just failed to reach statistical significance ($F_{(1,12)} = 4.19$, $p = 0.06$). However, if group size was controlled for using an ANCOVA, the difference between twins and singletons was significant ($F_{(1,11)} = 7.19$, $p = 0.02$), although the effect of group size itself was not significant ($F_{(1,11)} = 2.85$, $p = 0.119$). A partial correlation between group size and time off, controlling for status, again just failed to reach statistical significance ($r = -0.45$, d.f. = 11, $p = 0.06$).

PLATE 3.1

An adult male cotton-top tamarin (left) and a sub-adult female carrying their infant male siblings.

FIGURE 3.1. Mean number of 15-second intervals per 30 minute observation session spent off carriers by seven litters of twins and seven singletons. Vertical bars indicate standard errors.

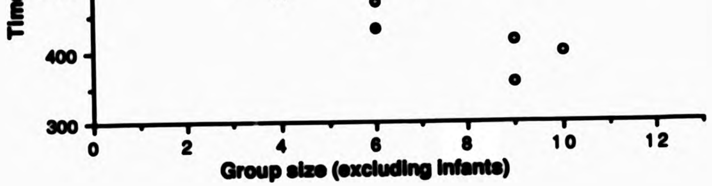


FIGURE 3.2. Relationship between group size and index of time off for seven twin litters and seven singletons. For calculation of index of time off, see text.

Graphical inspection of the data (see fig. 3.1) suggested that singletons were showing a delayed pattern of independence relative to twins: the difference began at the age of five weeks, but had disappeared by the time the infants reached ten weeks. Consistent with this pattern, Mann-Whitney U-tests for time off each week showed no significant differences between twin and singleton litters in weeks 1-4, 6, and 10-12, but significant differences in weeks 5 and 7-9 (table 3.2). However, a Mann-Whitney U-test found no significant difference in the age in days at which twins and singletons were first seen off (twins: median = 26 days, range 16-31 days; singletons: median = 24 days, range 21-37 days; $U = 23.5$, $n_1 = 7$, $n_2 = 7$, $p > 0.05$). Physical development, in terms of ability to move independently, did not therefore appear to be different for twins and singletons.

The mean number of 15-second intervals per session that infants in twin litters were on the same carrier was calculated. There was a significant negative correlation between group size and the mean number of intervals per session that twins were carried together (Spearman rank order correlation coefficient, $r_s = -0.82$, $n = 7$, $p < 0.05$; see fig. 3.3), i.e. in larger families, carriers were less likely to be carrying both infants at once. Although the mean number of intervals per session that twins were carried together decreased as they got older, this appeared to be largely a function of spending increasing periods off, as the percentage of time carried that they were carried together remained relatively constant (fig. 3.4).

Contributions to carrying by different family members

Every parent and older sibling was observed to carry infants at some time, but they did so to differing degrees.

To test whether any caretakers preferentially carried infants of a given sex, an ANOVA was conducted on the data from the six heterosexual twin litters, using four categories of caretaker (position in family subdivided according to sex: mothers (n = 5), fathers (n = 5), daughters (n = 9) or sons (n = 16)) as a group factor, and sex of infant as a within-subjects factor. The total number of 15-second intervals that each caretaker carried each infant over the 12-week observation period was used in the analysis. There was no significant main effect of

TABLE 3.2. Differences in time spent off by cotton-top tamarin infants in twin litters ($n = 7$) and singleton litters ($n = 7$) over the first 12 weeks of life. Mann-Whitney U-tests were used to compare the mean number of 15-second intervals per 30 minutes spent off carriers each week.

Age (weeks)	*U*	*p (2-tailed; corrected for ties)*
1	24.5	1.000
2	24.5	1.000
3	21.0	0.534
4	19.5	0.517
5	6.5	0.021*
6	12.0	0.110
7	9.0	0.048*
8	8.0	0.035*
9	7.5	0.030*
10	22.5	0.798
11	22.0	0.749
12	22.0	0.749

* $p < 0.05$

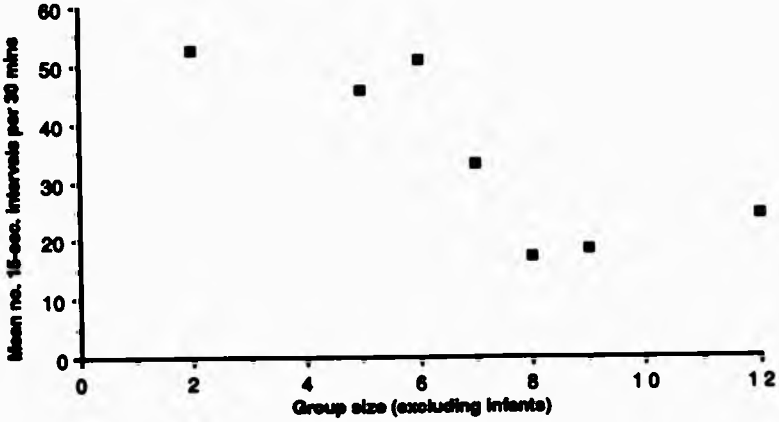


FIGURE 3.3. Relationship between group size and the mean number of 15-second intervals per 30 minutes spent on the same carrier by seven twin litters of cotton-top tamarins.

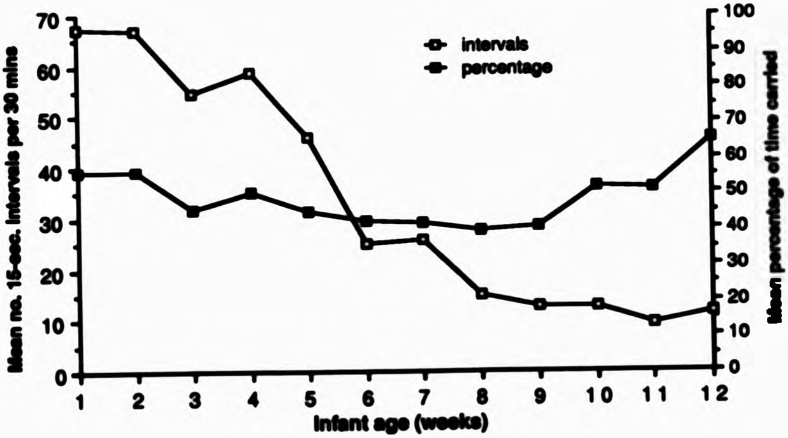


FIGURE 3.4. Mean number of intervals per 30 minutes, and mean percentage of time carried, that infants in twin litters were on the same carrier.

infant sex ($F_{(1,31)} = 0.38$, $p = 0.54$), and no interaction between category of caretaker and infant sex ($F_{(3,31)} = 0.34$, $p = 0.80$). However, there was a significant effect of category of caretaker on the total amount of carrying done by each individual ($F_{(3,31)} = 5.58$, $p = 0.0035$); this is discussed in more detail below. Subsequent Wilcoxon tests also showed no effect of infant sex on carrying for any particular category of carrier (mothers: $z = -0.944$, $p = 0.35$; fathers: $z = -0.405$, $p = 0.69$; daughters: $z = -0.178$, $p = 0.86$; sons: $z = -0.776$, $p = 0.44$). Thus there was no evidence that any category of caretaker invested preferentially in one sex rather than the other (fig. 3.5). Data for infants in twin litters were therefore combined for subsequent analysis.

Changes in the contribution of mothers, fathers and older siblings to infant carrying as infants got older are shown in figure 3.6. There was a mean of 4.6 (± 3.1 SD) older offspring per family, and these older siblings divided most of the carrying amongst themselves. For twin litters, more carrying was done by older sibs than by parents throughout the 12-week observation period, peaking at 4 weeks. Differences between mothers and fathers were most obvious in the first three weeks. Mothers' contributions decreased steadily over time, while fathers' reached a peak in week 3, temporarily overtaking mothers, and then declined. For singletons, the picture was basically similar, except that mothers did most of the carrying in week 1 despite the presence of older offspring, and both fathers and older offspring peaked one week later than for twins, in weeks 4 and 5 respectively. This pattern is consistent with the greater time that singletons spent carried overall.

Comparisons between the time infants spent on mothers, fathers and older siblings each weeks were made in two ways. First, the *total* time spent on sibs was compared with time on parents. The frequent zero scores in later weeks resulted in non-normal distributions, and non-parametric tests were therefore used. Relative amounts of time infants spent on mothers, fathers and siblings each weeks were compared separately for twins and singletons using Kruskal-Wallis one-way ANOVAs. If a significant overall difference was found in any week, post-hoc pair-wise Mann-Whitney U-tests were used to identify the source of the significant effect. The results are given in table 3.3. Significant overall differences for singletons were

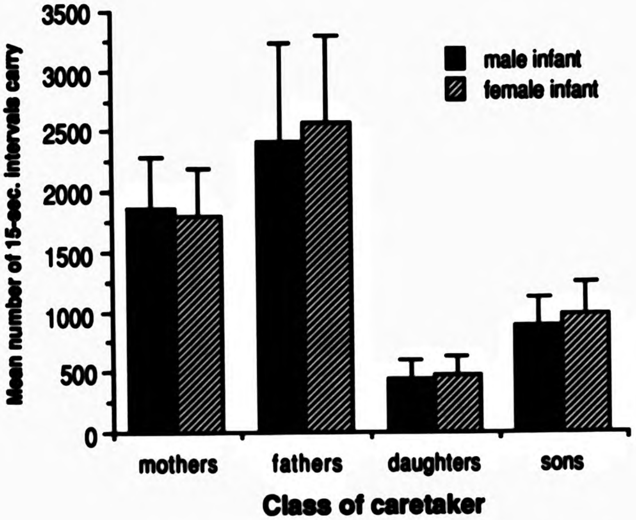
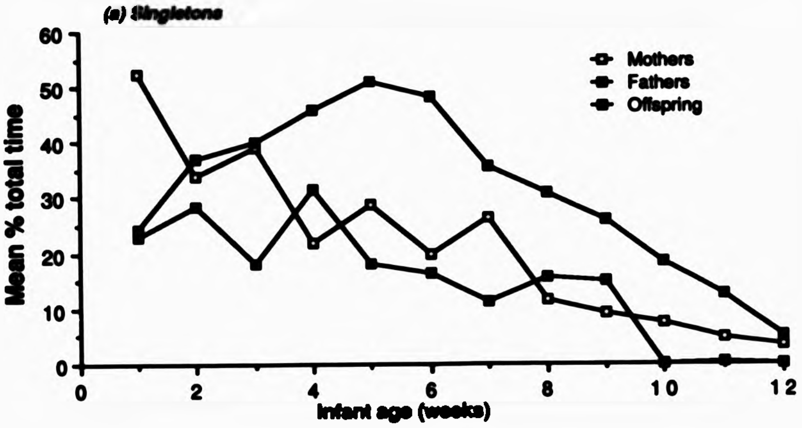


FIGURE 3.5. Carrying of male and female infants in mixed-sex twin litters of cotton-top tamarins by different classes of carrier. Vertical bars indicate standard errors.



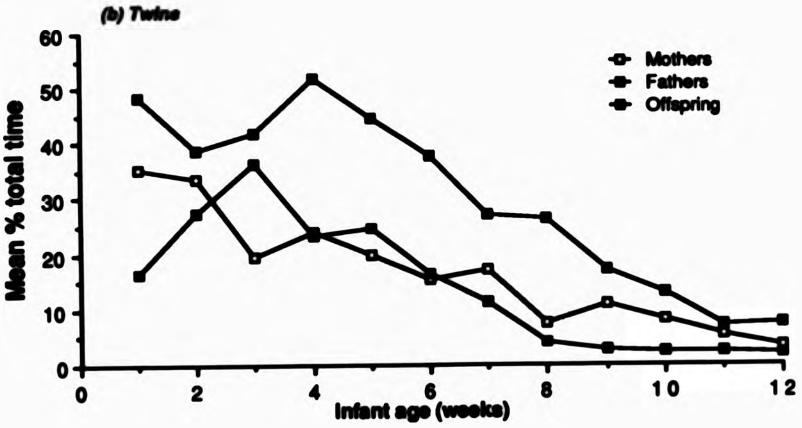


FIGURE 3.6. The mean percentage of observation time per week that (a) seven singletons and (b) seven twin litters of cotton-top tamarin infants were carried by mothers, fathers and older offspring.

TABLE 3.3. Differences between time spent on mothers, fathers and older siblings by seven singletons and seven twin litters of cotton-top tamarins over the first 12 weeks of life. Overall differences were tested by Kruskal-Wallis one-way ANOVAs; when a significant effect was found, pair-wise comparisons between groups were made with Mann-Whitney U-tests. M = mothers (n = 7 for both singletons and twins), F = fathers (n = 7), S = siblings (n = 6; total time on sibs). Values given are two-tailed and corrected for ties.

Age (weeks)	*Kruskal-Wallis one-way ANOVA*		*Mann-Whitney U-tests (if appropriate)*					
			M vs. F		*M vs. S*		*F vs. S*	
	χ^2	*p*	*U*	*p*	*U*	*p*	*U*	*p*
Singletons								
1	3.49	n.s	..	..	..	..	..	..
2	0.23	n.s	..	..	..	..	..	..
3	4.13	n.s	..	..	..	..	..	..
4	3.80	n.s	..	..	..	..	..	..
5	4.82	n.s	..	..	..	..	..	..
6	5.98	n.s	..	..	..	..	..	..
7	4.81	n.s	..	..	..	..	..	..
8	3.97	n.s	..	..	..	..	..	..
9	2.60	n.s	..	..	..	..	..	..
10	7.95	<0.02	7.0	<0.02 (M)	15.5	n.s	4.5	<0.02 (S)
11	6.52	<0.05	23.0	n.s	8.0	<0.05 (S)	5.5	<0.02 (S)
12	4.22	n.s	..	..	..	..	..	..
Twins								
1	2.39	n.s	..	..	..	..	..	..
2	4.04	n.s	..	..	..	..	..	..
3	4.47	n.s	..	..	..	..	..	..
4	7.96	<0.02	13.0	n.s	0.0	<0.001 (S)	6.0	<0.02 (S)
5	7.96	<0.02	31.0	n.s	1.0	<0.001 (S)	5.0	<0.02 (S)
6	6.00	<0.05	34.5	n.s	3.0	<0.004 (S)	6.0	<0.02 (S)
7	6.02	<0.05	19.0	n.s	7.0	n.s	3.0	<0.004 (S)
8	10.90	<0.01	17.0	n.s	0.0	<0.001 (S)	0.0	<0.001 (S)
9	9.62	<0.01	6.0	<0.02 (M)	10.0	n.s	1.0	<0.001 (S)
10	7.39	<0.05	10.0	n.s	12.0	n.s	4.0	<0.01 (S)
11	3.58	n.s	..	..	..	..	..	..
12	5.11	n.s	..	..	..	..	..	..

n.s = p > 0.05

Letters in brackets indicate the category of carrier that infants were on most for a given pair-wise comparison.

found only in weeks 10 and 11. In week 10, infants were on both sibs and mothers significantly more than they were on fathers, but there was no significant difference in time spent on mothers compared to sibs. In week 11, infants were on siblings significantly more than either mothers or fathers, but there was no significant difference in time spent on each parent. In the case of twin litters, significant overall effects were found in weeks 4-10. In all these weeks, infants were on older sibs significantly more than on their fathers. There were no significant differences between time spent on mothers and fathers except in week 9, when infants were on mothers more than fathers. In weeks 4-6 and 8, infants were on sibs significantly more than mothers, but in weeks 7, 9 and 10 there was no significant difference between time on mothers and sibs.

Secondly, the *mean* time infants spent on each *individual* sib was calculated for each litter, and compared to time on parents using similar methods. The results are shown in table 3.4. For singletons, there were significant overall differences in weeks 1-4, 7 and 10. Only in week 10 was there a significant difference between time on mothers and fathers, with mothers doing more. In weeks 1-4 and 7, infants were on their mother significantly more than on individual siblings, while in weeks 1, 2 and 4 they were on fathers more than sibs. There were no other significant differences in time on sibs and parents. For twins, there were significant overall effects in all weeks except weeks 6, 8 and 11. There were only two significant differences between mothers and fathers, in weeks 9 and 12. Infants spent more time on mothers in both cases. In all pair-wise comparisons between mothers and siblings, infants were on mothers significantly more. Infants were on fathers significantly more than sibs in weeks 1-3 and 5, but there were no differences in other weeks.

Thus, although infants often spent more time on siblings than on their mothers or fathers, they tended to spend less time on each *individual* sib than on either parent. It was noteworthy that the mean contribution by fathers was greater than the mean for individual offspring.

To investigate in detail the relative contributions made by different categories of caretaker to infant carrying, an ANOVA was conducted with carrying index as the dependent variable

TABLE 3.4. Differences between carrying by mothers, fathers and older siblings of seven singletons and seven twin litters of cotton-top tamarins over the first 12 weeks of life. Overall differences were tested by Kruskal-Wallis one-way ANOVAs; when a significant effect was found, pair-wise comparisons between groups were made with Mann-Whitney U-tests. M = mothers (n = 7 for both singletons and twins), F = fathers (n = 7 for both singletons and twins), S = siblings (n = 29 for singletons and n = 35 for twins). Values given are two-tailed and corrected for ties.

Age (weeks)	*Kruskal-Wallis one-way ANOVA*		*Mann-Whitney U-tests (if appropriate)*					
			M vs. F		*M vs. S*		*F vs. S*	
	χ^2	*p*	*U*	*p*	*U*	*p*	*U*	*p*
Singletons								
1	18.31	<0.001	11.0	n.s	10.5	<0.001 (M)	51.0	<0.02 (F)
2	10.52	<0.01	23.0	n.s	34.0	<0.01 (M)	49.5	<0.03 (F)
3	11.02	<0.01	11.0	n.s	23.0	<0.01 (M)	72.0	n.s
4	8.84	<0.02	22.0	n.s	43.0	<0.02 (M)	46.0	<0.03 (F)
5	4.48	n.s	..	..	..	..	..	..
6	3.55	n.s	..	..	..	..	..	..
7	8.39	<0.02	11.5	n.s	27.0	<0.03 (M)	98.0	n.s
8	1.19	n.s	..	..	..	..	..	..
9	1.98	n.s	..	..	..	..	..	..
10	6.50	<0.04	7.0	<0.02 (M)	64.5	n.s	58.5	n.s
11	0.32	n.s	..	..	..	..	..	..
12	2.06	n.s	..	..	..	..	..	..
Twins								
1	14.52	<0.001	19.0	n.s	23.0	<0.001 (M)	55.0	<0.03 (F)
2	16.95	<0.001	14.0	n.s	22.0	<0.001 (M)	42.0	<0.006 (F)
3	12.84	<0.002	15.0	n.s	50.0	<0.02 (M)	36.0	<0.004 (F)
4	9.38	<0.01	13.0	n.s	43.0	<0.01 (M)	70.5	n.s
5	11.30	<0.004	18.0	n.s	46.5	<0.02 (M)	47.0	<0.02 (F)
6	4.81	n.s	..	..	..	..	..	..
7	11.36	<0.004	19.0	n.s	32.0	<0.003 (M)	65.5	n.s
8	2.46	n.s	..	..	..	..	..	..
9	9.24	<0.01	6.0	<0.02 (M)	35.0	<0.004 (M)	118.0	n.s
10	8.37	<0.02	10.0	n.s	37.0	<0.004 (M)	118.0	n.s
11	4.80	n.s	..	..	..	..	..	..
12	13.57	<0.002	7.0	<0.03 (M)	26.0	<0.0001 (M)	87.0	n.s

n.s = $p > 0.05$

Letters in brackets indicate that individuals in that category carried infants more than those in the other category for a given pair-wise comparison.

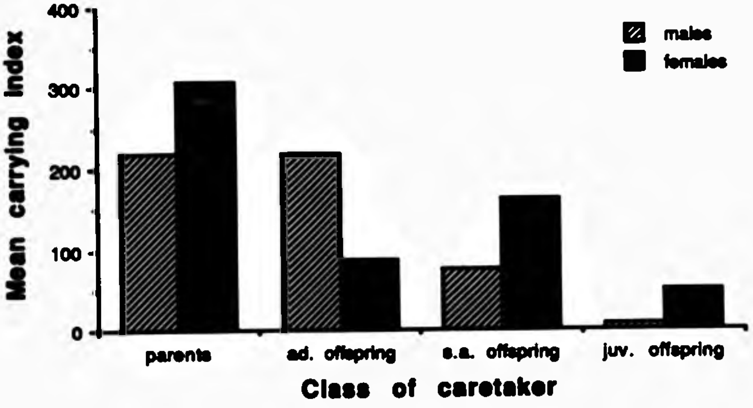
and using sex of caretaker, age class of caretaker (parent, adult offspring, sub-adult offspring or juvenile offspring) and litter size as group factors. There was no significant main effect of sex, but there were significant effects of age class ($F_{(3,76)} = 13.96$, $p = 0.000$) and of litter size ($F_{(1,76)} = 4.00$, $p = 0.049$). An ANCOVA showed that group size as a covariate had a significant effect ($F_{(1,75)} = 23.60$, $p = 0.000$), but the effects of age class and litter size were unchanged (age class: $F_{(3,75)} = 13.87$, $p = 0.000$; litter size: $F_{(1,75)} = 8.42$, $p = 0.005$). In addition, when group size was controlled for, the interaction between sex and age class only just failed to reach statistical significance ($F_{(3,75)} = 2.63$, $p = 0.057$). As figure 3.7 shows, parents carried more than individual offspring, and older offspring carried more than younger offspring. Mothers carried slightly more than fathers, and female sub-adults and juveniles carried more than males. However, adult sons carried more than adult daughters. This explains the lack of an overall sex difference but the the strong trend towards an interaction between age and sex, and supports the prediction outlined in the introduction. The absence of significant interactions between litter size and the other factors showed that the number of infants in the litter had no effect on the relative (as opposed to absolute) contributions made by each age-sex class.

Sons appeared to carry slightly more than daughters overall. However, the average age of the sons (27.7 ± 19.1 months) was greater than that of the daughters (20.9 ± 13.3 months), i.e. the average son was an adult, while the average daughter was only a sub-adult. A partial correlation controlling for litter size demonstrated that there was a significant correlation between sibling age and carrying index ($r = 0.693$, d.f. $= 55$, $p = 0.00$), i.e. older offspring carried more than younger offspring.

Effects of group size on individual contributions to infant carrying

A partial correlation controlling for litter size, using the mean carrying index per individual in each litter, showed that there was a significant negative correlation between group size and carrying index ($r = -0.907$, d.f. $= 11$, $p = 0.00$), i.e. each individual in a larger family carried less than individuals in smaller families.

(a) Singletons



(b) Twins

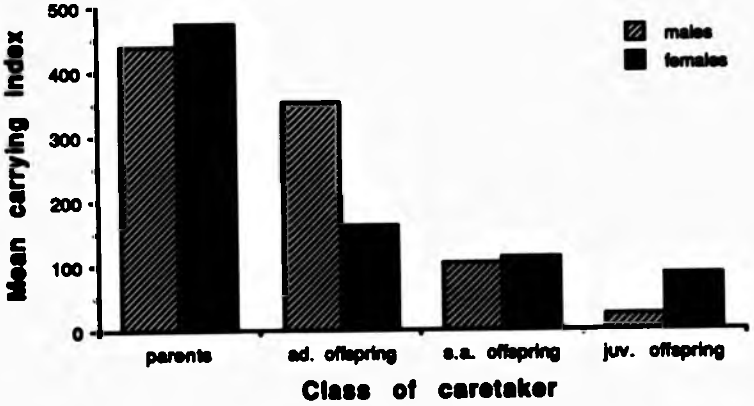


FIGURE 3.7. Mean carrying index for males and female caretakers in four age classes for (a) seven singletons and (b) seven twin litters of cotton-top tamarin infants. The carrying index was obtained by summing the 12 weekly mean scores per 30-minute sample for each individual caretaker. For further details, see text. Ad. = adult (> 24 months), s.a. = sub-adult (13-24 months), juv. = juvenile (4-12 months).

To look at the effect of group size on the separate contributions made by parents, partial correlations of group size and carrying index were conducted, controlling for litter size. The results showed no significant correlation between the mother's carrying index and group size (r = -0.23, d.f. = 11, p = 0.46), but a significant negative correlation for fathers (r = -0.76, d.f. = 11, p = 0.003). The mean index per sibling in each group was also calculated, but there was no significant correlation between the mean carrying index per sib for each litter and group size (r = -0.256, d.f. = 9, p = 0.225). Therefore, fathers' contributions to carrying appeared to be most affected by increases in group size.

However, if each sibling age class was considered separately, significant negative correlations between carrying index and group size were obtained (juveniles: r = -0.556, d.f. = 10, p = 0.030; sub-adults: r = -0.677, d.f. = 20, p = 0.000; adults: r = -0.415, d.f. = 19, p = 0.031).

In addition, in order to compare *relative* contributions to care, the following ratios were found for each litter: (a) mother's index/father's index; (b) mother's index/mean index per sib; (c) father's index/mean index per sib. There was no significant correlation between the mother/father ratio and group size (r = 0.357, d.f. = 11, p = 0.115) but the ratio between the father's contribution and the sib mean was significantly negatively correlated with group size (r = -0.523, d.f. = 9, p = 0.049), and that between the mother's contribution and the sib mean approached statistical significance (r = -0.473, d.f. = 9, p = 0.071). This confirms that fathers do both absolutely and relatively less as the number of siblings available to help increases, and suggests that while mothers may not decrease their contribution in absolute terms, they do *relatively* less as group size increases. Therefore, most of the additional care infants in large families receive comes from older siblings.

Suckling

The mean number of 15-second intervals per 30-minute observation session that infants were suckled by their mothers each week was calculated. Infants were suckled most in the first week (see fig. 3.8); suckling time then declined steadily over the 12-week observation period.

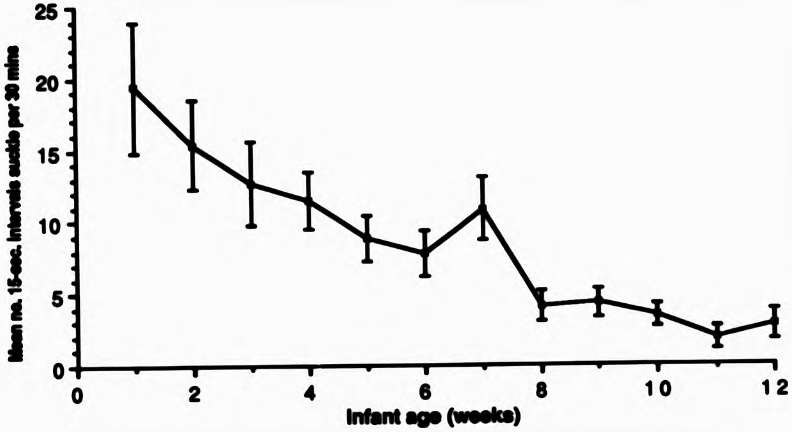


FIGURE 3.8. Mean number of 15-second intervals per 30 minutes spent suckling by infants in fourteen litters of cotton-top tamarins. Values were calculated using litter means for twins. Vertical bars indicate standard errors.

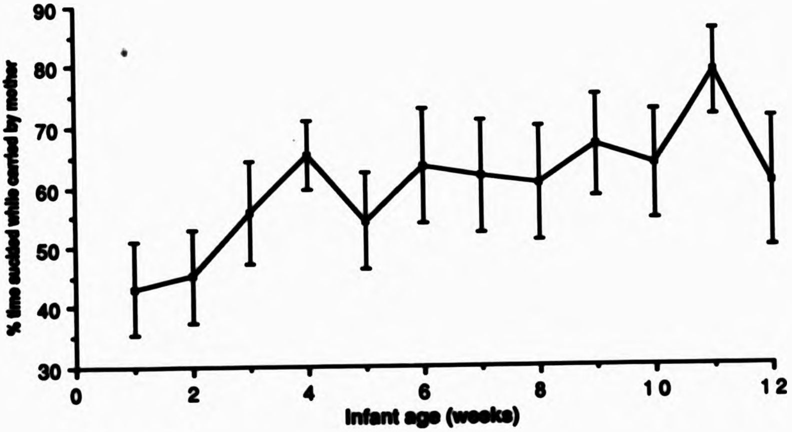


FIGURE 3.9. The mean percentage of time that infants were suckled while being carried by their mothers. Vertical bars indicate standard errors.

The weekly mean values for each infant were summed to give an overall index of the time each infant was suckled (*suckling index*). An ANOVA of suckling indices using sex of infant and status (singleton or twin) as group factors showed that there were no differences between male and female infants in the mean amount of suckling they received (males = 99.3 ± 46.6 SD; females = 97.0 ± 47.6 SD), and also no difference between single infants and twins (singletons = 113.7 ± 48.6 SD; twins = 90.2 ± 44.3 SD) (main effect of sex: $F_{(1,17)} = 0.46$, $p = 0.51$; main effect of status: $F_{(1,17)} = 1.88$, $p = 0.19$; sex x status interaction: $F_{(1,17)} = 2.93$, $p = 0.11$). Thus there was no evidence that mothers invested more in infants of one sex rather than another, or that singletons were suckled any more than twins. Twins' suckling indices were positively correlated (Spearman rank order correlation coefficient, $r_s = 0.79$, $n = 7$ litters, $p < 0.05$), and therefore litter means were calculated and used in subsequent analyses. There was no significant correlation between the mean suckling index per litter and group size (Spearman rank order correlation coefficient, $r_s = 0.04$, $n = 14$ litters, $p > 0.05$), and thus there was no evidence that infants in larger families were suckled more than those in smaller families.

The proportion of their carrying time that mothers spent suckling infants increased as infants got older (fig. 3.9). To test the prediction that mothers in larger families should spend a greater proportion of their carrying time feeding the infants, the percentage of mothers' total carrying time that infants were suckled was calculated. Values obtained for co-twins were not significantly correlated (Spearman rank order correlation coefficient, $r_s = 0.46$, $n = 7$ litters, $p > 0.05$), and each of the 21 infants was therefore treated as an independent subject. A Spearman rank order correlation coefficient showed that there was no effect of group size on the proportion of their carrying time that mothers spent suckling their infants ($r_s = 0.26$, $n = 21$, $p > 0.05$).

Food-sharing[1]

Effects of group size, litter size, and age and sex of infant on food-sharing

No food-sharing involving begging or offering was seen until infants reached the age of five weeks and were starting to become independent. Even in week 5, only one infant received one item of food. Thereafter, the frequency of food-sharing increased rapidly (fig. 3.10).

The total number of food items received by each infant over the 12 weekly lunchtime sessions was calculated. An ANOVA with two group factors, status and sex, was used to analyse differences in total food received by infants of different sexes, and by twins and singletons. A Spearman rank order correlation coefficient showed that the total number of food items received by co-twins was not significantly correlated ($r_s = 0.64$, $n = 7$ litters, $p > 0.05$). Each of the 21 infants was therefore treated as an independent subject. The results showed that there were no significant main effects of either sex or status, and no significant interaction between the two (sex: $F_{(1,17)} = 0.18$, $p = 0.679$; status: $F_{(1,17)} = 0.53$, $p = 0.476$; sex x status interaction: $F_{(1,17)} = 1.14$, $p = 0.300$). An ANCOVA showed that group size had a significant effect ($F_{(1,16)} = 7.75$, $p = 0.013$), but controlling for group size did not substantially alter the effects of the other factors (sex: $F_{(1,16)} = 0.39$, $p = 0.453$; status: $F_{(1,16)} = 0.03$, $p = 0.858$; sex x status interaction: $F_{(1,16)} = 0.17$, $p = 0.685$).

Data from mixed-sex twin litters were used to investigate any preference by particular individuals (mothers, fathers, daughters or sons) for sharing food with one sex rather than another. There were no differences in the amount of food shared with infants of each sex for any given category of caretaker, although there was a significant effect of category of caretaker on the total amount shared: this will be discussed further below (category: $F_{(3,31)} = 4.03$, $p = 0.016$; infant sex: $F_{(1,31)} = 0.30$, $p = 0.590$; category x infant sex interaction: $F_{(3,31)} = 0.07$, $p = 0.977$; see figure 3.11).

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1) Some of the data on food-sharing have also been presented in Feistner & Price (1990).

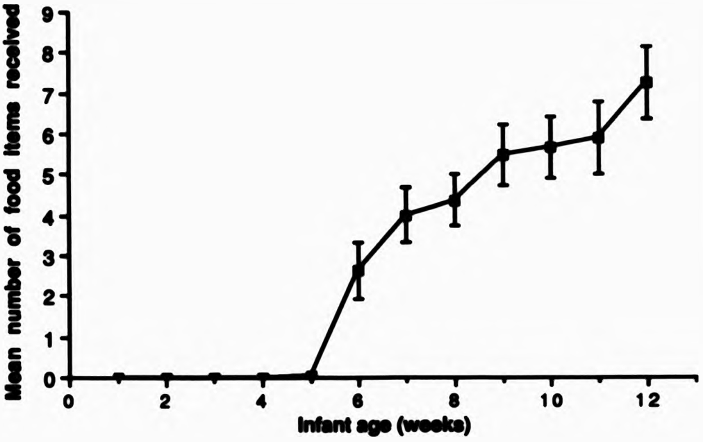


FIGURE 3.10. Changes in the amount of food received by cotton-top tamarin infants with increasing age.

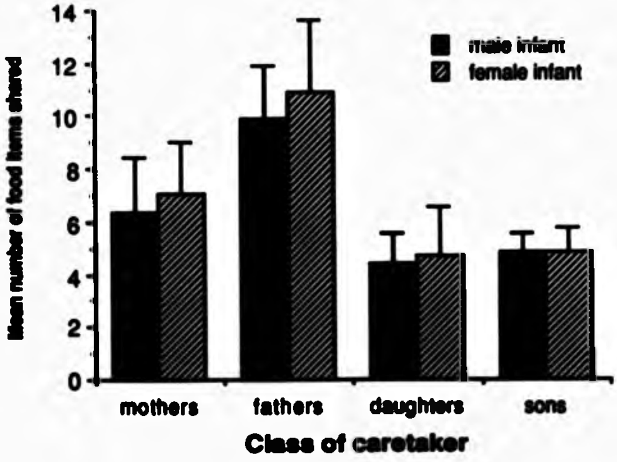


FIGURE 3.11. Food-sharing in six mixed-sex litters of cotton-top tamarins by different classes of caretaker. Vertical bars indicate standard errors.

There was a significant positive correlation between group size and the total amount of food received by an infant (Spearman rank order correlation coefficient, $r_s = 0.56$, $n = 21$, $p < 0.05$), i.e. infants in larger families received more food (fig. 3.12).

Begging success remained fairly constant over the observation period (fig. 3.13), with a little more than half the begs made being successful throughout (overall mean success for the 21 infants was 0.56 ± 0.11 SD). This suggests that the increase in the number of items received by infants as they grew older was due to their begging more frequently as they became more proficient at locomotion and were thus able to reach possessors of food more easily, rather than an increased willingness on the part of others to share food. The begging success of co-twins was not significantly correlated (Spearman rank order correlation, $r_s = 0.43$, $n = 7$, $p > 0.05$), and there was no difference between twins and singletons in their begging success (twins: mean = 0.56 ± 0.10 SD, n = 14; singletons: mean = 0.56 ± 0.14 SD, n = 7). There was no correlation between begging success and group size ($r_s = 0.27$, $n = 21$ infants, $p > 0.05$), i.e. infants in larger families were no more likely to be successful in their attempts to beg than those in smaller families.

A mean of 14.6% (± 7.3 SD) of total items received were from offers (twins, n = 14: 15.6 ± 8.4 SD; singletons, n = 7: 12.6 ± 4.1 SD). The percentage of offers for co-twins was not significantly correlated ($r_s = 0.36$, $n = 7$, $p > 0.05$). There was no significant correlation between the percentage of offers and group size ($r_s = 0.02$, $n = 21$ infants, $p > 0.05$), i.e. there was no evidence that infants received more or less food from offers in smaller families compared to those in larger families.

Contributions to food-sharing by different family members

To test for correlations among the various measures of food-sharing, Spearman rank-order correlations were conducted (using means per litter for the 24 individuals who were present for more than one set of infants). The results are presented in table 3.5. The only negative correlation was, not surprisingly, between the proportion of positive responses to

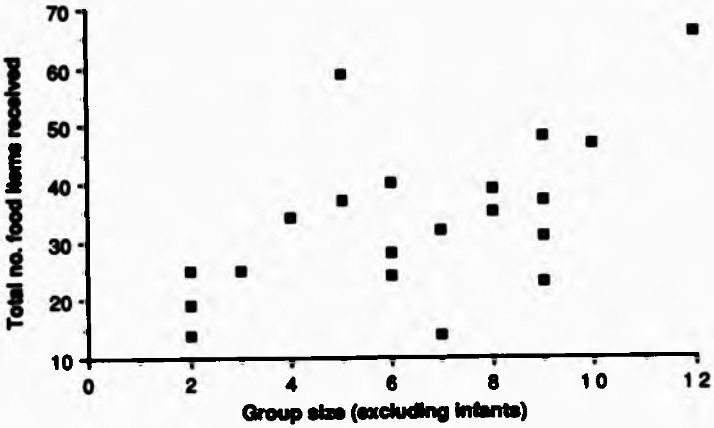


FIGURE 3.12. Relationships between group size and the total number of food items received by 21 cotton-top tamarins in 12 weekly observation sessions.

FIGURE 3.13. Begging success in infant cotton-top tamarins over the first 12 weeks of life. Begging success = (no. of successful begs)/(no. of successful begs + no. of unsuccessful begs). N = number of infants seen food-sharing in a given week. Vertical bars indicate standard errors.

TABLE 3.5. Spearman rank order correlations among six measures of food-sharing by 62 cotton-top tamarins.

	Resisted begs	*Offers*	*Total shared*	*Offers as % of total*	*Proportion of positive responses to begging*
Positive responses to begs	0.66***	0.43***	0.98***	0.16	0.56***
Resisted begs		0.32*	0.66***	0.16	-0.14
Offers			0.57***	0.91***	0.28*
Total shared				0.32*	0.55***
Offers as % of total					0.07

* $p \leq 0.05$; *** $p \leq 0.001$

infant begs and the number of resisted begs. However, the correlation was small. Most other measures were significantly positively correlated. Individuals who frequently responded positively to begging by infants shared more food overall, and also tended to offer food to infants more often. Individuals who offered more also shared a greater proportion from offers. The fact that positive responses and total amount shared were also positively correlated with resistance suggests that infants are perhaps likely to beg more often from those individuals who will be more willing to share food with them. However, a greater proportion of shares from offers was not related to the number of positive responses made to infant begging.

Tests were carried out to investigate the effects of sex and class of caretaker and of litter size on food-sharing. As juveniles in families with singletons were not observed to offer, the data for these cells for the frequency of offers and for the percentage of items shared that were offered did not meet the requirements for the application of parametric tests. Kruskal-Wallis one-way ANOVAs were therefore used to examine the effects of age on these two measures; effects of litter size, and of sex within each age class, were tested with Mann-Whitney U-tests. Each of the other four measures was subjected to ANOVAs and ANCOVAs (controlling for group size). Group size had a significant effect only on the frequency of resistance to infant begging, and therefore the results of the ANCOVA are reported only for this measure.

The results are presented in table 3.6 and figure 3.14. Age class had a significant effect on all measures. Younger tamarins responded positively to begging and offered food items less frequently, but resisted begging attempts more frequently than older tamarins. Parents both responded positively to and resisted begging attempts more frequently than offspring, and also offered more. Parents thus shared more items in total than offspring, and younger siblings shared less than older siblings. However, there was no marked difference in response to begging between parents and offspring.

Sex of caretaker had no significant effects on sharing except for the percentage of total items shared that were offered: Mann-Whitney U-tests showed that adult daughters shared a significantly higher proportion of items by offering than did adult sons, but there were no

TABLE 3.6. Results of statistical tests on measures of food-sharing. Only significant effects are listed; full results are given in appendix C. Age classes = parents, adult offspring, sub-adult offspring, juvenile offspring.

(a) Results of analyses of variance and covariance on four measures of food-sharing for all caretakers ($n = 92$). Results are for ANOVAs only if group size had no significant effect; otherwise both results are given.

Measure	*Factor/covariate*	*F value*	*d.f.*	*p*
Positive responses to begs	*Age class*	10.68	3,76	0.0000
	Litter size	13.27	1,76	0.0005
Resisted begs	*Age class*	5.68	3,76	0.002
	• Controlling for group size	2.82	3,75	0.045
	Litter size	14.57	1,76	0.0003
	• Controlling for group size	18.50	1,75	0.0001
	• Group size	10.72	1,75	0.0033
Total shared	*Age class*	12.37	3,76	0.0000
	Litter size	17.87	1,76	0.0001
Proportion of positive responses to begging	*Age class*	5.72	3,75	0.0014

• Results of analysis of covariance.

(b) Results of non-parametric tests on two measures of food-sharing. KW = Kruskal-Wallis one-way ANOVA; MW = Mann-Whitney U-test. Values are corrected for ties.

Frequency of offers	*Age class (KW)*	$\chi^2 = 18.99$, d.f. = 3, $p = 0.0003$
% of items shared that were offers	*Age class (KW)*	$\chi^2 = 9.35$, d.f. = 3, $p = 0.025$
	Effect of sex in adult offspring (MW)	$U = 20.0$, $p < 0.05$

FIGURE 3.14. Measures of food-sharing by cotton-top tamarins. (a) Mean frequency of positive responses to infant begs; (b) mean frequency of resistance to infant begs ; (c) mean frequency of offers; (d) mean number of food items shared in total; (e) percentage of total items shared that were offers; (f) proportion of positive responses to infant begging.Values used were totals from 12 weekly observation sessions of 7 singletons and 7 twin litters.

▨ **male caretakers** ☐ **female caretakers**

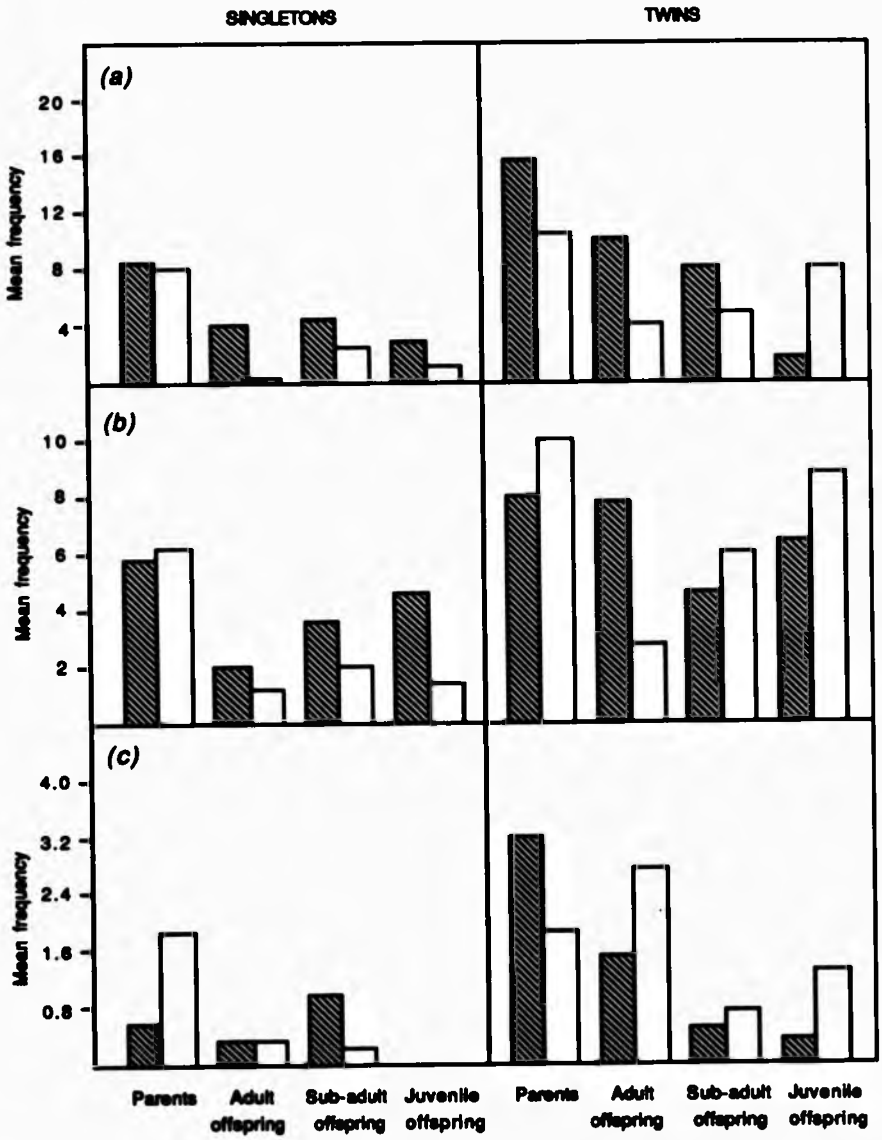
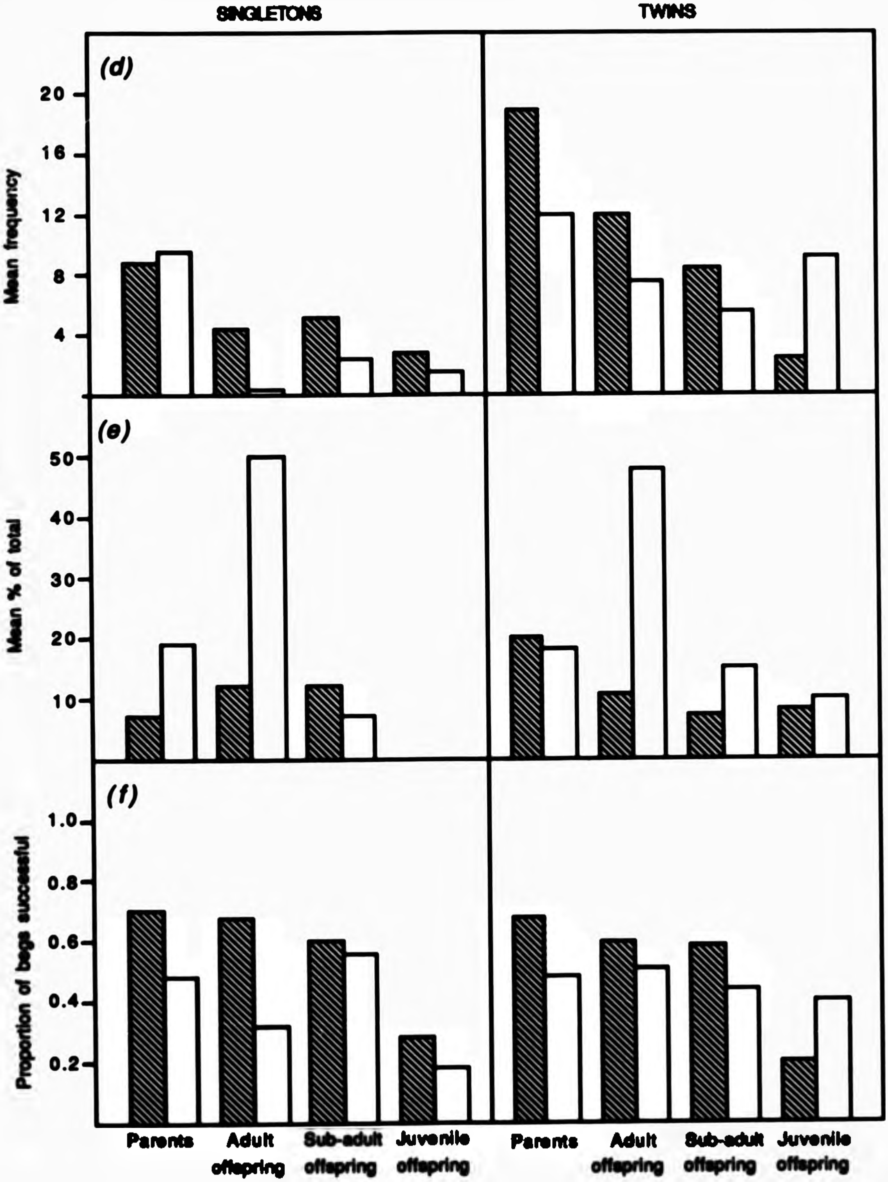


FIGURE 3.14 (cont.)



significant sex differences in the other age classes. However, there were strong trends for effects of sex on the frequency of positive responses to infant begs ($F_{(1,76)} = 3.77$, $p = 0.056$) and on the proportion of positive responses to begs ($F_{(1,76)} = 3.58$, $p = 0.062$), with males sharing more than females on both measures.

Litter size had several significant effects: caretakers in families with twins were begged from more and shared more in total, but there was no effect of litter size on the proportion of begs that were successful. Caretakers were therefore no more or less likely to respond positively to begging attempts by twins. Mann-Whitney U-tests showed that there were trends towards effects of litter size on the frequency of offers ($U = 843.5$, $z = -1.764$, $p = 0.078$) and the percentage of shares that were offers ($U = 716$, $z = -1.79$, $p = 0.073$), with twin litters producing higher scores in each case.

Partial correlations, controlling for litter size, confirmed that sibling age in months was significantly (though not highly) positively correlated with the frequency of offers ($r = 0.272$, d.f. = 55, $p = 0.019$), the total amount of food shared ($r = 0.282$, d.f. = 55, $p = 0.017$), the percentage of items shared that were offers ($r = 0.225$, d.f. = 55, $p = 0.046$) and the proportion of positive responses to infant begs ($r = 0.274$, d.f. = 55, $p = 0.019$). The correlation between age and the frequency of positive responses to begs approached significance ($r = 0.216$, d.f. = 55, $p = 0.053$). However, there was no significant correlation between age and the frequency of resistance to begs ($r = -0.027$, d.f. = 55, $p = 0.422$).

Effects of group size on contributions to food-sharing

When the mean amount of food shared by each individual caretaker was calculated for each infant, a significant negative correlation with group size was found ($r_s = -0.61$, $n = 21$, $p < 0.05$), i.e. in larger families, each older member of the family shared less than those in smaller families (fig. 3.15). Similarly, negative correlations were found when partial correlations, controlling for litter size, were used to look at the other measures: positive responses to begging ($r = -0.612$, d.f. = 11, $p = 0.026$) and resistance to begging ($r = -0.658$, d.f. = 11, $p = 0.014$). There were no significant correlations for the proportion of items shared

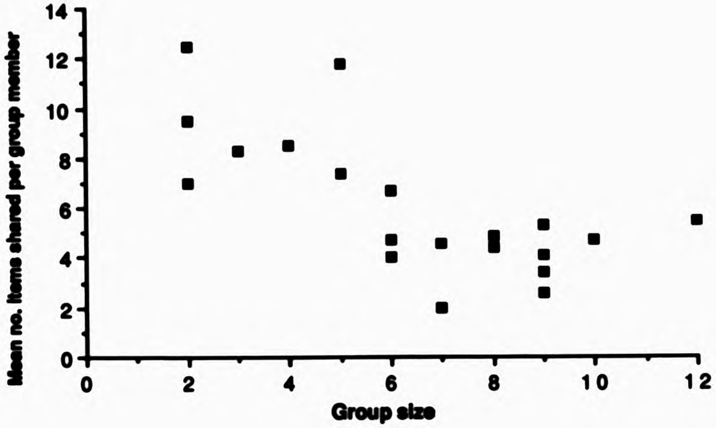


FIGURE 3.15. Relationship between group size and the mean number of food items shared by each non-infant group member for 21 cotton-top tamarin infants.

that were offers, or the proportion of positive responses to infant begging. These results suggest that infants tended to beg less from each group member as family size increased, but that there was no effect of group size on the likelihood that infant begging would receive a positive response. There was a non-significant trend for frequency of offers to be negatively correlated with group size ($r = -0.490$, d.f. = 11, $p = 0.089$), suggesting that motivation to offer food may have been less in bigger groups.

Partial correlations, controlling for litter size, were used to look for the effects of group size on the contributions to food-sharing made by parents and older sibs. Each of the six measures was analysed separately. For mothers, the only significant correlation was with begging success ($r = 0.634$, d.f. = 11, $p = 0.020$), i.e. mothers in larger families responded positively to a higher proportion of infant begging attempts than those in smaller families, but did not offer more or share more food overall (frequency of positive responses: $r = 0.508$, $p = 0.077$; frequency of resistance: $r = -0.393$, $p = 0.184$; frequency of offers: $r = 0.114$, $p = 0.710$; total items shared: $r = 0.443$, $p = 0.129$; % items that were offers: $r = -0.254$, $p = 0.401$). For fathers, there were significant negative correlations with group size for the frequency of positive response to infant begs ($r = -0.713$, d.f. = 11, $p = 0.006$) and the total amount of food shared with infants ($r = -0.681$, d.f. = 11, $p = 0.010$), and a trend towards a negative correlation for the frequency of resistance ($r = -0.514$, $p = 0.072$), but there were no other effects of group size on fathers' behaviour (frequency of offers: $r = 0.091$, $p = 0.768$; % items that were offers: $r = 0.420$, $p = 0.153$; proportion of positive responses to begs: $r = 0.411$, $p = 0.163$).

Each sibling age class was considered separately, and some interesting effects emerged (see table 3.7). There were no significant correlations between group size and the percentage of items shared by offering, or the proportion of positive responses to infant begs, in any age class. For juveniles, there were negative correlations for all six measures. Three of these were statistically significant, and a fourth approached significance. For sub-adults, there was only one significant correlation: frequency of offers was negatively correlated with group size. Four of the remaining five correlations, however, were also negative. For adults, although

TABLE 3.7. Correlations between measures of food-sharing and group size for three age classes of helper. Results are for partial correlations, controlling for litter size.

Measure		*Juveniles (d.f. = 10)*	*Sub-adults (d.f. = 20)*	*Adults (d.f. = 19)*
Frequency of positive responses to infant begs	*r*	-0.548	-0.030	+0.458
	p	0.003	0.447	0.018
Frequency of resistance to infant begs	*r*	-0.751	-0.062	+0.322
	p	0.002	0.393	0.077
Frequency of offers	*r*	-0.450	-0.408	-0.426
	p	0.071	0.030	0.027
Total number of items shared	*r*	-0.543	-0.154	+0.313
	p	0.034	0.247	0.083
Proportion of positive responses to infant begs	*r*	-0.126	0.093	-0.076
	p	0.348	0.340	0.372
% items shared that were offers	*r*	-0.372	-0.252	-0.258
	p	0.117	0.129	0.130

TABLE 3.8. Spearman rank order correlations between carrying index and measures of food-sharing for 62 cotton-top tamarins.

	Positive responses to begging	*Resisted begs*	*Offers*	*Total shared*	*Offers as % of total*	*Proportion of positive responses to begging*
Carrying index	0.50***	0.38**	0.49***	0.53***	0.39**	0.32*

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$

frequency of offers was significantly negatively correlated with group size, three of the other correlations were positive. One of these was statistically significant, while the remaining two showed strong trends towards significance. There was therefore a changing pattern of effects of group size on food-sharing by siblings that depended on age.

Correlations between different measures of infant care

A Kendall coefficient of concordance showed that all measures of care (carrying index plus the six measures of food-sharing) were significantly correlated ($\chi^2 = 250.2$, d.f. = 6, p = 0.00). Spearman rank order correlations were then used to compare the carrying index as a measure of one form of investment in infants with measures of food-sharing. The results are presented in table 3.8. All correlations were positive and statistically significant, the highest correlations being with number of successful begs, number of offers and the total number of items shared. This suggests that individuals who carry infants also share food with them more.

Discussion

In this section I will summarise the results of this part of the study and compare them with those of previous investigations of infant care in callitrichids. Investment in infants as a component of the reproductive strategies of callitrichids will be considered in chapter 8.

Distribution of care and changes over time

The pattern of infant care over time shown by the cotton-top tamarins in this study resembled that described in other reports. Mothers' contributions to carrying declined fairly steadily from birth onwards, whereas contributions by fathers and older offspring increased to peaks at 3-5 weeks before starting to drop. Siblings' contributions tended to peak slightly later than fathers'. Similar patterns showing a changing distribution of care over time have been reported before, with carrying by mothers decreasing but carrying by others increasing, at least temporarily, as infants get older (e.g. *Saguinus oedipus*: Wolters 1978; Welker *et al*. 1981; *S. fuscicollis*: Epple 1975*b*; Vogt *et al*. 1978; *S. labiatus*: Pryce 1988; Buchanan-Smith 1989; *Callithrix jacchus*: Chalmers & Locke-Haydon 1985; Arruda *et al*. 1986; *C. humeralifer*:

Rylands 1985; *Leontopithecus rosalia*: Hoage 1978; *Cebuella pygmaea*:Wamboldt *et al.* 1988). The fact that contributions to carrying by fathers tend to *increase* over the first few weeks is interesting. Although in studies with few or no older offspring, increases in carrying by the father over the first few weeks could simply be compensation for decreased carrying by the mother, this pattern of paternal carrying persists even in studies of larger groups (e.g. Wolters 1978; Cleveland & Snowdon 1984; Rylands 1985). One possible reason why fathers might carry most in this period is suggested in chapter 6.

The results agreed with those of previous studies of *Callithrix* and *Saguinus* that fathers and older siblings often carried infants from the first day of life. This is in contrast to data from *L. rosalia* showing that mothers generally do all the infant carrying until the infants reach the age of two to three weeks (Hoage 1978).

Carrying by older offspring in callitrichid families is frequently reported to be low, with infants spending more time on parents than on siblings (e.g. *Callithrix jacchus*: Ingram 1977; *S. labiatus*: Pryce 1988). However, in the present study, as well as that of Cleveland & Snowdon (1984), infant cotton-top tamarins often spent more time on siblings than on parents from birth onwards. This is probably explained by differences in group size and the number of adult offspring in each family: no adult offspring were present in any of the groups studied by Pryce (1988), and only one of Ingram's (1977) groups had an adult offspring. In contrast, both studies of cotton-top tamarins included several adult sons and daughters.

Food-sharing increased throughout the 12-week observation period. Further studies in the Stirling colony (Feistner 1985; Feistner & Price 1990) have shown that the frequency of food-sharing peaks at 12 weeks and then declines. Food-sharing in *S. fuscicollis* also reaches a maximum at 8-12 weeks (Cebul & Epple 1984). Thus the highest frequencies of food-sharing in *Saguinus* appear to coincide with the achievement of complete independence. However, a study of *Callithrix argentata melanura* (Buchanan-Smith 1984) found an earlier peak, at about 4-6 weeks, before the infants were fully independent. The reason for these differences is not clear, although the results of the latter study were based on only one group, and therefore may not be representative. Begging success in cotton-top tamarin infants did not alter noticeably as they got older; a similar result was reported for *C. jacchus* by Chalmers & Locke-Haydon (1984).

Effects of group size

The prediction that infants in larger groups would receive more care than those in smaller groups was supported for both carrying and food-sharing. However, there was no evidence that infants in larger families were suckled more.

Saddle-back tamarin infants in larger groups also spend less time off than those in smaller groups (Pook 1976). Ingram (1977) found that first litters in *C. jacchus* families tended to spend most time off, and fourth litters least, at comparable ages; presumably this was because group size had increased. On the other hand, another study of *S. fuscicollis* (Vogt *et al.* 1978) found no apparent effect of family size on infant independence; this study was, however, based on only one group.

The other main effect of group size was that the amount of care given by each individual was reduced as group size increased, both for carrying and for food-sharing. Previous studies (e.g. Cleveland & Snowdon 1984) have looked at the effects of increasing family size on parental contributions to care, but have generally not considered its effect on the distribution of care among all available caretakers. Nevertheless, one previous study of cotton-top tamarins (Feistner 1985; Feistner & Price 1990) found a similar negative correlation between group size and the amount of food shared with infants by each individual. There was no evidence, however, that infants received more or less food from offers in smaller families compared to those in larger families. Similarly, Feistner (1985; see also Feistner & Price 1990) found no significant correlation between group size and the frequency of offering. However, there was some indication in the present study that siblings (though not parents) offered less in bigger groups.

Factors affecting contributions to care by different individuals

Wolters (1978) found no evidence that any particular family members carried cotton-top tamarin infants more, and Cavalliere (cited in Cebul & Epple 1984) found no consistent relationship between attempts by infant saddle-back tamarins to steal food, or their success in doing so, and the type of group member at which the attempts were directed. In this study, on the other hand, there was evidence that age, sex, and position in the family influenced the extent to which individual cotton-top tamarins invested in infants. Group size also affected the contributions made by particular individuals.

Although the relatively large family sizes in this study meant that infants were generally more likely to be carried by an older sibling than either parent, nevertheless mothers consistently carried more than individual siblings. In the first five weeks in particular, fathers also tended to carry more than sibs. Consequently, parents contributed more to care than any class of helper, including adults, and this also proved to be true of food-sharing. This confirms and extends the results of previous studies (e.g. Ingram 1977; Hoage 1978), which were frequently based on small groups.

However, a greater number of helpers did have some effects on parental contributions to care. As predicted, fathers appeared to benefit more than mothers from increased group size, although it was surprising how little mothers' behaviour was affected. There was no evidence that their contributions to carrying or food-sharing were reduced significantly (although they tended to do a smaller proportion of the carrying in larger families), nor did they spend a greater proportion of their carrying time suckling infants. However, contributions by fathers to both food-sharing and carrying were significantly negatively correlated with group size. This contrasts with the results of Ingram (1977, 1978*a*) on *C. jacchus*, and Cleveland & Snowdon (1984) on cotton-top tamarins, who both found that increased group size had a greater effect on maternal than paternal contributions to carrying. In addition, Ingram (1977, 1978*a*) found that mothers tended to concentrate more on feeding infants in larger groups. However, some other studies of cotton-top tamarins have produced results similar to those reported here: Wolters (1978) found that fathers' carrying scores tended to decrease below the mean value in larger groups, and Tardif *et al.* (1989*a*) showed that fathers' contributions to infant carrying declined from 62% to 31% when helpers were present, but mothers' scores fell only slightly, from 33% to 26%. McGrew (1988) found that mothers' investment in infants did decrease with group size, but that fathers' contributions decreased not only in absolute terms, but also relative to the mother's contribution. No similar effect was found in the present study. McGrew's study was based on brief observations (two hours) of infants at widely varying ages (7-14 weeks), and used a broad measure of care that included playing with infants and simply being near them, as well as carrying and sharing food. These factors could account for the difference in the effects found.

One possible explanation for the lack of effect of group size on maternal care might be that factors other than family size could have important effects on maternal "styles" of care. Two such factors are maternal condition and weight, and parity. Snyder (1974) found that experienced *L. rosalia* mothers tended to transfer infants to others later than primiparous mothers, and that weak mothers, unlike stronger females, allowed fathers to carry immediately after birth. In the present study, one primiparous mother (Delaware), who might have been expected to contribute a considerable amount to infant care as she had only her mate's assistance, in fact did very little. She was a small female and appeared to suffer chronic back discomfort, and also showed a tendency to lose condition when she gave birth. She also seemed to have a difficult birth (Price, in press *b*), and this may have been one reason why she refused to carry the infants or feed them during the day. It is unlikely that the fact that she was a primipara could account by itself for her behaviour, as other primiparous mothers in the Stirling colony generally carry infants considerably more than Delaware did (personal observation).

The prediction that older siblings would care for infants more than younger siblings was supported by data from both carrying and food-sharing. Several previous studies have reported that older siblings carry more than younger ones (Epple 1975*b*; Box 1975*b*, 1977; Ingram 1977, 1978*a*; Bucher & Anzenberger 1980; Welker *et al.* 1981; Tardif *et al.* 1986*b*). In a study of wild *S. fuscicollis*, Goldizen & Terborgh (1986) found that juveniles in one group carried much more after three adult males had emigrated. Rylands (1985) also found that in large groups of wild *C. humeralifer*, siblings carried less than in small groups. In the present study, at least some effects of group size on care by siblings appeared to be age-dependent. Although, as predicted, juveniles invested less on all measures as family size increased, for the older age classes the results were not so consistent: although scores on carrying were negatively correlated with family size for both sub-adults and adults, food-sharing showed some unexpected patterns. Sub-adults showed few significant correlations with group size, whilst adults showed some positive correlations. This suggests that in larger families adult offspring may perform relatively more of the infant care duties than in smaller families.

The sex of the caretaker affected the extent to which it carried infants, but this effect was partly dependent on the age of the caretaker and whether it was a parent or a helper. Mothers carried slightly more overall than fathers, but there were few significant differences. There were few effects of sex on food-sharing. However, one potentially important factor was brought out by the present study: at least for infant carrying, age and sex showed a strong tendency to interact, so that adult males carried more than females, with the reverse being true for sub-adults and juveniles. Interestingly, Ingram (1977, 1978*a*) also found that adolescent (= juvenile) female common marmosets carried more than males, but while this sex difference was maintained in sub-adults it was much less marked. Thus there was evidence to confirm the prediction outlined in the introduction to this chapter that female callitrichids should attempt to acquire infant carrying experience early, before they leave their natal groups.

Previous reports of sex differences in care by both parents and siblings are often contradictory and few consistent patterns have emerged. In wild *S. mystax* (Ruth 1987), only males play with infants, but both sexes share food. Goldizen (1987*a*, 1989) found that adult males in wild groups of *S. fuscicollis* carried, groomed and stayed near infants more than lactating females did. Wolters (1978) found that fathers did 90% of the food-sharing in cotton-top tamarin families, with the remainder done by sons. However, another study in the Stirling colony (Feistner 1985; Feistner & Price 1990) found no evidence of a sex difference in food-sharing, supporting the results of the present study. Feistner (1985) also found that females tended to offer more than males; a similar effect emerged in the present study. In captive groups of *S. fuscicollis*, Cebul & Epple (1984) found that fathers shared food *less* than mothers or older sibs.

Some studies report that fathers or adult males tended to carry more than mothers or adult females (e.g. *S. fuscicollis*: Epple 1975*b*; *C. jacchus*: Ingram 1977), though the differences are often not statistically significant. Others (e.g. *C. jacchus*: Box 1977) have found that mothers carry more, while yet others report that mothers and fathers split the carrying duties approximately equally between them (e.g. *S. geoffroyi*: Moynihan 1970, Lindsay 1979; *S. labiatus*: Pryce 1988). Some studies have emphasised the role of sons as well as fathers in infant care (e.g. *S. fuscicollis*: Vogt *et al.* 1978; *S. oedipus*: Wolters 1978, McGrew 1987), others have found that female offspring may carry more than males (e.g. *C. jacchus*: Box 1975*b*, 1977; Ingram 1977, 1978*a*). Female juveniles may also direct more social behaviour towards infants (e.g. *C. jacchus*: Ingram 1977; *S. fuscicollis*: Cebul & Epple 1984), but Wamboldt *et al.* (1988) found that juvenile female pygmy marmosets (*Cebuella pygmaea*) were less likely than males to retrieve infants who had been temporarily separated from their families.

Many of these contradictions may result from differences in group size or composition - as noted above, group size can affect the way in which care is divided among family members - or in methodology. For example, Tardif *et al.* (1986*b*) did not distinguish between the carrying of one versus two infants. Sex differences in both parents and helpers may also depend on the age at which infants are observed: as discussed above, in this study and in many others, mothers' scores tended to be highest in the early weeks, whereas fathers' scores peaked later. Hoage (1978) also reported that juvenile female *L. rosalia* started to carry earlier than males, but the relative amount done by juveniles of each sex varied as infants grew older.

The existence of species differences is also possible, though as yet it is difficult to see any consistent pattern. However, a study by Tardif *et al.* (1986*b*) comparing infant care in *Callithrix jacchus* and *S. oedipus* found that male marmoset siblings tended to carry more than females, whereas the opposite was true of the tamarins. The expression of sex differences may also depend on the measure of involvement in infant care used. For example, Locke-Haydon & Chalmers (1983) found that while juvenile female common marmosets carried more than their brothers, the males played more with infants.

Effects of infant variables

The sex of an infant had no effect on any measures of care: there was no evidence that infants of one sex received more care than those of the other, or that any category of caretaker invested preferentially in infants of a given sex. Not all previous studies have considered the effects of infant sex. Of those that have, some, like the present study, have found that it did not influence the pattern of care (e.g. *C. jacchus*: Box 1977; *C. argentata melanura*: Buchanan-Smith 1984; *S. oedipus*: Cleveland & Snowdon 1984). These results are in contrast with two reports of differences in the distribution of infant care according to infant sex, both of which emphasised same-sex preferences in infant care by parents. In *C. jacchus* (Ingram 1977, 1978*a*), mothers fed female infants more than males, while male infants were carried more by their fathers. In *L. rosalia* (Hoage 1978, 1982), parents preferentially carried infants of their own sex.

Litter size, on the other hand, did have some effects, although these were not consistent across all measures of care. Singleton infants were carried more than individual twins, but did not receive more food and were not suckled more. The prediction than singletons would receive more care was therefore confirmed for one measure but not for the others. The fact that there was no difference between individual twin and singleton infants in the amount of suckling received suggests that mothers of twin litters must be investing twice as much energy in milk production as mothers of singletons (however, it is not known whether time on the nipple is directly related to the amount of milk obtained). In addition, caretakers in families with single infants must invest half as much in terms of sharing food; on the other hand, although caretakers carrying twins invest more, it is not double that for singletons.

Other studies have reported that singleton infants tend to become independent later than twins (Box 1977; Brand 1981*a*; Buchanan-Smith 1984). Cleveland & Snowdon (1984), on the other hand, found no effect of litter size on time carried, although when off, single infants were in contact with other group members more than twins. This may be because twins tend to spend a lot of time together (personal observation).

The pattern of distribution of infant care amongst parents and helpers was basically similar for twins and singletons, except that mothers were the primary carriers of singletons in week 1. Twins, in contrast, were always more likely to be on a sibling. Box (1977) also found that common marmoset parents were more involved in caring for a single infant than for twins. Hoage (1978) found that experienced golden lion tamarin mothers transferred singleton infants later than twins; however, Ingram (1977, 1978*a*) reported that singleton common marmosets were carried more by their fathers.

As predicted, twin infants were carried together less in larger groups. No previous study has investigated this. However, it was surprising that as twins got older the *proportion* of time they were on the same carrier did not alter to any great degree. Vogt *et al*. (1978) found that twins were carried together for the first few weeks, but were more likely to be on different carriers as they got older, as would be expected as the burden of carrying them increased. Goldizen (1987*a*), in a study of two sets of wild saddle-backed tamarin infants, found that the time they spent on the same carrier first increased until the age of about one month, and then declined again. Nothing resembling this pattern was seen in the present study.

Differences according to the measure of infant care used

Comparisons of the pattern of investment for two different measures of care, carrying and food-sharing, show some similarities but also some differences. Individuals who carried more also tended to share more food with infants. For both measures, parents tended to invest more than siblings, and older offspring to invest more than younger offspring. However, while there was a strong trend towards an interaction between age and sex in carrying (with adult sons doing more than adult daughters, but younger sons doing less than younger daughters), few significant or consistent effects of sex emerged for food-sharing. Males tended to respond more positively to infant begging, but females tended to offer more food to infants. In fact, adult daughters showed the highest percentage of food items shared by offering. These results suggest that although there was a tendency for adult daughters to share less than sons, females were no less motivated than males to share.

One obvious difference between food-sharing and carrying is that some individuals could potentially *control* carrying by others, either by taking infants from those individuals, or by preventing them from taking infants when they tried to do so. Carrying might therefore be influenced by the behaviour of others, not simply by the individual's motivation to carry. Food-sharing, on the other hand, would be less likely to be affected in this way. This possibility is considered in more detail in the next chapter.

Summary

(1) Infant cotton-top tamarins in larger families received more care (in terms of carrying time and food-sharing) than those in smaller families.

(2) Individual caretakers in large families invested less care in infants than those in smaller families, in terms of both food-sharing and infant carrying.

(3) Singleton infants were carried more than individual twins, but did not receive more food and were not suckled more. Caretakers therefore performed twice as much care in terms of food-sharing and suckling when there were twins in the group, but less than twice as much carrying.

(4) Paternal contributions to carrying and food-sharing decreased as family size increased, but maternal contributions did not. However, mothers did a smaller *proportion* of the carrying in larger groups. Mothers carried more than fathers, particularly in the first two weeks, but there were otherwise few significant sex differences in care by parents.

(5) Parents of both sexes gave more care to infants than did any individual older sibling, but infants spent more time being carried by siblings than by either fathers or mothers.

(6) Older siblings invested more in infants than younger siblings. There was a trend for sex differences in infant carrying by older siblings to be age-dependent: adults sons tended to invest more in infants than adult daughters, but sub-adult and juvenile daughters tended to

invest more than sub-adult and juvenile sons. However, the effects of sex on food-sharing were inconsistent.

(7) Some of the conclusions drawn about patterns of investment in cotton-top tamarins, particularly with regard to sex differences, depended on the measure of care used.

Chapter 4

Infant transfers in cotton-top tamarins

Introduction

To study infant care purely in terms of the *amount* of care contributed by each individual in a group is to ignore the influences that competition between caretakers, attempts by some caretakers to control the caretaking activities of others, and the preferences of infants for particular caretakers, might have on the pattern of care that eventually emerges. To investigate these factors, I collected data on *transfers* of infant cotton-top tamarins, i.e. movements of infants from one carrier to another.

Competition

Competition to carry infants in callitrichid groups, and efforts by some individuals to prevent others from taking infants, have been briefly mentioned in a few previous reports (e.g. Epple 1975*b*; Box 1977; Cleveland & Snowdon 1984), but only one study (Pryce 1988) has quantified competition to carry and its effects on the distribution of carrying within a tamarin family (*Saguinus labiatus*). Interestingly, a study of captive common marmosets (Locke-Haydon & Chalmers 1983; Chalmers & Locke-Haydon 1985) found no evidence of competition. However, Scanlon *et al*. (1987) found in a field study of the same species that all group members cared for infants, and suggested that they might do so as a means of gaining the advantages of group membership. If this is true, then competition to carry infants would also be expected.

If competition to carry infants does occur in cotton-top tamarins, then it should lead to the following:

(1) more frequent transfers in larger groups;

(2) more frequent transfers for singletons than for twins;

(3) higher frequencies of active attempts to take infants, resistance by carriers to attempts by others to take over, and interventions in transfers by third parties, in larger groups.

(4) less frequent rejection of infants in larger groups.

There are several possible reasons why tamarins in their natal families might compete with one another to carry infants, and they lead to different predictions about which individuals should compete most strongly:

(1) They might need experience in carrying infants. Competition might therefore be expected to be most severe among younger tamarins, i.e. we might expect individuals with less experience to try and take infants more frequently in order to gain that experience. Following the same logic outlined in chapter 3, young females would be predicted to compete most strongly, as they have a greater need to acquire parenting skills and a shorter time in which to do so.

(2) They might be attempting to increase their chances of inheriting their natal territory. Again, the arguments put forward in chapter 3 suggest that older male offspring, as the ones most likely to stay on their parents' territory rather than disperse, should compete most strongly as by doing so they may "pay" their parents for permission to stay (McGrew & McLuckie 1986). Males should therefore be more likely to be active takers of infants, and to resist takeovers by other individuals.

There seems to be no obvious reason why parents should compete to carry, as their presumed benefit from the presence of helpers is release from carrying duties. However, the energetic costs of lactation mean that mothers might be expected to reject infants more than fathers, and this has been reported for common marmosets (Ingram 1977, 1978*b*; Arruda *et al.* 1986).

Control of carrying

Engel (1985*b*) has reported that if a juvenile common marmoset attempts to contact an infant, the carrier shows "dissociative behaviour" towards the juvenile (although she did no define "dissociative", this presumably involves behaviour such as mild aggression). Carriers therefore appear to try and avoid the establishment of physical contact between infants and juveniles. This led Engel (1985*a*) to suggest that adult members of the group may exert a "controlling function" in interactions between infants and juveniles. This seems a reasonable hypothesis, because juveniles are inexperienced and consequently may be a threat to the safety of the infants. However, adults may tolerate some interactions in order to give juveniles the opportunity to learn the necessary parenting skills. I therefore predicted that older family members would try to limit carrying by juveniles more than other age classes, by preventing them from taking infants, removing infants from them, and intervening in transfers in which juveniles were involved.

A further aspect of control was mentioned briefly in chapter 3. Although adult daughters carried less than adult sons, they showed little tendency to share food less. This suggested that their motivation to care for infants was not reduced. It is possible, then, that other family members prevented adult daughters from carrying infants in the same way that they might control carrying by juveniles.

Development of infant independence

Although early studies (e.g. *Callithrix jacchus*: Epple 1967; *Saguinus geoffroyi*: Moynihan 1970) reported that infant callitrichids transferred between carriers by themselves and rarely received assistance, more recent reports have found that infants tend to be relatively passive in transfers in the first two to three weeks of life, gradually becoming more active as they grow older (e.g. *C. jacchus*: Box 1977; *C. argentata melanura*: Buchanan-Smith 1984; *Leontopithecus rosalia*: Kleiman 1984). In these early weeks, then, parents and helpers are primarily responsible for the movements of infants from one group member to the next. As infants become more capable of moving from one carrier to another, the frequency of transfers is likely to increase. Then, as they start to spend longer periods of time off, the frequency of transfers should decline. I also expected that the role of infants in actively initiating transfers would increase over time.

Lindsay (1979) has suggested that the frequency of transfers is also affected by the increased weight of the infants as they grow, subjecting adults to a greater burden. Trivers (1974) has predicted that parent-offspring conflict over investment should arise when the benefits to parents of investing in the current offspring are outweighed by the costs of a reduction in their ability to invest in future offspring. Helper-infant conflict would also be expected in communally rearing species. Thus, rejection by carriers and by individuals that infants attempt to climb on to should increase with time. Correspondingly, active initiation of carrying by caretakers should decrease.

In addition, the data presented in chapter 3, showing that singletons were carried more than twins, suggested that singletons would be rejected less frequently than twins.

Preferences of infants for particular caretakers

Locke-Haydon & Chalmers (1983) have proposed that infants may not rate caretakers equally. For example, as mothers are the main source of nutrition for young infants, they might be perceived by infants as "better" than other caretakers. Older, more experienced and reliable caretakers might be perceived as better than younger ones. Similarly, Epple (1975*b*), who reported an increase in carrying by *S. fuscicollis* parents and a decrease by subordinates when infants became independent, speculated that this might be because infants prefer parents. These ideas are supported by data demonstrating that infant cotton-top tamarins showed a preference for contact and proximity with their mothers, and promoted contact with parents more than with siblings (Cleveland & Snowdon 1984). Infant *C. jacchus* (Ingram 1977) and *S. labiatus* (Pryce 1988) are also responsible for maintaining proximity with their mothers more than with their fathers. I therefore predicted that infants would be more likely to actively initiate carrying bouts with their mothers than with other caretakers, and with older caretakers rather than younger caretakers, as these individuals could perhaps provide "better quality" care.

Methods

Subjects

Data on transfers were collected simultaneously with the data on other aspects of infant care for the 21 cotton-top tamarin infants described in chapter 3. For details of the infants and their families, see table 3.1. Details of housing and husbandry are given in chapter 2.

Behavioural categories and recording methods

General methods and scheduling of observation sessions are described in chapter 3. All occurrences of transfers (either *completed* or *attempted*; for definitions, see chapter 2) were recorded for each 30-minute focal infant sample. The identities of the carrier and taker were noted for each transfer of the focal infant, and the behaviour of carrier, taker and infant was recorded and classified as *active*, *passive*, or *resistance* (full definitions of these classifications are given in table 4.1). If the infant was moving from the substrate on to another individual, the behaviour of the carrier was recorded as *none*; and similarly, the behaviour of the taker was scored as *none* if the infant was moving from a carrier on to the substrate. If for any reason the behaviour of any individual could not be seen, it was recorded as *unknown*. Any *interventions* in transfers by third parties were also noted. Interventions generally took the form of mild threats (e.g. frowning and piloerection directed at the potential taker) or attempts to move between the carrier/infant and the potential taker. More serious aggression was rare. The outcome of the transfer (*completed* or *attempted*), and the identity of the carrier(s) of the other infant(s) in the case of twin or triplet litters, were also recorded.

Active behaviour by carriers and resistance by takers were interpreted as infant rejection; resistance by carriers and active behaviour by takers as indicating an interest in carrying or continuing to carry infants. For clarity, active behaviour by carriers will be referred to as "rejection" in the text. An example of a transfer involving active behaviour by both the carrier and the taker is illustrated in plate 4.1.

Data were usually recorded on standardised checksheets. However, if transfers occurred very frequently (e.g. in four samples when infants were about six weeks old, and beginning to move about independently in short bouts, there were more than 40 transfers in 30 minutes), the data were dictated on to audio tape and subsequently transcribed on to the checksheets.

PLATE 4.1

An infant transfer. A breeding female cotton-top tamarin (right) rejects the infant she is carrying and it is taken by one of her sub-adult sons, who is carrying the other infant.

TABLE 4.1. Definitions of the behaviour of carrier, taker and infant during transfers.

	Type of behaviour		
	Active	*Passive*	*Resistance*
Carrier	Carrier bites or pulls at infant, or rubs it against substrate in an attempt to dislodge it. Attempt terminated if behaviour ceases for at least 10 secs. (Rejection)	Carrier makes no attempt to dislodge infant or to prevent another individual taking infant.	Carrier attempts to prevent another individual taking infant (by moving away or threatening taker), or to stop an infant climbing off. Attempt terminated if behaviour ceases for more than 10 secs.
Taker	Taker places hands on infant (usually round head) and pulls infant towards it. Attempt terminated if behaviour ceases for at least 10 secs.	Taker does not actively try to pull infant on, or resist when an infant climbs on.	Taker attempts to dislodge infant within 10 secs of the infant climbing on, by biting or pulling at it, or rubbing against substrate.
Infant	Infant initiates transfer by attempting to move on to another individual or on to the substrate before a potential taker has touched it. Attempt terminated if behaviour ceases for at least 10 secs.	Infant does not initiate transfer or resist attempts by taker to take it, or by carrier to dislodge it.	Infant remains on carrier for at least 10 secs after carrier attempts to dislodge it, or moves away from an individual trying take it.

Analysis of data

As before (see chapter 3), infants were described in terms of their sex and status (singleton or twin), and caretakers (either carriers or takers of infants) in terms of their sex and age class (parent, adult offspring, sub-adult offspring or juvenile offspring).

For most analyses, parametric techniques were desired as I was interested in the effects of several variables on behaviour. The data were inspected to see if they met the necessary assumptions for the application of parametric tests. Kolmogorov-Smirnov goodness-of-fit tests were used to test whether the data were normally distributed. If the data did not meet the assumptions, non-parametric tests were used.

As the frequency of transfers varied from one age-sex class of carrier or taker to another, in order to compare behaviour among these classes more easily, proportions of the total transfers in which a particular behavioural category occurred were calculated, and used in place of actual frequencies.

Most data were analysed by ANOVAs, using litter size, and the sex and age class of the caretaker as group factors. Analyses were repeated using ANCOVAs, introducing group size as a covariate. If group size had no significant effects, then only the results of ANOVAs are reported. If a significant effect ($p < 0.05$) was found in an ANOVA, post-hoc Scheffé tests were used to identify the source of the effect. Spearman rank order correlations were used to test for associations between variables.

All significant results are reported here, but for clarity, in general non-significant results are not given. Full results are presented in appendix C.

Results

Frequency of transfers: effects of group size, litter size, and sex of infant

In all, 5949 transfers were recorded, of which 86% (n = 5142) were completed transfers, and 14% (n = 807) were attempted transfers. ANOVAs and ANCOVAs (controlling for group size) were performed to analyse the effects of birth status and sex on the total number of transfers per infant (n = 21) that occurred, the number of completed and attempted transfers, and the number of transfers in which a third party intervened. ANOVAs produced no significant main effects or interactions on any of these measures. Repeating the analyses using ANCOVAs showed that group size had significant effects on the total number of transfers per infant ($F_{(1,16)} = 8.03$, $p = 0.012$), the number of attempted transfers ($F_{(1,16)} = 4.95$, $p = 0.041$), and the number of completed transfers ($F_{(1,16)} = 6.68$, $p = 0.020$), but not on the number of interventions. If group size was controlled for, status had an effect on the number of attempted transfers that occurred: there were more attempted transfers in singletons than in twins ($F_{(1,16)} = 6.34$, $p = 0.023$). There were no significant effects of the other factors on any measure.

To test the effects of infant sex on behaviour, caretakers were categorised as mothers, fathers, daughters or sons, and ANOVAs conducted on the data from the six heterosexual litters. These showed that infant sex had almost no effect on the behaviour of carriers or takers of any category, i.e. caretakers did not in general treat male and female infants differently. The only exception was a significant interaction between infant sex and category of caretaker for passive behaviour by carriers ($F_{(3,31)} = 3.63$, $p = 0.024$). The data from the heterosexual litters was also used to investigate the influence of infant sex on infants' behaviour towards carriers and takers. ANOVAs showed no significant main effects of infant sex on any aspect of infant behaviour, and no interactions between infant sex and the category of carrier or taker involved. There was therefore no evidence that male and female infants behaved differently, or showed any sex-specific preferences for particular caretakers. Furthermore, there were high, and often statistically significant, correlations between the total scores of co-twins on several measures of infant transfers (see table 4.2). Litter means were therefore calculated and used in subsequent analyses.

Changes in behaviour with infant age

Figure 4.1 shows the changes in the frequency of transfers that occurred as infants grew older. Completed transfers increased in frequency to a peak at six weeks, and then declined.

TABLE 4.2. Spearman rank order correlations (r_s) between frequencies of four measures of infant transfers in twin litters ($n = 7$ litters). p-values given are two-tailed.

	Total number of transfers	*Number of completed transfers*	*Number of attempted transfers*	*Number of interventions*
r_s	0.714	0.571	0.775	0.882
p	0.071	0.180	0.041	0.009

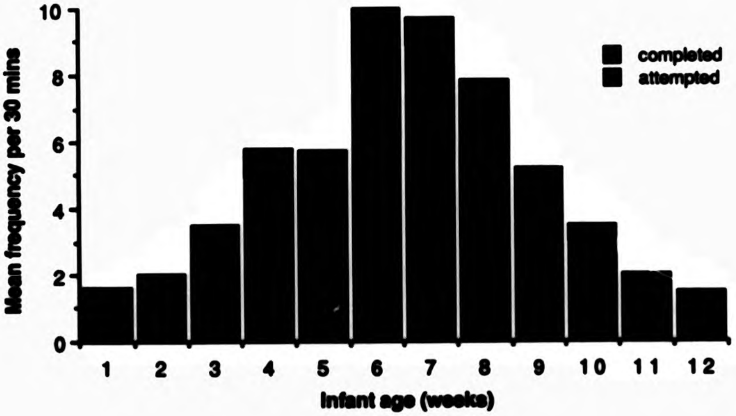


FIGURE 4.1. Mean frequency of completed and attempted transfers per 30 minutes in 21 infant cotton-top tamarins over the first 12 weeks of life.

The frequency of attempted transfers, on the other hand, remained relatively constant over time.

Changes in the behaviour of carriers, takers and infants over the 12-week period are illustrated in figure 4.2. All transfers (both completed and attempted) and data from twin and singleton litters have been combined. Infants' first forays off carriers were always initiated by the infants themselves, and indeed caretakers often seemed to try and limit their explorations by picking them up again. Infants were followed closely by their older siblings, and often avoided attempts to pick them up. Rejections by carriers before this time did occur, but were always followed by a taker retrieving the infant before it came off.

Carriers were predominantly passive (in those transfers in which a carrier was involved) until week 12 (fig. 4.2*a*). Resistance by carriers to attempts by others to take infants occurred most frequently during the first five weeks, with a maximum in week 1. By week 10, resistance had ceased altogether. Active behaviour by carriers (i.e. attempts to reject infants) occurred throughout the study period, but was most frequent in weeks 6-8. Transfers involving no carriers (i.e. movements of infants from the substrate to a taker) began in week 3 and peaked in week 6, then declined as the overall number of transfers fell. However, they remained the predominant form throughout the second half of the observation period.

Takers were mostly active in transfers in weeks 1-5 (fig. 4.2*b*). In week 6, active behaviour by takers decreased and passive behaviour began to predominate as infants themselves moved around more. Resistance by takers was rare until week 6, after which it remained common as takers rejected attempts by infants to climb on. The number of transfers in which no taker was involved peaked in week 7. Note that not all transfers involving no taker resulted in movement of infants on to the substrate; particularly in the early weeks, there were failed attempts by carriers to "dump" infants.

Infants were most commonly passive in transfers in weeks 1-3 (fig. 4.2*c*). Beginning in week 4, there was a considerable increase in the frequency of transfers in which infants were active, and this continued to be by far the most common category of infant behaviour for the rest

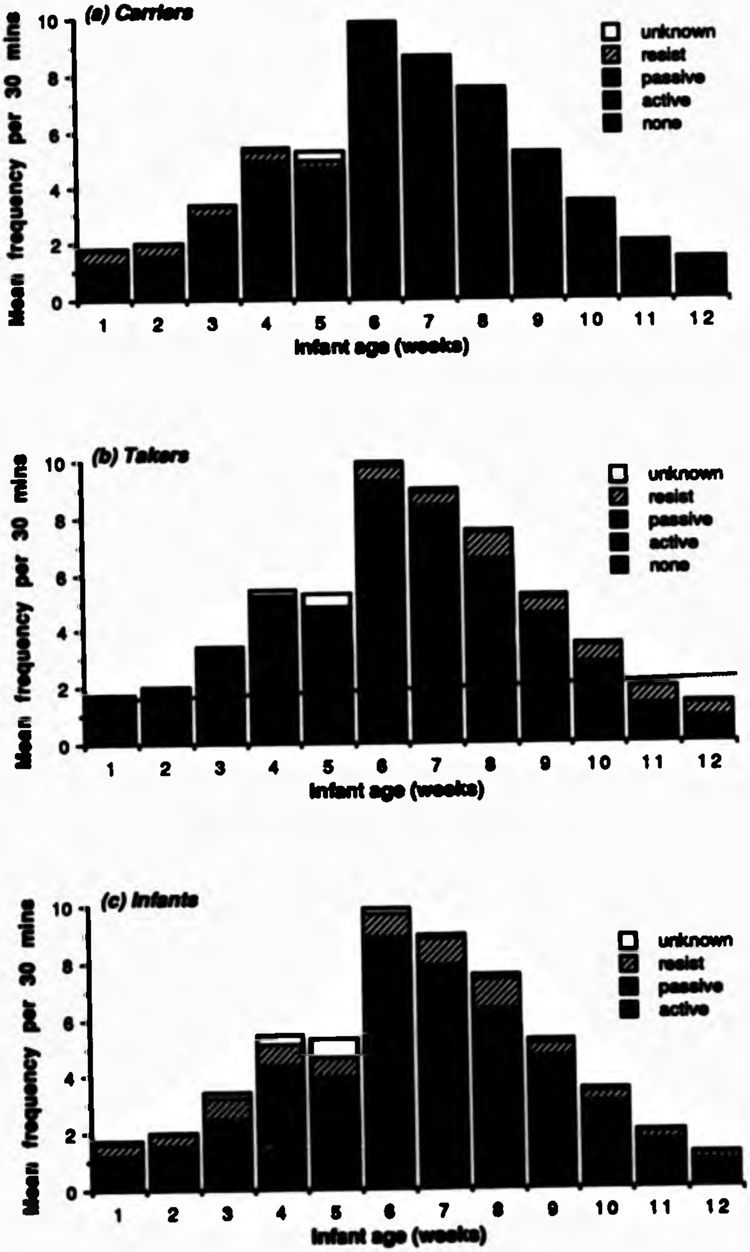


FIGURE 4.2. Changes in the behaviour of carriers, takers and infants during transfers over the first 12 weeks of life. For definitions of each behavioural category, see table 4.1.

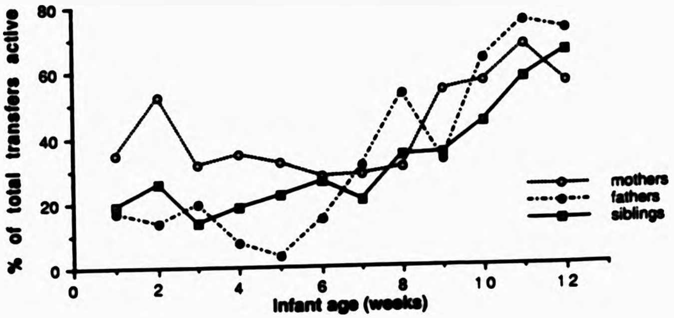
of the study period. Infants resisted some transfers throughout; infant resistance peaked in weeks 6-8 when carriers were most likely to reject them. Some resistance, particularly in weeks 3-5, was also due to avoidance by infants of individuals who were trying to retrieve them.

The behaviour of mothers, fathers and siblings as carriers and takers was investigated in more detail by calculating for each individual the percentage of transfers in which each type of behaviour occurred. The behaviour of each type of caretaker when carrying is illustrated in figure 4.3. Mothers rejected infants in a higher percentage of transfers than either fathers or siblings in weeks 1-6. Fathers, on the other hand, tended to reject infants least in the first few weeks, with a minimum in week 5. After week 6, sibs tended to reject infants less than either parent. Passive behaviour was most common in fathers and least common in mothers in weeks 1-5, but by weeks 11-12, fathers showed the lowest percentage of passive behaviour. Sibs resisted attempts by others to take infants most in weeks 1-4, mothers least. Resistance to takeovers by fathers peaked in week 2, reaching the same level as resistance by sibs. After week 5, there were few differences in the amount of resistance by the different categories of carrier.

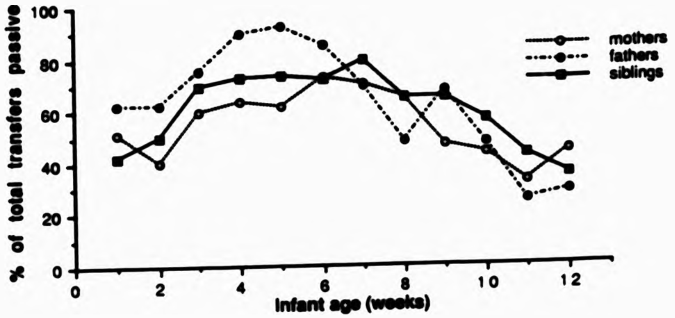
Similarly, the behaviour of mothers, fathers and siblings as takers is illustrated in figure 4.4. In weeks 1-3, mothers showed the lowest percentage of active takeovers of infants, siblings the highest. Active taking by fathers peaked in week 2, again reaching the same level as that by sibs. In later weeks, mothers actively took infants in a higher percentage of transfers than either sibs or fathers. In weeks 1-3, passive behaviour was most frequent in mothers and least frequent in sibs. In weeks 4-6, fathers were most likely to be passive. Resistance (i.e. rejection of infants) in weeks 1-5 was most commonly seen in mothers; fathers rejected infants less than either siblings or mothers until week 6, when their levels of resistance increased steeply. After week 6, there were few differences in either passive behaviour or resistance amongst caretakers.

Effects of group size on the behaviour of carriers and takers

A Spearman rank order correlation coefficient showed that there was a significant positive correlation between group size and the mean number of transfers per infant in a given litter (r_s = 0.67, n = 14 litters, $p < 0.05$, two-tailed; fig. 4.5), i.e. infants in larger families transferred more *(a) Active*



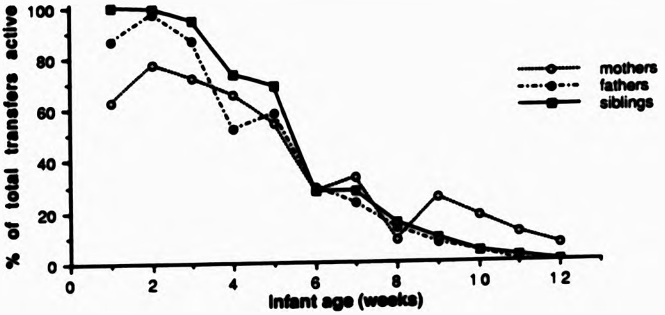
(b) Passive



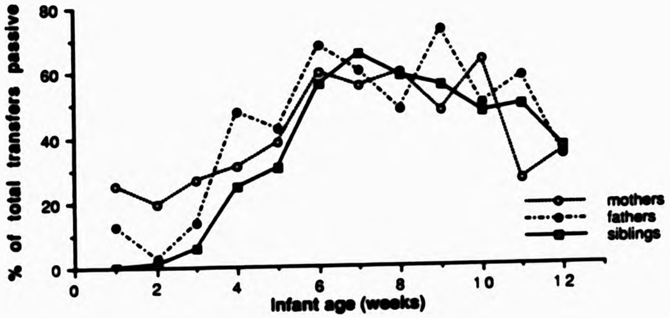
(c) Resist

FIGURE 4.3. Changes in the behaviour of cotton-top tamarins carrying infants with increasing infant age. (a) Percentage of active behaviour by carriers; (b) percentage of passive behaviour by carriers; (c) percentage of resist behaviour by carriers.

(a) Active



(b) Passive



(c) Resist

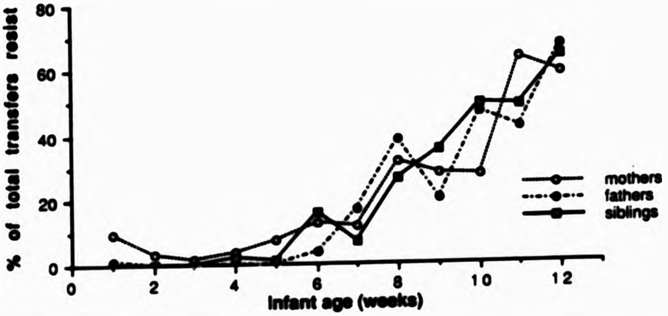


FIGURE 4.4. Changes in the behaviour of cotton-top tamarins taking infants with increasing infant age. (a) Percentage of active behaviour by takers; (b) percentage of passive behaviour by takers; (c) percentage of resist behaviour by takers.

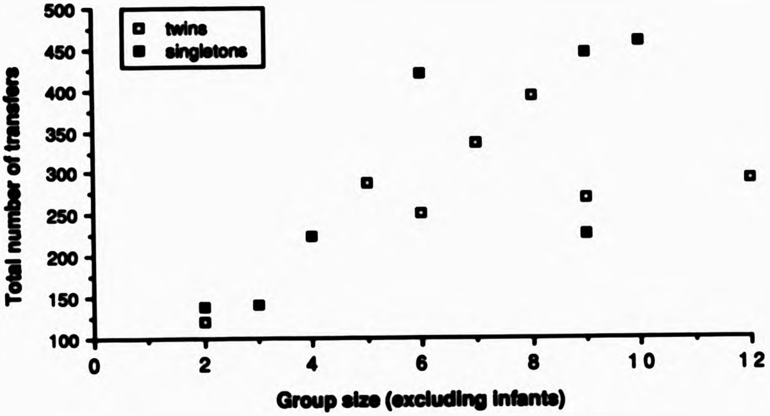


FIGURE 4.5. Relationship between group size and the mean number of transfers per infant in 14 litters of cotton-top tamarins.

often than those in smaller families.

The relationship between group size and the proportion of active behaviour and resistance by carriers and takers during infant transfers was also investigated. There was a significant negative correlation between group size and the proportion of transfers per litter ($n = 14$) in which *takers* resisted (Spearman rank order correlation coefficient; $r_s = -0.82$, $p < 0.05$, two-tailed), but a positive correlation with the proportion of transfers in which takers were active ($r_s = +0.69$, $p < 0.05$, two-tailed). Conversely, there was a significant positive correlation between group size and the proportion of transfers in which *carriers* resisted ($r_s = +0.54$, $p < 0.05$, two-tailed), and a negative correlation with the proportion of transfers in which they were active, i.e. rejected infants ($r_s = -0.64$, $p < 0.05$, two-tailed). Thus, individuals in larger groups were less likely to reject infants, more likely to actively take infants, and more likely to resist attempts by others to take.

In addition, Spearman rank order correlations were used to look at the effects of group size on the behaviour of mothers, fathers and siblings separately, again using proportions of total transfers. Mothers were unaffected by changes in group size: there were no significant correlations with group size on any category of maternal behaviour for mothers either carrying or taking infants. Fathers carrying infants rejected them in a smaller proportion of transfers as group size increased ($r_s = -0.57$, $p < 0.05$, two-tailed), and also resisted infants' attempts to climb on less ($r_s = -0.69$, $p < 0.05$, two-tailed). They also actively took infants more in larger groups ($r_s = 0.54$, $p < 0.05$, two-tailed); however, they did not resist attempts by other individuals to take any more in larger groups. Siblings carrying infants were less likely to reject them as group size increased ($r_s = -0.61$, $p < 0.05$, two-tailed), and also resisted attempts by infants to climb on less ($r_s = -0.83$, $p < 0.05$, two-tailed). However, siblings did not actively take infants more in larger groups, nor were they more likely to resist attempts by others to take.

Behaviour of carriers

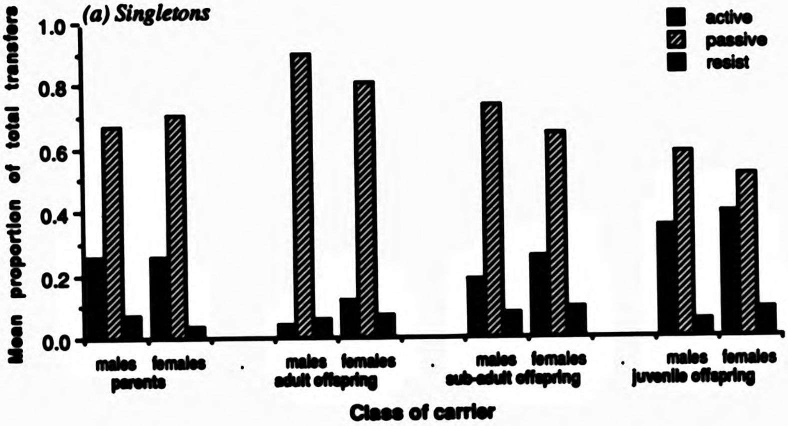
The total number of transfers that each caretaker was involved in as a carrier was calculated and compared. ANOVAs showed that there was a significant effect of litter size: carriers were involved in fewer transfers per infant for singletons than for twins ($F_{(1,76)} = 5.23$, $p = 0.025$). There was also a significant main effect of the age class of the carrier ($F_{(3,76)} = 7.42$, $p = 0.0002$). Post-hoc Scheffé tests showed that juveniles were involved in significantly fewer transfers as carriers than any other age class ($p < 0.05$).

There was also a significant interaction between age class and sex of the carrier ($F_{(3,76)} = 3.03$, $p = 0.035$). Post-hoc Scheffé tests showed that for male carriers, juveniles were involved in significantly fewer transfers than all the other age classes ($p < 0.05$), but for females, only the difference between parents and juveniles was significant, since adult female siblings were involved in only slightly more transfers than juvenile females.

The analyses were repeated using ANCOVAs to investigate the effects of group size. Group size as a covariate had a significant effect on frequencies of transfers for carriers ($F_{(1,75)} = 14.20$, $p = 0.0003$). However, controlling for group size did not alter the effects of the other factors (litter size: $F_{(1,75)} = 4.37$, $p = 0.040$; age class: $F_{(3,75)} = 7.53$, $p = 0.0002$; sex x age class interaction: $F_{(3,75)} = 3.58$, $p = 0.018$).

The proportion of total transfers that were completed was calculated for each carrier. These were then subjected to ANOVAs to investigate whether any particular age-sex classes were more successful in preventing other individuals from retrieving infants; however, there were no significant effects of any factor. In addition, ANCOVAs showed that group size had no significant effects.

The variations in the extent to which carriers of different age-sex classes were involved in transfers meant that in order to compare different types of behaviour meaningfully, it was necessary to analyse proportions rather than actual frequencies. The proportion of total transfers in which each carrier showed active, passive and resistance behaviour was therefore calculated. ANCOVAs showed that there were no significant effects of group size on the behaviour of carriers; therefore only the results of ANOVAs are reported. The results are illustrated in figure 4.6. There was a significant effect of litter size on the proportion of active behaviour (i.e.



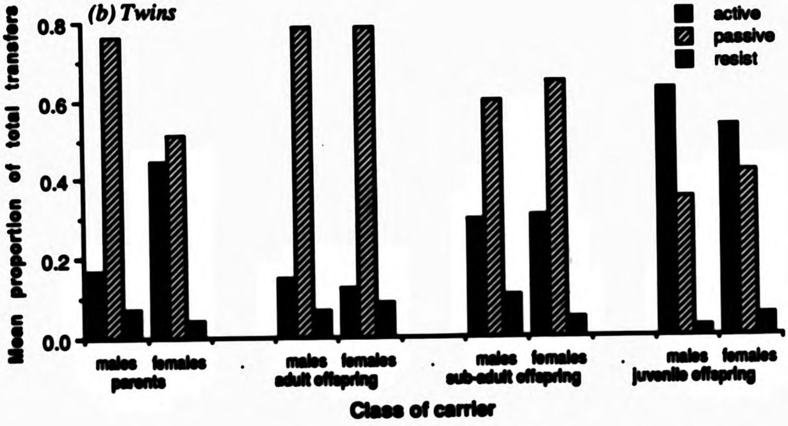


FIGURE 4.6. Behaviour of carriers in transfers of (a) seven singletons and (b) seven twin litters of cotton-top tamarins. Litter means were used for twin litters.

rejection of infants) by carriers ($F_{(1,76)} = 5.40$, $p = 0.023$): carriers were more likely to reject twins (mean = 0.305) than singletons (mean = 0.228). The age class of the carrier also had a significant effect ($F_{(3,76)} = 11.01$, $p = 0.00$): juveniles rejected most frequently, adult siblings least frequently. Post-hoc Scheffé tests showed that all pair-wise differences except that between adult siblings and sub-adult siblings were significant ($p < 0.05$). There was no evidence that either sex rejected more in any age class.

Passive behaviour by carriers again showed significant effects of litter size ($F_{(1,76)} = 4.61$, $p = 0.035$; mean for twins = 0.630; mean for singletons = 0.704) and age class of the carrier ($F_{(3,76)} = 10.11$, $p = 0.00$). In the reverse of the picture for rejection, adult carriers were most often passive in transfers, juveniles least often. All pair-wise comparisons between means except that between parents and sub-adults were significant ($p < 0.05$, Scheffé tests).

There were no significant effects of any factor on resistance by carriers to attempts by other individuals to take infants.

Behaviour of takers

The total number of transfers that each caretaker was involved in as a taker was calculated and compared. ANOVAs showed that there were significant effects of litter size and the age-sex class of the caretaker. Takers were involved in fewer transfers per infant for singletons than for twins ($F_{(1,76)} = 6.98$, $p = 0.010$). There was a significant main effect of age class of the taker ($F_{(3,76)} = 10.14$, $p = 0.000$). Post-hoc Scheffé tests showed that juveniles were involved in significantly fewer transfers as takers than any other age class ($p < 0.05$).

There was also a significant interaction between age class and sex ($F_{(3,76)} = 4.04$, $p = 0.010$). Juvenile males were involved in significantly fewer transfers as takers than older males in any other age class, but for females, both juvenile and adult daughters were involved significantly less than either parents or sub-adults ($p < 0.05$).

The analyses were repeated using ANCOVAs to investigate the effects of group size.

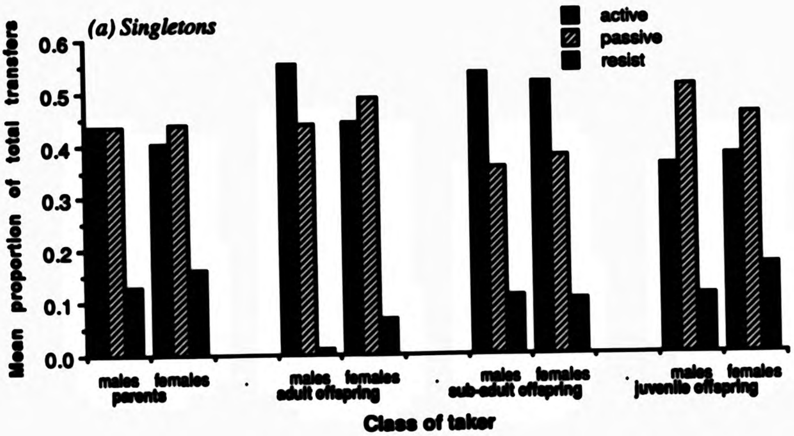
Group size as a covariate had a significant effect on frequencies of transfers ($F_{(1,75)}$ = 10.80, p = 0.002). However, controlling for group size did not alter the effects of the other factors (litter size: $F_{(1,75)}$ = 6.08, p = 0.016; age class: $F_{(3,75)}$ = 10.41, p = 0.000; sex x age class interaction: $F_{(3,75)}$ = 4.70, p = 0.005).

The proportion of total transfers that were completed was calculated for each taker. These were then subjected to ANOVAs to investigate whether any particular age-sex classes were more successful than others in obtaining infants. An ANOVA showed that the only significant effect was an interaction between litter size and the age class of the taker ($F_{(3,76)}$ = 3.83, p = 0.013). Post-hoc Scheffé tests showed that juveniles were significantly less likely to obtain an infant in twin litters (mean = 70% of transfers completed) than in singleton litters (mean = 89.6% of transfers completed). There were no other significant differences between means. ANCOVAs showed that group size had no significant effects and did not alter the effects of the other factors.

As in the case of carriers, the variations in the extent to which individuals of different age-sex classes were involved in transfers as takers meant that in order to compare different types of behaviour meaningfully, it was necessary to analyse proportions rather than actual frequencies.

The proportion of transfers in which each taker showed active behaviour, passive behaviour or resistance was calculated (fig. 4.7). ANCOVAs showed that there was a significant effect of group size on active behaviour by takers ($F_{(1,75)}$ = 4.14, p = 0.045); otherwise there were no statistically significant effects of any variable on either active or passive behaviour by takers. However, there was a tendency for mothers, adult daughters and juvenile daughters to be active takers in a smaller proportion of transfers than males in the same age classes.

ANOVAs showed that resistance by takers (i.e. rejection of infants) was significantly affected by the age class of the taker ($F_{(3,76)}$ = 4.44, p = 0.006). ANCOVAs demonstrated that group size had a significant effect ($F_{(1,75)}$ = 5.32, p = 0.024), but controlling for group size did not alter the effect of age ($F_{(3,75)}$ = 3.39, p = 0.023). Juveniles rejected infants most, adult



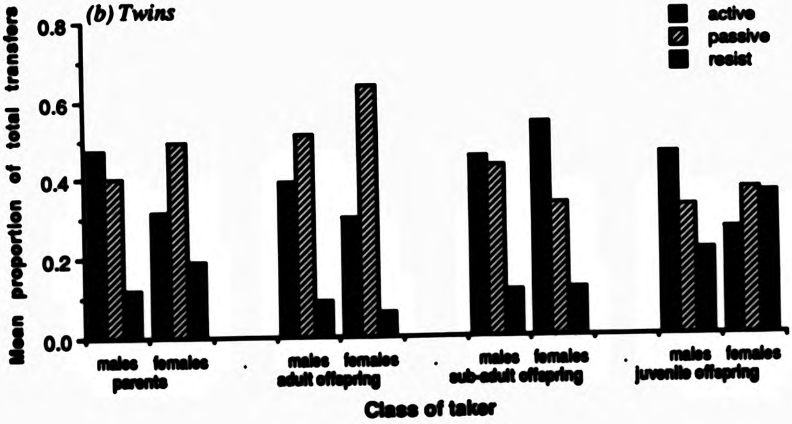


FIGURE 4.7. Behaviour of takers in transfers of (a) seven singletons and (b) seven twin litters of cotton-top tamarins. Litter means were used for twin litters.

siblings least; post-hoc pair-wise comparisons between means using Scheffé tests showed that only this comparison was significant ($p < 0.05$). Controlling for group size with an ANCOVA produced an additional effect of litter size ($F_{(1,75)} = 4.11$, $p = 0.046$), with takers rejecting a smaller proportion of transfers of singletons (mean = 0.107) than of twins (mean = 0.169). There was no significant effect of sex, although mothers and juvenile females tended to reject infants more than their male counterparts.

Behaviour of carriers according to the identity of the taker

In order to find out whether carriers were any more or less likely to allow other individuals from a particular age-sex class to take infants, the behaviour of carriers during transfers was investigated for each individual taker. Proportions were again used. ANCOVAs showed there were no effects of group size. ANOVAs showed that litter size also had no significant effects; figure 4.8 therefore combines the data from twin and singleton litters. Rejection of infants by carriers (i.e. active behaviour) was significantly affected by the sex of the taker ($F_{(1,75)} = 12.37$, $p = 0.001$): carriers were more likely to reject infants if the potential taker was a male (mean = 0.214) than if it was a female (mean = 0.099). There were no statistically significant interactions, although there was a trend towards an interaction between age and sex ($F_{(3,75)} = 2.39$, $p = 0.075$): the carrier was more likely to be active if the taker was the father rather than the mother, or an adult or juvenile male rather than a female. However, there was little difference for sub-adults.

Passive behaviour by carriers varied significantly according to the sex of the taker ($F_{(1,75)} = 6.16$, $p = 0.015$): carriers were less likely to be passive if the taker was a male (mean = 0.674) rather than a female (mean = 0.738). There was a trend towards an interaction between the age and sex of the taker ($F_{(3,75)} = 2.46$, $p = 0.069$): carriers were more likely to be passive if the taker was the mother rather than the father, or a juvenile female rather than a male, but there was little difference for adults or sub-adults.

There were no statistically significant effects on resistance by carriers to takeover attempts by other individuals, but there were trends towards effects of age ($F_{(3,75)} = 2.45$, $p = 0.070$) and

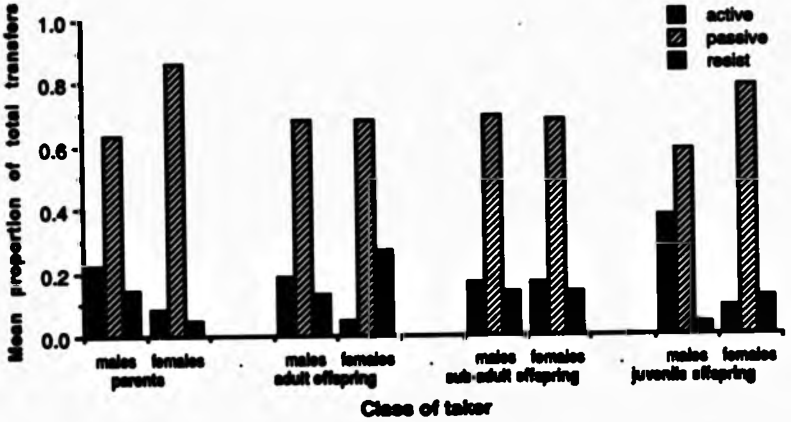


FIGURE 4.8. The behaviour of carriers during transfers in 14 litters of cotton-top tamarins according to the age-sex class of the taker.

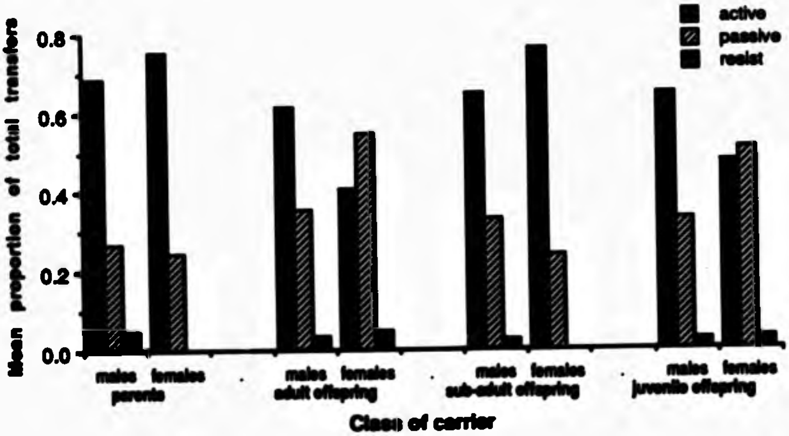


FIGURE 4.9. The behaviour of takers during transfers in 14 litters of cotton-top tamarins according to the age-sex class of the carrier.

an interaction between age and sex ($F_{(3,75)} = 2.63$, $p = 0.056$). Carriers were less likely to resist a transfer if the taker was a parent or a juvenile than if it was an adult or sub-adult. Carriers were more likely to resist if the taker was the father than the mother, but less likely if the taker was an adult or juvenile male than a female. There was little difference for sub-adults. Carriers were therefore most likely to resist a transfer if the taker was an adult daughter, and least likely if it was the mother or a juvenile male.

Behaviour of takers according to the identity of the carrier

The response of takers according to the age-sex class of the carrier was investigated to discover whether or not other individuals were more or less likely to retrieve infants from any particular class of carrier. The results are illustrated in figure 4.9. The occurrence of zero means and variances (e.g. for juvenile females) meant that the assumptions necessary for the application of parametric techniques were violated, and non-parametric tests were therefore used. There were no significant effects of litter size on any category of behaviour (Mann-Whitney U-tests), and therefore data for all litters were combined. Kruskal-Wallis one-way ANOVAs showed that takers were significantly more likely to be active if the carrier was a parent or a sub-adult than an adult or a juvenile ($\chi^2 = 7.80$, $p = 0.050$); and correspondingly, there was a strong trend for takers to be passive less often if the carrier was a parent or sub-adult ($\chi^2 = 7.50$, $p = 0.058$). Mann-Whitney U-tests within each age class produced no significant sex differences.

Interventions

Interventions by third parties occurred in only 2% (n = 122/5949) of all transfers recorded. Serious aggression - biting and chasing - was rare, but when it did occur was occasionally so severe that injury to the infant was a real possibility. In an extreme case, an adult daughter who had obtained an infant was attacked and chased by her mother, two adult brothers and a sub-adult brother, and in the ensuing struggle the infant was dislodged and fell to the floor. Fortunately it was quickly retrieved by its mother and was uninjured; however, this illustrates the potentially damaging consequences of competition to carry infants.

There was a significant positive correlation between group size and the proportion of transfers for each litter in which interventions occurred ($r_s = 0.60$, $n = 14$, $p = 0.023$, two-tailed), again suggesting that competition to carry infants is heavier in larger groups.

There were changes in the frequency of interventions with increasing age of infants (fig. 4.10), with a peak at the age of 3 weeks. To investigate whether interventions by third parties had any effect on the outcome of a transfer, the proportion of transfers that were completed both when interventions occurred and when they did not was calculated for each litter. A Wilcoxon test showed no significant difference between the proportion of completed transfers in each condition ($n = 14$, $T = 21$, $p > 0.05$), i.e. there was no evidence that interventions influenced the outcome of a transfer.

As interventions were so rare, some cells had zero means and variances. The data could not therefore be assumed to meet the requirements for parametric tests, and so in order to investigate the occurrence of interventions across different categories of caretaker, non-parametric tests were used. Kruskal-Wallis one-way ANOVAs were used to look for variations in the occurrence of interventions across age classes (parents, adult siblings, sub-adult siblings and juvenile siblings), and Mann-Whitney U-tests were used to investigate sex differences within each age class. The value used for each subject was the proportion of transfers in which interventions occurred when it was the carrier or taker.

First, the occurrence of interventions according to the identity of the potential *taker* of the infant was examined. There was a significant difference between age classes in the proportion of transfers in which interventions occurred (Kruskal-Wallis one-way ANOVA; χ^2 (corrected for ties) = 9.64, d.f. = 3, $p < 0.05$), with interventions least common if a parent was the taker. There were no significant sex differences for parents, sub-adult offspring or juvenile offspring (Mann-Whitney U-tests; parents: $n_1 = 14$, $n_2 = 14$, $U = 68.5$; sub-adults: $n_1 = 15$, $n_2 = 9$, $U = 52.5$; juveniles: $n_1 = 7$, $n_2 = 10$, $U = 25$; all $p > 0.1$). However, interventions occurred in a significantly higher proportion of transfers when adult daughters were takers than when adult sons were takers ($n_1 = 16$, $n_2 = 7$, $U = 0$, $p < 0.002$). Figure 4.11 shows that male offspring in all classes were less likely to be takers in transfers involving interventions than females were,

FIGURE 4.10. Mean frequency per 30 minutes of interventions by third parties in infant transfers in 14 litters of cotton-top tamarins. Litter means were used for twin litters. Vertical bars indicate standard errors.

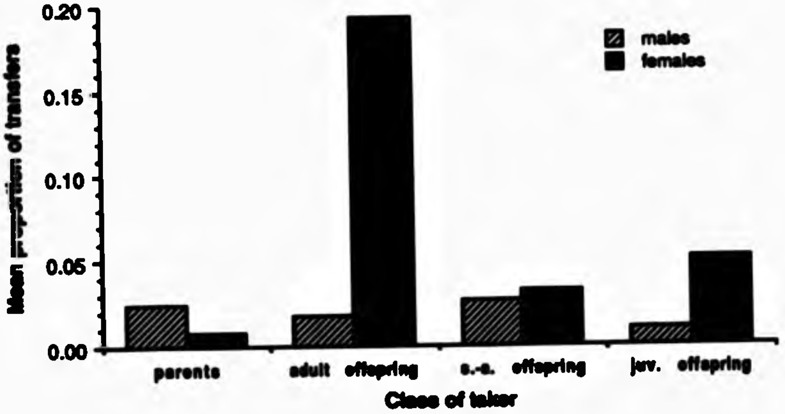


FIGURE 4.11. Proportion of transfers in which interventions by third parties occurred according to the identity of the taker.

whereas the reverse was true for parents.

Secondly, the occurrence of interventions according to the identity of the *carrier* was investigated. There was a significant effect of age class on the proportion of transfers in which interventions occurred (Kruskal-Wallis one-way ANOVA, χ^2 (corrected for ties) = 8.42, d.f. = 3, $p < 0.05$), but there were no significant sex differences in any age class (Mann-Whitney U-tests; parents: $n_1 = 14$, $n_2 = 14$, $U = 101$; adult offspring: $n_1 = 16$, $n_2 = 7$, $U = 54.5$; sub-adult offspring: $n_1 = 15$, $n_2 = 9$, $U = 53.5$; juvenile offspring: $n_1 = 7$, $n_2 = 10$, $U = 33.0$; all $p > 0.1$). As figure 4.12 shows, the likelihood of interventions was highest when parents were carriers, and lowest when juvenile offspring were carriers.

To investigate which classes of individuals were most likely to intervene in transfers, the percentage of those transfers in which a given individual could have acted as a third party (i.e. those in which it was neither carrier nor taker) that it actually did so was calculated. There was a significant effect of age class on the likelihood of intervening (Kruskal-Wallis one-way ANOVA; χ^2 (corrected for ties) = 13.80, d.f. = 3, $p < 0.01$). There were no significant effects of sex on intervention for parents, sub-adult offspring or juvenile offspring (Mann-Whitney U-tests; parents: $n_1 = 14$, $n_2 = 14$, $U = 94.5$; sub-adults: $n_1 = 15$, $n_2 = 9$, $U = 61.0$; juveniles: $n_1 = 7$, $n_2 = 10$, $U = 21.5$; all $p > 0.1$). However, there was a significant sex difference for adult offspring ($n_1 = 16$, $n_2 = 7$, $U = 17.5$, $p < 0.02$): adult daughters were never seen to intervene in transfers. As figure 4.13 shows, the individuals most likely to intervene were adult and sub-adult sons, and sons in all age classes intervened more than daughters. Sub-adult daughters also intervened relatively frequently. Juvenile offspring intervened less frequently than older offspring, and parents intervened less than offspring overall.

Response of infants to different classes of carrier and taker

ANOVAs were conducted to investigate infant behaviour during transfers in relation to the identity of the carrier and taker involved. Proportions of total transfers that involved each type of infant behaviour (*active*, *passive*, or *resistance*) were calculated and subjected to ANOVAs, using the age class of the carrier or taker, its sex, and litter size as group factors. Means per infant

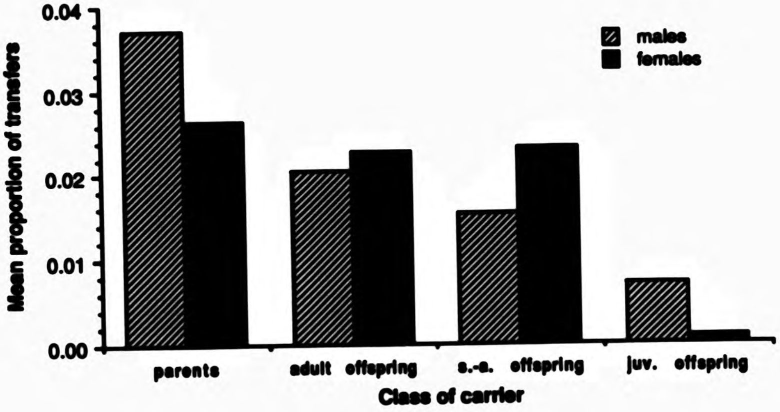


FIGURE 4.12. Proportion of transfers in which interventions by third parties occurred according to the identity of the carrier.

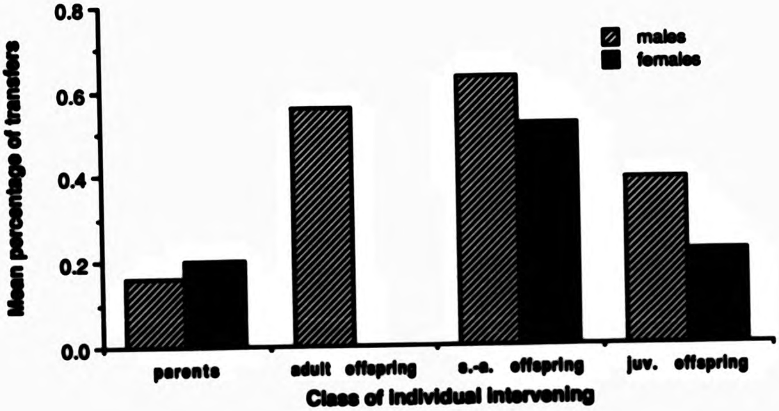
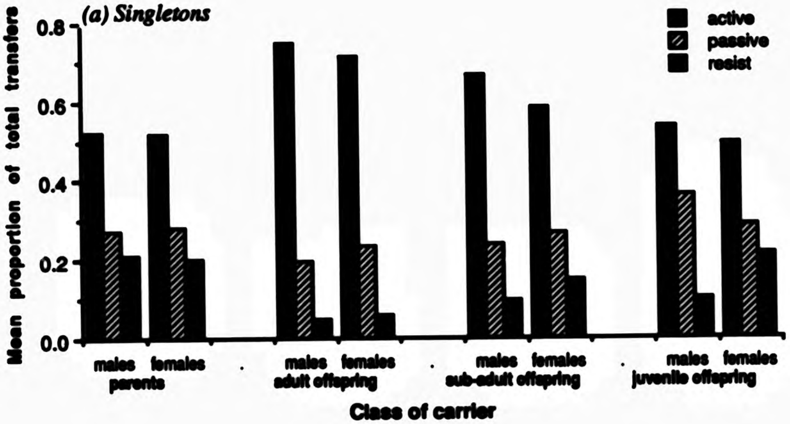


FIGURE 4.13. The percentage of transfers in which individuals of different age-sex classes intervened as third parties.

were used for twin litters. Repeating the analyses with ANCOVAs demonstrated that group size had no significant effects; therefore only the results of the ANOVAs are reported.

The effects of the age-sex class of the *carrier* on each category of infant behaviour are illustrated in figure 4.14. There were no significant effects of sex of carriers on any measure. The only significant effect on active behaviour by infants was of age class of the carrier ($F_{(3,76)} = 3.44$, $p = 0.021$): infants were most likely to actively leave adult carriers, and least likely to leave parents or juveniles. Post-hoc Scheffé tests demonstrated that the differences between adults and parents, and between adults and juveniles, were significant ($p < 0.05$). The only significant effect for passive behaviour by infants was the interaction between age class of the carrier and litter size ($F_{(3,76)} = 2.84$, $p = 0.043$). Post-hoc Scheffé tests showed that the only significant difference between means occurred in twin litters, where infants were passive significantly less when the carrier was a juvenile than when it was a sub-adult ($p < 0.05$). There were significant effects on resistance by infants for age class of the carrier ($F_{(3,76)} = 5.28$, $p = 0.002$), litter size ($F_{(1,76)} = 9.15$, $p = 0.003$), and the interaction between these two factors ($F_{(3,76)} = 3.95$, $p = 0.011$). Twins resisted attempts to remove them from carriers more than singletons. All infants resisted transfers off both parents and juveniles significantly more than off adult sibs ($p < 0.05$, Scheffé tests). However, while singleton infants were most resistant to transfers off parents (Scheffé tests showed that the differences between parents and both adult and sub-adult sibs were significant; $p < 0.05$), twins resisted transfers off juvenile sibs most (the differences between juveniles and both parents and adult sibs were significant; $p < 0.05$, Scheffé tests).

The effects of the age-sex class of the *taker* on each category of infant behaviour are illustrated in figure 4.15. There were no statistically significant effects on active behaviour by infants, although there was a trend towards an effect of the age class of the carrier ($F_{(3,76)} = 2.42$, $p = 0.072$): both twins and singletons were most likely to be active if the taker was a parent, particularly the mother; singletons were also more likely to be active in transfers on to juveniles than on to adult or sub-adult siblings. There were no significant effects on passive behaviour by infants. Resistance by infants was significantly affected by the age class of the


(a) Singletons

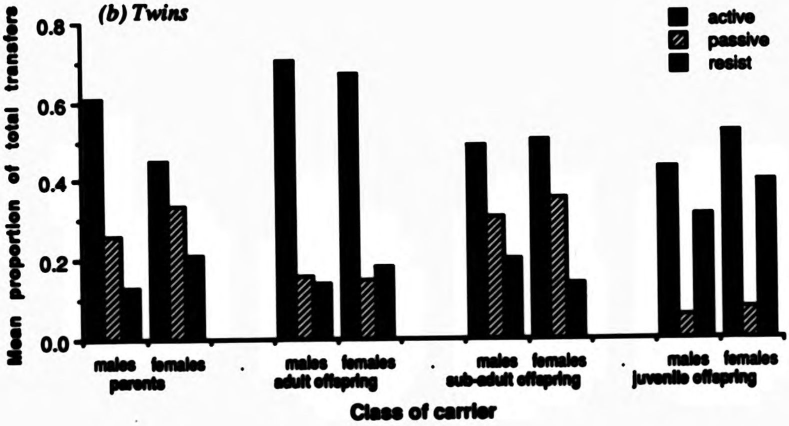
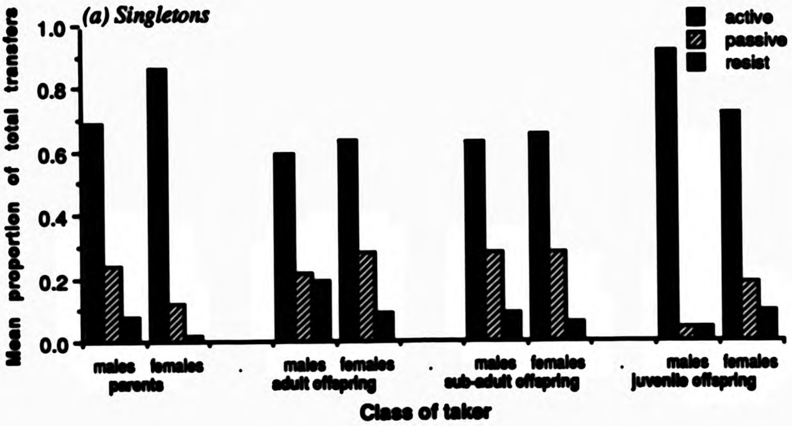

(b) Twins

FIGURE 4.14. Behaviour of infants during transfers in relation to the identity of the carrier in (a) seven singletons and (b) seven twin litters of cotton-top tamarins. Litter means were used for twin litters.



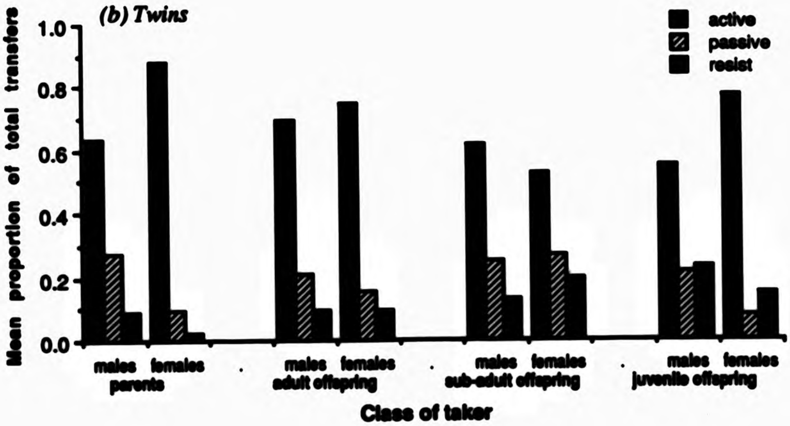


FIGURE 4.15. Behaviour of infants during transfers in relation to the identity of the taker in (a) seven singletons and (b) seven twin litters of cotton-top tamarins. Litter means were used for twin litters.

taker ($F_{(3,76)} = 2.82$, $p = 0.044$), although post-hoc Scheffé tests produced no significant differences between pairs of means. Both twins and singletons resisted attempts by parents to take least; however, while twins were most likely to resist if the taker was a juvenile, singletons were most likely to resist if the taker was an adult sibling. Consequently, there was a trend towards an interaction between age class and litter size ($F_{(3,76)} = 2.36$, $p = 0.078$). There was also a strong trend towards an effect of litter size ($F_{(1,76)} = 3.72$, $p = 0.057$): takers in families with singletons were resisted by infants on a smaller proportion of transfers (mean = 0.082) than those in groups with twins (mean = 0.114).

Discussion

Development of infant independence

As predicted, the frequency of infant transfers in cotton-top tamarins initially increased as infants got older, but then declined as they approached complete independence. Infants were initially passive in transfers, but as they developed locomotor skills they became primarily responsible for initiating transfers. Similarly, Lindsay (1979) also found that transfers in *S. geoffroyi* increased in frequency as infants grew.

Carriers resisted takeovers only in the first few weeks. This could either be because competition is heavier in these weeks, or because infants are more vulnerable and carriers make more attempts to prevent some individuals from taking infants. As the weight of infants increases it is also less likely that a carrier will prevent another individual from taking over the task of carrying. Pryce (1988) also found that "retrieving" (i.e. actively taking infants) and "retaining" (i.e. resisting other individuals' attempts to take over) by *S. labiatus* caretakers were most common with young infants.

Rejection of infants by carriers and takers increased over time. In marmosets, the onset of infant independence appears to be largely controlled by rejections from parents and helpers (*Callithrix jacchus*: Ingram 1977; Locke-Haydon & Chalmers 1983; Arruda *et al.* 1986; *C. argentata melanura*: Buchanan-Smith 1984). This also appears to be true of *S. labiatus* (Pryce 1988; H. Buchanan-Smith, pers. comm.). However, in cotton-top tamarins, the infants themselves initially promote their independence: a comparative study of *C. jacchus* and *S. oedipus* (Tardif *et al.* 1986*b*) showed that infant marmosets were off more in weeks 5-8, and were rejected significantly more than infant tamarins, but that tamarin infants exhibited more infant-initiated transfers off carriers. Tardif *et al.*'s results were confirmed in the present study: the early explorations of infants were initiated by the infants themselves.

The reason for this species difference is not entirely clear. Tardif *et al.* (1986*b*) suggested that the energy demands of rearing a given infant may be less for *C. jacchus* groups than for *S. oedipus* groups. However, although the total energy required may be less for marmosets if the infants are carried for a shorter period, seen from a slightly different perspective these results also suggest that marmosets are less able to bear the energetic costs of infant care, and therefore are forced to promote infant independence earlier. This is supported by the fact that in the present study, singleton infants, which at a given age are presumably less energetically costly to carry than twins, were carried more and rejected less than twin infants. In addition, twins resisted transfers off carriers more than singletons did, while attempts to take were resisted less by singletons than by twins. This is again consistent with the finding of the present study (chapter 3) that singletons were carried for a greater amount of time than twins.

There was little evidence in this study that the behaviour of infants or caretakers varied in any way with the sex of the infant, and indeed, only one study has reported differences in transfer behaviour according to infant sex: Ingram (1977) found that infant female common marmosets tended to be rejected more than males.

Different caretakers varied in the pattern of behaviour they showed over time. Mothers rejected infants most in the first few weeks, fathers least. However, after infants reached the age of six weeks, both parents tended to reject more than older siblings. Siblings resisted up to 40% of attempts by other individuals to take infants from them. Fathers also resisted as carriers (and at the same level as sibs in weeks 2), but mothers rarely did so. Fathers also actively took infants at the same level as sibs in week 2. Mothers were the least active takers in weeks 1-3, but the most active later on. The prediction that mothers should reject infants more frequently than fathers was confirmed.

Infant preferences

There was evidence that infants preferred to be carried by some individuals rather than others. Infants were most likely to climb off adult or juvenile siblings but least likely to leave their parents. Infants also resisted moving off parents and juveniles most, but adult siblings least. Both twins and singletons were most likely to actively initiate a transfer if the taker was a parent, particularly the mother, and also to resist attempts by parents to take them less; singletons were also more likely to be active in transfers on to juveniles than on to adult or sub-adult siblings. Locke-Haydon (1984*b*) also concluded that rejection by mothers may be most traumatic for *Callithrix jacchus* infants, as they tended to follow such rejections by attempting to climb on to the individual most likely to carry them, their father. This also suggests that infant prefer to be carried by their parents.

Thus the predictions outlined in the introduction to this chapter were only partially confirmed: infants did appear to have a preference for their parents as carriers, but there was little indication that they preferred older siblings over younger ones. Some of the transfers on to juveniles may have represented the beginnings of playful behaviour: infants play most with the older sibs closest to them in age (personal observation). The high levels of carrying observed by adult offspring, especially adult males (see chapter 3), are therefore not apparently due to a preference by infants for these individuals.

Control and competition

In parallel to the results for carrying presented in chapter 3, juvenile males and females, and adult daughters, were involved in fewer transfers than other age-sex classes. The data presented in this chapter suggest that the distribution of carrying was affected both by competition and by control, as well as by each individual's own motivation to carry. Competition and control are likely to be related: competing to carry necessarily involves attempting to maximise one's own carrying and limit that of others. However, some behaviour appeared to be directed at controlling the carrying of specific classes of individuals, and I will therefore consider them separately.

There were several lines of evidence indicating that some individuals were controlling the carrying activities of others. Carriers were more likely to reject an infant if the potential taker was a male than if it was a female; there was also a trend towards greater resistance by carriers to takeovers by others if the taker was an adult daughter, and less resistance if the taker was the mother or a juvenile daughter. This suggests that other family members try to limit carrying by females, particularly adult daughters. Juvenile daughters taking infants may be less likely to be resisted by carriers as they need experience; it also makes sense for carriers not to resist attempts to take by a mother as she is the primary source of nutrition for young infants. However, tamarins tended to actively retrieve infants more from parents and sub-adults, which does not fit with the prediction that older individuals should attempt to take infants from juveniles.

Interventions in transfers by third parties were uncommon, and were least frequent if the taker was a parent, especially the mother. They occurred more often if the taker was a sibling, especially a female, and appeared to be particularly directed at adult daughters taking infants. On the other hand, interventions were most frequent if a parent was carrying, and least frequent if the carrier was a juvenile. This provides support for the idea that caretakers as well as infants might perceive the mother as being a "better" caretaker.

There was therefore some evidence to support the predictions outlined in the introduction to this chapter that other family members might attempt to limit carrying by juveniles, and by adult daughters, although there is no obvious reason why adult daughters should be singled out for such treatment: all those observed were competent caretakers and never abused infants.

Reports of control in other species are uncommon and generally lacking in detail. Snyder (1974) reported that an adult female *L. rosalia* chased a juvenile female who had a five-day-old infant and retrieved it. Bucher & Anzenberger (1980) found that transfers from dominants to subordinates in *Callithrix jacchus* were of a different type than transfers in the opposite direction, although details were not given. In Pryce's (1988) study of *S. labiatus*, parents most frequently retained infants against siblings when infants were young. This suggests that parents tried to control carrying by inexperienced individuals when infants were most vulnerable. Pryce also suggested that fathers might be selected to regulate carrying by mothers because of milk production, since fathers "retained" infants (i.e. successfully resisted attempts to take infants from them) more against mothers than against sibs, while the opposite was true for mothers - they retained more against sibs than against fathers.

There was also evidence that individuals competed to carry infants. As predicted, transfers were more frequent in larger groups, although only attempted transfers were more frequent in singletons than in twins. Active behaviour by takers, resistance to takeovers by carriers, and interventions, all increased in larger groups, while rejection of infants by both carriers and takers decreased. Thus individuals in larger groups were less likely to reject infants, more likely to actively take, and more likely to resist takeovers. A reduction in infant rejection could be explained by the reduction in the costs of infant care to individuals produced by spreading carrying duties among a larger number of caretakers. However, there would be no reason to resist takeovers or actively take infants more often if this was the only explanation.

I also predicted variations in the degree of competition to carry shown by particular individuals: specifically, that adult sons and juvenile daughters would compete most. However, although as expected adults rejected infants least when carrying, juveniles did so most. This does not support the prediction that young tamarins should try and gain as much experience in carrying as possible; however, it is perhaps not surprising given that juveniles are not fully grown and thus infants are likely to be a greater burden on them.

There was some evidence to support the prediction that mothers should reject more and actively take infants less than fathers. Perhaps surprisingly, there were also indications that fathers do compete to carry infants despite the presence of helpers: fathers were seen to resist attempts to take by other individuals, and to actively take infants, at levels that sometimes reached those shown by sibs. Tardif *et al.* (1989*a*), in another study of cotton-top tamarins, also found that fathers were more likely to actively retrieve infants than mothers were. Furthermore, although there were no effects of group size on maternal behaviour in the present study (mothers in larger groups were no more or less likely to reject infants or take them than those in smaller groups), group size influenced the behaviour of fathers as well as that of siblings: fathers in larger groups rejected infants less and actively took them more; siblings in bigger families also rejected less, although they did not actively take more.

Adult daughters never intervened in transfers involving other caretakers; the individuals most likely to intervene were adult sons and sub-adult sons and daughters. Parents intervened less than offspring. This suggests that sub-adult offspring and adult sons were more competitive and more likely to attempt to limit carrying by other family members. There were, however, no clear sex differences in the proportion of active attempts to take infants or resistance by carriers to takeover attempts by others. Thus the distribution among age-sex classes of carrying by offspring may be attributable less to differences in the extent to which individuals are motivated to compete than to other factors, notably control by others.

Locke-Haydon & Chalmers (1983) have proposed that the amount of time infant common marmosets are carried is controlled primarily by the tendency of caretakers to reject, and that caretakers do not compensate for high levels of rejection by others. Their model suggests that at each age, there is a tendency for an infant to seek and for each caretaker to offer an age-specific amount of care. If the amount of care sought by infants is more than the amount that caretakers are willing to provide, this predicts no competition and no compensation. A study in which the care given by fathers and older sibs was experimentally reduced by drugging them (Locke-Haydon 1984*a*) supported the idea that no compensation or competition would occur, although there was no evidence that infants spent more time seeking care when carriers were drugged.

The situation in tamarins appears to be different: both this study and that of Pryce (1988) found evidence of competition. Pryce's (1988) study of *S. labiatus* showed that the distribution of infant carrying in a tamarin family was determined not only by the individual characteristics of particular carriers, but also by interactions with other group members, and provided the first quantitative evidence of competition to carry infants: the amount of carrying was determined both by an individual's own competitive behaviour and that of other family members, and thus group members can have a marked effect on the caretaking behaviour of other individuals: individuals who retained more carried more. The data presented in this chapter confirm these findings.

One possible explanation for these differences is as follows. As discussed above, cotton-top tamarin infants, unlike common marmosets, initiate their own independence to begin with, rather than being rejected by caretakers, and this suggests that caretakers are willing to provide more care than infants seek, at least in the early stages of the development of infant independence. However, there are also other possible explanations, particularly given that Ingram (1977) and Arruda *et al.* (1986) found that other group members *would* compensate for the loss or lack of care from some caretakers in common marmosets. Group size may be one important factor, although Pryce (1988) also had small group sizes in his study of tamarins (a maximum of five non-infants, and no adult offspring). Thus Locke-Haydon & Chalmers' model may be more applicable to marmosets and/or to small families.

In conclusion, the results presented in this chapter suggest that infant transfers may be a useful way of studying the distribution of care in a callitrichid family. However, other factors might also influence behaviour. For example, if threats are directed to individuals *before* they attempt to take, they may not even try. Prior experience might also have an effect; for example, an individual who has been threatened before may be reluctant to make any further attempts. These factors could not be assessed in the present study, and remain to be investigated in detail.

It is also important to discover *why* caretakers might only be willing to provide a certain maximum amount of care to infants. An obvious explanation is that caring for infants involves certain costs to the caretaker. This is investigated in the following chapter.

Summary

(1) Transfers of infants in families of cotton-top tamarins increased in frequency from birth to six weeks, and then declined.

(2) Infants were initially passive in transfers, but became more active as they gained independence. Caretakers actively took infants and prevented other individuals from taking them most in the early weeks. Infants were responsible for initiating their independence, but as they got older, they were rejected more frequently by caretakers.

(3) Infants preferred to be carried by parents rather than siblings, but did not prefer older sibs to younger ones.

(4) Mothers rejected infants more frequently than fathers; young tamarins rejected infants more than older tamarins. Singletons were rejected less than twin infants.

(5) Individuals in larger groups were less likely to reject infants, more likely to actively take infants, more likely to resist attempts by others to take, and more likely to intervene in transfers, suggesting increased competition to carry in large groups.

(6) There was evidence that carrying by juvenile siblings and by adult daughters was limited by other group members.

(7) There was evidence that adult sons and sub-adult sons and daughters competed most strongly, and were more likely to attempt to control carrying by other group members.

Chapter 5

The costs of infant carrying

A. Changes in the behaviour of tamarins carrying infants

Introduction

In marmosets and tamarins, the additional costs of transporting twin infants over and above those that all female primates incur in pregnancy and lactation (Altmann 1980, 1983) appear to be so great that females require assistance to rear twin offspring successfully (Garber *et al.* 1984; Goldizen 1987*a*; Dunbar 1988). It therefore seems reasonable to assume that by aiding breeders in caring for offspring, helpers in callitrichid groups incur immediate costs in terms of expenditure of time and energy, although they may gain compensating benefits (see chapter 1).

Taylor *et al.* (1980, cited in Dunbar 1988), have shown that an animal carrying a weight consumes additional energy in direct proportion to the ratio of the carried weight to its own body weight. Thus, an adult cotton-top tamarin weighing about 500-600g (see chapter 2) carrying twin neonates weighing about 50g each (see figure 5.1) will consume up to 20% more energy. It follows that callitrichid helpers are paying energetic costs by carrying infants. Preliminary data from field studies of tamarins suggest that in addition, carriers are unable to feed and forage at normal levels. For example, Terborgh & Goldizen (1985, p. 297) noted in a field study of the saddle-back tamarin (*Saguinus fuscicollis*) that an individual carrying infants "travels in a conspicuously labored fashion in the cover of the understory and neither feeds nor insect forages". Goldizen (1987*a*) provided quantitative data on these changes in the behaviour of tamarins carrying infants: although adult tamarins normally spent 10-15% of their time feeding, carriers of infants spent only about 5% of their time feeding.

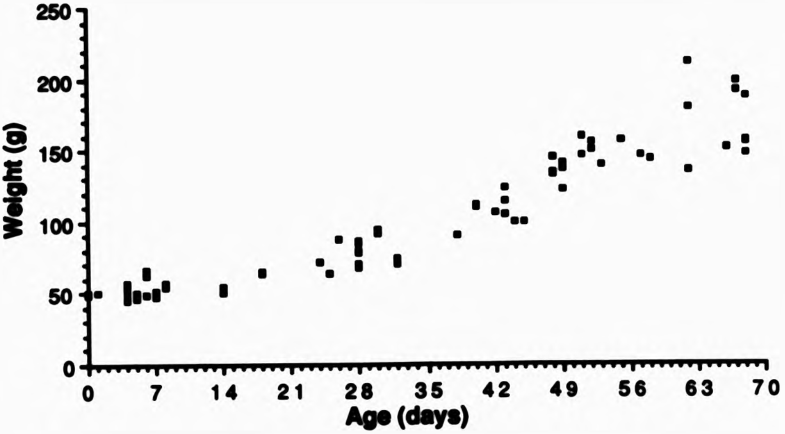


FIGURE 5.1. Changes in the weight over the first ten weeks of life of infant cotton-top tamarins born in the Stirling colony between 1/6/82 and 16/11/88. Infant weights were obtained on an opportunistic basis whenever infants were caught up to be marked for identification purposes. Each point represents one of 72 weight records from 59 infants. Individual infants contributed either one or two records.

In captivity, however, the relative ease with food could be obtained may mean that infant carrying involves few costs (Goldizen 1989). One major aim of this section of the study was therefore to investigate whether similar changes in feeding time and other behaviour would occur in captive tamarin helpers, and to quantify these changes in an attempt to see if helpers were indeed incurring costs.

A second aim of the study was to investigate reasons why any such changes might occur. Two possible explanations suggest themselves. First, as Terborgh & Goldizen (1985) remarked, carriers appear to have difficulty moving, and thus one possibility is that general mobility might be decreased, leading to difficulty in reaching food sources and catching live prey. To investigate this, data were collected on behaviour that required mobility in the limbs: scratching, auto-grooming and scent-marking. These were the only correlates which could be practically assessed without disruptive experimental manipulation.

A second, not necessarily competing, explanation is that carriers need to spend more time in vigilant behaviour in order to protect vulnerable infants, as well as themselves, from predators. Since vigilance is incompatible with foraging, this may lead to reduced feeding times. Predator pressure may be considerable in these small species (Terborgh 1983), and predation on tamarins in the wild by raptors and snakes has been witnessed: Terborgh (1983) saw a juvenile *S. fuscicollis* taken by a small hawk, and an adult emperor tamarin (*S. imperator*) being carried by an ornate hawk eagle (*Spizaetus ornatus*). Tamarins in the same population are also known to have been eaten by ocelots, *Felis pardalis* (Goldizen 1987*b*). Heymann (1987) observed predation by an anaconda (*Eunectes murinus*) on an adult female moustached tamarin (*Saguinus mystax*). Goldizen (1987*b*) also reported that unsuccessful raptor attacks on tamarin groups occurred every one or two weeks, and wild tamarins frequently respond to potential predators by giving alarm calls or mobbing. Bartecki & Heymann (1987), for example, saw a group of *S. fuscicollis nigrifrons* mobbing two snakes (*Corallus enydris*), while Goldizen (1987*b*) remarked that *S. f. weddelli* gave frequent false alarms about once an hour throughout the day, and there was usually at least one adult tamarin scanning for predators at all times. A series of studies of captive *S. labiatus* by Caine (1984, 1986, 1987, 1990; Caine & Marra 1988) has demonstrated that vigilance remains important to tamarins even in the predator-free conditions of captivity. Cotton-top tamarins in the Stirling colony also frequently responded with characteristic alarm calls to overhead movements, such as birds flying over the skylights, and mobbed unfamiliar stimuli with loud vocalisations (type A chirps and slicing screams (Cleveland & Snowdon 1982); personal observation). Thus, if tamarins carrying young need to be especially vigilant, either to protect the infants, or because they are themselves less able to escape potential threats, they may have less time available to devote to activities such as foraging which require their attention to be directed away from sources of potential danger. To investigate this, data on aspects of vigilant behaviour were collected.

The initial design of this study allowed for comparisons of changes in behaviour according to the number of infants carried, and with the age of infants. However, it became apparent soon after the study was initiated that collecting sufficient adequately-controlled data would be difficult, as competition among family members to carry infants (see chapter 4) meant that infants frequently changed carriers and carrying bouts were therefore short. In addition, in larger families it was uncommon for infants to be carried by the same individual (see chapter 3). The focus of the study was therefore narrowed to concentrate on the effects on behaviour of carrying one infant, versus carrying no infants. Although a more detailed study that takes account of these other factors is needed, pilot studies, and also previous field work (Goldizen 1987*a*) suggested that there were likely to be few additional effects of carrying more than one infant.

If changes in behaviour did occur, I predicted that there would be a decrease in time spent feeding, foraging and moving while carrying an infant. Preliminary observations also suggested that, since the tamarins tended to forage in particular areas of the cage, notably the floor, changes in use of space might also occur. The reduced mobility hypothesis predicts that tamarins carrying infants should show reduced movement and levels of behaviour such as scratching. The increased vigilance hypothesis predicts that tamarins carrying infants should show more behaviour aimed at detecting potential predators.

Methods

Subjects and housing

The subjects for this study were drawn from five families of cotton-top tamarins. All subjects except one breeding male (Elvis) were captive born. Three groups lived in separate rooms, one was housed in a type I colony cage, and the remaining group lived in two type II colony cage units. For further details of housing and husbandry, see chapter 2.

Because of the difficulty of predicting in advance which members of a family were likely to carry infants most frequently, no attempt was made to select subjects prior to birth. The only exception to this was that no data were collected from breeding females. There were two reasons for this: (1) nursing infants may have had qualitatively or quantitatively different effects on behaviour than carrying them dorsally; and (2) females showed marked changes in behaviour associated with lactation (primarily marked increases in feeding and foraging, and decreases in social interactions; see chapter 6) that may have influenced the results.

Data were collected from any individual who carried an infant during an observation session. Two hours proved to be the maximum amount of data that it was feasible to collect if both carrying and non-carrying data were to be collected from the same subjects and matched for time of day. However, since some individuals carried more than others (see also chapter 3), sufficient data for analysis were obtained only from 11 adult and sub-adult male tamarins (see table 5.1). Data collected from other individuals was discarded.

Behavioural categories and recording methods

Data were collected on checksheets divided into 15-second intervals. The focal subject's activity was recorded using instantaneous sampling, and classified into one of seven exhaustive and mutually exclusive categories: *sit*, *locomote*, *feed*, *forage*, *affiliative* (i.e. allogrooming and affection), *play*, or *other* (including aggressive and sexual behaviour). Observations of the first subject (Fideaux) suggested that use of space might also be affected by carrying infants, and therefore, although not recorded for Fideaux, data on cage location were collected from the

TABLE 5.1. Details of the subjects observed during the investigation of the costs of carrying.

Family and litter	*Subject*	*Age-sex class*	*Infant age (days)* *(a) during carrying condition*	 *(b) during control condition*
Erica Twins 20/5/88	Fideaux	Breeding male	2-6	5-42
Roxanne Triplets 19/1/89	Elvis	Breeding male	1-7	32-36
	Alistair	Adult son	1-2	33-38
	Vincent	Sub-adult son	1-6	32-37
	William	Sub-adult son	1-11	32-36
Elsa Twins 3/3/89	Romulus	Adult son	4-6	22-33
	Zeus	Sub-adult son	5-7	23-34
Shoshone Twins 17/4/89	James	Adult son	1-3	24-35
	Kansas	Sub-adult son	1-5	22-34
Delaware Twins 22/4/89	Arnold	Breeding male	1-7	19-33
	Alan	Adult son	1-7	18-31

remaining ten subjects. The subject's location (classified as being in the *upper*, *middle* or *lower* third of the cage) was again recorded using instantaneous sampling, as were spatial relationships with other group members (*solitary*, *near* or *contact*). In addition, actual frequencies of *autogrooming*, *scratching* and *anogenital scent- marking* were recorded. Definitions of these behavioural categories can be found in chapter 2.

Two methods of assessing vigilance were used. A measure of vigilance, *look up* (see plate 5.1) was operationally defined as looking directly up at the skylight or ceiling (excluding looking at other family members), and was scored using one-zero sampling. *Alarm calls* were also recorded with one-zero sampling; the following vocalisations were considered alarm calls: Type A chirp, slicing scream, Type E chirp, Type E chirp chatter, inverted U + whistle call (all descriptions of vocalisations followed Cleveland & Snowdon (1982), and all calls were grouped together for analysis).

Procedure

Data collection commenced as soon as infants were born into a group. Two hours of data were collected from each subject using focal animal sampling for each of two conditions: (1) *carry infant* (carrying one and only one infant); and (2) a control condition, *not carrying* (carrying no infants). Infants in Stirling approximately doubled their weight over the first six weeks of life, with the most rapid weight gain beginning in about the third week (fig. 5.1). Dronzek *et al*. (1986) recorded an increase in weight of 6% over the first two weeks of life in hand-reared cotton-top tamarins, but a 37% increase between weeks 2 and 4. Data for the *carry infant* condition were therefore collected only during the first two weeks of life (see table 5.1), to minimise additional changes in behaviour resulting from increased age and therefore weight of the infants. Observations on a given subject were spread over at least three days in each condition. Attempts were also made to make observations at various different times of day, although this was not always easy due to the difficulty of predicting when and for how long a given individual would carry an infant. Observation sessions varied in length according to the length of the carrying bout, but were at most 45 minutes long, in order to ensure that the data for each subject came from at least three different sessions. Thus, data for a given subject

PLATE 5.1

A breeding male cotton-top tamarin "looking up" at the skylight overhead.

were collected from three or more observation sessions until two hours had been accumulated; data collection for that subject then ceased.

Almost all the data for the control condition were obtained after data collection for the *carry infant* condition had been completed (see table 5.1). Although it could be argued that it would have been best to collect both types of data over the same period, this method was chosen for two reasons: (1) It allowed control data collection to be accurately matched for time of day to the *carry infant* data, and was similar to the timing of observations in Goldizen's (1987*a*) field study; (2) Because tamarins who carried sufficiently often during the first fortnight to be subjects continued to carry a great deal in the following weeks, it was often extremely difficult to obtain data for the *not carrying* condition until the infants began to move independently, especially given the constraint that time of day had to be matched. However, all control data were collected before infants reached the age of six weeks (i.e. while the infants were still almost entirely dependent; see chapter 3), to ensure that the simple presence or absence of young infants in the family was not contributing substantially to any observed changes in behaviour.

All data were analysed using non-parametric techniques for matched samples (Siegel 1956).

Results

Changes in activity

There were marked changes in the behaviour of individuals carrying infants. Figure 5.2 shows the changes in activity that occurred, and table 5.2 gives the results of statistical analyses carried out on the data. Time spent sitting was greater when tamarins were carrying infants, while time spent locomoting, feeding, foraging and engaging in social activities (affiliation and play) was lower. All the differences between the two conditions were statistically significant, with the exception of the category *other*, which showed no difference between the two conditions. Associated with these changes in activity, frequencies of autogrooming, scratching and anogenital marking were significantly lower when subjects were

TABLE 5.2. Results of Wilcoxon tests performed on data obtained from 11 male cotton-top tamarins when carrying an infant and when not carrying.

Behavioural category	*N*	*z value*	*p (2-tailed)*
Activity			
Sit	11	-2.93	0.003
Locomote	11	-2.93	0.003
Feed	11	-2.93	0.003
Forage	11	-2.93	0.003
Affiliative	11	-2.60	0.009
Play	11	-2.67	0.007
Other	11	-0.18	0.859
Other behaviour			
Autogroom	11	-2.80	0.005
Scratch	11	-2.85	0.004
Anogenital mark	11	-2.80	0.005
Spatial relationships			
Solitary	11	-2.93	0.003
Near	11	-1.11	0.266
Contact	11	-2.93	0.003
Location in cage			
Upper	10	-2.80	0.005
Middle	10	-2.80	0.005
Lower	10	-2.80	0.005
Vigilance behaviour			
Look up	11	-2.93	0.003
Alarm call	11	-1.72	0.086

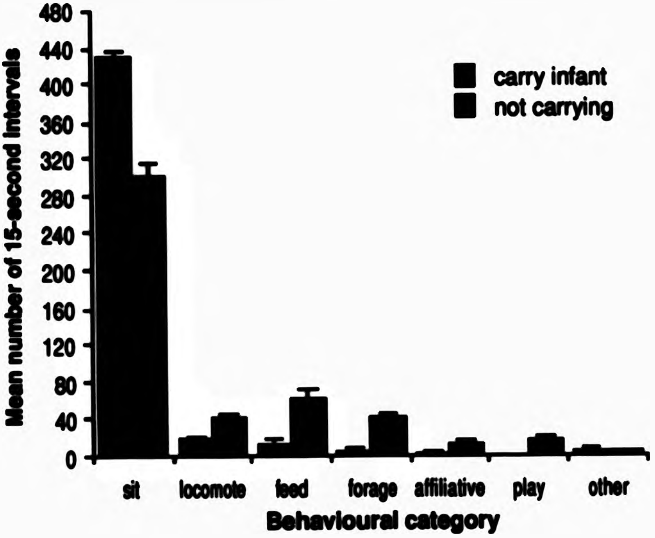


FIGURE 5.2. Mean number of 15-second intervals in two hours observation that 11 male cotton-top tamarins spent in seven categories of activity when carrying an infant and when not carrying. Vertical bars indicate standard errors.

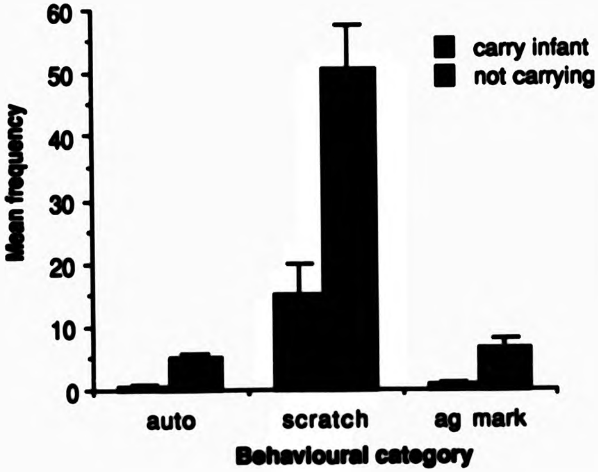


FIGURE 5.3. Changes in the actual frequencies of three categories of individual behaviour (autogroom [auto]*, scratch, and anogenital scent-mark* [ag mark]*) for 11 male cotton-top tamarins when carrying an infant and when not carrying. Vertical bars indicate standard errors.*

carrying an infant (fig. 5.3).

The same data are presented in the form of a time budget in figure 5.4, which shows that carriers spent most of their time sitting (90%, compared with 63% when not carrying), and very little time moving, feeding, foraging or engaging in any social activities. For example, carriers spent only 3% of their time feeding and 1% foraging, compared to 13% feeding and 9% foraging when not carrying.

Changes in spatial relationships

The tamarins spent considerably more time in contact with other family members (53% versus 17%) , and less time solitary, i.e. more than 20cm from any other group member (30% versus 71%), when they were carrying infants (fig. 5.5). These differences were statistically significant (table 5.2). Time spent near other individuals did not differ between the two conditions.

Changes in cage location

The effect of carrying an infant on the way tamarins used different areas of the cage is shown in figure 5.6. Carriers spent almost all their time (90%) in the upper third of the cage or room. Only 0.5% of their time was spent in the lower third. When not carrying infants, the tamarins spread their time more evenly through the cage, although they still spent more time in the upper third (53%, compared with 33% in the middle areas and 14% low down). The differences in cage use between the two conditions were statistically significant (table 5.2).

Changes in vigilance

In contrast to effects on activity, the results for vigilance behaviour were unexpected. There was no significant effect of carrying an infant on alarm calling by the focal subject, although it occurred in slightly fewer intervals when tamarins were carrying. There was a significant decrease in the number of intervals in which *look up* behaviour occurred when subjects were carrying infants (fig. 5.7; table 5.2).

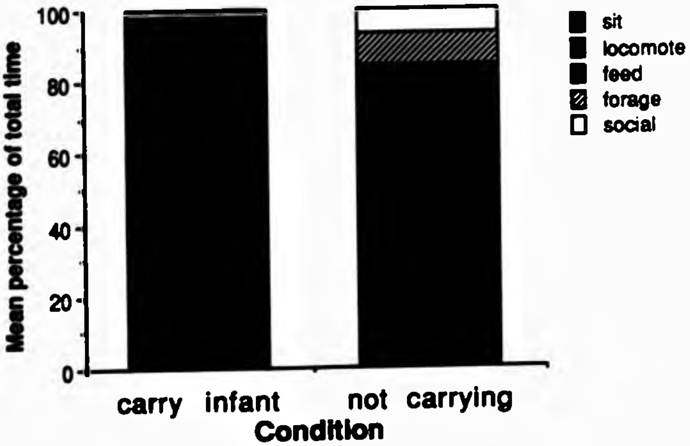


FIGURE 5.4. Mean percentage of two hours observation time spent by 11 male cotton-top tamarins in each of five behavioural categories when carrying an infant and when not carrying. (Social = affiliative + play + other).

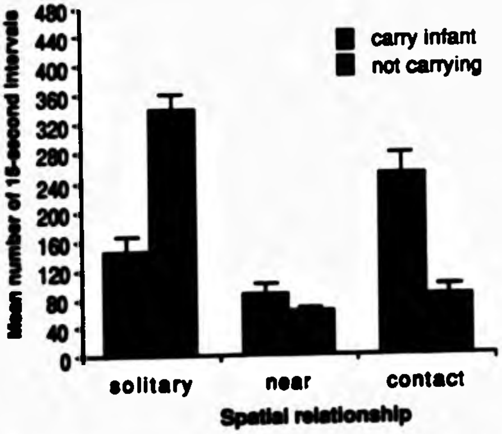


FIGURE 5.5. Changes in the spatial relationships of 11 male cotton-top tamarins when carrying an infant and when not carrying. Vertical bars indicate standard errors.

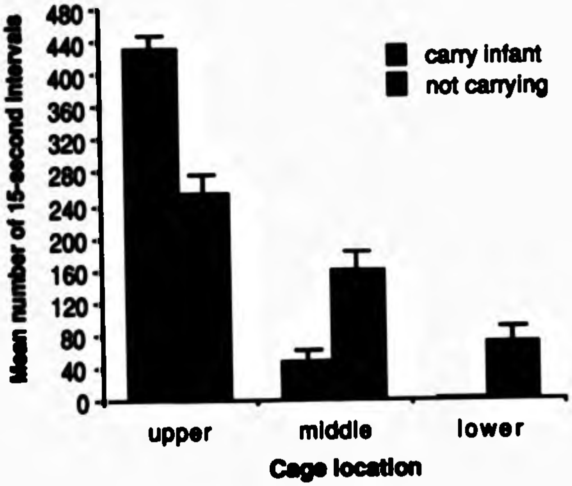


FIGURE 5.6. Changes in the use of space by 11 male cotton-top tamarins when carrying an infant and when not carrying. Vertical bars indicate standard errors.

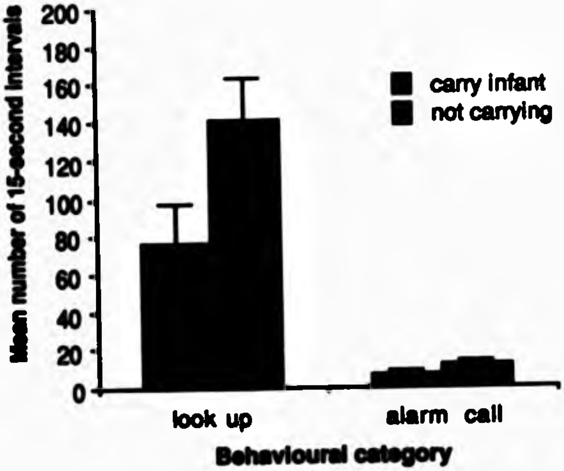


FIGURE 5.7. Changes in the number of 15-second intervals during which look up behaviour and alarm calling occurred in 11 male cotton-top tamarins when carrying an infant and when not carrying. Vertical bars indicate standard errors.

Conclusions

Most of the expected effects of carrying an infant on the activity of cotton-top tamarins occurred. When carrying infants, tamarins spent much less time feeding, foraging or moving. The changes in use of space suggested by changes in cage location were expected given the lack of feeding and foraging behaviour in carriers, since most foraging occurred in the lower levels of the cages. It was surprising that although carriers spent more time with other group members, they were nevertheless significantly less likely to be involved in affiliative behaviour such as allogrooming. This may reflect decreased mobility on the part of the carrier, and interest in the infant rather than the carrier by other family members. Although data were not collected on the identity of the individuals they remained close to, much of the time carriers of twin infants appeared to stay together. It is therefore possible that an individual carrying all the infants in a group would show a different pattern of spatial relationships - for example, it might spend more time alone. Further data are required to clarify this.

Data collected on aspects of individual behaviour showed that levels of activities such as scratching and autogrooming were lower when tamarins when carrying infants. This suggests that their general mobility may be reduced, providing at least a partial explanation for the decrease in feeding, foraging, and moving. Such effects could be confirmed by experimental studies of the ability of carriers to gain access to resources.

In addition, as carriers were also groomed less by other group members, a reduction in the ability to clean oneself may represent a decreased ability to maintain adequate hygiene and thus a further cost incurred by caring for infants.

However, the results for vigilance behaviour were unexpected: contrary to the predicted change, not only was there no increase in vigilance, but carriers of infants in fact performed significantly *less* vigilance behaviour than when they were not carrying. There are at least three possible explanations for this: (1) the measure used, *look up*, was not a good indicator of vigilance; (2) the fact that the control data were collected when the infants were older may have affected the results; for example, family members may be more vigilant when infants start to spend short periods of time off their carriers and are presumably very vulnerable to predation; or (3) instead of spending more time in looking for potential threats, carriers were adopting a different anti-predator strategy, such as spending more time in areas of the cage that offered concealment. (Simply staying still may make carriers less obvious to predators, but this would not explain the *decrease* in vigilant behaviour that occurred in carriers.) Additional experiments were therefore conducted to investigate these possibilities.

B. "Looking up" as vigilance

Introduction

One possible explanation for the unexpected effect of carrying on vigilance is that the measure used, *look up*, was not in fact a good indicator of vigilance. An experiment was therefore designed to test this. Caine (1984) found that visual scanning in *Saguinus labiatus* increased following the presentation of threatening stimuli, confirming that it was a form of vigilance. I therefore predicted that if *look up* was indeed an appropriate measure of vigilance in captive cotton-top tamarins, it would increase following the presentation of a potentially threatening stimulus.

Methods

Subjects

The subjects for this study were seven breeding pairs of cotton-top tamarins (i.e. 14 individuals in all) living in families ranging in size from two to 12 independent individuals. Two of the pairs were wild-caught, but had been in captivity for 12 or more years. The remaining ten subjects were all captive-born, and ranged in age from 64 to 112 months at the time of the experiment. The four largest groups were housed in separate rooms; the remaining three lived in separate cages in a single room which was also shared by a fourth group not taking part in the experiment. Each room contained a skylight (dimensions 1.75m x 1.15m) which was at least partially visible to all groups. Further details of housing and husbandry are given in chapter 2.

Behavioural categories and recording methods

The data were collected by 14 undergraduate students in an Animal Behaviour class. However, all data analysis was my responsibility. The behaviour of interest, *look up* (as defined previously) was scored on check-sheets using one-zero sampling at 30-second intervals. (This interval was selected rather than a 15-second interval as few of the observers had had previous experience in observing tamarins). Additional data on activity, social behaviour and spacing were collected, but only the results for *look up* are presented here.

Apparatus

In an attempt to mimic a predator-like stimulus, a model bird designed by E. Moodie and A. Chamove was presented to the tamarins. The model consisted of a black silhouette of a bird with a wingspan of about 1m, attached to a pole. Three of the groups had previously been exposed to the model once each, about 18 months before this experiment (Moodie & Chamove, in press).

Procedure

A experimental design similar to that used by Caine (1987) in an investigation of the effect of light levels on vigilance in *Saguinus labiatus* was adopted. Baseline data were collected first, followed by post-stimulus data, and a final session after a break in which no stimulus was presented.

All the data were collected on two mornings between 1015 and 1245. One subject from each pair of tamarins was observed on each occasion. Order of testing within each pair was determined randomly prior to the start of the experiment. All the groups were tested at the same time, with a two-week interval between the two tests to minimise any habituation to the stimulus. Each data collection period took the following form:

(1) A 30-minute baseline observation session between 1015 and 1100 (session 1).

(2) Presentation of the stimulus. The bird model was "flown" over all the animal-room skylights for about five minutes by a technician. She used the pole to pass the model

back-and-forth 2-3 times across each skylight. Each group received five presentations, each lasting about five seconds and separated by approximately one-minute intervals; skylights were passed in the same order on each circuit. No data were collected during this period.

(3) Immediately following presentation of the stimulus, there was a second 30-minute observation session between 1100 and 1145 (session 2).

(4) Following session 2, there was a break of 20-30 minutes during which the observers left the room and no stimulus was presented.

(5) A final 30-minute observation session was carried out between 1200 and 1245 (session 3).

Non-parametric tests were used to analyse the data.

Results

Response to stimulus

The tamarins responded to the presentation of the model bird with alarm calls (most frequently Type E chirps and Type E chirp chatters; Cleveland & Snowdon (1982); see also section A), freezing, piloerection, and monitoring of the skylight (see also Moodie & Chamove, in press).

Effect on look up behaviour

Changes in the number of 30-second intervals in which subjects looked up are shown in figure 5.8. Both male and female tamarins showed increased levels of *look up* in session 2 (post-stimulus) compared to session 1, with a return to baseline levels in session 3. These differences are statistically significant (Friedman two-way analysis of variance; males: $\chi_r^2 = 6.5$, d.f. = 2, n = 7, p = 0.039; females: $\chi_r^2 = 10.6$, d.f. = 2, n = 7, p = 0.005; overall: $\chi_r^2 = 16.75$, d.f. = 2, n = 14, p = 0.0002).

Conclusion

The measurement used, *look up*, does reflect levels of vigilance in captive cotton-top tamarins. The unexpected results obtained in section A cannot therefore be explained by the

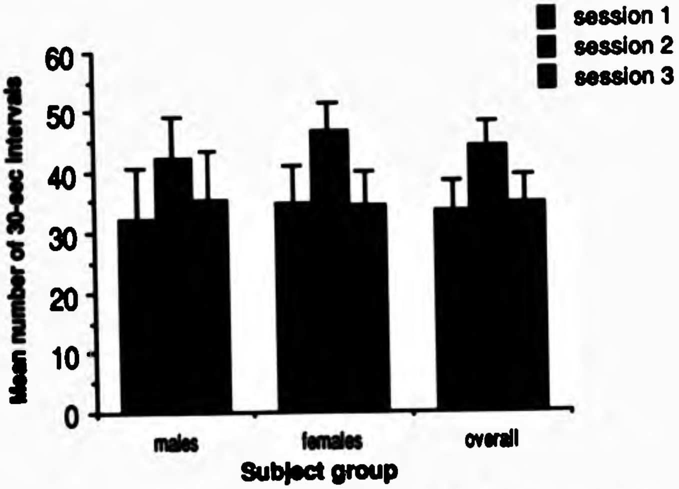


FIGURE 5.8. Mean number of 30-second intervals in which **look up** *behaviour occurred for seven male and seven female cotton-top tamarins in three consecutive 30-minute observation sessions. Session 1: baseline; session 2: following presentation of a predator simulation; session 3: following a break in which no stimulus was presented. Vertical bars indicate standard errors.*

use of inappropriate measure of vigilance.

C. Changes in vigilance with age of infants

Introduction

The second possibility investigated to explain the unexpected effect of infant carrying on vigilance was that older family members increased their levels of vigilant behaviour when infants were starting to become independent, a time when they might be particularly vulnerable to predation as their locomotor and other skills are not fully developed. To assess this, additional data on vigilance in whole groups were collected.

Methods

Subjects

The subjects were the 12 members (six males and six females) of two cotton-top tamarin groups: Shoshone (n = 4) and Delaware (n = 8). Delaware's group lived in a room of their own; Shoshone's group lived in a cage in a room shared with other families. For further details of housing, see chapter 2. All subjects were captive-born, and ranged in age from 11 to 131 months at the start of observations.

Procedure

Each group was observed during two different periods: (1) when infants were 1-2 weeks old; and (2) when infants were six weeks old. One hour's data was collected from each subject during each period. This hour was divided into 12 five-minute focal samples, three taken at each of the following times: 1000-1100, 1200-1300, 1400-1500, and 1600-1700. During each sample, time spent *looking up* (defined as before) was recorded directly to the nearest second using a stopwatch; even the briefest bout was timed. No account was taken of whether the subject was carrying an infant or not.

Observation sessions lasted for up to one hour, depending on the size of the family. Order of testing for the subjects was determined randomly prior to the start of each session, and individual subjects were observed only once in any given session.

The total time each subject engaged in *look up* behaviour was then calculated for each condition, and compared using a Wilcoxon matched pairs signed-ranks test.

Results

When taken together, the subjects showed no significant changes in *look up* behaviour with the age of the infants (Wilcoxon test: n = 12, z = -1.51, p = 0.13; fig. 5.9). However, there appeared to be a difference between the two groups when they were considered separately. While Shoshone's group showed no significant change with the age of the infants (Wilcoxon test: n=4, z=-0.53, p=0.59), Delaware's group rather surprisingly showed a significant *decrease* in *look up* behaviour when the infants were older (Wilcoxon test: n = 8, z = -1.96, p = 0.05).

Conclusions

Groups of cotton-top tamarins did not increase their overall level of vigilance as infants increased in age, and there was some evidence that they decreased it. The results in section A could not therefore be explained by differences between conditions in the ages of the infants.

D. Use of concealment by carriers

Introduction

The final possibility investigated was that carriers of infants spent more time in concealed areas of the cage than normal, and therefore either did not need or were unable to spend much time actively looking for potential threats. For example, a tamarin in a concealed area of the cage would also be less able to monitor its surroundings (e.g. the skylight may not be visible to it), which may have led to the reduced levels of *look up* seen in section A.

Crypticity appears to be an important component of the anti-predator strategies of wild marmosets and tamarins. Terborgh (1983) found that groups of three sympatric callitrichid

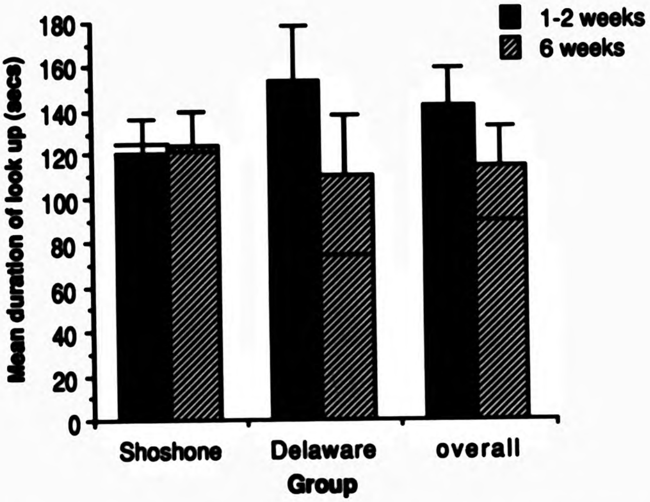


FIGURE 5.9. Mean time spent looking up by 12 members of two cotton-top tamarin groups during one hour's observation per subject at each of two different infant ages. Vertical bars indicate standard errors; horizontal lines indicate median values.

species (*Saguinus fuscicollis*, *S. imperator* and *Cebuella pygmaea*) spent much of their resting time in thick cover (commonly dense vine tangles), rarely moved in the highest levels of the canopy away from the protection of vines and foliage, and chose vine-shrouded sleeping sites affording a good view of the forest. When resting, saddle-back tamarins also reduced their movement and vocalisations (Goldizen 1987*b*). The importance of a safe sleeping site to wild cotton-top tamarins was clear from Neyman's (1980) field study: if unaware of the observer, the tamarins would quieten down and spend long periods looking round before entering the sleeping tree. If they noticed the observer, they would move on and keep travelling in an attempt to "lose" her. Similar behaviour was reported by Caine (1990) in captive *S. labiatus*: the tamarins were more reluctant to enter their sleeping boxes if an observer was present.

Data were therefore collected to determine whether or not cotton-top tamarins carrying infants were using a cryptic strategy to reduce the threat of predation.

Methods

Subjects

The subjects for this study were drawn from four groups of cotton-top tamarins. An additional one hour's data in each condition (*carry infant* and *not carrying*, as before) was collected from four of the subjects in two groups in section A. One hour's data in each condition was also collected from a further seven subjects in two additional families. Thus, 11 subjects in all (nine males and two females; see table 5.3) contributed data.

Behavioural categories and recording methods

As well as noting location in cage (*upper*, *middle*, or *lower*, as before), a more detailed record was made of where the subject was at each 15-second interval. Certain areas of the cage or room were assumed to afford at least partial concealment, with concealment defined as hidden from overhead view from the skylight: nest-boxes, curtains, ducting, and platforms or perches beneath other furnishings or very high in the cage that could not be seen from the skylight. Areas of partial concealment were designated before observations began, and a tamarin with at least half of its torso in one of these areas was said to be *hidden*.

TABLE 5.3. Details of the subjects observed during the investigation of the use of concealment by tamarins carrying infants.

Family and litter	*Subject*	*Age-sex class*	*Infant age (days)* *(a) during carrying condition*	*Infant age (days)* *(b) during control condition*
Shoshone Twins 17/4/89	James	Adult son	1-3	24-35
	Kansas	Sub-adult son	1-5	22-34
Delaware Twins 22/4/89	Arnold	Breeding male	1-7	19-33
	Alan	Adult son	1-7	18-31
Hopi Twins 18/6/89	Jim	Breeding male	10-12	24-40
	Cameron	Adult son	9-11	19-40
	Ceilidhe	Adult daughter	9-12	19-40
Roxanne Twins 7/8/89	Alistair	Adult son	8-11	14-17
	Urquhart	Adult son	6-11	13-15
	Ursula	Adult daughter	6-13	14-16
	Vincent	Adult son	6-13	14-17

The procedure for collecting data was as in section A, with data collection for the *carry infant* condition completed before data for the control condition were collected, in order to match the two sets of data from each subject for time of day. The only change was that observation sessions lasted a maximum of 30 minutes rather than 45 minutes, again to ensure that data for each subject were collected from several different sessions.

Non-parametric statistical techniques were used to analyse the data.

Results

Tamarins carrying infants spent significantly more time hidden than when they were not carrying (Wilcoxon test; $n = 10$ pairs of scores where $d \neq 0$, $T = 2$, $p < 0.01$; see figure 5.10). However, most of the furnishings providing concealment were in the upper sections of the cages, and since the tamarins spent most of their time in the upper part of the cage when carrying (95%, versus 55% when not carrying), this difference could be due simply to their spending more time at high levels. The proportion of time the subjects spent hidden while in the upper sections was therefore compared for the two conditions. Again, tamarins spent a significantly greater proportion of their time hidden whilst in the upper level when carrying an infant (Wilcoxon test; $n = 10$ pairs of scores where $d \neq 0$, $T = 2.5$, $p < 0.01$; see figure 5.10).

Conclusions

Cotton-top tamarins carrying infants appeared to adopt a strategy of concealment from potential sources of danger. This may explain the fact that they did not engage in more overt anti-predator behaviour such as looking for overhead threats. The concealment hypothesis would be further supported if it could be shown that tamarins carrying infants reduced the levels at which they vocalised. A reduction in vocalisations at times when tamarins are vulnerable, for example when settling down for the night or resting, has been noted in field studies (e.g. Neyman 1978, 1980; Goldizen 1987*b*), and has been demonstrated experimentally in captivity by Caine (1987). Future studies should show whether carriers adopt similar strategies to avoid predation.

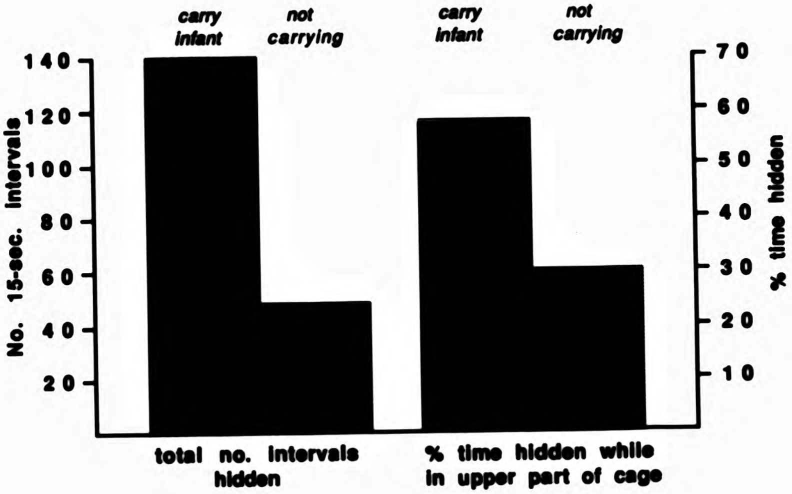


FIGURE 5.10. Time spent hidden by 11 cotton-top tamarins when carrying an infant and when not carrying.

Discussion

Cotton-top tamarins in captivity decrease the time they devote to feeding, foraging, moving and socialising when they carry infants, partly because their mobility is decreased, and partly because they spend more time concealed. Similar effects of infant carrying on behaviour have been described in captive *Callithrix jacchus* (Clarke 1987), and in wild *Saguinus fuscicollis* (Goldizen 1987*a*; Snowdon & Soini 1988) and *S. geoffroyi* (Moynihan 1970).

Goldizen (1989) has recently suggested that in captivity, tamarins may be unlikely to form stable polyandrous groups as they will not be paying significant costs by carrying infants. It would therefore not be necessary for monogamous pairs to recruit a third polyandrous male, as they could successfully rear twins by themselves. If true, this would have important implications for the study of callitrichid reproductive strategies in captivity. However, the present study has demonstrated that carriers in captive tamarin families *do* pay costs in some form, most notably in terms of lost feeding and foraging time. Feeding/foraging times in the captive cotton-top tamarins studied here were in fact remarkably similar to those for the wild saddle-back tamarins described by Goldizen (1987*a*) for both carriers of infants and non-carriers. Thus, even in captivity, tamarins may be paying costs in terms of time budgetting by helping to rear infants. Further studies are needed to determine whether the time lost in feeding translates into other changes such as weight loss, or whether captive tamarins can easily make up the energy lost. However, these results suggest that the reproductive strategies of callitrichids can feasibly be studied in captivity.

Summary

(1) Cotton-top tamarins carrying an infant moved, fed, foraged and socialised significantly less than when not carrying, and their general mobility appeared to be reduced.

(2) Carriers of infants also performed less vigilant behaviour than when not carrying.

(3) Reduced vigilance in carriers could not be explained by the use of an inappropriate measure of vigilance or by the method of sampling.

(4) Carriers spent more time concealed than when they were not carrying, and this may explain the reduced levels of actively vigilant behaviour.

Chapter 6

The behaviour of monogamous pairs of cotton-top tamarins

Introduction

Investment in infants by fathers and other individuals within the group appears to be extremely important for successful reproduction in callitrichids (Kleiman 1977; Garber *et al.* 1984; Goldizen 1987*a*). Garber *et al.* (1984), for example, presented data indicating that infant survival in moustached tamarins (*Saguinus mystax*) may be correlated with group size, and that adult males may be particularly important. The relationships between breeding males and females are therefore of great interest, and the aim of this part of the study was to investigate these relationships along with other aspects of the behaviour of breeding cotton-top tamarins.

Previous authors have proposed various hypotheses covering several aspects of the behaviour of callitrichid pairs. These generate some specific predictions which I hoped to test in this part of the study.

Changes in sociosexual behaviour over the breeding cycle.

As discussed above, it has been suggested that parental investment by the male is essential for the successful rearing of twin infants. If this is so, females would be expected to use strategies aimed at keeping males nearby when it is most important to them - i.e. just before the infants are born - to ensure that there will be sufficient care available at the right time. This is supported by data suggesting that mating increases prior to parturition in common marmosets (Evans & Poole 1983). It is possible, then, that females become more attractive and receptive at this time, encouraging males to stay. Investment in pair bond maintenance by females would also be predicted to be highest immediately before birth, and perhaps in the weeks just after birth when care is likely to be most important to infant survival.

Males, on the other hand, should show a different pattern of investment in their relationships with females: the greatest investment in pair bond maintenance would be expected when the female is likely to conceive. In cotton-top tamarins, as in other callitrichids, a post-partum oestrus occurs two to four weeks following birth (Ziegler *et al.* 1987*a*). Male interest in females should thus increase after birth and peak at the time of oestrus, and studies of the common marmoset suggest that this may be true at least of this species (Kendrick & Dixson 1983; Dixson & Lunn 1987). However, it has also been hypothesised that concealed ovulation may have evolved in female marmosets and tamarins in order to keep males around throughout the breeding cycle (e.g. Stribley *et al.* 1987): if males cannot detect ovulation they are forced to stay near the female to ensure that they do not miss it. Females show no visible signs of oestrus such as sexual swellings, and do not menstruate (Hampton *et al.* 1966; Hearn & Lunn 1975). In addition, several studies combining hormonal analysis with behavioural observations in species other than the common marmoset have found few correlations between sociosexual behaviour and the stage of the ovarian cycle (e.g. French 1982; Brand & Martin 1983; Stribley *et al.* 1987). These data suggest that males may be unable to detect ovulation, and would be consistent with either a monogamous or a polyandrous mating system (Stribley *et al.* 1987). In this case, no changes in male behaviour over the breeding cycle should be apparent.

A female might also be expected to assess those males who are potential fathers for her offspring on the basis of their skills in caring for infants, since it should pay females to choose as mates males who are competent in infant care. This hypothesis leads to the prediction that males should develop strategies aimed at convincing females that they would be good parents. Since older offspring can take over much of the infant care in callitrichid families, in principle breeding male tamarins in large families need do no infant care at all (McGrew 1988). Nevertheless, despite the fact that most of them had older offspring who were eager to carry infants, all breeding male tamarins in this study did carry and share food with infants, especially in the first month (chapter 3), and appeared to seek out opportunities to carry infants and to resist attempts by other individuals to take infants, particularly in the first few weeks (chapter 4). This is perhaps surprising, since infant carrying is a costly activity, particularly in terms of lost feeding time (chapter 5). Furthermore, during the study of infant care (chapters 3 and 4), it was noticeable that breeding males often appeared to attempt to mate with the breeding female as soon as the male had taken an infant. This suggested that males may have been using infant carrying as a "courtship" strategy in order to increase the chance that the females would accept them as mates, and I investigated this further in a study of breeding pairs.

Changes in sociosexual relationships with the duration of the "pair bond".

Changes in the levels of social and sexual behaviour with the length of time pairs have been together have also been predicted. Dunbar (in prep.) has suggested that as group size increases and therefore the number of helpers available increases, breeding tamarins should have less incentive to invest time in maintaining the pair bond. This would predict a decrease in sociosexual interactions between breeding callitrichids as family size increases, and data from callitrichid species support this (e.g. Kleiman 1977; Evans & Poole 1984; Savage *et al.* 1988). One problem, however, is that in the present study and in many others the effects of group size are confounded with the duration of the pair bond, a factor which has also been predicted to lead to decreased sociosexual behaviour in callitrichid pairs (Kleiman 1977): this hypothesis states that in order to form a bond between the male and female initially, relatively high levels of social and sexual interactions are necessary, but once the bond has become well-established, less energy need be expended in sociosexual behaviour.

Changes in activity over the breeding cycle.

Other aspects of the behaviour of breeding tamarins, particularly females, might also be expected to vary over the breeding cycle as a consequence of the changing energetic demands at different stages of the cycle. First, weight gain during pregnancy may affect a female's ability to move around her environment. Terborgh (1983), for example, noticed that a wild female *Saguinus imperator* could move only with difficulty in late pregnancy. Evans & Poole (1984) noted a decline in the activity of captive female *Callithrix jacchus* in the latter half of pregnancy, when body weight increases conspicuously (Ingram 1975; Lunn 1983), while in a pair of captive *Leontopithecus rosalia* studied by Wilson (1976) the female considerably reduced her level of activity in late pregnancy and spent long periods in the nestbox. Kirkwood & Underwood (1984) found that weight conspicuously increased during the final eight weeks of pregnancy in captive cotton-top tamarins, but that the energy intake of pairs was not noticeably higher than in non-breeding groups. Thus pregnancy did not appear to impose greatly increased energetic demands on females. Consequently, female tamarins were predicted to reduce their activity during pregnancy, but not to increase the time they spent feeding.

Secondly, lactation is energetically costly for female primates (Altmann 1980, 1983; Dunbar 1988). Goldizen (1987*a*) found that wild female saddle-back tamarins (*S. fuscicollis*) had to double their feeding time from 10-15% to about 30% when lactating, while Kirkwood & Underwood (1984) noted that captive pairs of cotton-top tamarins doubled their energy intake after infants were born. Presumably much of this was due to the female's need to counteract the costs of lactation. Garber & Teaford (1986) found that one wild female saddle-back tamarin lost 21% of her body weight during lactation. Increases in the time that female tamarins spent feeding and foraging during lactation were therefore predicted. In addition, Dunbar (1988) has suggested that females should cut into their resting time rather than their social time to make up for the increased time they need to spend feeding, since maintaining investment in relationships with other individuals may be important in securing their help when needed. Therefore, since it is presumably particularly important for callitrichid females to maintain their social relationships in order to ensure adequate help when infants are born, little change was expected in the time female tamarins devoted to social interactions, despite any changes in feeding time that might occur.

The aims of this part of the study were therefore to investigate (1) changes in the relationship of breeding cotton-top tamarins over the breeding cycle, and the strategies adopted by males and females; (2) changes in activity over the breeding cycle; and (3) comparisons between pairs housed together for varying lengths of time and with different numbers of offspring.

Methods

Subjects

The subjects of this study were seven groups of cotton-top tamarins (table 6.1). Five established breeding pairs, who had been living together for periods varying between 6.5 months and 11 years when observations began, were each observed for approximately 12 weeks before and 12 weeks after a birth (i.e. from about midway through pregnancy until the infants were independent). This regime, rather than the alternative of following pairs from one birth to the next, was chosen for two reasons: (1) interbirth intervals were not always regular, particularly in the younger females, which meant that scheduling data collection to fit other aspects of the study would have been more difficult; and (2) it allowed the same litter to be followed through gestation and lactation. Stage of pregnancy was estimated from regular visual inspections of the breeding females, and from a knowledge of previous birth dates. (Erica's stage of pregnancy was misjudged as she was unexpectedly carrying the first singleton infant to be born in the colony. Lunn (1983) has also found that adult female *Callithrix jacchus* carrying singletons were not noticeably pregnant even at term.) All the females had previously produced infants, and with the exception of one of Roxanne's triplets, which died three days after birth, all infants born to the five pairs during the study were successfully reared. Dates of conception during the observation period were estimated by subtracting 184 days (the average gestation period in this species; Ziegler *et al.* 1987*a*) from the date of the next parturition.

A further two pairs were observed for a period of six weeks following pair formation, in order to compare the behaviour of recently formed pairs with that of established pairs.

To investigate in more detail the hypothesis that males mated more when they were carrying infants, the eight-week period after each birth was examined in more detail in the five established pairs. For two of these pairs (Delaware & Arnold, and Erica & Fideaux) additional data were collected for eight weeks following subsequent births. The two sets of data for Delaware & Arnold and for Erica & Fideaux were combined to give one data set for each of the five pairs.

TABLE 6.1. Details of the pairs of cotton-top tamarins observed

Group no.	*Names (female first)*	*Date of birth*	*Group size*[1]	*Date paired*	*Observations: Start*	*Observations: Finish*	*Infants born*	*No. weeks observation: Before birth*	*No. weeks observation: After birth*	*Total observation time (hrs)*
(a) Established pairs										
1	Erica[2] Fideaux	11/4/83 25/9/82	2	18/2/87	1/9/87	8/2/88	6/10/87 (singleton)	5	18	70
2	Delaware[2] Arnold	4/12/83 16/3/81	4	24/10/85	1/9/87	11/2/88	5/11/87 (twins)	10	14	77.5
3	Hopi Jim	28/4/82 16/10/80	7	26/9/84	1/9/87	13/3/88	7/12/87 (twins)	14	14	89.5
4	Roxanne Elvis	wild-caught wild-caught	10	1977	2/11/88	13/4/89	19/1/89 (triplets)	12	12	76
5	Elsa[3] Mario	wild-caught wild-caught	11	24/1/79	11/12/88	25/5/89	3/3/89 (twins)	12	12	78
(b) Newly formed pairs[4]										
6	Viva Windsor	11/6/85 2/12/87	2	27/6/89	27/6/89	7/8/89	-	-	-	22.5
7	Alpha Xavier	1/3/85 21/12/86	2	3/7/89	3/7/89	13/8/89	-	-	-	24

1. Group size excluding infants born during study.
2. An additional 8 weeks of data were collected from pairs 1 and 2 following a subsequent birth.
3. Elsa's eldest daughter Viva gave birth to a single stillborn male infant on 17/5/89.
4. Observed for 6 weeks following pair formation.

In one group (Elsa's) the oldest daughter, Viva, unexpectedly became pregnant, giving birth to a single stillborn male infant 10.7 weeks after Elsa had produced twins. Date of conception was estimated as 15/11/88, about one month before observations on her parents began. There was no evidence that she mated with her father. Further details of this incident, and data on Viva's relationship with her parents during her pregnancy, are presented in chapter 7.

Apart from the birth and occasional loss of infants, the composition of all the groups in the study remained stable during the observation period.

Housing

Groups 4 and 5 lived in separate rooms, while groups 1, 2 and 3 lived in one or two type I colony cages, and groups 6 and 7 in type II colony cages. Further details of housing and husbandry are given in chapter 2.

Behavioural categories and recording methods

Each pair was observed for 3-4 hours per week (mean = 3.24 hours, n = 135 group-weeks) divided into 30-minute observation periods. Samples each week were spread evenly between 1000 and 1800. Each 30-minute period was split into two consecutive 15-minute sampling sessions in which first one and then the other member of the pair served as the focal subject, so that its activity and its interactions with other members of the family, if present, could be recorded. (The majority of the data on relationships between parents and offspring will be presented elsewhere.) Interactions between the breeding pair were recorded for the whole 30-minute period. In addition, the identities of the carriers of infants were noted every 15 seconds. Order of testing within pairs was determined randomly before each observation period began.

All data were collected on checksheets divided into 15-second intervals. The behavioural categories scored and the methods used to record them are listed in table 6.2. Definitions of these categories can be found in chapter 2.

TABLE 6.2. Behavioural categories and recording methods for the study of the behaviour of breeding cotton-top tamarins.

Behavioural category	*Recording method*	*Other information noted*
Sexual behaviour		
Attempted mounts	All occurrences	-
Partial mounts	All occurrences	-
Full mounts	All occurrences	-
Female mounts	All occurrences	-
Male head-shake	One-zero	-
Female head-shake	One-zero	-
Male tongue-flick	One-zero	-
Female tongue-flick	One-zero	-
Male trill	One-zero	-
Social behaviour		
Allogroom	One-zero	Identity of participants; direction
Affection	One-zero	Identity of participants; direction
Anogenital sniff	One-zero	Identity of participants; direction
Aggression	One-zero	Identity of participants; direction
Face press*	All occurrences	Identity of participants; direction
Allomark	All occurrences	Identity of participants; direction
Approach	All occurrences	Identity of participants; direction
Leave	All occurrences	Identity of participants; direction
Offer food	All occurrences	Identity of participants; direction
Beg food	All occurrences	Identity of participants; direction; outcome
Steal food	All occurrences	Identity of participants; direction; outcome
Spatial relationships	Instantaneous	*Solitary*, *near*, or *contact*; identity of other individuals near or in contact
Activity	Instantaneous	*Sit*, *move*, *feed*, *forage*, or *social*.

* Face-pressing was not observed between members of pairs

Analysis of data

Behaviour of established pairs. Depending on the level of analysis required, fortnightly or four-weekly means were calculated for the activity and sociosexual interactions of each pair, and the data were inspected graphically and statistically for changes over the period of observation. Most data were collapsed into six four-week blocks or "months". Months -3 to -1 covered the 12 weeks preceding birth, while months 1 to 3 comprised the 12 weeks following birth. As Erica was further on in her pregnancy than estimated when observations began, data were lacking for Erica & Fideaux for month -3. This month was therefore excluded from statistical analyses, although the data from month -3 from the other four pairs are presented in the figures for comparison. For some analyses involving categories of behaviour that occurred only relatively rarely, 12-week means for behaviour before and after birth were calculated and compared.

The choice of statistical tests depended on the type of behaviour under investigation. The effects of both sex and time on behaviour, and also any interactions between them, were of interest in this study. As non-parametric methods were not available for investigating interactions, parametric techniques were desirable. Kolmogorov-Smirnov goodness-of-fit tests showed that the data on activity did not deviate significantly from normality. Parametric analyses of variance, with sex as a between-subjects factor and time as a within-subjects factor with five levels (months -2 to +3), were therefore conducted to test for sex differences in activity, variations in activity over the breeding cycle, and interactions.

Social and sexual interactions, however, showed considerably more variability between pairs, and in many cases the frequent occurrence of zero values meant that the data were unlikely to be normally distributed. The assumptions underlying parametric techniques were therefore violated, and for this reason, non-parametric tests were used. Friedman two-way analyses of variance were used to look for changes in behaviour over time, using monthly scores as before, while sex differences in behaviour were evaluated using Wilcoxon matched pairs signed rank tests on the total scores obtained for each pair. It was not possible to test for interactions between sex and time with these methods. In order to obtain a more detailed picture of changes in the relationship between members of breeding pairs over time, fortnightly means were also calculated and inspected graphically.

The index developed by Hinde (1983; Hinde & Atkinson 1970) was used to investigate which member of the pair was primarily responsible for maintaining close spatial associations. An idea of relative responsibility for maintaining proximity can be obtained by subtracting the percentage of all *leaves* that were made by the male from the percentage of all *approaches* that were made by him:

$$\text{Hinde index} = \%A_m - \%L_m = \frac{100A_m}{(A_m + A_f)} - \frac{100L_m}{(L_m + L_f)}$$

where A_m = frequency of approach by male
A_f = frequency of approach by female
L_m = frequency of leave by male
L_f = frequency of leave by female

The resulting index is positive if the male is more responsible for promoting proximity than the female, and negative if the female is largely responsible.

Sexual interactions can be analysed in terms of three features of female sexual behaviour (Beach 1976): *proceptivity* (i.e. female initiative in establishing or maintaining sexual interactions), *receptivity* (i.e. female readiness to allow copulation), and *attractivity* (i.e. the female's stimulus value in evoking sexual responses by the male, which can be inferred from the male's behaviour). In the present study, female tongue-flicking, head-shaking and mounting were considered as indicators of proceptivity; the proportion of male mounts rejected as an indicator of receptivity; and male mounts, head-shakes, tongue-flicks and approaches as indicative of attractivity. Similar measures were used by Brand (1984). Female mounts have not been described in previous studies of cotton-top tamarins, but in other primates are considered as proceptive behaviour (Beach 1976).

Infant carrying and "courtship" by male tamarins. To obtain sufficient data for analysis of male infant care and sexual behaviour it was necessary to combine together the three types of mount recorded (attempted mounts, partial mounts, and full mounts). All frequencies given therefore refer to total numbers of mounts. The data were divided into four categories:

(1) male carrying, female not carrying (M√Fx)
(2) both male and female carrying (M√F√)
(3) male not carrying, female carrying (MxF√)
(4) neither male nor female carrying (MxFx)

For each pair, the proportion of time that was spent in each of these categories over the eight week period was calculated. Expected frequencies of mounts were then calculated, assuming a null hypothesis that mounts were distributed randomly among the categories. Expected frequencies for each category were therefore obtained by multiplying the total number of mounts seen by the proportion of time spent in that category (e.g. if 25% of the time the male was carrying but the female was not, 25% of the total mounts were expected to be in that period). These expected mount frequencies were then compared with the actual number of mounts that occurred in each category. In order to analyse the data statistically, the data for the categories M√Fx and M√F√ were combined into one condition, *male carrying*, and the categories MxF√ and MxFx into another, *male not carrying*. Rates of mounts per half hour were calculated for each condition for each pair, and a Wilcoxon matched pairs signed ranks test was then used to compare rates of mounts across the two conditions. Rates per 30 minutes of other aspects of sexual behaviour were compared in a similar way.

Comparisons of data from pairs housed together for varying periods. To facilitate comparisons between the behaviour of newly-formed and established pairs, the data for all groups were collapsed further into six-week blocks. For the newly-formed pairs these blocks included all the data collected, while for the established pairs the data were grouped into four separate blocks: (A) weeks -12 to -7 before birth; (B) weeks -6 to -1 before birth; (C) weeks +1 to +6 after birth; (D) weeks +7 to +12 after birth. The sample sizes were too small for direct statistical comparisons between new and established pairs. However, as the established pairs had been housed together for widely-varying periods, it was possible to conduct correlational analyses to investigate the effects of length of pairing on behaviour, using Spearman rank order correlation coefficients.

Results

The behaviour of tamarins in established breeding pairs

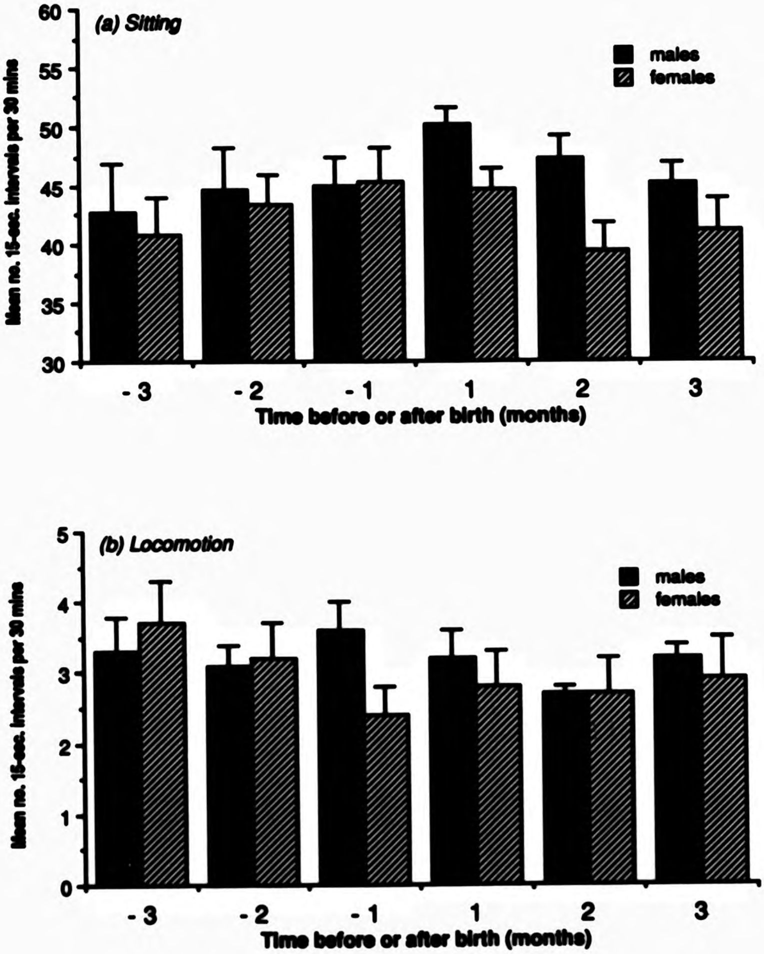
Changes in activity

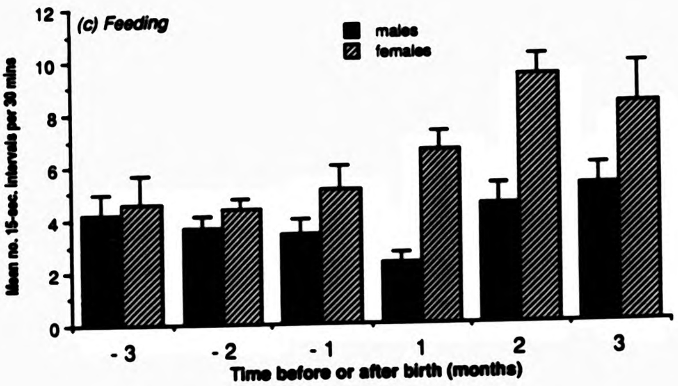
Changes in the way that breeding pairs of tamarins distributed their time before and after birth are shown in figure 6.1. *Sitting* increased slightly in both sexes during the latter half of pregnancy (fig. 6.1*a*). Although males tended to spend slightly more time sitting than females, the difference was not marked. After birth, however, the sitting scores for the two sexes diverged: males spent more time sitting after birth than before, whereas females reduced their time sitting, reaching a minimum during the second month postpartum. An ANOVA showed that there was a significant main effect of time on sitting ($F_{(4,32)} = 2.68$, $p = 0.049$), but there was no overall sex difference ($F_{(1,8)} = 1.61$, $p = 0.240$). There was a trend, although non-significant, towards an interaction between time and sex ($F_{(4,32)} = 12.24$, $p = 0.087$), suggesting that females may have altered their behaviour differently from males over the breeding cycle.

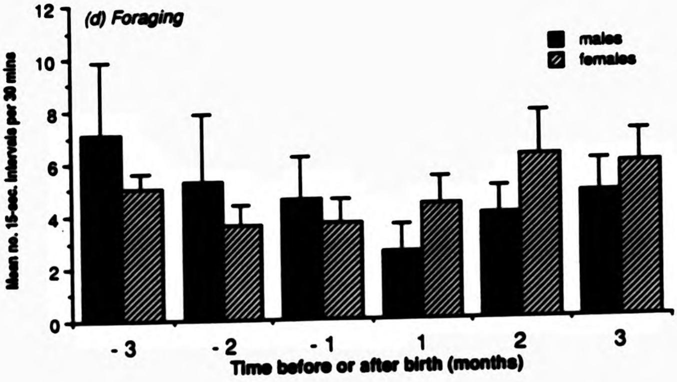
Locomotion showed less clearcut differences both over time and between the sexes (fig. 6.1*b*). As expected, locomotion by females decreased steadily in the 12 weeks before infants were born, reaching a minimum in the month preceding birth. This led to the greatest difference between males and females at this point. Female locomotion levels increased again slightly after birth. Males showed no clear changes over the observation period. None of these effects was statistically significant (main effect of sex: $F_{(1,8)} = 2.13$, $p = 0.183$; main effect of time: ($F_{(4,32)} = 0.31$, $p = 0.872$; interaction between sex and time: $F_{(4,32)} = 0.69$, $p = 0.605$).

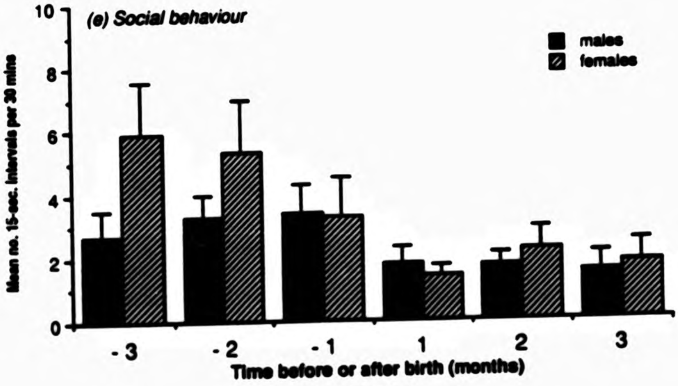
Feeding (i.e. consuming or holding food or drink) showed clear sex differences: females consistently spent more time feeding than males throughout the observation period (fig. 6.1*c*). Female feeding times did not vary a great deal in the months before birth, but increased

FIGURE 6.1. Changes in the activity of five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants: (a) sitting; (b) locomotion; (c) feeding; (d) foraging; (e) social behaviour. Vertical bars indicate standard errors.




(c) Feeding


(d) Foraging


(e) Social behaviour

postpartum to a maximum during month 2, at levels approximately twice as high as those before birth. Although males did alter their feeding time over the observation period (showing a slight decrease during pregnancy and immediately after birth, and then an increase in the final two months of observation) the changes were not so dramatic as for females. The difference in feeding time between males and females was greater after birth than before. An ANOVA showed that the overall difference between the sexes was significant ($F_{(1,8)} = 10.08$, $p = 0.013$), as was the main effect of time ($F_{(4,32)} = 13.57$, $p = 0.000$). The interaction between sex and time was also significant ($F_{(4,32)} = 5.10$, $p = 0.003$). Thus, changes in feeding behaviour over time differed between males and females.

Foraging showed a rather surprising reversal (fig. 6.1*d*). Before birth, males consistently spent more time foraging (mostly scanning the ground) than females, particularly in month -3. Male foraging times reached a minimum during month 1 and then rose again. However, there was considerable individual variability. Although female foraging times remained at fairly constant levels before birth, immediately after birth females began to forage more, increasing steadily to reach a peak during the second month postpartum. However, none of these effects was significant (main effect of sex: $F_{(1,8)} = 0.13$, $p = 0.731$; main effect of time: $F_{(4,32)} = 1.03$, $p = 0.405$; interaction between sex and time: $F_{(4,32)} = 1.43$, $p = 0.248$).

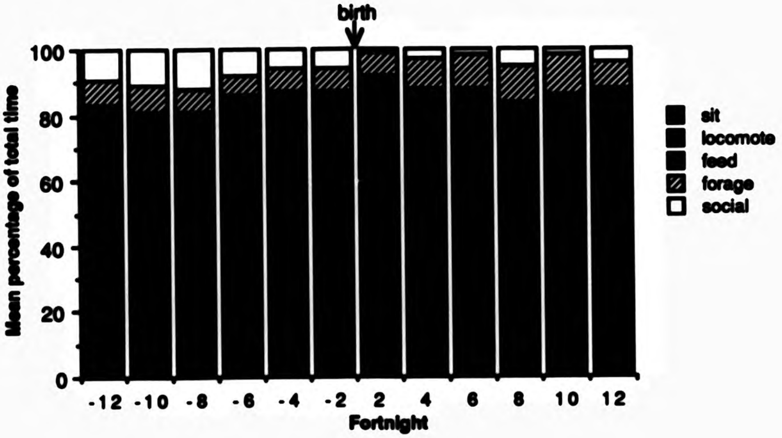
Social behaviour (including allogrooming, affection, play and aggression involving all family members, and sexual behaviour with the partner) was also affected by the birth of infants (fig. 6.1*e*). A sex difference was apparent in months -3 and -2, when females socialised nearly twice as much as males. After this, the levels for each sex were similar. Both sexes showed a drop in social interactions after birth, and this low level remained for the rest of the observation period. An ANOVA showed that the change in level of social activity over time was significant ($F_{(4,32)} = 4.66$, $p = 0.004$), but there was no significant difference between the sexes ($F_{(1,8)} = 0.40$, $p = 0.546$), and no significant interaction between sex and time ($F_{(4,32)} = 0.66$, $p = 0.625$).

These data are presented in the form of separate time budgets for breeding males and females in figure 6.2. In order to give a more detailed picture of changes in activity over time, fortnightly means are given. Females spent 65-76% of their time sitting, peaking around birth. After birth, feeding and foraging took up an increasing proportion of the females' time, and at week +6 comprised 28% of their total time, compared to a mean of 15% for the six two-week blocks before birth. Males did not show such conspicuous changes, spending a mean of 16% of their time feeding or foraging before birth, compared to 13% after birth. The increase in females' feeding and foraging activities appeared to be largely at the expense of active social time, which decreased to a minimum of 1% of total time in week +2. Social time after birth averaged 3%, compared to a mean of 9% before birth. However, the category *social* included only active forms of social interaction such as allogrooming. Tamarins spend a good deal of their time resting in contact with other group members without engaging in more overt forms of interaction, and this time could also be seen as social time. This was therefore investigated by looking at the proportion of their time that tamarins spent solitary, near or in contact with other group members. The results are shown in figure 6.3. There were few changes over time in the spatial relationships of breeding tamarins. ANOVAs demonstrated that there were no differences between males and females in the time they spent solitary or in the time they spent in contact with others, no effects of time (i.e. month), and no interactions (*solitary* - main effect of sex: $F_{(1,8)} = 2.00$, $p = 0.195$; main effect of time: $F_{(4,32)} = 1.43$, $p = 0.245$; sex x time interaction: $F_{(4,32)} = 0.21$, $p = 0.931$; *contact* - main effect of sex: $F_{(1,8)} = 0.78$, $p = 0.404$; main effect of time: $F_{(4,32)} = 1.59$, $p = 0.201$; sex x time interaction: $F_{(4,32)} = 0.38$, $p = 0.821$. Thus, the fact that there was no change in the amount of time females spent in contact with other family members suggests that in fact they conserved their social time.

Changes in sociosexual behaviour within breeding pairs

Social relationships between members of established pairs showed changes over the observation period. Pairs spent more time close to one another as parturition approached. Time spent in contact was always greater than time spent near each other. After birth, time spent near or in contact decreased again (fig. 6.4). There was a trend towards statistical significance for the changes in contact time over the observation period (Friedman two-way ANOVA; $\chi_r^2 =$

(a) Females



(b) Males

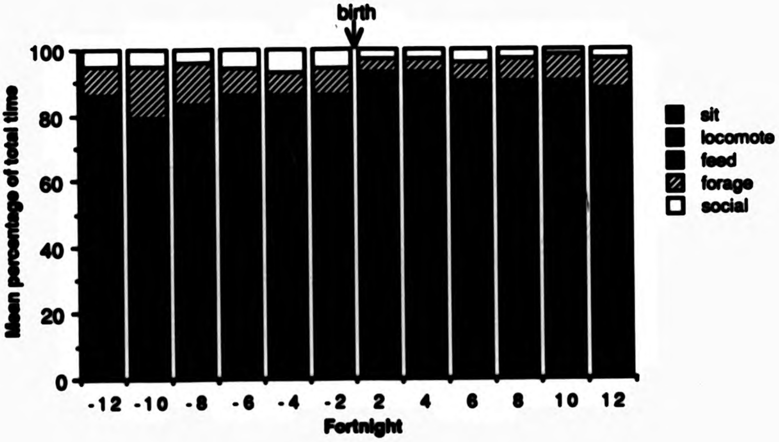
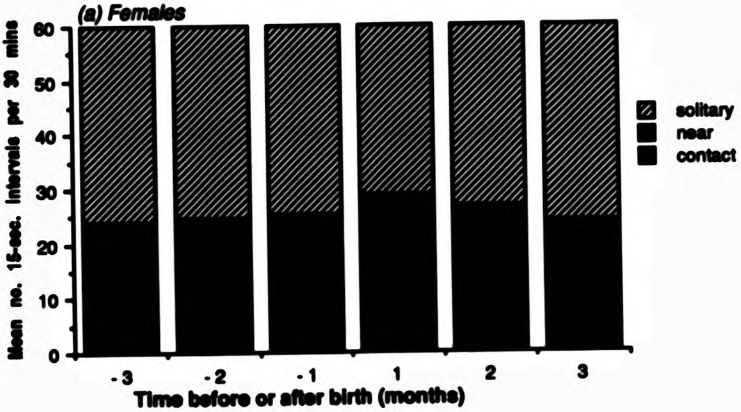


FIGURE 6.2. Time budgets of five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants. (a) Females; (b) Males.



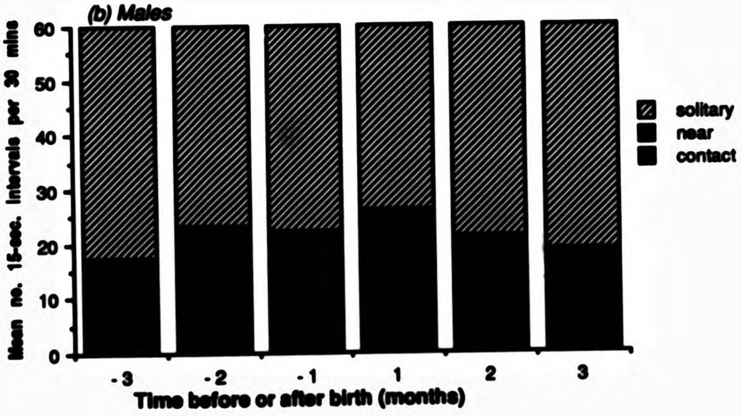


FIGURE 6.3. Spatial relationships of five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants. (a) Females; (b) Males. Values given are mean number of 15-second intervals per 30 minutes spent solitary, near any other group member or in contact with any other group member.

8.48, d.f. = 4, $0.05 < p < 0.1$), but there was no significant change in the time mates spent near one another (Friedman two-way ANOVA; $\chi_r^2 = 7.2$, d.f. = 4, $p > 0.1$). Analysis of Hinde's index (fig. 6.5) showed that before birth, females were consistently responsible for maintaining proximity, while after birth there was a sudden reversal of the relationship and males became primarily responsible for promoting proximity. After 5-6 weeks the pattern reversed once more and females again became more responsible for maintaining proximity. These changes over time were statistically significant (Friedman two-way ANOVA; $\chi_r^2 = 14.9$, d.f. = 4, $p < 0.01$), and although varying in degree, the pattern was consistent for all five pairs studied. The changes in responsibility for maintenance of proximity were reflected in changes in the frequency with which partners approached and left one another (fig. 6.6). Females showed a peak in approaching their mate before birth, while male approach peaked after birth. Males left their mates much more frequently than females did before birth, but after birth male leaving declined while female leaving peaked, so that during the first month after birth leaves by both sexes occurred at similar frequencies.

Females consistently groomed their mates more than *vice versa* before birth (fig. 6.7). However, after birth there was a decline in the amount of grooming done by both sexes, and females groomed only slightly more than males. The overall difference between the sexes in grooming was significant (Wilcoxon test; T = 0, n = 5, $p < 0.05$). The change over time in the amount of grooming done by females was also significant, but for males it was not (Friedman two-way ANOVAs; females: $\chi_r^2 = 15.2$, d.f. = 4, $p < 0.01$; males: $\chi_r^2 = 3.92$, d.f. = 4, $p > 0.3$). Affection showed the opposite pattern: males showed more affection to females than the reverse throughout the observation period, with a peak in the month after the female gave birth (fig. 6.8). The sex difference in affection was significant (Wilcoxon test; T = 0, n = 5, $p < 0.05$). There was a trend towards statistical significance in the changes over time in levels of affection shown by males, but not by females (Friedman two-way ANOVAs; males: $\chi_r^2 = 8.0$, d.f. = 4, $0.05 < p < 0.1$; females: $\chi_r^2 = 6.92$, d.f. = 4, $p > 0.1$). Aggressive behaviour was rare in all pairs, and occurred at similar levels in both sexes during most of the observation period. The only exception was that females showed a sudden increase in aggression towards males in the month after giving birth (fig. 6.9). There was no sex difference in the amount of

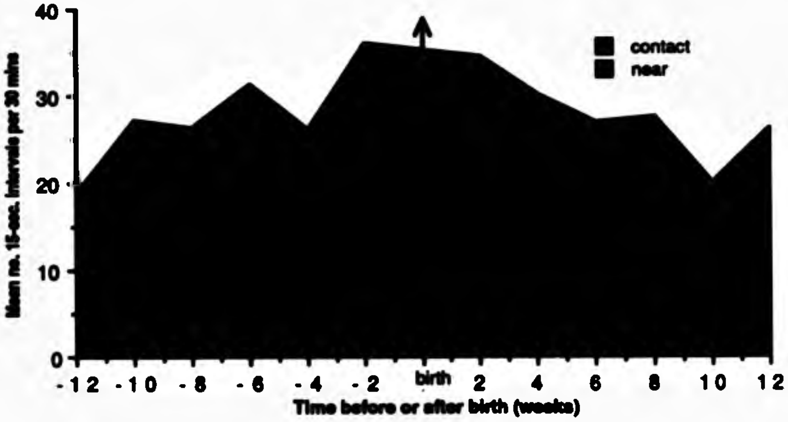


FIGURE 6.4. Spatial relationships in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

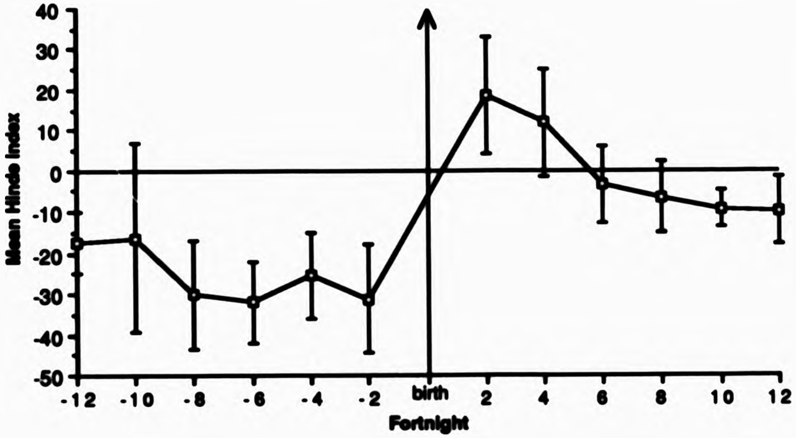
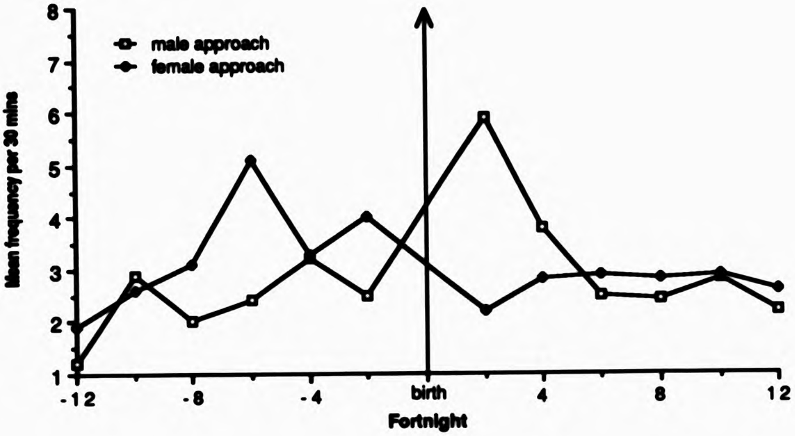


FIGURE 6.5. Maintenance of proximity, as determined by Hinde's index, in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants. For method of calculation of the index, see text. Vertical bars represent standard errors.

(a) Approach



(b) Leave

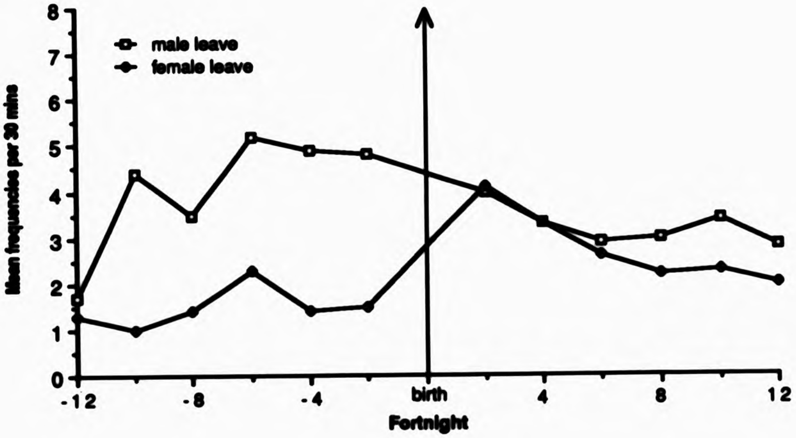


FIGURE 6.6. Frequencies of (a) approaching the partner, and (b) leaving the partner in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

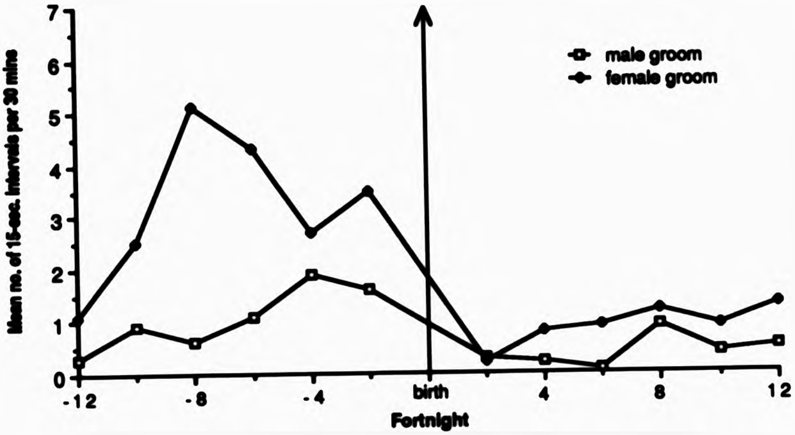


FIGURE 6.7. Allogrooming in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

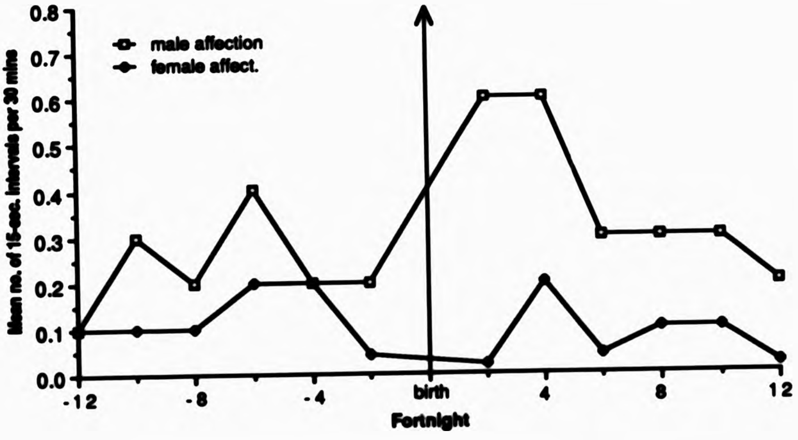


FIGURE 6.8. Affection in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

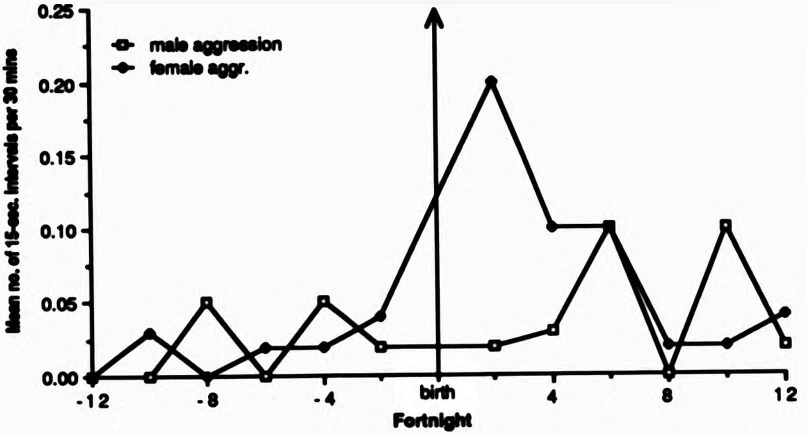


FIGURE 6.9. Aggression in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

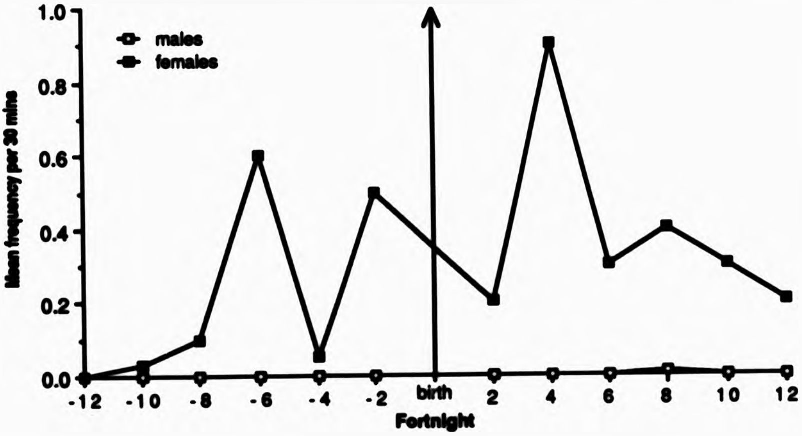


FIGURE 6.10. Partner-marking in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

aggression shown (Wilcoxon test; $T = 4$, $n = 4$ where $d \neq 0$, $p > 0.05$), and no significant changes over time for either sex (Friedman two-way ANOVAs; males: $\chi_r^2 = 1.32$, d.f. = 4, $p > 0.8$; females: $\chi_r^2 = 5.16$, d.f. = 4, $p > 0.2$). Females scent-marked their partners much more than males did (partner-marking was seen only once by a male; see fig. 6.10), but as one female was not seen to partner-mark the difference was not statistically significant (Wilcoxon test; $T = 0$, $n = 4$ where $d \neq 0$, $p > 0.05$). There were no significant changes over time in partner-marking by either sex (Friedman two-way ANOVAs; males: $\chi_r^2 = 0.4$, d.f. = 4, $p > 0.98$; females: $\chi_r^2 = 1.96$, d.f. = 4, $p > 0.7$).

Food-sharing was seen in only two pairs. Food was always transferred from the male to the female. Delaware received food from Arnold once, when he offered it to her, only a few hours before she gave birth. Roxanne received food from Elvis more frequently (14 occurrences), both by begging (11 times) and by offering (3 times). Elvis was only seen to refuse Roxanne once, in the fortnight immediately before she gave birth. There were fluctuations in the frequency with which food passed from Elvis to Roxanne over the observation period (fig. 6.11), but these did not appear to be associated with particular phases of the breeding cycle.

Figures 6.12 to 6.16 show changes in sexual and related behaviour by breeding males and females. Males sniffed their mates' anogenital areas much more than females (Wilcoxon test; $T = 0$, $n = 5$, $p < 0.05$; see fig. 6.12). There was a significant reduction in the frequency with males sniffed their mates anogenitally after birth (Friedman two-way ANOVA; $\chi_r^2 = 13.28$, d.f. = 4, $p < 0.01$), but females showed no changes over time (Friedman two-way ANOVA; $\chi_r^2 = 2.84$, d.f. = 4, $p > 0.5$). Male trill peaked after birth, and this change showed a trend towards statistical significance (Friedman two-way ANOVA; $\chi_r^2 = 8.36$, d.f. =4, $0.05 < p < 0.1$; see fig. 6.13). There were no sex differences in head-shaking or tongue-flicking (Wilcoxon tests; head-shake: $T = 4$, $n = 4$ where $d \neq 0$, $p > 0.05$; tongue-flick: $T = 4.5$, $n = 5$, $p > 0.05$; see fig. 6.14*a* and *b*). Male head-shake reached a maximum after birth, but this was not significant (Friedman two-way ANOVA; $\chi_r^2 = 4.84$, d.f. =4, $p > 0.3$), while male tongue-flick showed little variation with time (Friedman two-way ANOVA; $\chi_r^2 = 1.24$, d.f. =

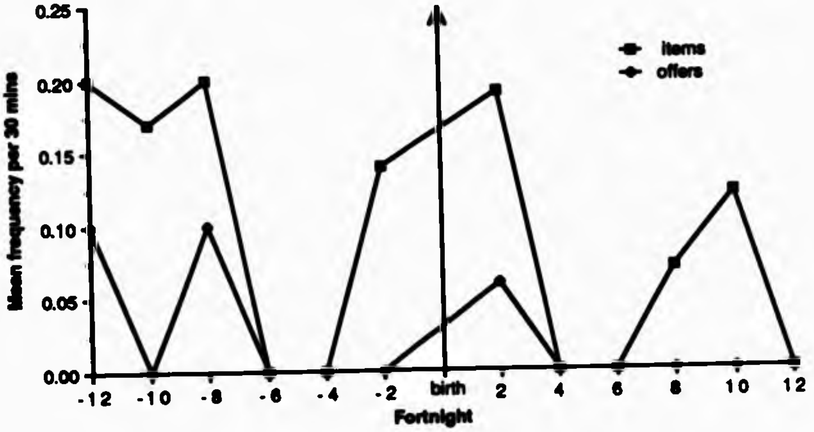


FIGURE 6.11. Food-sharing in a breeding pair of cotton-top tamarins. All food was transferred from the male (Elvis) to the female (Roxanne). Values given are means per 30 minutes for the total number of items transferred, and the number of offers.

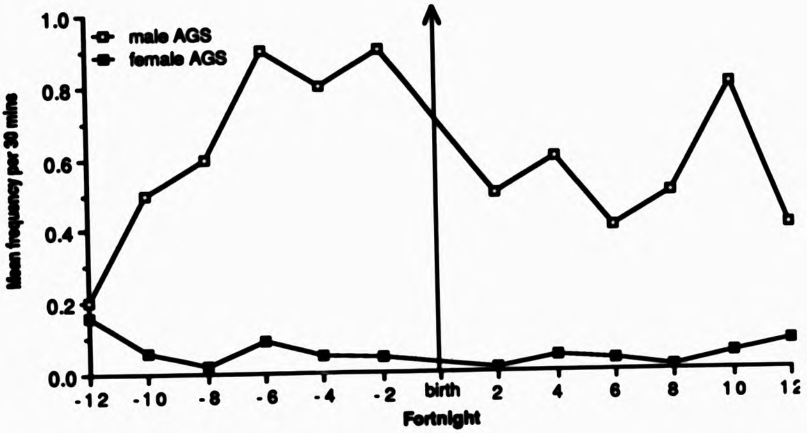
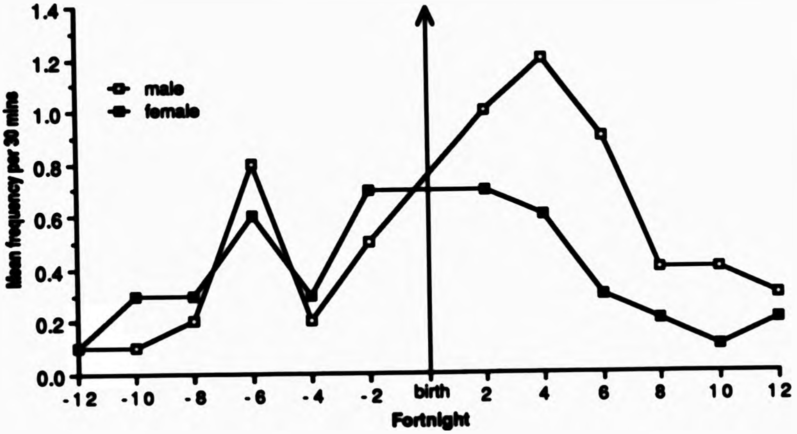


FIGURE 6.12. Anogenital sniffing in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

FIGURE 6.13. Frequency of male trill in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

(a) Head-shake



(b) Tongue-flick

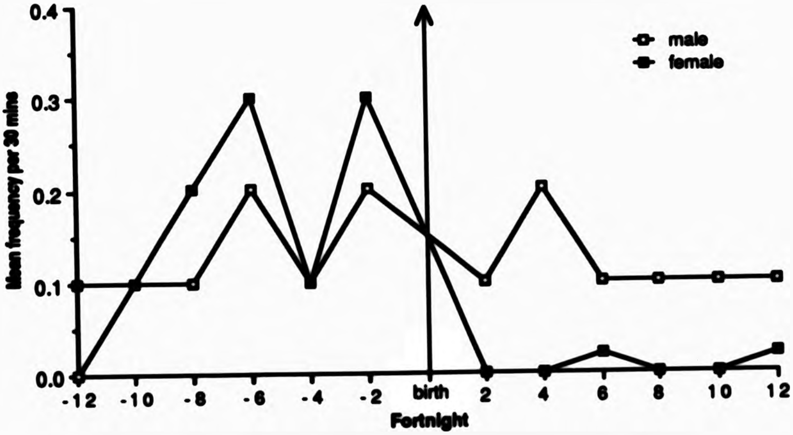


FIGURE 6.14. Frequency of head-shaking and tongue-flicking in five breeding pairs of cotton-top tamarins for 12 weeks before and 12 weeks after the birth of infants.

4, $p > 0.8$). Females, on the other hand, showed significant changes in levels of both tongue-flicking and head-shaking (Friedman two-way ANOVAs; tongue-flick: $\chi_r^2 = 12.36$, d.f. = 4, $p < 0.02$; head-shake: $\chi_r^2 = 10.12$, d.f. = 4, $p < 0.05$). Female tongue-flick was rare after birth, while female head-shake reached a peak just before and after birth. Female mounts were seen in three pairs before birth, but were rare afterwards; however, the differences over time were not significant (Friedman two-way ANOVA; $\chi_r^2 = 4.48$, d.f. = 4, $p > 0.3$; see fig. 6.15).

As the females did not all conceive at the same time relative to giving birth, the data on mounts were graphed separately for each pair (fig. 6.16). Although absolute frequencies varied considerably from pair to pair, they all showed the same basic pattern of change over time. There was a peak in mounting in the weeks immediately preceding birth. Although mounts were not seen in one pair (Elsa & Mario), they did show increases in head-shaking and tongue-flicking. The peak before birth led to no significant differences in overall mounting frequencies over time (Friedman two-way ANOVA; $\chi_r^2 = 5.16$, d.f. = 4, $p > 0.2$). In all five pairs, there was also a marked peak in mounting following birth. Mounting was rare in the first week postpartum, but increased over the following two to six weeks. This corresponds with the period of postpartum oestrus in cotton-top tamarins, which generally occurs in the four weeks following parturition (Ziegler *et al.* 1987*a*). However, subsequent levels of sexual behaviour appeared to be dependent on when conception occurred: in the three pairs in which the female conceived within a few weeks of giving birth, mounting became relatively infrequent soon after the estimated date of conception. The females in the remaining two pairs did not conceive during the study period, and sexual behaviour continued throughout observations.

Female rejections of male attempted and partial mounts were never seen before birth. After birth, a mean of 21% of male mounts were rejected overall, most commonly in the first four weeks postpartum. As there were insufficient data on rates of rejection for monthly values to be used, 12-week means for before and after birth were calculated and compared. The difference in the proportion of mounts rejected before and after birth was significant (Wilcoxon test; $T = 0$, $n = 5$, $p < 0.05$).

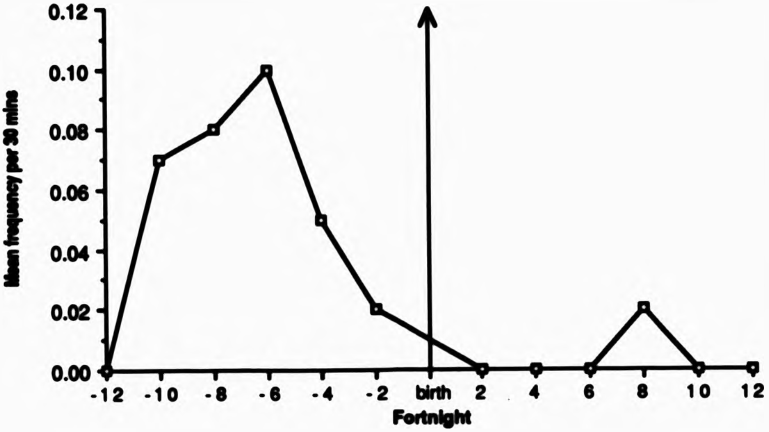


FIGURE 6.15. Frequency with which breeding females mounted their mates in five pairs of cotton-top tamarins.

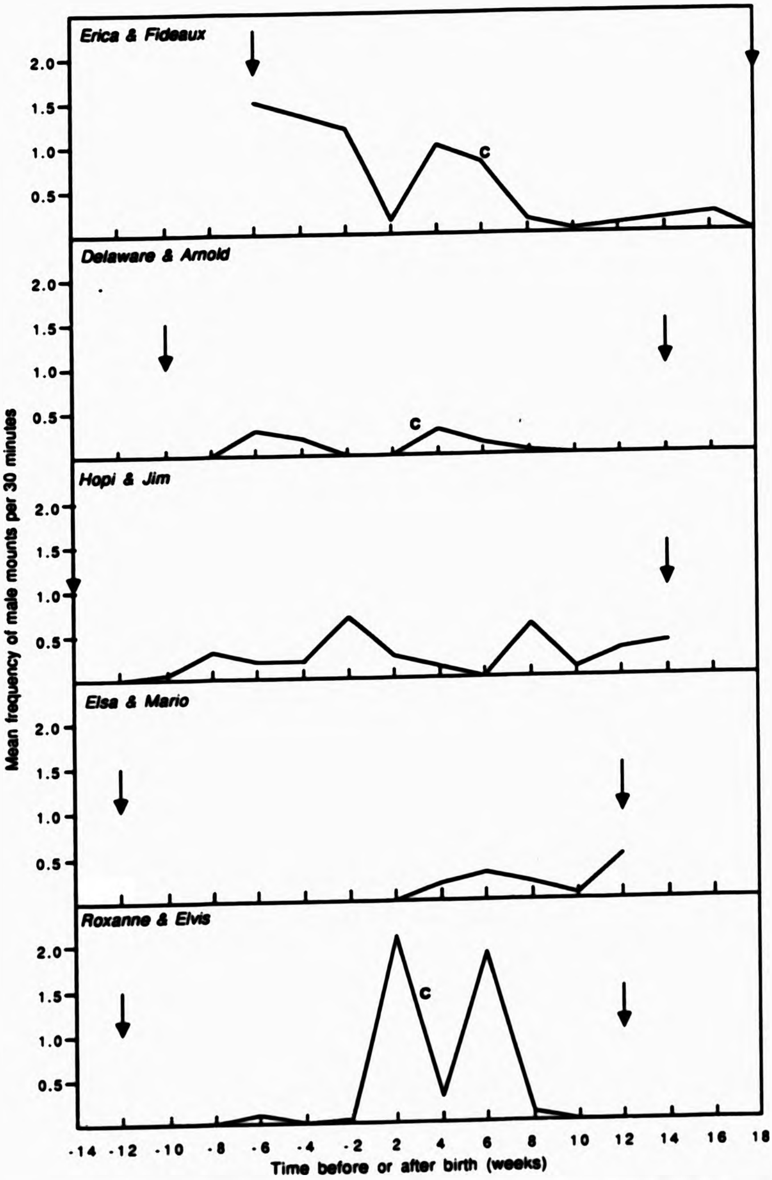


FIGURE 6.16. Mounting during the reproductive cycle in five pairs of cotton-top tamarins. Fortnightly means were calculated for frequency of mounts per 30 minutes. Arrows indicate start and end of observation period on each pair. C = estimated week of conception.

The breeding pair in each group were seen to mate only with each other, and in three of the four pairs with older offspring, no interference by other family members in copulations occurred. However, in Roxanne's family, the second-eldest son (Urquhart, b. 10/11/86) was seen to interfere between his father (Elvis) and his mother. He showed a great deal of interest in his mother in the two months before and after she gave birth. Before parturition, he was seen to maintain close contact with Roxanne, push between her and her mate Elvis, and show aggressive threats to Elvis over a period of five days. This behaviour ceased temporarily about a month before Roxanne delivered triplets. About two weeks after the infants were born, Urquhart again began to follow Roxanne closely, moved between her and Elvis, stopping them making contact, prevented Elvis from mounting her, and frequently sniffed her anogenital region. This behaviour continued for a period of two weeks, and was associated with a conspicuous drop in the frequency with which Elvis mounted (fig. 6.16). On one occasion, Urquhart was seen to move behind Roxanne three times, put his hands on her waist, and give slow tongue-flicks (these were rather different from the tongue-flicks normally associated with sexual behaviour, which were rapid). Conception apparently occurred during this time, but as no intromissions by Urquhart were seen and Roxanne rejected his advances, Elvis was probably the father of the resulting infants. Urquhart was not seen to behave in this fashion again, although two weeks after Roxanne's next delivery, another son, William (b. 2/12/87), a sub-adult and the fourth oldest son in the group, was also seen on one occasion to nuzzle his mother and tongue-flick slowly.

One other example of unusual behaviour involving an adult son and a parent occurred during observations of Elsa & Mario. One of the eldest male twins in the group (Remus, b. 5/4/83) was seen persistently following his father, sniffing him anogenitally, and mounting him over a period of about two weeks, 4-6 weeks before Elsa gave birth. This behaviour was repeated before Elsa's next delivery. No aggression was involved, although Mario appeared to be somewhat irritated by his son's attentions. Unlike his twin brother (see chapter 7) or the sons in Roxanne's family, Remus showed no signs of sexual interest in his mother or sisters.

Infant carrying as a "courtship" strategy[1]

As described in the methods section, expected numbers of mounts were calculated according to the amount of time each pair spent in each of the four carrying conditions. To simplify the presentation of the results, the expected number of mounts was subtracted from the observed number for each condition. Therefore, in figure 6.17, a positive result indicates that there were more mounts than expected for that condition, and a negative result shows that there were fewer mounts than expected.

Two males, Elvis and Fideaux, mounted their mates quite frequently (fig. 6.17*a* and *b*). For both males, the results were almost exactly as the hypothesis would predict and confirmed my previous impression that males mated more when carrying: there were generally more mounts than expected when the male was carrying one or more infants, and fewer than expected when he was not. There are two anomalies - Elvis mounted Roxanne slightly more than expected when she was carrying but he was not, while Fideaux mounted less often than expected when both he and Erica were carrying - but the deviations from the predicted pattern are only slight.

Figures 6.17*c* and 6.17*d* show data for another two males, Mario and Jim. Although they did not mount as frequently as Elvis or Fideaux, they showed exactly the predicted pattern.

However, as figure 6.17*e* shows, the final male, Arnold, did not conform to the predicted pattern. Although he was observed for two births, only 14 mounts were seen in all. There is in fact some suggestion that it was whether or not his mate Delaware was carrying that affected the frequency of mounts: Arnold mounted less often than expected when Delaware was carrying than when she was not.

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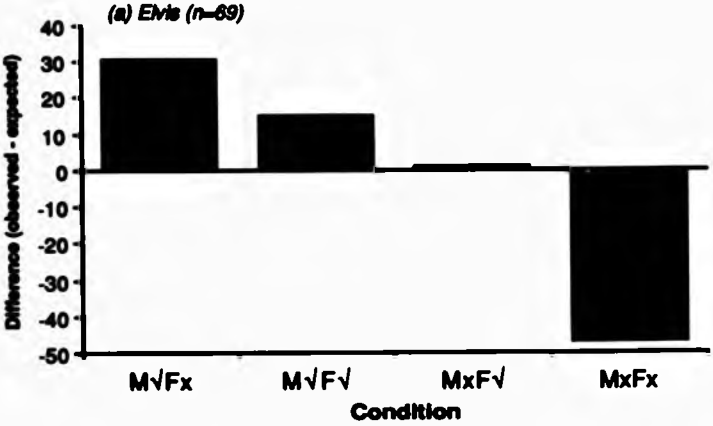
1) Data from this section are also presented in Price (in press *a*).

FIGURE 6.17. Mounting in relation to infant carrying by breeding males in five pairs of cotton-top tamarins. (a) Elvis; (b) Fideaux; (c) Mario; (d) Jim; (e) Arnold. Bars represent the difference between the number of mounts observed in each condition and the number of mounts expected. For calculation of expected frequencies of mounts, see text.

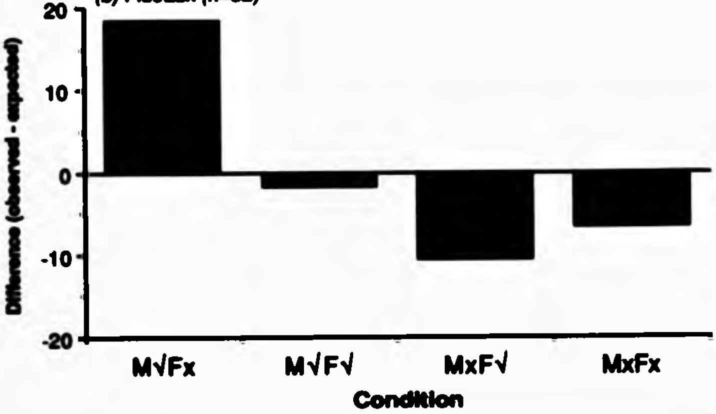
n = total number of mounts observed by each male.

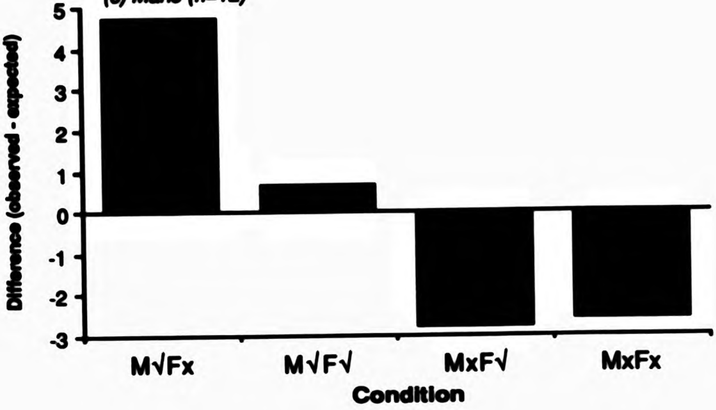
M√Fx = *male carrying, female not carrying*
M√F√ = *both parents carrying*
Mx F√ = *female carrying, male not carrying*
MxFx = *neither parent carrying*

(a) Elvis (n=69)

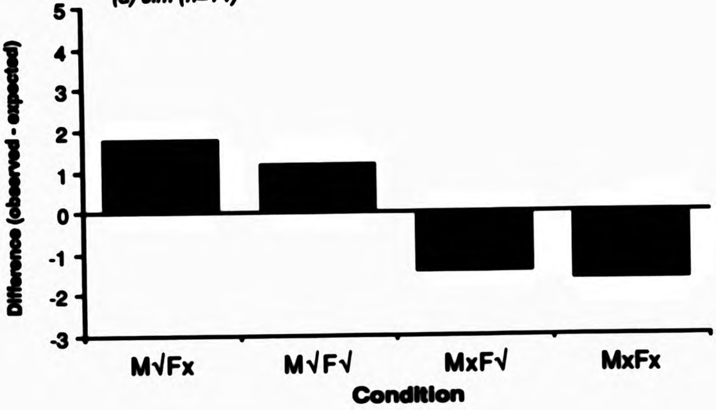


(b) Fideaux (n=52)

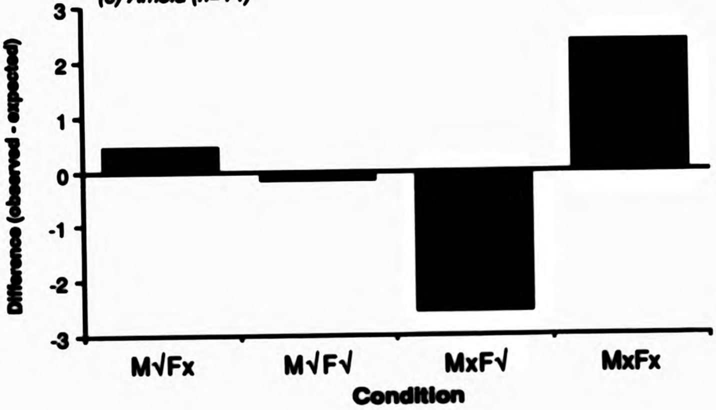




(c) Mario (n=12)



(d) Jim (n=14)



(e) Arnold (n=14)

The mean rates of mounting for the five males when carrying and not carrying are shown in figure 6.18. For all five males, including Arnold, mounts were more frequent when the males were carrying infants, and less frequent when they were not carrying. The difference in rates between the two conditions was statistically significant (Wilcoxon test; $T = 0$, $n = 5$, $p < 0.05$). To ensure that female carrying was not influencing this effect, the time spent in each condition was subdivided into times when the female was carrying and when she was not. There were no significant effects of female carrying in either condition (median number of mounts per 30 minutes; (a) M√F√ vs. M√Fx: 0.48 vs. 0.67, $p > 0.05$; (b) MxF√ vs. MxFx: 0.24 vs. 0.17, $p > 0.05$; Wilcoxon tests).

The results for other aspects of sexual behaviour are summarised in table 6.3. Rates of male trilling and female head-shaking were significantly increased when males were carrying. There were no significant differences between the two conditions for male head-shaking or for tongue-flicking by either sex, although males more than doubled their rates of head-shaking when carrying. Females rejected on average almost twice as great a proportion of male mounts when the males were not carrying, but again this difference was not statistically significant.

The behaviour of newly-formed pairs

The sociosexual behaviour of two newly-formed pairs (Viva & Windsor, and Alpha & Xavier; see table 6.1) was investigated during the first six weeks of cohabitation. Some changes in behaviour were apparent over the six-week observation period in both pairs. Information on social relationships is given in table 6.4. Levels of contact and time near were high in the first week, and then declined. As for established pairs, time spent near each other was less than time spent in contact. The males were largely responsible for maintaining proximity, although the females began to play a more active role in later weeks. For Alpha & Xavier, Xavier was consistently more responsible for maintaining proximity; for Viva & Windsor, however, Viva became more responsible in week 6. Both males groomed their mates more than the females groomed them, but female grooming, very low or nonexistent in the first week, began to increase as time went on. The males consistently showed more affection to their mates than they received. Aggression was rare, although the males appeared

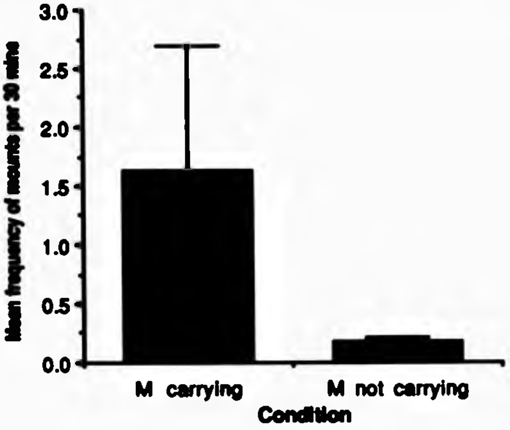


FIGURE 6.18. Mean rates of mounting per 30 minutes by five breeding male cotton-top tamarins when carrying infants and when not carrying. M = male. Vertical bars represent standard errors.

TABLE 6.3. Sexual behaviour in pairs of cotton-top tamarins when the male was carrying an infant compared with when he was not carrying.

	Median (range)		
Category	*Male carrying*	*Male not carrying*	*p (2-tailed)* *(Wilcoxon test, n = 5)*
Male trill [a]	1.29 (0.07 - 7.43)	0 (0 - 0.32)	< 0.05
Male tongue-flick [a]	0.12 (0 - 0.62)	0.10 (0 - 0.26)	n.s.
Female tongue-flick [a]	0 (0 - 0.02)	0 (0 - 0.03)	n.s
Male head-shake [a]	0.74 (0 - 4.23)	0.35 (0.02 - 1.08)	n.s.
Female head-shake [a]	0.21 (0.10 - 0.91)	0.04 (0 - 0.72)	< 0.05
% female rejection [b]	16.0 (0 - 75)	29.0 (0 - 83)	n.s.

[a] Number of 15-second intervals per 30 minutes.
[b] Percentage of male mounts rejected by female.
n.s. = not significant ($p > 0.05$).

TABLE 6.4. Social relationships in two newly-formed pairs of cotton-top tamarins. Weekly values represent mean scores per 30-minute session.

	Time after pairing (weeks)					
	1	*2*	*3*	*4*	*5*	*6*
Viva & Windsor						
Contact	53.8	23.0	28.2	26.8	27.9	35.1
Near	8.2	16.5	10.6	13.2	8.6	10.5
Hinde's index	+18.5	+23.2	+24.4	+19.7	+13.7	-12.6
Male groom	10.2	2.9	3.5	1.7	4.5	6.1
Female groom	0	0	0.9	4.3	3.6	4.5
Male affection	2.8	1.8	3.0	1.7	1.9	1.4
Female affection	0.2	0	0.6	0.2	0.1	0.4
Male aggression	0.2	0.5	0	0	0	0.2
Female aggression	0.2	0	0	0	0	0
Male partner-mark	0	0	0	0.2	0	0
Female partner-mark	0.2	0.1	0	0	0	0
Female anogenital sniff	0	0.1	0	0.2	0	0.2
Male anogenital sniff	1.9	0.4	1.5	0.5	0.8	1.0
Alpha & Xavier						
Contact	48.8	34.6	21.5	24.1	27.0	28.9
Near	8.8	11.1	11.1	9.1	9.4	11.1
Hinde's index	+15.3	+16.7	+1.3	+15.8	+12.9	+4.7
Male groom	10.1	4.8	1.0	6.5	4.5	5.2
Female groom	0.4	5.9	3.2	0.6	1.9	6.4
Male affection	2.8	1.5	1.2	2.8	0.4	0.8
Female affection	0.6	0.9	0.2	0.2	0.8	0.6
Male aggression	0	0.1	0	0	0	0
Female aggression	0	0	0	0	0	0
Male partner-mark	0	0	0	0	0	0
Female partner-mark	0.8	1.0	0.8	0.5	0.6	0.6
Female anogenital sniff	0	0.1	0.2	0.2	0	0.4
Male anogenital sniff	0.4	0.4	0.1	0.4	0.1	0.6

TABLE 6.5. Sexual behaviour in two newly-formed pairs of cotton-top tamarins. Weekly values represent mean scores per 30-minute session.

	Time after pairing (weeks)					
	1	*2*	*3*	*4*	*5*	*6*
Viva & Windsor						
Male trill	0	0.1	0.1	0.2	0.2	0.2
Male tongue-flick	0.6	0.4	0.2	0.7	0.5	0.5
Female tongue-flick	1.4	2.1	1.4	1.7	0.6	0.8
Male head-shake	1.0	0.9	0.4	1.2	0.4	0.6
Female head-shake	3.1	2.0	1.5	1.5	0.4	0.5
No. female mounts	0.1	0.1	0.1	0	0	0.2
No. attempted mounts	0.5	0.1	0.5	0.3	0.6	0.2
No. partial mounts	0.6	0.1	0	0.2	0	0
No. full mounts	0.1	0.1	0.1	0	0	0.2
% mounts rejected by female	11.0	0	0	0	0	0
Alpha & Xavier						
Male trill	0.6	0.6	0.1	0	0	0.5
Male tongue-flick	2.2	0.8	0.1	0.1	0.4	0.9
Female tongue-flick	2.4	1.6	0.6	0	0.2	1.1
Male head-shake	3.2	1.8	0.6	0.5	0.5	1.1
Female head-shake	2.9	2.1	1.0	0.5	0.4	1.2
No. female mounts	0	0	0	0	0	0
No. attempted mounts	1.3	0.8	0.9	0.2	0	0.1
No. partial mounts	0.5	0.8	0.2	0	0	0.2
No. full mounts	0.4	0.2	0	0	0.2	0.2
% mounts rejected by female	5.6	0	0	0	0	0

slightly more aggressive than the females. Males sniffed their mates anogenitally more, while females partner-marked more.

Food transfer was rare in both pairs. Alpha was seen to steal food from Xavier once, although Xavier resisted. Windsor quite frequently tried to steal food from Viva (19 occurrences), but as she always resisted he succeeded only twice. No offering or begging resembling behaviour seen infants or in two of the established pairs was observed.

Table 6.5 shows changes in several aspects of sexual behaviour over the six-week observation period. Frequency of mounts was high, particularly in the early weeks. There was a decline in sexual behaviour over the six-week period. Viva & Windsor showed lower levels of mounting than Alpha & Xavier. The two females showed more tongue-flicking and head-shaking than their mates. Only one rejected mount was seen in each pair (2% of 50 mounts for Alpha & Xavier; 3.4% of 29 mounts for Viva & Windsor). Both rejected mounts occurred in the first week after pairing.

The behaviour of pairs housed together for varying lengths of time

Previous studies (e.g. Evans & Poole 1984; Savage *et al*. 1988) have compared the behaviour of new pairs (i.e. with non-pregnant females) with that of established pairs during the female's pregnancy. However, as described above, the established pairs in this study showed changes in their relationship over the observation period, and thus behaviour during pregnancy is not necessarily an accurate reflection of behaviour at other times. Each period of the cycle in established pairs (A, B, C and D; see methods section) was therefore compared separately with the data from the newly-formed pairs. These comparisons showed both similarities and differences between the interactions of new and established pairs, the extent of which depended in part on the stage of the cycle at which established pairs were compared.

Comparisons of social behaviour in new and established pairs are illustrated in figure 6.19. While during periods A and D (mid-pregnancy and late lactation) established pairs spent somewhat less time than new pairs near and in contact with one another, immediately before

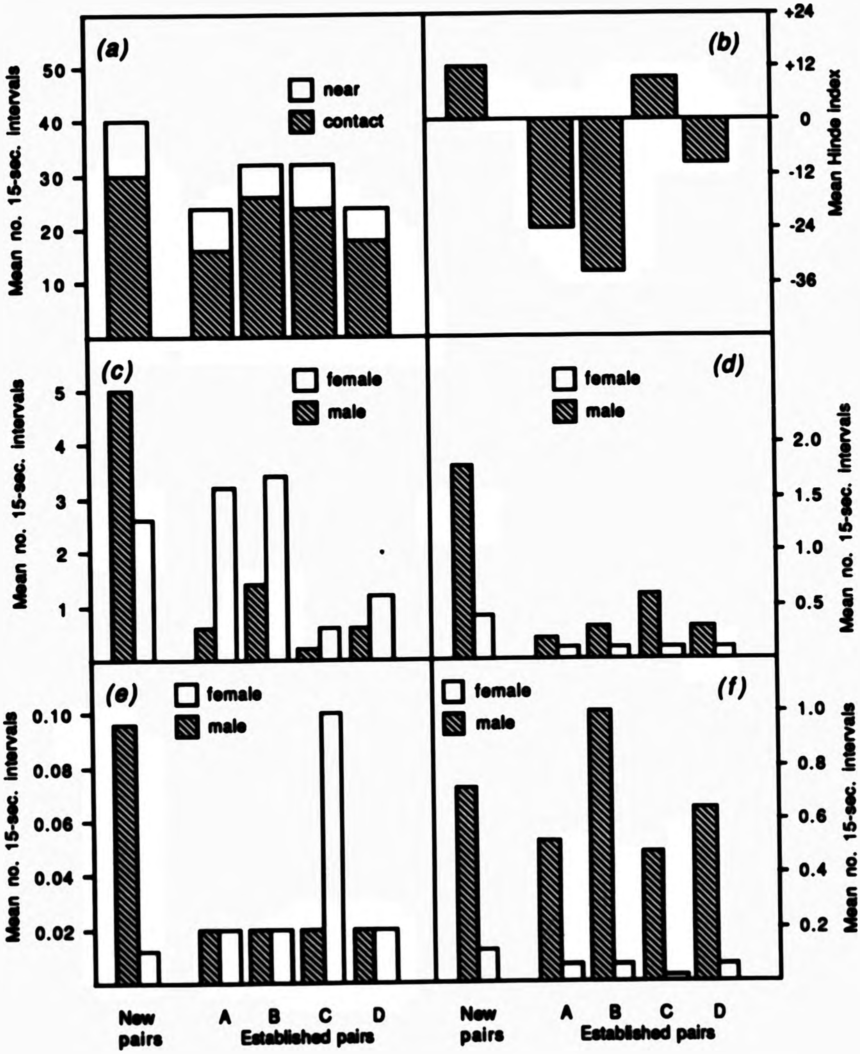


FIGURE 6.19. Comparisons of social relationships in two newly-formed pairs and five established pairs of cotton-top tamarins. (a) Spatial relationships; (b) Hinde index; (c) allogrooming; (d) affection; (e) aggression; (f) anogenital sniffing of mate. Values are expressed as means per 30 minutes, with the exception of (b). Periods for established pairs: A = weeks -12 to -7 before birth; B = weeks -6 to -1 before birth; C = weeks 1 to 6 after birth; D = weeks 7 to 12 after birth.

and after birth they were together more of the time, at levels approaching those shown by the new pairs (fig. 6.19*a*). Furthermore, during the six-week period (C) after the infants were born, breeding males were almost as active in maintaining proximity with their mates as males in new pairs (fig. 6.19*b*). This contrasted with the other three periods, when females in established pairs were largely responsible for maintaining proximity.

One obvious difference between new and established pairs was that, throughout the observation period, females in established pairs groomed their mates more than they were groomed in return, while the opposite was true for new pairs (fig. 6.19*c*). This change appeared to be due to a dramatic drop in grooming by males in established pairs: females in both new and established pairs groomed at approximately the same level overall. Both males and females in new pairs showed more affection to their mates than those in established pairs, but in all seven pairs, males showed more affection than females (fig. 6.19*d*). Again, the drop in affection in established pairs was greater for males than for females. Aggression was rare in all pairs, although females in established pairs showed slightly more aggression than their mates, while in the new pairs it was males who were more aggressive (fig. 6.19*e*). Anogenital sniffing by males showed no distinct differences (fig. 6.19*f*), while anogenital sniffing by females was rare in all groups, although slightly more frequent in the two new pairs.

Comparisons of sexual behaviour are shown in figure 6.20. The frequency of trilling by males in established pairs changed considerably over the observation period, but overall there was no clear difference from the levels shown by males in new pairs (fig. 6.20*a*). Tongue-flicking and head-shaking by both males and females occurred more frequently in new pairs (figs. 6.20*b* and *c*), but during the six weeks postpartum (period C), levels of head-shaking in established pairs reached similar levels to those in new pairs. Females in new pairs showed more head-shaking and tongue-flicking than their mates, but there were no clear sex differences in the established pairs. Frequencies of all types of male mount were higher in the new pairs (fig. 6.20*d*), although during the postpartum period levels of mounting in established pairs approached those of new pairs. Frequencies of female mounts differed from one period to the next in established pairs (fig. 6.20*e*); before birth they were similar to those in new pairs, but

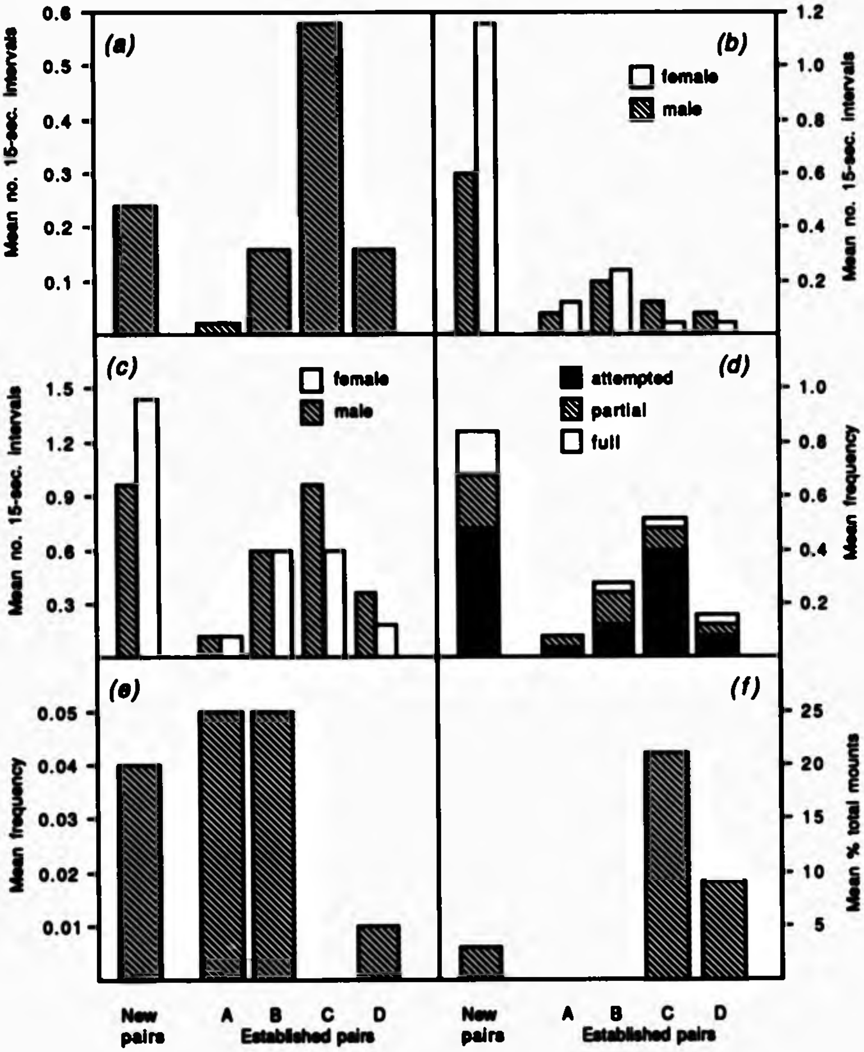


FIGURE 6.20. Comparisons of sexual behaviour in two newly-formed pairs and five established pairs of cotton-top tamarins. (a) Male trill; (b) tongue-flick; (c) head-shake; (d) mounts by male; (e) female mounts; (f) percentage of male mounts rejected by female. Values are expressed as means per 30 minutes, with the exception of (f). Periods for established pairs: A = weeks -12 to -7 before birth; B = weeks -6 to -1 before birth; C = weeks 1 to 6 after birth; D = weeks 7 to 12 after birth.

dropped dramatically after birth. Rejection of male mounts by females was unusual in new pairs, and was never observed before birth in established pairs. However, after birth rejection of mounts was not uncommon (fig. 6.20*f*).

Spearman correlation coefficients were used to compare frequencies of various categories of sociosexual behaviour with the length of time pairs had been housed together. Four sets of coefficients were calculated, corresponding to each of the four periods of the cycle for the established pairs. The same data from the new pairs were used in all four sets of calculations. Based on previous findings, I predicted that social and sexual interactions would decrease with the duration of pairing, and therefore used one-tailed tests. The results (see table 6.6) confirm that the effect of length of time paired on sociosexual behaviour varies to some extent with the stage of the breeding cycle at which established pairs are observed. Although almost all the correlations were negative (the only exception was the Hinde index in period C), supporting the prediction that interactions would decrease in frequency with time, they varied in degree from one stage to another. Period A (which corresponded roughly to mid-pregnancy in the established pairs, and is comparable to the time of observation in many other studies) showed few significant correlations between sociosexual behaviour and duration of pairing: only male tongue-flicking was significantly negatively correlated with time paired, i.e. males in longer-established pairs tongue-flicked less. This is not surprising given the relative lack of sexual behaviour at this stage of the breeding cycle. Correlations between contact and proximity were also virtually zero. However, the lack of data from Erica & Fideaux for this period (see methods section) made the sample size too small to reach significance on some measures (e.g. male grooming, affection, approach and leave). Period D (late lactation, and, in three pairs, early pregnancy) also produced no significant correlations for social or sexual behaviour, although there were some significant effects on spatial relationships. The greatest numbers of significant negative correlations were found in periods B and C (corresponding in the established pairs to late pregnancy, and postpartum oestrus/early lactation respectively), with significant negative correlations for several measures of social behaviour and spatial relationships. This was rather surprising since, as discussed above, it appeared to be during periods B and C that many differences between new and established pairs were smallest - for

TABLE 6.6. Correlations between length of time paired and measures of sociosexual behaviour in seven pairs of cotton-top tamarins. Separate Spearman rank order correlation coefficients are given for each of four time periods for five established pairs: (A) weeks -12 to -7 before birth; (B) weeks -6 to -1 before birth; (C) weeks 1 to 6 after birth; (D) weeks 7 to 12 after birth. For two newly-formed pairs, the same data (for six weeks following pairing) were used in all calculations. As predictions were made about the direction of the correlations, one-tailed significance levels were used.

	Period of breeding cycle in established pairs			
	A†	*B*	*C*	*D*
Spatial relationships				
Contact	-0.04	-0.72*	-0.83*	-0.83*
Near	-0.04	-0.94*	-0.17	-0.58
Male approach	-0.79	-0.83*	-0.47	-0.79*
Female approach	-0.90*	-0.63	-0.94*	-0.63
Male leave	-0.74	-0.63	-0.87*	-0.97*
Female leave	-0.56	-0.97*	-0.62	-0.65
Hinde index	-0.56	-0.44	+0.10	-0.29
Social behaviour				
Male groom	-0.79	-0.83*	-0.83*	-0.37
Female groom	-0.21	-0.65	-0.79*	-0.31
Male affection	-0.73	-0.94*	-0.83*	-0.36
Female affection	-0.16	-0.87*	-0.90*	-0.68
Male anogenital sniff	-0.53	-0.40	-0.53	-0.51
Sexual behaviour				
Male trill	..	..	-0.19	-0.24
Male tongue-flick	-0.90*	-0.83*	-0.59	-0.36
Female tongue-flick	-0.61	-0.40	..	..
Male head-shake	-0.58	-0.79*	-0.42	-0.60
Female head-shake	-0.61	-0.53	-0.91*	..
Total male mounts	..	-0.79	-0.09	-0.58

† $n = 6$ due to missing data from Erica & Fideaux. All other periods: $n = 7$.
.. Too many zero observations to calculate coefficient.
* $p < 0.05$ (one-tailed)

example, time spent in contact, responsibility for maintaining proximity, and sexual behaviour.

However, the negative correlation between time paired and frequency of mounting did disappear almost completely in the postpartum period (C). Frequencies of male tongue-flicking and head-shaking were significantly negatively correlated with time paired before birth, but not afterwards. Only female head-shaking produced a significant correlation, in period C, suggesting as before that females may have been less proceptive at this time. The relationships between frequencies of approach and leave by pair-mates also changed between periods B and C: in period B (late pregnancy), there were significant negative correlations for approaching by the male and for leaving by the female. In period C, in contrast, these correlations became non-significant, while the negative correlations between female approach and male leave became significant. Although not always statistically significant, negative correlations for grooming were always higher for males than for females, again indicating that males altered their behaviour more than females as the duration of pairing increased. There was a similar pattern for affection in the two periods before birth, but after birth females showed larger negative correlations than males. These results agree well with the pattern of pair relationships and responsibility for maintenance of proximity described above.

One possible reason for the less frequent interactions between established pairs around birth may be that lactating females needed to spend more time foraging than nulliparous females in new pairs. This is shown in figure 6.21. Established females spent slightly less time sitting and moving than females in new pairs. Before giving birth (periods A and B), they spent about the same time feeding as females in new pairs, but after birth they increased their feeding time to much higher levels than newly-paired females. In addition, established females always spent more time foraging. However, before giving birth they also tended to spend more time socialising than females in new pairs. Males in established pairs spent less time feeding but more time foraging than males in new pairs; about the same amount of time sitting and locomoting, except for period C when they spent more time sitting; and about the same amount of time in social interactions in periods A and B, but less in C and D.

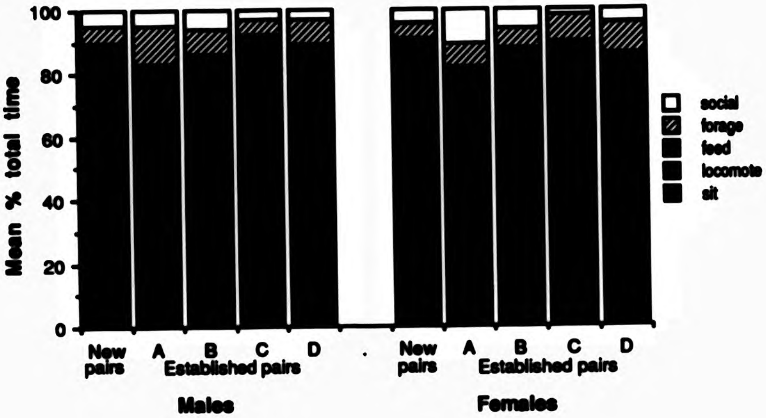


FIGURE 6.21. Activity of new and established pairs of cotton-top tamarins. For established pairs, activity budgets are given for four stages of the breeding cycle. A = weeks -12 to -7 before birth; B = weeks -6 to -1 before birth; C = weeks 1 to 6 after birth; D = weeks 7 to 12 after birth.

A further possibility is that breeding male and female tamarins have only a limited time available to spend in maintaining social relationships, and so as the size of their family increases they may share the time available amongst more individuals. In the pairs in this study, length of time paired was significantly correlated with group size (Spearman rank order correlation coefficient; $r_s = 0.94$, $n = 7$, $p < 0.05$). Thus, although breeding tamarins might spend the same *total* amount of time in social interactions, the time they spent with each individual group member, including the mate, might be decreased. In other words, alterations in the relationship between the breeding pair might be a secondary effect of changes in group size, rather than (or in addition to) a result of length of time paired. I investigated this by correlating time spent in contact with or near any other group member (as an indicator of how much time breeding tamarins spent socialising) with length of time paired. As before, separate correlations were calculated for each of the four phases of the observation period for established pairs. The results are shown in table 6.7. There were no significant correlations between length of time paired and how much time either males or females spent with other group members. However, it is of interest to note that for females, all the correlations were positive, while for males they were either near zero, or negative. This suggests that females tend to *increase* their levels of social interaction as the size of their families increases, whereas males tend to *decrease* them.

Discussion

In this section I will summarise the results of this part of the study and compare them with data from other studies of pair behaviour in callitrichids. Unfortunately, all the data currently available on relationships in monogamous pairs of marmosets and tamarins are from captive studies. Nevertheless, some interesting features have emerged from these studies which may have more general relevance. The results will be put into the broader context of callitrichid reproductive strategies in chapter 8.

Activity

Breeding tamarins changed the way they distributed their time over the breeding cycle, and the predictions outlined in the introduction to this chapter were confirmed. The most

TABLE 6.7. Correlations between length of time paired and time spent in proximity to other family members in seven pairs of cotton-top tamarins. Separate Spearman rank order correlation coefficients are given for each of four time periods for five established pairs: (A) weeks -12 to -7 before birth; (B) weeks -6 to -1 before birth; (C) weeks 1 to 6 after birth; (D) weeks 7 to 12 after birth. For two newly-formed pairs, the same data (for six weeks following pairing) were used in all calculations. Data from independent samples for males and females were used.

		Period of breeding cycle in established pairs			
		A[1]	*B*	*C*	*D*
Females	r_s	0.21	0.42	0.63	0.20
Males	r_s	0.07	-0.08	-0.24	-0.54

All p-values > 0.05.

1. n = 6 for period A; n = 7 for all other periods.

obvious changes were in the behaviour of female tamarins. As predicted, pregnancy produced little change in feeding or foraging times, but a slight (though non-significant) decrease in activity as measured by levels of locomotion. During lactation, however, females spent up to twice as much time feeding and foraging during lactation as during pregnancy. Although active social interactions decreased, the fact that there were no changes in the time spent in contact with other group members suggests that females were attempting to conserve social time, as Dunbar (1988) predicted they should. Males showed fewer changes, but their feeding and foraging scores reached a minimum in the month following birth.

Few studies have attempted to evaluate systematically changes in activity over the breeding cycle in marmosets and tamarins. The results of the present study are consistent with an investigation of energy intake in captive pairs of cotton-top tamarins during pregnancy and lactation (Kirkwood & Underwood 1984), in which energy intake, not significantly greater during pregnancy than in non-breeding pairs, doubled in two pairs during the first seven weeks of lactation. Assuming that males did not change their intake substantially, females therefore needed to increase their energy intake considerably to compensate for the demands of lactation.

The way captive tamarins distributed their time was comparable to values found in other captive studies. As in studies of *Callithrix jacchus* (Box & Pook 1974) and *Saguinus fuscicollis* (Vogt 1978*a*), sitting took up the greatest proportion of the tamarins' time. However, comparisons between studies are hampered by the fact that different authors use widely varying definitions of behavioural categories, and concentrate on different age-sex classes. For example, studies by Vogt (1978*a*) and Molzen & French (1989), which included juveniles, found much higher levels of both locomotion and social behaviour (10-15% and 20-40% respectively) than the present study (adult cotton-top tamarins spent only about 5% of their time in each of these activities).

Because data collection did not cover all the tamarins' waking hours, the data cannot be regarded as a true time budget, and a more detailed study of time budgets in captive cotton-top tamarins is still required. Furthermore, as there are at present no available data on activity budgets in wild cotton-top tamarins, it is difficult to assess the extent to which captive tamarins distribute their time in a similar way to their wild counterparts. Nevertheless, the figures obtained for feeding and foraging by females are remarkably similar to those reported by Goldizen (1987*a*) for wild saddle-back tamarins: about 15% during pregnancy, increasing to about 30% during lactation. Previous studies of time budgets in captive callitrichids have suggested that time spent foraging may be low in captivity compared to wild tamarins (e.g. *S. fuscicollis*: Vogt 1978*a*; *Leontopithecus rosalia*: Molzen & French 1989). However, as field studies have demonstrated the existence of considerable species differences in time budgets (Terborgh 1983), it is not yet possible to comment on the relationships between the time budgets of wild and captive callitrichids.

One obvious extension of this study would be to investigate weight changes in lactating females. Lunn (1983) found no effect of lactation on weight for the first 3-4 weeks postpartum in common marmoset mothers, except for a slight drop in weight in females who produced triplets. It is possible that the ease with which food could be obtained in captivity minimised weight loss; however, since in the present study feeding time increased beyond this point, a longer-term study may find subsequent weight loss in lactating females. Apart from increasing their feeding time, it is also possible that females altered their dietary preferences. As data were not collected on which foods females chose to eat, however, the present study cannot address this question.

Changes in sexual and social behaviour over the breeding cycle

Because no facilities for hormonal analysis were available, it was not possible to correlate social and sexual interactions with stages of the ovarian cycle. However, there was considerable evidence from this study that the female's reproductive state (pregnant, in postpartum oestrus, lactating) had a substantial effect on relationships between breeding male and female cotton-top tamarins, and there were changes in attractivity, proceptivity and receptivity over time. There was a peak in mounting in the weeks immediately preceding birth, and a marked peak following birth. This corresponds with the period of postpartum oestrus in cotton-top tamarins, which generally occurs in the four weeks following parturition (Ziegler *et* *al.* 1987*a*). However, subsequent levels of sexual behaviour appear to be dependent on when conception occurred: pairs in which conception occurred during the observation period showed subsequently reduced levels of mounting, suggesting that female attractivity declines if the female is pregnant, but is maintained if she does not conceive. Although there was no overall change in mounting frequency over time, the pre- and post-birth peaks were associated with differences in other components of sexual behaviour. One interesting finding was that female proceptive behaviour (female mounting, head-shaking and tongue-flicking) was most frequent before birth, while the fact that frequency of rejected mounts was higher postpartum suggested that they were least receptive after birth. Male behaviour suggested that females were also more attractive at this time, however. These patterns of behaviour have not previously been described in callitrichids; indeed, changes in sociosexual interactions over the breeding cycle in established pairs have received relatively little attention. Mounting may occur throughout pregnancy in most species (Epple 1978*b*), but there are some reports that mounts are not distributed with equal frequencies over time. Peaks appear to occur at two main points:

(1) at the estimated time of conception, for example during postpartum oestrus (e.g. *Callithrix jacchus*: Rothe 1975; Stevenson & Poole 1976; *L. rosalia*: Kleiman 1984).

(2) shortly before parturition (e.g. *C. jacchus*: Evans & Poole 1984; *S. labiatus*: Coates & Poole 1983; *S. oedipus*: Muckenhirn 1967; this study). One study (Kleiman & Mack 1977) found a peak in mounting during mid-pregnancy in *L. rosalia*, but this has not been reported in other species.

The data on changes in sexual relationships over the breeding cycle suggested that males were indeed sensitive to changes in the reproductive condition of females. However, this is a rather controversial area. Some studies attempting to relate sociosexual interactions more accurately to ovarian events by using hormonal analysis as an independent measure of cyclicity have found correlations between sociosexual behaviour and the phase of the ovarian cycle (e.g. *C. jacchus*: Kendrick & Dixson 1983, Dixson & Lunn 1987). However, a study of *L. rosalia* (Stribley *et al.* 1987) found no correlations between oestrogen levels and sociosexual behaviour. Confusingly, though, an earlier description, apparently of the same study but with one fewer pair (Stribley & French 1984) reported clear cycles in grooming, contact and proximity-maintaining behaviours with a periodicity of 19.1±1.4 days, very close to the ovarian cycle length, while acyclicity in ovarian function led to no cycles in social behaviour. Peaks in sexual behaviour were temporally associated with the cycles in social behaviour, although females were continuously receptive and mating occurred throughout the cycle. Kleiman (1978*a*) also found that cycles in *L. rosalia* were detectable from changes in sociosexual behaviour. Furthermore, while a study by French (1982) found no significant changes in behaviour in pairs of cotton-top tamarins associated with hormonal cycles, and Brand & Martin (1983) concluded that mating in cotton-top tamarins was not related to oestrogen activity, Brand (1984) reported that anogenital sniffing of the female by male cotton-top tamarins varied significantly over the cycle. There were also trends towards changes over time in male mounting, mounting success, and close-contact sitting. Brand (1984) also found that female tongue-flicking (an indicator of proceptive behaviour) tended to be highest at the low point in the oestrogen cycle, and there was some evidence that pregnant and non-cycling females were the most proceptive but the least attractive.

Some of these apparent contradictions may arise from methodological problems inherent in many studies. First, most have concentrated on newly-formed pairs (e.g. Brand & Martin 1983; Stribley *et al.* 1987). Since sexual interactions are high when marmosets and tamarins are first paired, but decline over time (e.g. Kleiman 1977; Evans & Poole 1983; Savage *et al.* 1988; this study), any short-term changes with the stage of the ovarian cycle may be masked. Kleiman (1984) pointed out that oestrus may be hard to detect in new pairs of golden lion tamarins, because sexual behaviour may occur after animals are first introduced, independently of the ovarian cycle. However, in established pairs of this species, peaks in mating that are roughly equivalent to the length of the oestrous cycle can be detected. Woodcock (1982) also reported that initial sexual interest by newly-paired male common marmosets was unrelated to the female's reproductive state. A recent study of golden lion tamarins (Stribley *et al.* 1987) also found that one established pair showed different patterns of some types of sociosexual behaviour to recently-formed pairs. This pair showed similar changes in the Hinde index to those described in cotton-top tamarins in the present study, with the male being primarily responsible for maintaining proximity only in the postpartum period. This suggests that the male could detect changes in the female's reproductive state.

Other studies (e.g. Brand & Martin 1983; Kendrick & Dixson 1983) have restricted physical access between members of pairs to brief observation periods each day. Stribley *et al.* (1987) suggest that such limited access paradigms involving repeated separations and reunions may result in perturbations in the relationship and thus in apparent cycles. However, Brand & Martin (1983), whose results, as discussed above, did not provide conclusive evidence of a relationship between ovarian cyclicity and mating, suggest the opposite effect: since temporary separation may lead to increased sexual activity when the pair is reunited (e.g. Evans 1981), this again may mask other changes in behaviour. Furthermore, Kendrick & Dixson's (1983) results were confirmed by Dixson & Lunn's (1987) study of pairs living together permanently with their families. A further problem may be that, as sexual behaviour in callitrichids does not occur very frequently, observation protocols involving only 30 or so minutes a day of observation may not be sufficient. Dixson & Lunn's (1987) study used 12-hour video taping, which may be the best method for investigating sexual behaviour in this species. Finally, at least in the cotton-top tamarin the oestrogen peak does not coincide with ovulation (Ziegler *et al.* 1987*a,b*).

Rothe (1975) reported that 90% of copulations in families of *C. jacchus* were disturbed by offspring. He also saw a juvenile male attempt to mate with his mother, but the father intervened. Evans (1986), however, saw no mating between parents and offspring in families of the same species. Interference by offspring in copulations in this study was rare, and occurred in only one family. The reason for the unusual behaviour of the sons in Roxanne's and Elsa's families was not clear. Kleiman (1979) found that young male *L. rosalia* may follow and attempt to mount their mother without serious repercussions. It may be significant that in the two families in which sons behaved atypically, the parents were wild-caught and may be well into their teens. In support of this, Price & Hannah (1983) saw one adult son in a cotton-top family follow his mother closely and groom and sniff her frequently, although no sexual behaviour was observed. Like the parents in the present study, the breeding adults in this group were more than 11 years old, and it is possible that such behaviour reflects the age of the parents.

There were also changes in the social relationships of breeding cotton-top tamarins over the breeding cycle. Investment by females in the pair bond in terms of grooming was higher before birth than after, and was consistently higher than that of males. One striking finding was that responsibility for maintaining close spatial associations varied considerably over time, but in a consistent way. In the period leading up to parturition, females were more responsible for maintaining proximity than males. During the first weeks postpartum, males became more responsible, but females later took over again. These data suggest that, as predicted, the time at which most investment in pair bond maintenance occurs differs between males and females.

There are few data from other species indicating such changes in behaviour over the breeding cycle. Vogt (1978*b*) found decreases in the distance between the members of the breeding pair in a captive group of *S. fuscicollis* occurred in the week prior to parturition, and again two weeks following one parturition. Qualitative observations suggested that these changes were largely due to the male approaching and following the female. Evans & Poole (1984), on the other hand, found that male common marmosets became more responsible for initiating contact during the latter part of pregnancy, but this appeared to be due to fewer approaches by the females, associated with a decrease in activity, rather than more frequent approaches by males. This contrasts with the results of the present study, where despite a decrease in female locomotion, female approaches peaked in late pregnancy.

Box (1975*b*) found a peak in both male and female grooming in common marmosets just before birth. Brown & Mack (1978) found that the total number of food items transferred among members of lion tamarin pairs declined during pregnancy and for 90 days postpartum; however, the relative proportion going to the female increased in late pregnancy. Ferrari (1987*a*) also observed that the breeding female in a wild group of *Callithrix flaviceps* received food from other group members, but only during the month or two before and after giving birth. In the cotton-top tamarin intra-pair food-sharing appears to be much less common than in lion tamarins (Feistner 1985, Omedes & Carroll 1980), and was seen regularly in only one established pair. Furthermore, almost all food appeared to be transferred from the male to the female, in contrast to lion tamarins where food is transferred both ways. There were no obvious changes over the cycle.

The data presented in this chapter also suggested that there may be a relationship between infant carrying by cotton-top tamarin fathers, and sex. Nearly 80% of conceptions in the Stirling colony have occurred within eight weeks of birth, and over 50% within four weeks postpartum. There is therefore a period after birth of relatively intense sexual activity that generally results in conception, and when male interest in staying close to the female is at a peak. This coincides with the period in which infants are still largely dependent and in which fathers show a lot of interest in carrying their offspring (see chapters 3 and 4). Although based on a small sample, the fact that males mounted their mates more frequently than expected when they were carrying infants, and less frequently than expected when they were not carrying confirmed the hypothesis that breeding males may use infants as part of a "courtship" strategy. There was also some evidence that females responded more positively to males' attempts to mount if the male was carrying an infant. Although no previous study has reported this phenomenon, there does seem to be a pattern that requires explanation. This is discussed further in chapter 8.

Changes in sociosexual behaviour with the duration of the pair bond.

Previous studies of pair-bond maintenanse and changes over time have suggested that levels of social and sexual interaction decrease with time, with changes in sociosexual interactions over time often being attributed to pair-bond formation and maintenance. However, in several studies this is confounded with the female's reproductive state: comparative data on established pairs in previous studies has usually been taken only for a limited period, often in mid-pregnancy. The present study has shown that behaviour in established pairs varies from one stage of the breeding cycle to another, and thus the level of any changes that are seen may depend on the point in the breeding cycle (pregnancy, cycling, or lactation) at which observations are made. Perhaps the most meaningful comparison to make is more likely to be between new pairs and established pairs during postpartum oestrus. This removes the possibility that any differences seen are due to pregnancy, although in established pairs there was evidence that lactation may also have an effect, producing reduced levels of social interactions. The presence of new infants may also affect levels of social interactions.

The data presented here contradict some previous studies in that there were few correlations between time paired and sociosexual behaviour in mid-pregnancy, but several negative correlations in late pregnancy and the postpartum period. This was somewhat unexpected given the increased levels of sexual behaviour seen postpartum in established pairs, but may be explained by the fact that lactating females were spending less time generally in active social interactions, and more time feeding. Note that the high levels of several behavioural categories in the first week after pairing will have further emphasised the difference between new and established pairs - it is likely that behaviour would be much more similar if this week was excluded.

There have been two previous studies of pair formation in cotton-top tamarins. Brand (1984; Brand & Martin 1983) investigated pair behaviour for the first 40 days of cohabitation. There were decreases over time in several measures of sexual behaviour, and in male allogrooming. However, there was an *increase* in female allogrooming, and also in close-contact sitting. Although in the present study, contact decreased over time in new pairs, in general Brand's results agree well with those presented here. Savage *et al.* (1988) also found that new pairs showed higher rates of affiliative behaviour (contact, grooming, huddling and copulations) than established pairs.

Several studies of other callitrichid species have found decreases in levels of social and sexual interactions between the members of the pair as the length of cohabitation increased. Evans & Poole (1983, 1984) and Woodcock (1982) found high levels of mating when male and female common marmosets were first paired. Kleiman (1977, 1978*a*) and Stribley *et al.* (1987) have found that sexual behaviour in *L. rosalia* was more frequent in new pairs, but then declined until in pairs that had been together for a long time it was rare. Kleiman (1978*a*) also suggested that sexual activity may be related to whether or not a pair had borne and raised offspring, although she did not say in what way. Kleiman (1977) and Evans & Poole (1983, 1984) conclude that the high levels of sexual behaviour observed when pairs are first put together may have a significant role in pair formation. Although not stated explicitly, this implies a reduced role for sexual behaviour in pair-bond maintenance. However, the present study has shown that when established female cotton-top tamarins are in oestrus, levels of sexual behaviour comparable to those seen in new pairs may occur.

As well as changes in the level of sexual behaviour, changes in social interactions over time have also been observed. Box (1975*b*) found that the breeding pair in one group of *C. jacchus* associated less as the family grew larger. Brown & Mack (1978) reported that the frequency of food transfer between members of lion tamarins pairs was highest for the first conception, and then declined. There was no evidence from the present study that food-sharing was more common in new pairs.

However, some other studies have found little evidence of changes in sociosexual behaviour over time. In a study of the red-bellied tamarin (*Saguinus labiatus*), Buchanan-Smith (1989) found no changes over the first four weeks of pairing in grooming or huddling, and sexual behaviour was rare. Infrequent sexual behaviour in this species compared to other callitrichids has also been reported by Coates & Poole (1983). One possible factor that could have affected Buchanan-Smith's results was that pairs were in restricted contact for four days before pairing; in other studies, pairs have been placed together immediately without prior contact. Therefore, some of the initial effects of pairing may have been reduced. Furthermore, both these studies took place over relatively short periods; longer-term studies may pick up more changes in behaviour.

One confounding factor in investigations of the effects of pair bond duration on social behaviour is likely to be group size. There was evidence in this study that the longer pairs of cotton-top tamarins lived together and the larger their families became, the less attention they directed towards their mate. However, they compensated for this by spending more time with their offspring, so that overall the amount of time spent with other family members altered little. This is supported by data from a study by Savage *et al.* (1988): established pairs of cotton-tops began to direct more attention towards their offspring than their mates.

Sex differences in the behaviour of breeding tamarins

In both new and established pairs of cotton-top tamarins, some sex differences in behaviour were apparent. However, the direction of the difference for some behaviours was different for new and established pairs: in new pairs, males groomed more and were more responsible for maintaining proximity, whereas in established pairs the opposite was true. The duration of the pair bond may thus have a considerable effect on the expression of sex differences in contributions to pair bond maintenance. Some behaviours, however (such as affection and anogenital sniffing) were consistently shown more by males than by females.

Most previous studies of cotton-top tamarins support these changes over time. Brand (1984) found that male cotton-tops in new pairs groomed more than females, but towards the end of her 40-day observation period, females began to groom more than males. This agrees with the results of the present study on new pairs. Several studies that have investigated established pairs of cotton-top tamarins have also found that females living in families groomed more than males (Muckenhirn 1967; Wolters 1978; Welker & Lührmann 1978; Price & Hannah 1983). In addition, Wolters (1978) and Welker & Lührmann (1978) found that females initiated contact more than males. This led Wolters (1978) to conclude (p. 267) that females' "affinity to their mate is more developed than that of the males to the females". Price & Hannah (1983) also showed that breeding males in both *S. oedipus* and *L. rosalia* families were the least likely to maintain proximity with other group members. In two cotton-top families, the males groomed less than the females, while in a pair which had bred unsuccessfully, the male groomed slightly more than the female. This pair was observed mating during the observation period, and the female was probably in postpartum oestrus (Price, unpublished observations). Savage *et al.* (1988), on the other hand, found that although new pairs of *Saguinus oedipus* showed higher rates of affiliative behaviour, in both new and established pairs males were more likely to initiate contact, grooming and sniffing. However, in established pairs the differences were not significant, and this decline in the magnitude of sex differences over time lends further support to the conclusions of this study.

Studies of pair relationships in other species have often reported that males groom more than females, show more sniffing, both anogenital and of other body areas, and are often more responsible for promoting proximity and contact (e.g. *C. jacchus*: Poole 1978; Woodcock 1978, 1982; Evans & Poole 1983, 1984; Dixson & Lunn 1987; *L. rosalia*: Omedes & Carroll 1980; Kleiman 1978*a*, 1984). This is opposite to the usual primate pattern (Evans & Poole 1983, 1984). Evans & Poole (1983), however, found that in new pairs of common marmosets, males were primarily responsible for establishing contact only during the first week. Poole (1978) found that male common marmosets were responsible for maintaining contact and showed more affection; otherwise there were no consistent sex differences. However, Evans & Poole (1984) point out that the females in this study may well have been pregnant, and a reduction in female activity may have influenced the results.

However, sex differences in other species, particularly *Saguinus*, are less conclusive. A study by Coates & Poole (1983) of established pairs of *S. labiatus* produced little evidence of any clear sex differences; males groomed more than females, while two of three females left more than males. When comparing new and established pairs in the same species, Buchanan-Smith (1989) found that males groomed more than females. However, in a further study of pair formation, Buchanan-Smith (1989) found no obvious sex differences in grooming or in maintenance of proximity. Vogt (1978*a*), who studied one family of *S. fuscicollis*, found that the mother groomed more than the father. In a study of common marmosets by Box (1975*a,b*), in some families the male groomed more, while in others it was the female. In captive *S. mystax* (Box & Morris 1980), there was a non-significant tendency for females to groom more than males, but it was not clear how long the pairs studied had been together. In one family, the male initiated contact and groomed more than the female. However, this pair had not bred again, and it is therefore possible that the female was cycling.

The pattern of behaviour seen in established pairs of cotton-top tamarins in this study contrasts with the usual picture of relationships in breeding pairs, in which males are generally seen as promoting close spatial associations more than females. However, some of the contradictions in previous reports of sex differences in the behaviour of callitrichid pairs may be due to variations in the time after pair formation at which observations have been made. New pairs in the present study exhibited the pattern most frequently reported: males were more responsible for maintaining proximity, and groomed more. However, established pairs showed, except during postpartum oestrus, the opposite pattern: females were more responsible for maintaining proximity and groomed more. Other affiliative behaviours, for example affection and anogenital sniffing, were always performed more by males. This suggests that these have different functions to other social interactions: they may allow males to monitor the female's reproductive condition and therefore determine how much to invest in their relationship. The pattern in this study is very similar to the one described in a recent study of pairs of golden lion tamarins (Stribley *et al.* 1987): in recently-formed pairs, male tamarins were responsible for maintaining contact, while in one established pair, the female was responsible except in the period immediately after birth.

Summary

(1) Breeding pairs of cotton-top tamarins showed changes in their activity over the breeding cycle. Female tamarins fed and foraged more during lactation, and were less active in late pregnancy.

(2) There were changes in social and sexual interactions over the breeding cycle. Female investment in pair bond maintenance, measured by grooming and promotion of proximity, was greatest shortly before birth, while male investment in terms of affection and promotion of proximity was greatest during postpartum oestrus. Female proceptivity and receptivity were greatest before birth, but attractivity was greatest after birth.

(3) Breeding males mounted females more frequently when carrying infants, suggesting that they were attempting to demonstrate their competence in infant care to the female in order to encourage her to accept them as mates.

(4) There were changes in behaviour with the length of time that pairs had lived together,

but the nature and degree of the changes seen was dependent in part upon the stage of the breeding cycle at which established pairs were observed. Established pairs showed frequencies of mounting during postpartum oestrus that were equivalent to those seen in new pairs.

(5) Sex differences in behaviour were different for new and established pairs: in new pairs, males groomed more and were responsible for maintaining proximity, but the reverse was true in established pairs.

(6) Levels of social behaviour decreased more in males than in females with increased duration of the pair bond and increased group size. Breeding tamarins devoted less attention to their mates but more to their offspring as group size increased.

Chapter 7

Polyandry, polygyny and incest in captive cotton-top tamarins

Introduction

The traditional view of marmosets and tamarins as monogamous (e.g. Epple 1975*a*), has been based largely on the observation that in captivity they breed successfully in pairs. However, it has recently been questioned following findings from long-term field studies on several species (Neyman 1978; Dawson 1978; Terborgh & Goldizen 1985; Rylands 1985) which seem to suggest that at least some callitrichids in the wild are not monogamous. Unfortunately, conclusive evidence for any mating system in wild marmosets and tamarins is sparse, as copulations are rarely seen (see chapter 1). Neyman's (1978, 1980) field study of the cotton-top tamarin produced no data on mating, though she considered that more than one breeding female per group was unlikely since no group had more than one set of juveniles at once. Although most of her study groups had more adult males than females, this could be explained if sons were more likely to stay in their natal groups than daughters (McGrew & McLuckie 1986), and thus data on group composition cannot be seen as evidence for a polyandrous mating system. A more recent study (Savage *et al*. 1989*a*) found two pregnant females in one group, although only one set of infants was subsequently seen.

A recent investigation of non-monogamous mating in captive cotton-top tamarins (Price & McGrew, in press *b*) agrees with captive studies of other callitrichid species (e.g. Hampton *et al*. 1966; Epple 1975*a*; Rothe 1975; Kleiman 1978*b*, 1979; Abbott 1978, 1984) that groups with more than one potentially breeding female are rarely stable. Groups with more than one male, on the other hand, may be less likely to break up (Price & McGrew, in press *b*).

In this chapter, I present data from two opportunistic case studies of non-monogamous mating in captive cotton-top tamarins, one in a polyandrous group, and one in a group in which incestuous mating resulting in polygyny occurred.

A. Behaviour in a polyandrous group

Introduction

The available evidence for mating by more than one male per group (or indeed any data on mating at all) in wild populations of callitrichids is largely limited to two of the twenty-five callitrichid species, and a total of no more than seven or eight groups. Rylands (1985), working on the marmoset *Callithrix humeralifer*, and Terborgh & Goldizen (1985), working on the saddle-back tamarin *Saguinus fuscicollis*, both saw groups in which more than one adult male mated with the breeding female. This does not prove that all of the males who mated had an equal chance of fathering offspring, since whether or not such mating occurred when the female was in oestrus and could therefore conceive was usually not known. The existence of a breeding system involving multiple paternity has therefore not been demonstrated as yet. Also, some groups in Terborgh & Goldizen's study population were monogamous, suggesting a flexible mating system that might depend on the number of non-breeding helpers available (Goldizen 1987*a*). Finally, Terborgh & Goldizen (1985) saw the formation of apparent "consortships", in which one male saddle-back tamarin attempted to sequester a female and prevent other males from associating with her. On the other hand, Goldizen (1989) has recently described peaceful interactions between the males in one polyandrous group of wild saddle-back tamarins; both males mated with the breeding female without interference. Buchanan-Smith (1989) also suggested that her observation of one wild red-bellied tamarin (*S. labiatus*) closely following another and attempting to mount may have indicated a form of consort relationship; however, the observation period was short, and the sexes of the individuals were unknown. Mounting occurs between males in cotton-top tamarins (personal observation; see also chapter 6). Other studies have suggested the possibility that more than one male might mate or breed (*C. flaviceps*: Ferrari 1987*b*; *Cebuella pygmaea*: Soini 1987*b*), but few detailed data are available for these cases. Soini (1988) observed that while subordinate *Cebuella* males attempted in mate, they were always thwarted by the dominant male.

In studies of captive groups, there is some evidence that while more than one male may mate, they do not necessarily have equal access to the female. Kleiman (1978*b*) and Epple (1972) have investigated trios of two males and one female in golden lion tamarins (*Leontopithecus rosalia*) and saddle-back tamarins respectively. Both found that while the males often coexisted peacefully for long periods (up to two years in the case of Epple's study), and sometimes both mated with the female, one male usually mated more often than the other.

However, there were some early indications in the literature that although more than one breeding female in a callitrichid group was unlikely, polyandry might occur. Hampton *et al.* (1966) described a group of three adult female and two adult male cotton-top tamarins. One female evicted both the others a few months after the group was established, and although one of the expelled females had apparently become pregnant only the winner reproduced successfully. The males showed no similar aggression, though there is no information on whether or not both mated. Hampton *et al.* (1966) also reported that cotton-top adults housed in adjacent cages often tried to reach neighbouring animals of the opposite sex, and one male who was temporarily moved copulated both with the female in the next cage, and with his own mate on return.

The existence in the Stirling colony of a group consisting of a father, two adult sons and an unrelated female, in which all the males had been observed to mate with the female, provided an opportunity to make a preliminary comparison between behaviour in monogamous and polyandrous groups.

Methods

Subjects and background

The group was established when Sioux, the breeding female of a monogamous family, died (for details, see chapter 2) and was replaced by an unrelated female (Shoshone, b. 24/3/86), from another colony. The composition of the group was subsequently altered substantially following intra-sexual aggression (see table 7.1). Twin males were born to Shoshone on 17/4/89, and a six-week period of detailed observation began immediately. At the start of these observations, the group consisted of five non-infant members: Shoshone; the original breeding male, Mohican (b. 2/5/78); and three of Mohican's offspring by his previous mate Sioux: an adult son, James (b. 4/4/87), and sub-adult male/female twins, Kansas and Kiowa (b. 22/10/87). The female twin, Kiowa, was evicted by Shoshone four days after the infants were born. As so little data were collected on Shoshone's relationship with Kiowa, all analysis concentrated on her interactions with the three males.

Kansas died following a fight with James 11 weeks after detailed data collection was completed. The fight occurred outside working hours, and when first noticed, both males had numerous wounds. However, they were both alert and neither appeared frightened, and the group as a whole was calm. No action was therefore taken. However, the following morning Kansas appeared listless, and was removed for about 30 minutes to be treated with antibiotics. He was also given a steroid injection in an attempt to stave off shock, and was returned to the group. However, his condition deteriorated during the afternoon. He was placed in the nestbox, but was attacked there, without warning, by James. Although he was removed immediately, he died of post-traumatic shock during the night.

Behavioural categories and recording methods

The group was observed for 3-4 hours a week divided into 30-minute observation sessions for a total of 20.5 hours over the six-week period following the birth of Shoshone's infants.

As the amount of time available was limited, I decided to concentrate observations on Shoshone, the breeding female, so that all instances of sexual behaviour could be recorded accurately. Shoshone therefore served as focal subject throughout, and her activity and interactions with all other group members were recorded during each 30-minute period, using a

TABLE 7.1. History of the polyandrous group

Date	*Events*
3/5/88	Breeding female, Sioux, dies. Left in group are her mate, Mohican (b. 2/5/78), five sons (Chickasaw, b. 2/4/83; Hogan, b. 18/2/86; Iroquois, b. 22/9/86; James, b. 4/4/87; Kansas, b. 22/10/87) and three daughters (Idaho, b. 22/9/86; Jessie, b. 4/4/87; Kiowa, b. 22/10/87).
12/9/88	Idaho removed and sent to Marwell Zoo.
3/10/88	A replacement female, Shoshone (b. 24/3/86), arrives from Marwell and is paired with Mohican in a small satellite cage, in visual, auditory, olfactory and limited physical contact with Mohican's offspring. Shoshone and Mohican observed mating.
	Iroquois and James fight, resulting in minor injuries to James.
5/10/88	Iroquois and Kansas fight.
6/10/88	Shoshone and Mohican observed mating.
7/10/88	Shoshone and Mohican observed mating.
	Iroquois and Kansas fight.
10/10/88	Shoshone and Jessie attempt to fight through mesh of cages.
11/10/88	All Mohican's offspring except for Kiowa and Kansas temporarily removed, while Shoshone and Mohican are allowed into the main cage.
12/10/88	Whole group allowed together. Shoshone and Chickasaw observed mating.
15/10/88	Iroquois attacks James. Iroquois removed from group as James is immature.
17/10/88	Chickasaw and Hogan fight. Hogan removed.
18/10/88	Following threats from Shoshone, Jessie is allowed access to Hogan and Iroquois, and refuses to return to main group.
24/10/88	Chickasaw attacks James. Chickasaw removed.
11/11/88 - 2/12/88	Kansas observed to mount Shoshone four times.
4/12/88 - 7/12/88	Aggression between Kansas and James.
8/12/88 - 13/1/89	Kansas and James follow Shoshone and attempt to mount her frequently. Minor fights occur when one of them tries to mount.
17/4/89	Shoshone gives birth to twins; detailed observations begin.
21/4/89	Shoshone attacks Kiowa. Kiowa removed after attacks from Shoshone.
27/5/89	Detailed observations end.
13/8/89	Kansas dies after a fight with James.

15-second time interval. The behavioural categories and recording methods were the same as those used to collect data from monogamous pairs. Instantaneous sampling was used to score Shoshone's activity, and her spatial relationships with the other group members: the identity of each individual in proximity or in contact with her was noted every 15 seconds. One-zero and all occurrences sampling were used to record other aspects of social relationships such as allogrooming, approaches and leaves, and sexual behaviour. (For full details of the behavioural categories and recording methods used, see chapter 6.)

Although using this sampling technique meant that systematic data could not be collected on the relationships between the males, a record was made of any notable occurrences, such as aggression, that occurred during data collection sessions. In addition, the identity of the carriers of both infants were recorded every 15 seconds; an individual was given a score of one if carrying one infant, and two if carrying two infants. Data were not collected on infant transfers.

Additional information on the previous history of the group, and events that occurred outside data collection periods, was compiled from colony records. Shoshone did not apparently conceive during the postpartum period.

Analysis of data

Runs tests above and below the median (Sokal & Rohlf 1981) for each behavioural category, using series of ten samples beginning at randomly chosen points in the set of 41 observations, demonstrated that the scores obtained for each male from consecutive samples were independent. Furthermore, when weekly means for most categories were calculated and inspected, there were no consistent trends over the six-week period. Average scores per 30-minute session were therefore calculated for each week and were considered to be independent samples for statistical purposes. Exceptions to this were sexual behaviour and infant carrying, which showed changes over the six-week observation period. Sign tests were used to test for differences between the males and the female in maintenance of proximity as assessed by Hinde's index (see chapter 6) for each week. As the scores of the males for each session appeared to be correlated on some measures, Wilcoxon tests and Friedman two-way analyses of variance for related samples, rather than tests for independent samples, were used to look for differences between the males in their other interactions with Shoshone. A χ^2 test was used to look for differences in the frequency with which the males mounted Shoshone.

Results

History of the group

Details of notable events and of the changes in group composition that occurred from Sioux's death until the end of the study period are given in table 7.1. During the five months between Sioux's death and the arrival of Shoshone as a replacement, no aggression was seen and the group remained stable, although some health problems were observed: intermittent diarrhoea was observed in most group members, and Mohican and Hogan both developed granulomas[1] on one leg which took several months to heal. Although no systematic observations were made, it also appeared that Idaho, the eldest daughter, had started to scent-mark more frequently. Idaho was removed four months after her mother's death, and sent to Marwell Zoo in return for Shoshone.

It was hoped that giving Mohican prior access to the new female would increase the chance that she would form a preference for him: Anzenberger (1985, 1986) has noted that already-paired female common marmosets will not mate with other males even if given the opportunity. So, in an attempt to encourage the formation of a pair-bond between Mohican and Shoshone, they were first paired in a separate cage (0.48m wide x 0.60m deep x 0.68m high) from the rest of the group, attached by flexible ducting to a bank of similar cages in a different room. This "satellite" cage had clear perspex sides, and was placed about 10cm from the front of the home cage. Mohican and Shoshone were therefore in visual, vocal and olfactory, but only very limited physical contact with Mohican's family. The new pair appeared to get on well, slept together in the satellite cage's nest box at night, and were observed to mate.

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1) Collections of granulocytes around a wound that has difficulty healing.

Fighting between two of Mohican's sons was seen on the day Shoshone was introduced to Mohican, and there was clearly tension between Jessie, now the eldest remaining daughter, and Shoshone. Both were seen to threaten the other with frowning and piloerection displays, and both scent-marked frequently. They made one attempt to fight through the mesh of the cages. Nine days after Mohican and Shoshone were paired, the whole group was allowed together. (We felt that no further purpose would be served by keeping them apart, and were concerned that prolonged separation might result in difficulties in reintroducing Mohican to his family.) Shoshone was observed mating with Chickasaw the same day, and Jessie immediately began showing submissive behaviour to Shoshone.

Three days after the group was mixed, a series of serious fights between the sons began that resulted in the three oldest being removed in the following nine days. Typically, an older son would attack a younger one. Mohican, however, was never involved in the aggression. Jessie also left the group, by retreating down the flexible ducting and refusing to return, after being threatened by Shoshone.

Shoshone's estimated date of conception was 16/10/88 (±3-4 days; Ziegler *et al.* 1987*a*), and therefore any of the five males in the group at the time who were more than 18 months old could have fathered the twin offspring born six months later. Both Kansas and James were observed to mount Shoshone (without pelvic thrusting) during her pregnancy, and sometimes interfered with one another's attempts to mate by pushing in next to Shoshone. However, in general the remaining five group members remained together in relative harmony, with only brief squabbles (usually involving only cuffing), until Shoshone's infants were born. The twins were successfully reared, with all group members sharing in their care.

Shoshone evicted Kiowa four days after the infants were born. On 12/8/89, when the infants were 17 weeks old, there was a severe fight between James and Kansas, resulting in numerous superficial injuries to both. Although there was no clear winner, Kansas' condition deteriorated (see methods section). James attacked Kansas on 13/8/89, and Kansas died the same day. No other group members were observed to take any part in the aggression.

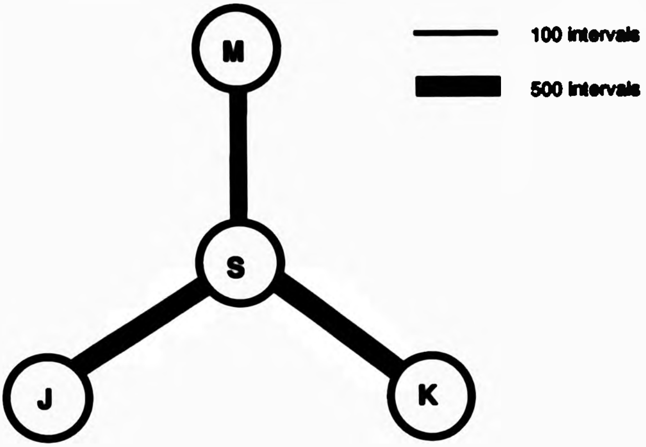
Detailed observations during the six weeks after the birth of twins

Spatial relationships between Shoshone and the three males are illustrated in figure 7.1. All the males showed basically similar patterns of association with Shoshone, although Mohican spent less time both in proximity and in contact with her than either of his sons. Kansas spent more time in proximity than the other two males, while James spent the most time in contact. However, neither of these differences was statistically significant (Friedman two-way ANOVAs; contact: $\chi_r^2 = 0.33$, d.f. = 2, $p = 0.85$; proximity: $\chi_r^2 = 1.33$, d.f. = 2, $p = 0.51$).

Figure 7.2 shows allogrooming, affection and aggressive interactions between Shoshone and each of the three males. Shoshone groomed Mohican more than she groomed either of his sons, although this difference was not statistically significant (Friedman two-way ANOVA; $\chi_r^2 = 0.58$, d.f. = 2, $p > 0.05$). However, the younger males groomed the female more than Mohican did, and the differences in male grooming were statistically significant (Friedman two-way ANOVA; $\chi_r^2 = 7.58$, d.f. = 2, $p = 0.029$). Subsequent pair-wise comparisons using Wilcoxon tests showed that the only significant difference was between Mohican and Kansas (Mohican-Kansas: $T = 0$, $n = 6$, $p < 0.05$; Mohican-James: $T = 1.5$, $n = 5$ where $d \neq 0$, $p > 0.05$; James-Kansas: $T = 5$, $n = 6$, $p > 0.05$). Mohican and Shoshone groomed one another at approximately equal levels ($T = 4$, $n = 4$, $p > 0.05$), but the two younger males groomed Shoshone significantly more than she groomed them (Kansas: $T = 0$, $n = 6$, $p < 0.05$; James: $T = 0$, $n = 5$, $p < 0.05$).

All three males gave and received approximately the same amount of affection, and Friedman two-way analyses of variance confirmed that there were no significant differences between the males in the amount of affection they gave or received (affection given: $\chi_r^2 = 1.58$, d.f. = 2, $p > 0.05$; affection received: $\chi_r^2 = 0.08$, d.f. = 2, $p > 0.05$). However, all males showed much more affection to Shoshone than they received from her, although this difference was not significant for Mohican (Kansas: Wilcoxon tests; $T = 0$, $n = 6$, $p < 0.05$; James: T =), $n = 5$, $p < 0.05$; Mohican: $T = 1$, $n = 5$, $p > 0.05$).

(a) Near



(b) Contact

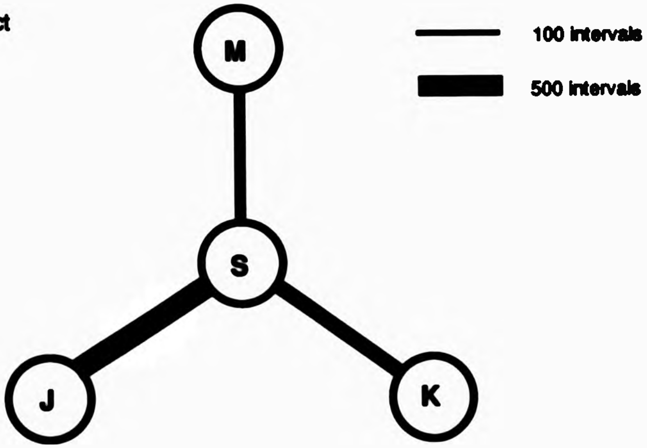


FIGURE 7.1. Spatial relationships in a polyandrous group of cotton-top tamarins.
(a) Total number of 15-second intervals that each male was near Shoshone.
(b) Total number of 15-second intervals that each male was in contact with Shoshone. Number of intervals is directly proportional to the width of the connecting line. S = Shoshone, M = Mohican, J = James, K = Kansas.

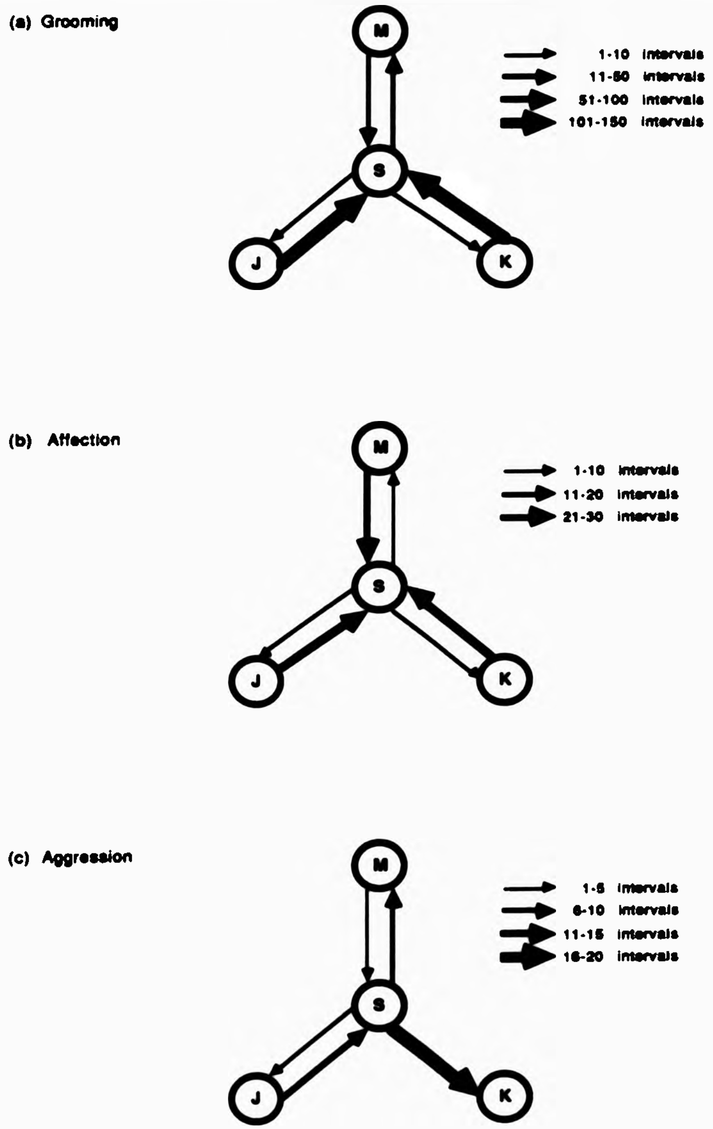


FIGURE 7.2. Social relationships in a polyandrous group of cotton-top tamarins. (a) Total numbe of 15-second intervals in which grooming occurred. (b) Total number of 15-second intervals in which affection occurred. (c) Total number of 15-second intervals in which aggression occurred. Arrows indicate direction of interaction. S = Shoshone, M = Mohican, J = James, K = Kansas.

Like grooming, the pattern of aggression showed differences between the males. Friedman two-way ANOVAs showed that there were no significant differences between the males in the amount of aggression they received from Shoshone or directed to her (aggression given: $\chi_r^2 = 3.0$, d.f. = 2, $p > 0.05$; aggression received: $\chi_r^2 = 4.75$, d.f. = 2, $p > 0.05$). Both Mohican and James gave and received low levels of aggression; Mohican received slightly more aggression from Shoshone than he gave in return, while James gave more than he received, but neither of these differences was significant (Wilcoxon tests; Mohican: $T = 0$, $n = 4$, $p > 0.05$; James: $T = 0.5$, $n = 4$, $p > 0.05$). However, Kansas, the youngest male, received much more aggression from Shoshone than either of the other two males, and was never seen to be aggressive to her. This difference was significant ($T = 0$, $n = 5$, $p < 0.05$).

None of the males was seen to share food voluntarily with Shoshone. Kansas stole food from her twice, and she attempted to steal from him once, but failed. All these occurrences involved resistance on the part of the possessor of the food.

Maintenance of proximity, as assessed by Hinde's index for each week, showed a clear difference between Mohican and the younger males. Overall, Shoshone was slightly more responsible for maintaining proximity than Mohican, but this was not statistically significant (overall Hinde index = -5.7; $x = 2$, $n = 6$, $p = 0.344$; sign test). In contrast, James and Kansas were both significantly more responsible for maintaining proximity than Shoshone (James: overall Hinde index = +38.6; $x = 0$, $n = 6$, $p = 0.032$; Kansas: overall Hinde index = +25.6; $x = 0$, $n = 6$, $p = 0.032$; sign tests). Changes in maintenance of proximity over the six week observation period are shown in figure 7.3. Mohican became more responsible for maintaining proximity in weeks 2-4. James also showed a peak in week 3, although he was always primarily responsible for maintaining proximity. Kansas, however, showed a different pattern: like James, he was responsible for maintaining proximity with Shoshone, but rather than showing a peak midway through observations, the values increased towards the end of the study period.

All the males mounted Shoshone during the six weeks after birth, and at least one full mount was seen by each male (fig. 7.4). On one occasion, full mounts by James and Kansas

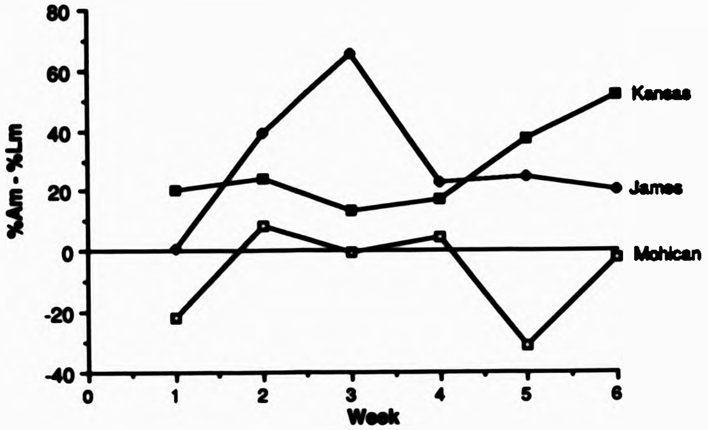


FIGURE 7.3. Maintenance of proximity in a polyandrous group of cotton-top tamarins for six weeks following the birth of infants. %Am - %Lm = Hinde's index (the percentage of approaches due to the male minus the percentage of leaves due to the male). Positive values indicate that the male is primarily responsible for maintaining proximity with the female, negative values that the female is primarily responsible.

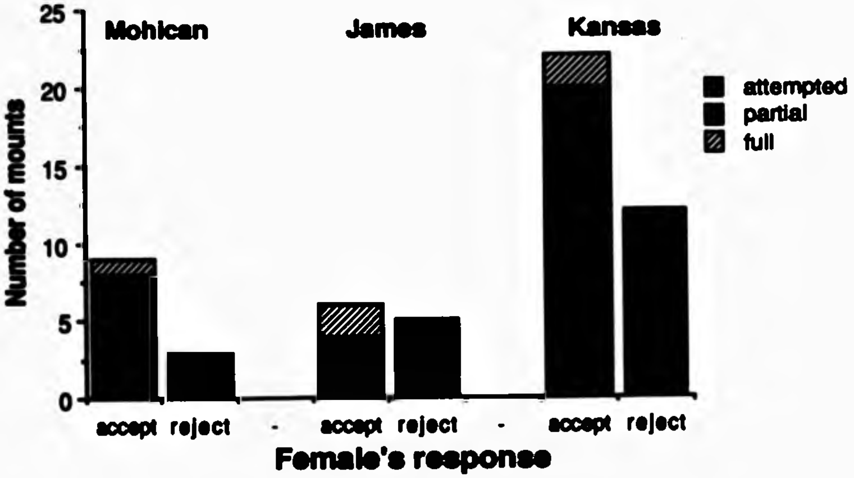


FIGURE 7.4. Total frequency of attempted, partial and full mounts by each of three males in a polyandrous group of cotton-top tamarins, and the female's response.

and one partial and two attempted mounts by Mohican occurred within six minutes of one another. James and Mohican mounted with approximately equal frequencies (Mohican: n = 12; James: n = 11). Kansas mounted more frequently (n = 34), and the difference in total mounting frequency by the three males was significant (χ^2 test; $\chi^2 = 17.8$, d.f. = 2, $p < 0.001$). Shoshone rejected quite a high proportion of each male's attempted or partial mounts (Mohican: 25%; James: 45%; Kansas: 35%). Mounting frequency was low in the first week and then increased (fig. 7.5). Both Mohican and James showed a tendency to mount Shoshone more often in weeks 2-4, suggesting an effect of Shoshone coming into oestrus, but Kansas increased his number of mounts steadily throughout the observation period. This pattern closely parallels that for maintenance of proximity.

Any form of interference by one male in the mounts of another was extremely rare, and occurred on only three occasions (5% of the 57 mounts seen). On one occasion, Mohican attempted to mount Shoshone, but stopped following an approach by Kansas. Similarly, Kansas stopped in an attempt to mount Shoshone when James approached. In the third case, James mounted Kansas while Kansas was mounting Shoshone. No threats or aggression were seen in any case.

Table 7.2 summarises aspects of sociosexual behaviour. The data were insufficient for statistical analysis. Soliciting behaviour by Shoshone was extremely rare: she was never seen to tongue-flick, and head-shook once near Mohican, and once near James. Male soliciting was more frequent, though not common. All three males sniffed Shoshone anogenitally far more frequently than she sniffed them; however, while Shoshone scent-marked each male several times, only Kansas was seen to mark her, and he did so only once.

Carrying of infants is illustrated in figure 7.6. Kiowa was not seen carrying during data collection sessions. The majority of infant carrying was done by James. To determine the effect that carrying infants had on male sexual behaviour, observed and expected frequencies of mounts were calculated for each male when carrying infants and when not carrying. (For details of the

TABLE 7.2. Sociosexual behaviour in a polyandrous group: total scores

Pair	*Male trill*	*Male tongue-flick*	*Female tongue-flick*	*Male head-shake*	*Female head-shake*	*Male anogen. sniff*	*Female anogen. sniff*	*Male partner-mark*	*Female partner-mark*
Mohican & Shoshone	3	0	0	1	1	20	1	0	13
James & Shoshone	62	2	0	5	1	11	0	0	5
Kansas & Shoshone	8	3	0	2	0	18	1	0	11

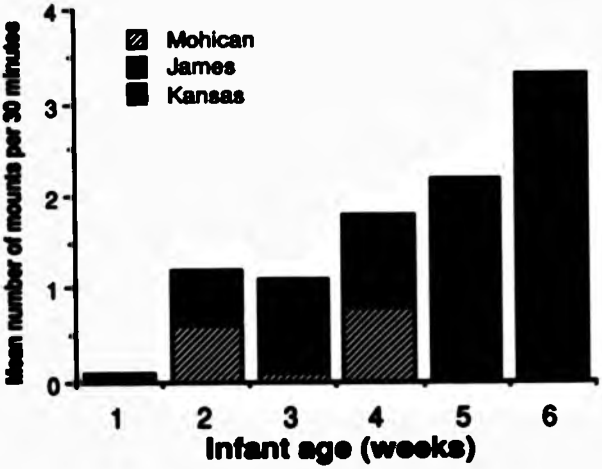


FIGURE 7.5. Mean number of mounts per 30 minutes performed by each male in a polyandrous group of cotton-top tamarins.

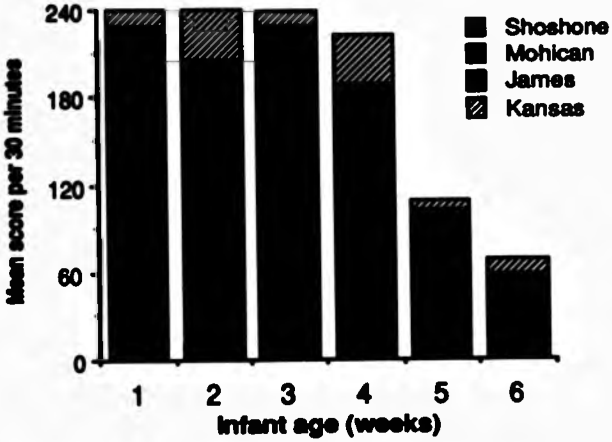


FIGURE 7.6. Mean number of 15-second intervals per 30 minutes that the members of a polyandrous group of cotton-top tamarins carried infants. Maximum score = 240 (carrying two infants for 30 minutes).

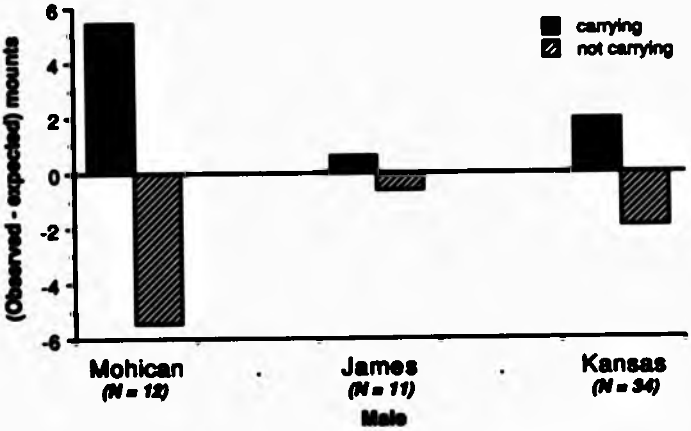


FIGURE 7.7. Mounting in relation to carrying of infants in a polyandrous group of cotton-top tamarins. Expected values for number of mounts when carrying and not carrying were calculated by multiplying the total number of mounts for each male by the proportion of time spent in each category. Expected values were then subtracted from the actual number of mounts observed. Positive values therefore indicate that more mounts than expected occurred in a given category, negative values that fewer mounts than expected occurred. N = total number of mounts by each male.

calculations involved, see chapter 6). The results are shown in figure 7.7. All three males mounted Shoshone more than expected when carrying infants, and less than expected when not carrying. However, only for Mohican was there a strong effect.

Relationships between the three males appeared to be almost entirely amicable during the observation period. Only three aggressive incidents occurred, and these were confined to minor aggression such as cuffing. All three involved James and Mohican: James was aggressive to Mohican twice, while Mohican showed aggression to James once. None of these aggressive episodes appeared to be associated with Shoshone. Although not involved in any aggression, for a brief period approximately one month after the infants were born, Kansas was often seen displaying (piloerecting his body and crown hair). He also scent-marked frequently. Some of these displays appeared to be directed at James.

Conclusions

Before the introduction of a new female, the group lived together peacefully for several months, despite the presence of several sexually mature males. However, the health problems that occurred were unlike anything that had previously been observed in the colony, and it is possible that the lack of a breeding female, although not leading to any obvious signs of tension, may have been affecting the remaining family members.

It was impossible to know whether or not more than one male was sexually active around the time of ovulation or conception, as Shoshone did not conceive during the observation period, and no hormonal data were obtained. The difficulty of assessing male sexual access in relation to paternity is a problem shared with many other studies. However, sexual activity by more all three males was observed during the postpartum period, with no apparent interference.

As in all monogamous pairs, all three males showed more affection and anogenital sniffing to Shoshone than they received, while she in turn scent-marked them more frequently than they did her. Like females in established pairs following birth, Shoshone rarely showed proceptive behaviour, and rejected a fairly high proportion of each male's attempts to mount.

Finally, although during the study period there was virtually no aggression between the males, and no overt competition to mate with the female, serious aggression between brothers in the group did occur both when Shoshone was first introduced, and also after the group had been together for some time, resulting in one fatality. Groups with more than two breeding males may therefore be unstable in the long term, particularly in captivity. It was interesting to note that all severe aggression involved brothers; the father was never involved.

A comparison with the data from monogamous pairs presented in chapter 6 shows both similarities and differences in behaviour. In contrast to both new and established monogamous pairs, all three males in the polyandrous group spent less time in physical contact with Shoshone than near her. There were also some differences between the father and his two sons in their relationships with the female. Mohican behaved more like males in established monogamous pairs in that he gave no more grooming than he received, and was less responsible than Shoshone for maintaining proximity. His sons, on the other hand, behaved more like newly paired monogamous males in that they groomed the female more than she groomed them, and were always primarily responsible for maintaining proximity. One possible explanation for these differences is that when the group was first formed, aggression from their older brothers (see table 7.1) may have meant that James and Kansas were unlikely to have been permitted to mate. It is possible, then, that although all the males had been in the group with Shoshone for the same length of time, only Mohican had originally established a relationship with her corresponding to that between a breeding male and female, and that James and Kansas had reached a similar stage much more recently.

Other aspects of behaviour showed differences between Mohican and James on the one hand, and Kansas on the other. Aggression between males and the female was rare in the case of Mohican and James, as in the monogamous pairs described in chapter 6. However, Shoshone directed aggression much more frequently at Kansas. Like males in established pairs, Mohican and James showed an increased tendency to maintain proximity with the female in weeks 2-4, followed by a decrease. Kansas, however, showed a different pattern. Age may have had an influence on this. When Shoshone was first introduced into the group, James was approximately 18 months old, but Kansas only a year old. Male callitrichids reach sexual maturity at about 18 months (e.g. Abbott & Hearn 1978), and thus Kansas at least was unlikely to have been sexually mature at the time of Shoshone's arrival, although he was seen to mount her. Whether his behaviour in relation to Shoshone more resembles that of offspring than that of breeding males in monogamous families cannot be determined at present. His fight with James may have been related to the onset of sexual maturity in Kansas - he was 22 months old at the time.

B. Behaviour in a polygynous group

Introduction

There is as yet little convincing evidence for simultaneous and successful rearing of infants by more than one female in a callitrichid group (Price & McGrew, in press *b*; see also chapter 1). Although more than one female has occasionally been seen to be pregnant or lactating in field studies of several species (*S. fuscicollis*: Terborgh & Goldizen 1985; *S. mystax*: Ramirez 1984, Ruth 1987; *S. oedipus*: Savage *et al*. 1989*a*; *C. humeralifer*: Rylands 1985; *C. jacchus*: Roda & Roda 1987, Scanlon *et al*. 1988; see chapter 1), simultaneous and *successful* reproduction (i.e. rearing of infants) appears to be extremely rare in wild callitrichid groups. Only one example exists: two females bred in a single *Leontopithecus rosalia* group observed by Baker (cited in French *et al*. 1989*a*). Immigration by parous females, and/or transitions between breeding females, could often explain the other observations.

Data from captive callitrichids generally agree that groups containing more than one unrelated adult female are unstable because of frequent and severe aggression between females (e.g. Epple 1975*a*), and relationships in groups containing more than one potentially breeding female (excluding daughters still in their natal families) remain to be described in detail. There have been few reports of more than one female breeding in captive groups. Christen (1974, cited in Epple 1975*a*) reported that both a dominant and subordinate female in groups of *Cebuella pygmaea* and *S. midas* produced full-term young; however, no female succeeded in rearing her offspring. Anzenberger & Simmen (1987) described a group of *Callithrix jacchus* in which a mother and daughter became pregnant, but the two females had to be separated. Simultaneous breeding by more than one female in captive cotton-top tamarins has occurred, but has never been successful (Price & McGrew, in press *b*) - at least one female always loses her infants.

An opportunity to investigate polygyny in cotton-top tamarins arose when the oldest daughter in one Stirling group unexpectedly became pregnant. This was an unusual situation as it was both polygynous and incestuous, and as the data were available, this daughter's relationship with her parents during the 24-week observation period was examined, and compared with that of an adult daughter in a monogamous but otherwise similar family.

Methods

Subjects

The subjects of this study were the parents and eldest daughters in two families of cotton-top tamarins, Elsa's and Roxanne's. Both sets of parents were wild-caught, but were at least 12 years old at the start of observations. The eldest daughter, Viva, in Elsa's family became pregnant although Elsa was still reproducing successfully and regularly. The control female, Ursula, from Roxanne's family, was chosen as she was in a group of similar size and composition to Viva's family. Details of the composition of each group at the time of observations are given in table 7.3.

Behavioural categories and recording methods

The data were obtained from the study of pair relationships described in chapter 6, and details of behavioural categories and recording methods can be found there. As data were collected on each parent's relationships with its offspring, the information on their relationships with their eldest daughter could easily be extracted from the check-sheets. Data were collated on spatial relationships, allogrooming, affection, aggression and anogenital sniffing.

Analysis of data

The number of samples obtained from each group was very similar (Roxanne's: 60 before

TABLE 7.3. Details of the composition of the polygynous group and the comparison group.

Parents[1] *(female first)*	*Eldest daughter*	*Other offspring present (age at start of observations)*			*Period of observation of parents*	*Infants born during study*
		>2yrs	*1-2yrs*	*<1yr*		
Polygynous group						
Elsa Mario	Viva b. 11/6/85	3M	1F	2M,2F	11/12/88- 25/5/89	3/3/89 Elsa (twins) 16/5/89 Viva (singleton)
Comparison group (monogamous)						
Roxanne Elvis	Ursula b. 10/11/86	2M	1M,1F	2M,1F	2/11/88- 13/4/89	19/1/89 Roxanne (triplets)

1. All parents wild-caught.

TABLE 7.4. History of the polygynous group.

Date	*Events*
Oct/Nov 1988	Romulus (b. 5/4/83), one of twin males who are eldest offspring in group, seen following Viva and sniffing her anogenital area frequently; possible attempted mounts also observed. Viva appears to reject his advances.
11/12/88	Observations on breeding pair, Elsa & Mario, begun.
3/3/89	Elsa gives birth to twin females; infants reared successfully.
1/5/89	Staff agree that Viva looks pregnant on visual inspection. Appears to be about mid-term for a twin litter.
5/5/89	Romulus seen tongue-flicking and attempting to mount Viva; Viva rejects him.
16/5/89	A single large male infant found dead with numerous injuries. Post-mortem reveals it to have been stillborn.
25/5/89	Observations on Elsa & Mario ended.
24/6/89	Viva attacks her younger sub-adult sister, Yolanda (b. 27/7/87); Yolanda is injured, and is removed temporarily.
26/6/89	Viva removed from family to be paired with an unrelated male, and Yolanda returned to group.

birth and 92 after; Elsa's: 62 before birth and 94 after). Therefore, as the frequencies of many behavioural categories were low, total scores for the whole period were compared directly. Analysis of the data was divided into two sections: interactions that involved both parents, and interactions that occurred only between mothers and daughters. The data were insufficient to allow statistical analysis.

Results

History of the group

Details of the history of the polygynous group during the relevant period are given in table 7.4. Viva gave birth to a single stillborn male infant 10.7 weeks after Elsa had produced surviving twins. Date of conception of Viva's infant was estimated as 15/11/88, about one month before observations on her parents began, and when Elsa was approximately two months pregnant. There was no evidence that Elsa was in ill-health or that she was ceasing to breed. The father of Viva's infant was unknown, but was suspected to be her brother, one of the oldest male twins in the family: he had been observed to show a great deal of interest in Viva in October and November 1988, frequently sniffing her anogenital area and following her, and was also seen attempting to mount her a few days before her infant was born.

The infant was unusually large (64g, compared to an average of 45-50g for newborn infants; see also fig. 5.1), and post-mortem revealed that the infant was stillborn (the lungs did not float), and that death was probably the result of trauma experienced during delivery. However, there were numerous injuries (primarily bite-marks) on the body, inflicted after death by one or more group members, although no monkey was actually seen touching the infant.

Detailed behavioural observations

Spatial relationships between parents and daughters are shown in figure 7.8. Both daughters were close to or in contact with their mother more than their father, but Viva was near and in contact with both her parents less than Ursula was. Allogrooming relationships showed a similar pattern (fig. 7.9). Both daughters groomed both their parents more than they were groomed in return, and had more frequent grooming interactions with their mothers than with

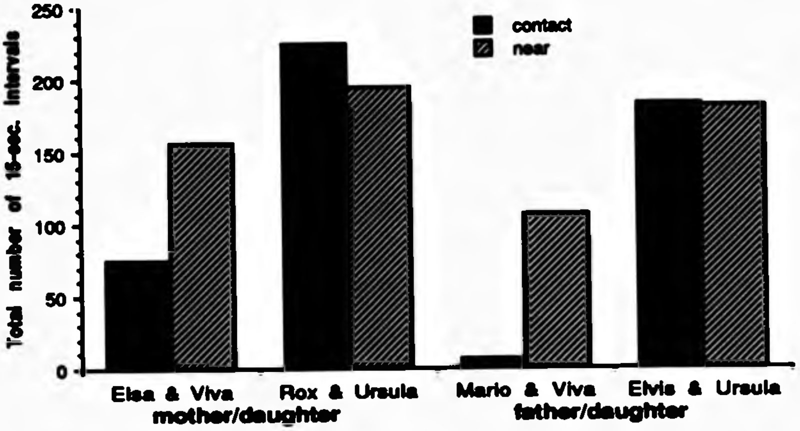


FIGURE 7.8. Spatial relationships between parents and eldest daughters in a polygynous group (Elsa/Mario/Viva) and a monogamous group (Roxanne/Elvis/Ursula).

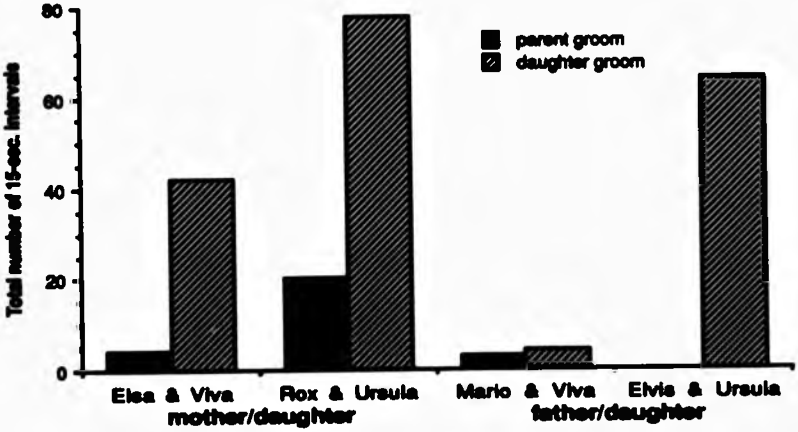


FIGURE 7.9. Allogrooming relationships between parents and eldest daughters in a polygynous group (Elsa/Mario/Viva) and a monogamous group (Roxanne/Elvis/Ursula).

their fathers. However, Viva again showed lower levels of interaction than did Ursula. Levels of affection (fig. 7.10), on the other hand, did not show such a clear pattern. Viva showed more affection to her mother than her father, while for Ursula the opposite was true, and Viva did not appear to have noticeably lower levels of interaction than Ursula for this behavioural category. Levels of aggression (fig. 7.11) were similar for the two daughters. Both received considerably more aggression from both their mother and their father than they gave. Perhaps surprisingly, there was no evidence that Elsa was more aggressive to her daughter than Roxanne. Anogenital sniffing between parents and daughters is shown in figure 7.12. Both daughters sniffed their mothers more than their fathers, and directed more sniffs at their mothers than they received in return. However, while Ursula sniffed her father Elvis more than he sniffed her, the opposite was true of Viva and Mario.

Two categories of behaviour were seen only in mothers and daughters. Only the females were seen to scent-mark one another, and they did so infrequently. Roxanne marked Ursula three times, while Ursula did not mark Roxanne at all. However, the reverse was true in the polygynous group: Elsa did not mark Viva, but Viva marked her mother twice. Face-pressing was also confined to mother-daughter interactions. It occurred at similar frequencies in the two groups (Roxanne & Ursula: 12 times; Elsa & Viva: 13 times), and was always initiated by the daughter in both groups. Furthermore, the timing of face-pressing was identical in the two families: mothers and daughters were seen face-pressing *only* in the 12-week period leading up to the birth of the mother's infants, and never afterwards.

Conclusions

Although Viva was less involved in affiliative interactions with her parents than the daughter in the monogamous group, there was no evidence to suggest that she received any more aggression from either her mother or her father, and her eventual removal from the family was due to the aggression she directed at her younger sister. The functions of scent-marking and face-pressing are unclear. Breeding female cotton-top tamarins scent-mark at much higher frequencies than other individuals (French & Snowdon 1981; French & Cleveland 1984; S. Evans, pers. comm.), and so it is interesting that Viva was seen marking her mother. In

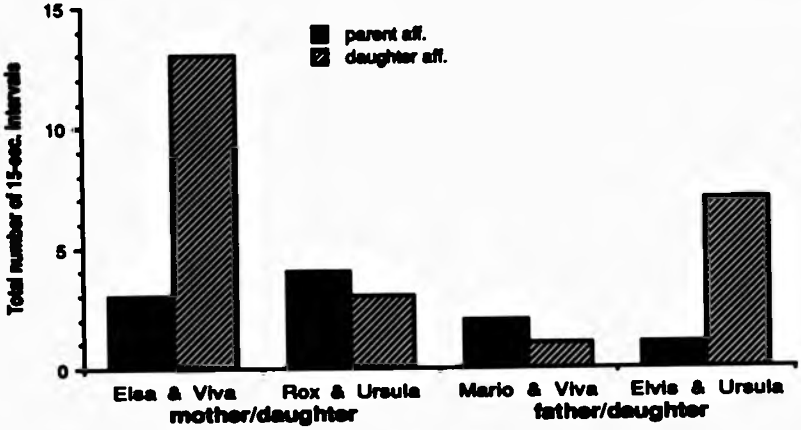


FIGURE 7.10. Affectionate behaviour between parents and eldest daughters in a polygynous group (Elsa/Mario/Viva) and a monogamous group (Roxanne/Elvis/Ursula).

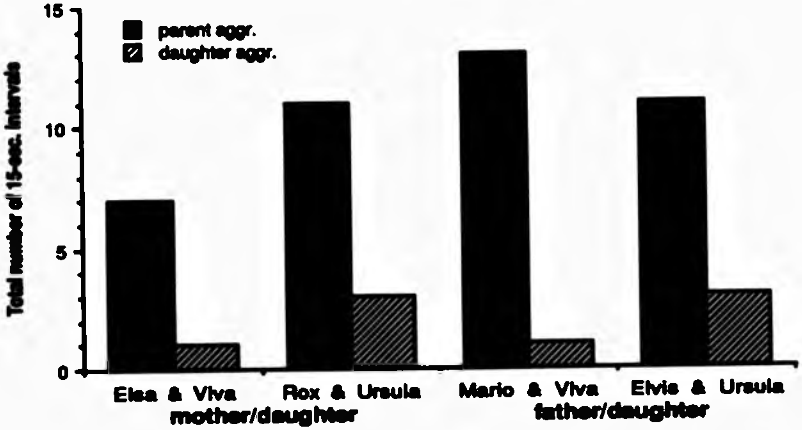


FIGURE 7.11. Aggressive behaviour between parents and eldest daughters in a polygynous group (Elsa/Mario/Viva) and a monogamous group (Roxanne/Elvis/Ursula).

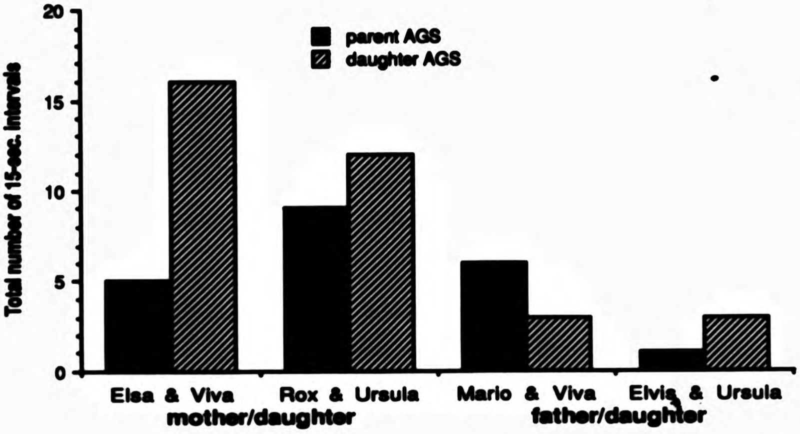


FIGURE 7.12. Anogenital sniffing [AGS]between parents and eldest daughters in a polygynous group (Elsa/Mario/Viva) and a monogamous group (Roxanne/Elvis/Ursula).

addition, although data were not collected on Viva's scent-marking rates at the time of her pregnancy, data collected about 18 months earlier showed that she marked at equivalent rates to breeding females (personal observation).

Viva's father appeared to monitor her anogenital area more than the control female's father did, so it is possible that he was aware of her reproductive condition. However, although following the birth of her infant and the end of data collection he was observed attempting to mount her, he showed no sexual interest in her during observations, in contrast to his relationship with her mother.

Elsa did not conceive during the observation period (although she did so subsequently). This was unusual for her: in ten of 11 previous pregnancies, she had conceived within a month of giving birth. It is interesting to speculate that the onset of fertility in her daughter may have affected Elsa's own breeding capabilities. Alternatively, a faltering in Elsa's own hormonal activity may have initiated fertility in Viva.

The injuries to Viva's infant suggest that it might not have survived even if live-born. Other infants who have died as a result of illness, or were stillborn, have rarely been found with injuries. Although the identity of the infant's attacker(s) was unknown, an obvious candidate is Elsa given previous reports of aggressive behaviour by dominant females to the young of subordinates (Roda & Roda 1987; Price & McGrew, in press *b*).

Discussion

Mating exclusivity and the confinement of breeding to one adult of each sex in a group, which have been included among the defining characteristics of a monogamous system (Kleiman 1977) seemed to be abandoned in these cases. Mechanisms proposed to account for the limitation of breeding to one adult of each sex within a group include a preferential attraction for the pair-mate, and intra-sexual aggression (Epple 1978*a*, French & Inglett 1989), although different mechanisms may apply to each sex (Anzenberger 1985). Parents also have several means of limiting breeding by their offspring, including physiological suppression of fertility, behavioural suppression involving aggression and prevention of copulation, or incest avoidance.

Preference for one pair-mate

Although no systematic data were collected on male relationships, the picture obtained from the polyandrous group in this study is similar to the one drawn by Goldizen (1989) in a recent description of social and sexual relationships in polyandrous groups of wild saddle-back tamarins. In both studies, males groomed the females more than vice versa, and tended to initiate proximity. Relationships between males were amicable, and interference in copulations was rare. The female was rarely seen to solicit males. Males were more involved in infant care than the female. Although the youngest male in the present study attempted to mount more, the female rejected a higher proportion of his attempts than those of the other two, and complete copulations by all three males occurred at similar frequencies. Thus there was no evidence either from the present study or from that of Goldizen (1989) that the female had a preferred sexual partner. These results differ from those of Epple (1972) and Kleiman (1978), who both found that one male in trios of saddle-back tamarins and lion tamarins respectively had priority of access to the female. In Epple's study, one male performed 88-100% of the observed mounts in three of four groups, and in Kleiman's study, only one male was seen mating in five of the seven groups in which neither of the males was related to the female.

In the polygynous group, there was no evidence that either of the breeding pair mated with any of their offspring during detailed observations, and the daughter was seen to interact sexually with only one of her brothers. It is possible that this represents a situation in which a preference for one pair-mate did exist. However, the incestuous nature of this relationship makes it difficult to interpret in a wider context, and more detailed data are required to understand the nature of relationships in groups such as this.

Aggression

At least during detailed observations, neither group appeared to use aggression as a means of limiting breeding, with the exception of the attack by the breeding female on the young female in the polyandrous group. The minimal aggression seen between males in the polyandrous group and between the mother and her daughter in the polygynous group was somewhat surprising, particularly given reports of frequently serious aggression between adults in groups of unrelated animals. In the polyandrous group, aggression might have been expected during the first weeks postpartum, since Rothe (1975) reported that interference by the dominant male in the copulations of the others appeared to be more frequent when the dominant female was in oestrus.

Kleiman (1984) has found that once a relationship is established between one male and the female, two-male/ one-female trios of golden lion tamarins may remain stable for long periods (e.g. up to a year), with the third individual assuming the role of a sub-adult or juvenile. Brown & Mack (1978) found that such individuals preferentially receive food. This may have originally been the position of the youngest male in the present study; however, shock following a sudden and serious fight after a long period of stability resulted in his death. Death from shock with wounds not severe enough in themselves to be fatal has been reported for golden lion tamarins (Inglett *et al*. 1989), although in this species females appeared to be more susceptible than males. The youngest male was also the only one seen displaying at other group members. Kleiman (1979) found that the more assertive individual in golden lion tamarins may eventually be the most seriously wounded, and a similar pattern may have occurred in this study.

An interesting feature of the polyandrous group and those described by Price & McGrew (in press *b*) is that aggression was almost always between brothers; fathers rarely became involved. A lack of parent-offspring aggression was also notable in the polygynous group in this study, despite the fact that aggression between female callitrichids is often described as more frequent and perhaps more severe than that between males (*S. fuscicollis*: Epple 1975*a*; *L. rosalia*: Kleiman 1979; Inglett *et al*. 1989). For example, Kleiman (1979) and Inglett *et al*. (1989) both indicate that cases of fatal injury to female golden lion tamarins are more frequent than those to males.

However, several studies also report that parents tend to be less involved in aggression within families, while it is more likely among sibs (Epple 1975*a*; Kleiman 1979). Wolters (1978) and McGrew & McLuckie (1986) found that mothers were more often involved in intra-sexual conflicts in families of cotton-top tamarins than were fathers. However, although several cases of aggression against daughters in McGrew & McLuckie's (1986) study involved mothers, these cases were confined to one family line, and subsequent occurrences in the same colony (K. Moore, unpublished data; personal observation) suggest that mothers are rarely the primary aggressors, even in evictions of daughters. One study of common marmosets (Rothe 1975) described one mother who attempted to hinder contact between her eldest daughter and the father, but there were no serious fights. In addition, Tardif (1983, 1984) found no effect of female maturation on mother-daughter relationships.

Another possible explanation for the fact that neither of Viva's parents were unduly aggressive to her may have been that was not seen to mate with her father: at least during detailed data collection, observations suggested that the most likely father of her infant was one of her elder brothers. Rothe (1975) found that dominant animals in artificial groups were less likely to interfere in copulations between subordinates, although they would intervene in copulations between their "mate" and a subordinate.

Evans & Hodges (1984) have suggested that the low frequency of evictions by parents indicates that aggression is unlikely to be an important factor in controlling breeding in families, but it seems strange that such a mechanism would not come into play if fertility suppression failed, as it clearly did in the polygynous group. However, one recent study has produced results which closely parallel those reported here. Following a field observation of extra-group mating by a young *C. jacchus* female, Hubrecht (1989) allowed four daughters in a captive colony, at least one of whom had ovulated in her natal family, access to unrelated males for a series of brief periods. One became pregnant. She was removed from her family after attacking her younger sister, but there was no evidence of increased mother-daughter aggression.

The case of polygyny raised two other interesting issues: first, the breakdown of physiological mechanisms of fertility suppression; and second, the possibility of incestuous mating in callitrichids.

Suppression of fertility in offspring

Investigations of daughters in their natal families have revealed the possibility of species differences in the nature of fertility suppression, although the mechanisms are still not well understood. Epple & Katz (1984) found that no daughters in *S. fuscicollis* showed regular cycles while in their family. Studies of cotton-top tamarins (French *et al.* 1984; Savage *et al.* 1988) have also consistently found that daughters were acyclic in the presence of their mothers, although Tardif (1984) reported that some daughters in their natal families exhibited progesterone spikes. However, although suppression of ovarian activity in *Saguinus* appears to be almost total, in other species daughters have been found to cycle whilst still in their natal groups. Abbott (1984) and Hubrecht (1989) reported that some daughters in families of *C. jacchus* ovulated, although another study of the same species by Evans & Hodges (1984) failed to find signs of cyclicity in daughters. In *L. rosalia*, French & Stribley (1987) and French *et al.* (1989) reported that daughters cycle regularly. In these species, behavioural rather than physiological suppression may be more important.

If a cotton-top tamarin mother dies, the eldest daughter begins cycling, although younger daughters remain suppressed (Heistermann *et al.* 1989). Although Ziegler *et al.* (1987*b*) and Savage *et al.* (1988) have argued that the presence of an unrelated male as well as the daughter's removal from the mother's influence is necessary to induce cycling, the results of Heistermann *et al.* do not support this. Savage *et al.*'s sample size was only two, however. Furthermore, a study of the common marmoset (Evans & Hodges 1984) found that isolated females did cycle very quickly after removal from their families. Access to an unrelated male also appears to be insufficient by itself to induce cycling in anovulatory daughters: Tardif (1983, 1984) found that cotton-top tamarin daughters housed with their mother and an unrelated male did not cycle, while Hubrecht (1989) reported that an anovulatory daughter in a *Callithrix jacchus* group did not begin to cycle even when exposed to an unrelated male.

Suppression in daughters may be mediated by olfactory cues in scent-marks (Epple & Katz 1984; Savage *et al.* 1988): the onset of ovulation in paired females exposed to scent secretions from their natal families was delayed. Evans & Poole (1983) also found that female *Callithrix* *jacchus* conceived later if housed near dominant relatives. Increases in scent-marking by daughters following removal from their families or the death of their mothers have been reported in cotton-tops (Savage *et al.* 1988; Heistermann *et al.* 1989) and common marmosets (Box 1975*a*). It is therefore very interesting that Viva appeared to mark as frequently as breeding females.

The conditions necessary for mothers to suppress daughters are not clear, and there are several possible explanations for breakdown of suppression. First, isolated cases might occur occasionally anyway. Second, illness of the mother may affect her ability to suppress her offspring, one of whom may then take over the breeding position (e.g. Price & McGrew, in press *b*), but in this case there was no evidence that Elsa was ill or that her fertility was failing. However, Elsa was aging: she was wild-caught and imported into the UK in 1976, and was therefore at least 12 years old, and probably more, when her daughter conceived. Tardif & Ziegler (1986) have studied the effects of age on ovarian function in saddle-back and cotton-top tamarins. Females older than about 12 years showed atypical hormonal profiles. Old 14-15 year old females showed cyclicity, but great variation in hormone levels. Two 16-17 year old females did not cycle. Therefore it is possible that if Elsa's ovarian activity was beginning to decline, she was no longer able to suppress Viva. However, it is not known if ovarian hormones are necessary for suppression: ovariectomised female tamarins could still suppress young females fostered to them (Katz *et al.* 1986). This study is not conclusive, however, as the young females were all less than a year old, and may therefore have simply been too young to show regular cycles, regardless of the suppressive effect of the presence of a dominant female. Furthermore, Elsa was still reproducing regularly, suggesting that there had been little alteration in her cycles.

Finally, daughters may be more able to escape the suppressive effect of their mothers presence as they become older. However, Viva was 3 years and 5 months old when she conceived, and her age fell within the range investigated in previous studies of suppression in cotton-top tamarins (e.g. French *et al.* 1984; Ziegler *et al.* 1987*b*), which have found that daughters remain suppressed up to at least 42 months. Observations of 58 families of saddle-back tamarins with daughters up to 7 years old (Epple & Katz 1984), showed that only the mother bred, and sexual behaviour involving offspring was rare. This is also true of the Stirling colony, in which daughters have remained in their families for up to 6 years without showing signs of sexual activity. The reason for the onset of ovulation in Viva's case therefore remains a mystery.

Incest

The fact that daughters in some species may ovulate (e.g. Abbott 1984) has led Carroll (1986) to argue that incest avoidance, rather than physiological suppression, is the mechanism by which offspring are prevented from breeding in their natal families. He described cases in which replacement of the father by an unrelated male in groups of *Callimico goeldii* and *Callithrix argentata melanura* resulted in the new male mating with both the mother and daughter, and instances in which a group ceased to reproduce after the loss of a parent, and argued that this indicates that the genetic relationship between parents and offspring, and daughter, rather than suppression of fertility, is the important factor governing the expression of sexual behaviour in families. Other authors have also considered that incest is unlikely. Heistermann *et al.* (1989) found that reproduction in motherless families ceased despite the onset of cycling in the eldest daughter, while Herde *et al.* (1986) found that cotton-tops housed in peer groups from infancy did not form pair relationships. However, this cannot be a complete explanation, for two reasons: as discussed above, complete physiological suppression of daughters exists in some species; and secondly, incest does occur in some circumstances.

Isolated cases of incest have been described several times, but although it is not clear with what frequency it occurs, it appears to be rare in callitrichids. It seems to be most likely if a parent dies but is not replaced by an unrelated adult, and therefore may be an artefact of captivity, where restrictions imposed on dispersal may mean that incest is a preferable option to not reproducing at all. Cases of incest have been reported in *C. jacchus* (Box 1978; Rothe 1978; Anzenberger & Simmen 1987; Crook 1988; König *et al.* 1988), and cotton-top tamarins (Price & McGrew, in press *b*). For example, in a study by König *et al.* (1988), incest occurred in six of 17 families of *Callithrix jacchus* in which a parent was lost. However, in four of five groups in which unrelated individuals were present, these became involved in breeding. Groups which reproduced were more likely to be stable. In view of this it is interesting that in the polyandrous group in present study it was the unrelated female who assumed the breeding position; presumably this functions to reduce inbreeding.

However, while incest might be expected to occur when it was the only alternative for breeding adults who had no access to unrelated individuals after losing their mates, this was not the case in the polygynous group in the present study. One of the cases described by Price & McGrew (in press *b*) is similar to the one reported her. A mother and her daughter became pregnant by the daughter's father, who was the only sexually mature male in what was originally a straightforward nuclear family. Mother and daughter apparently became pregnant within two months of each other, so there was no suggestion that the mother was no longer able to breed. In another case described by Price & McGrew (in press *b*), a father mated with his daughter even though an unrelated female was available. The observations in chapter 6 of apparently sexual interest by sons in their mothers also suggest that any incest "taboo" that exists may not be sufficiently strong in some circumstances. However, whether and to what extent incest might occur in wild groups is unknown.

Summary

(1) A polyandrous group containing a father, one or more of his sons, and an unrelated female reproduced successfully and was stable for long periods.

(2) All three males present in the group during the female's postpartum oestrus had equal sexual access to her, had amicable relationships, rarely interfered with one another's copulations, and shared in infant care.

(3) Although aggression occurred between brothers, the father was never involved in intra-group conflicts.

(4) A daughter mated incestuously with her father and/or one or more brothers, and became pregnant while her mother was still breeding, resulting in a polygynous group. Her infant was still-born, but was apparently attacked by one or more family members.

(5) The daughter showed lower levels of affiliative behaviour with her parents than a control daughter in a monogamous family, but there was no evidence of increased aggression.

Chapter 8

General Discussion

As detailed comparisons between the results obtained in this study and previous work on callitrichids have been made in the relevant data chapters, in this concluding chapter I will broaden the scope of the discussion to consider the alternative strategies available to breeding and helping individuals, and the factors that might influence their choice amongst these options. The study of callitrichid social organisation has now reached the stage where simply amassing more data will provide little further insight. At this point, it is important to identify the most fruitful areas for further study and to develop a framework around which research can be structured. Testable hypotheses are needed if we are to understand callitrichid reproductive strategies (e.g. Goldizen 1987*a*; Dunbar 1988), and as data are lacking on many aspects of these strategies, I will focus on developing predictions, based on the results obtained in this and other studies, that can be tested in future research.

My starting point will be the more general framework of communal rearing outlined in chapter 1. In trying to fit cotton-top tamarins and other callitrichids into this scheme, the questions that immediately arise are:

(1) what advantages do callitrichids (both breeders and helpers) gain from adopting communal rearing, and how might such a system have evolved?

(2) what strategies are available to breeding marmosets and tamarins to maximise their reproductive success?

(3) what options are open to non-breeding helpers to gain access to breeding positions?

Why do callitrichid females need help?

To understand why callitrichids need help in rearing young, it is important to first establish the reasons why a callitrichid female is unlikely to be able to rear twins without assistance. There have been only three reports of successful rearing of twins by captive callitrichids in the absence of the father (Moynihan 1970; Mallinson 1975; König & Siess 1986), and none in wild populations. How often an unaided mother has failed to rear infants is unknown, but the few reports in the literature of successful rearing under such conditions, despite the fact that the energetic costs of reproduction to the mother are probably reduced in captivity, suggests that females in the wild may need a male's help in order to rear her infants successfully. Why is this?

All female mammals have to bear the energetic costs of pregnancy and lactation, and these costs can have consequences for their survival and future breeding success. However, the costs of gestation appear to be relatively slight compared to those of lactation. For example, the survival and subsequent fecundity of red deer hinds (*Cervus elaphus*) who lost calves soon after birth was not significantly reduced in comparison to that of barren hinds, but hinds who reared calves to weaning had a reduced chance both of survival and of subsequent calving (Clutton-Brock *et al.* 1989). Data presented in chapter 6 demonstrated that captive female cotton-top tamarins doubled the time they spent feeding and foraging during lactation, but did not feed or forage noticeably more during late pregnancy. Kirkwood & Underwood (1984) found similar results in a study of energy intake in captive cotton-tops. There is also supporting evidence for these results from several other species of primate. Field studies have rarely found increases in feeding time during pregnancy, but several have reported marked increases during lactation (e.g. *Saguinus fuscicollis*: Goldizen 1987*a*; muriquis, *Brachyteles arachnoides*: Strier 1987; titis, *Callicebus moloch*: Wright 1984; baboons, *Papio cynocephalus*: Altmann 1983); it may even be impossible for females to maintain a high enough energy intake to offset the costs of lactation, leading to weight loss (e.g. *Papio anubis*: Bercovitch 1987). Captive studies that have measured either energy or food intake have also found that these increase during lactation (e.g. *Saguinus oedipus*: Kirkwood & Underwood 1984; *Galago senegalensis*: Sauther & Nash 1987).

Furthermore, as infants grow but remain dependent on their mothers for most or all of their nutritional needs, the costs of lactation increase, forcing females to spend more and more time feeding and foraging. This was clear in the present study, in which feeding rates of female cotton-top tamarins did not reach a peak until the second month after birth (chapter 6). After this point, infant tamarins began to receive increasing amounts of solid food from other family members (chapter 3), presumably reducing the burden on their mothers and resulting in a drop in feeding and foraging times. Increases in feeding and foraging during the course of lactation have also been described in wild gelada, *Theropithecus gelada* (Dunbar & Dunbar 1988), wild *Papio cynocephalus* (Altmann 1983), and captive *Galago senegalensis* (Sauther & Nash 1987).

Female primates are therefore forced to increase their energy intake during lactation. Increasing litter size from the single infant typical of most anthropoids to two or more means that female callitrichids are likely to face an even greater burden than other primates. For example, triplet births in captive *Callithrix jacchus* were associated with a slight weight loss during lactation, whereas singleton and twin births were not (Lunn 1983). Although there are no comparative data from other primates, increased litter size was associated with a stress syndrome characterised by weakness in female cats studied by Deag *et al.* (1987): the larger the litter, the more weight the mother lost, although there was no effect of stress on the proportion of a mother's litter that survived. Stressed cats also tended to be smaller, and in view of this it is interesting that the smallest female tamarin in the present study showed signs of losing condition after parturition, and carried her offspring very little (chapter 3).

Although increasing litter size leads to an increase in the energetic costs of lactation, it is probably the considerable costs of *carrying* twin infants in addition to suckling them that has led to the requirement of female callitrichids for assistance in rearing. Dunbar (1988) has used Altmann's (1980, 1983) model of maternal time budgets and Terborgh's (1983) data on activity budgets of wild saddle-back tamarins to model the costs to tamarin mothers of carrying and suckling one or two infants. His model suggests that while a female tamarin could afford to suckle two infants if she did not also have to carry them, she could not feed enough to successfully rear twins if carrying as well as suckling was left to her.

Studying the costs of infant care can shed light both on how parents may benefit from retaining helpers, and on what costs non-breeding helpers have to bear. The need to carry infants continuously clearly imposes costs on caretakers. Data presented in chapter 5 suggested that even in captivity, carriers of infant cotton-top tamarins drastically reduce the time they spend moving, foraging and feeding. Similar results have been reported for *Callithrix jacchus* in captivity (Clarke 1987), and for wild saddle-back tamarins (Goldizen 1987*a*). The results of experiments on captive cotton-top tamarins (chapter 5) suggested that there may be two reasons for this: carriers' ability to move around their environment is limited by the burden of infants; and in addition, they attempt to remain concealed, probably to reduce the risk of predation. Although ease of access to food in captivity may mean that this does not affect, for example, a carrier's weight, and is therefore unlikely to significantly affect their ability to reproduce in the future, it does suggest that the costs of infant carrying are considerable.

One possible alternative to carrying infants around all the time would be to "park" them in nests or hollows while the parents foraged, a strategy that has been adopted by several prosimian species which, like callitrichids, often produce multiple litters (Bearder 1987; Richard 1987). One feature that distinguishes the neonates of prosimian species that use nests from those that do not is the length of gestation and consequently the stage of development of the infants at birth. For example, lorises, which do not use nests, have a longer gestation period than galagos, which do (Bearder 1987). Unlike lorises, which are relatively more precocial at birth, galago infants are unable to cling to their mother and therefore the use of a nest is essential. Nests have certain disadvantages, however; unguarded infants are, for example, likely to be vulnerable to predators. Callitrichid infants are able to cling firmly to a carrier's fur as soon as they are born; support from the adult is usually not needed, and is rarely given (Rothe 1973, 1974; Stevenson 1976; Price, in press *b*). Infants can therefore be carried around with the rest of the group right from the start, and a nest is unnecessary. In addition, marmoset and tamarin neonates cannot thermoregulate: their ventral hair is extremely sparse (Soini 1988; Snowdon & Soini 1988; personal observation), and if for any reason they become separated from their carriers they begin to lose heat very rapidly (personal observation). Tamarin infants become capable of thermoregulation only at the age of 3-4 weeks (Dronzek *et al.* 1986). Thus constant contact with a carrier may be very important for maintaining infants' body temperature.

Evolution of communal rearing in callitrichids

How have callitrichids evolved this complex system of reproduction involving twinning and extensive non-maternal care? The small size of the callitrichid species and the fact that they regularly twin led Hershkovitz (1977) to conclude that they were relatively primitive compared to other anthropoid primates. However, it is now fairly generally accepted that these traits are in fact derived (Eisenberg 1978; Ford 1980; Leutenegger 1980; Sussman & Kinzey 1984), and that twinning is a response to evolution of small body size: as maternal body size decreases, infants become relatively larger until a single infant becomes too large to pass through the mother's pelvis (Leutenegger 1973, 1979). If twinning is not an ancestral state, we need an explanation for how monogamy and twinning could have arisen in this family, and there has been some discussion over whether monogamy or twinning evolved first (Dunbar 1988).

There have been several attempts to explain the evolution of mating systems in general (e.g. Orians 1969; Emlen & Oring 1977), and primate mating systems in particular (e.g. van Schaik & van Hooff 1983; Terborgh 1986), with some authors focussing specifically on monogamy (e.g. Kleiman 1977; Wittenberger & Tilson 1980; Rutberg 1983). Although it is the predominant mating system in birds, monogamy is rare amongst mammals in general (about 3% of mammalian species are reported to be monogamous; Kleiman 1977), but is rather more prevalent among primates (about 14% of species; Rutberg 1983).

In primates, a popular approach (e.g. Wrangham 1980; Dunbar 1988) has been to assume that since female reproductive success is limited primarily by energetic and nutritional constraints, female grouping patterns are determined primarily by the distribution of food, and male grouping is then a response to the distribution of females. Using this approach, the evolution of monogamy in primates is considered by Rutberg (1983) to be based on territoriality. He suggests that when food patches that are rich enough to support groups are rare, solitary systems or monogamy will be favoured. The evolution of monogamy as a male strategy will then be determined by the defensibility of females and the availability of effective male parental investment. If females are so widely scattered that a male can defend only one at once, male parental investment may act as the incentive for a male not to abandon an impregnated female.

Kleiman (1977), on the other hand, suggested that monogamy might arise either when a female cannot rear young alone, or when the habitat cannot hold more than one female raising young at a time. Wittenberger & Tilson (1980) suggested that primate monogamy can best be explained by assuming that females do better if pairing with an already mated male is a disadvantage compared to pairing with an unmated male. Monogamy may evolve in these species even if it is not advantageous for the male, if female aggression prevents males from acquiring additional mates. Wittenberger and Tilson argue that this could arise if polygyny involved costs to females in terms of the loss of paternal care, and therefore this is a similar argument to that of Kleiman (1977). Rutberg (1983) has suggested that one problem with this hypothesis is the lack of evidence that offspring survival is enhanced by male parental investment. However, there is some evidence (Garber *et al.* 1984) that this may occur in tamarins. For female callitrichids, then, reproductive success may also be very dependent on the availability of *males*; males may then become the limiting sex. Moehlman (1989) has pointed out that this appears to be true in the larger canids which require allomaternal care.

Van Schaik & van Hooff (1983) suggest that no single hypothesis is sufficient to explain all cases of monogamy, and argue that Rutberg's explanation may apply to the monogamous Old World monkeys and the gibbons, while Wittenberger & Tilson's and Kleiman's explanations are more appropriate to callitrichids. Monogamy in *Aotus* and *Callicebus* may be correlated both with the distribution of food into small, predictable, uniform patches, and the need for male help with infant care (Wright 1986). However, Dunbar (1988) has suggested that male parental care is unlikely to have been the main factor promoting the evolution of monogamy in callitrichids. Assuming that a callitrichid female could produce two litters a year, but could not rear twins without a male's assistance, Dunbar constructed a pay-off matrix based on the alternative strategies available to females (produce one or two infants per litter) and to males (mate monogamously or polygynously - Dunbar in fact used the term "bigamous", but he did not define it, and it is not clear how it differs from polygyny). This is illustrated in figure 8.1*a*. On this basis it seems clear that the best strategy is for the male to be monogamous and for the female to twin, as both receive the highest payoff. However, it is difficult to see how monogamy could have developed *after* twinning, since if a female twins but does not have male assistance she is unlikely to be able to rear any infants at all. Dunbar therefore concluded that female callitrichids could only have afforded to develop twinning if the mating system was already monogamous for some other reason, and males were thus available to help.

Dunbar's model is based on some assumptions whose validity is questionable, however. Firstly, while marmosets may well have two litters per year, in tamarins one per year seems usual (see chapter 1). Redrawing Dunbar's payoff matrix for tamarins assuming that females produce only one litter per year (see figure 8.1*b*) shows that males would do just as well if females had a single infant and males were polygynous as they would if females twinned and males were monogamous. Second, there is no reason to assume that a female who twinned but had no help would necessarily lose both infants; abandoning one infant at birth, for example, might allow her to rear the other one successfully. Thus there seems no overwhelming advantage of monogamy to the male. Until we have more accurate data on annual litter frequency and the relative incidence of these different options, the question of whether monogamy or twinning arose first will remain open.

However, given the development of twinning and male parental care, it is relatively easy to see how polyandry could arise if the circumstances altered such that the care provided by a single male was insufficient for successful reproduction. Polyandry is an extremely rare form of mating system which has been described in a few bird species (Jenni 1974), humans (Crook & Crook 1988), and possibly in callitrichids (Terborgh & Goldizen 1985; Goldizen 1987*a*, 1988, 1989). Goldizen (1988, 1989) has compared polyandry in saddle-back tamarins to a specialised form of polyandry ("cooperative polyandry") found in some bird species (e.g. Ridpath 1972; Faaborg & Patterson 1981; Faaborg 1986). This can be defined as a system in

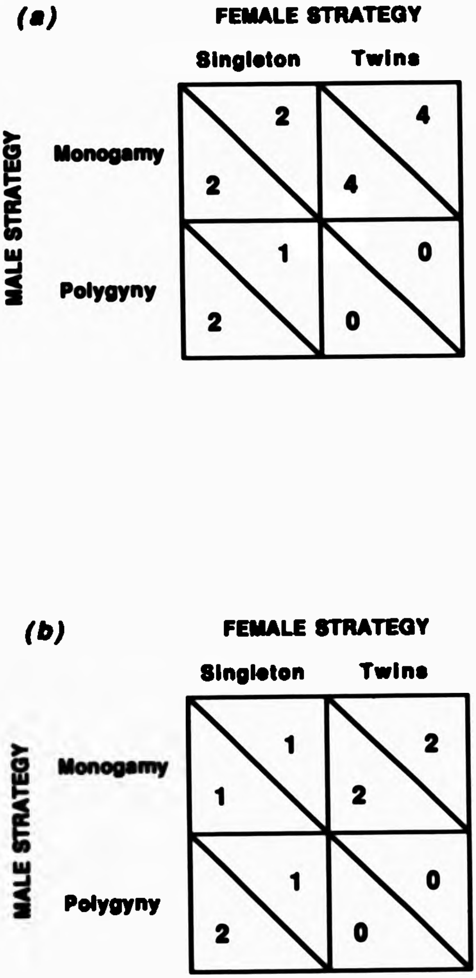


FIGURE 8.1. Pay-off matrices for alternate strategies of males (monogamy versus polygyny) and females (twins versus single infant). (a) Assuming female produces two litters per year (after Dunbar 1988, p. 284, table 12.6). (b) Assuming female produces one litter per year. For each quadrant, figure in the lower left is the payoff to the male in terms of number of offspring reared; upper right is payoff to female.

which two or more males mate with a single female during a single breeding season, and collaborate to raise her offspring (Terborgh & Goldizen 1985), and is therefore a communal rearing system, not simply a mating system.

Since arguments put forward to explain polyandry are typically based on the need for infant care (e.g. Sussman & Kinzey 1984; Sussman & Garber 1987), they are essentially extensions of arguments originally made to support the idea of monogamy, i.e. that single females are unable to rear twin infants alone (Kleiman 1977; Leutenegger 1980). It is rather difficult to test this hypothesis, however: although Terborgh & Goldizen (1985) and Goldizen (1987*a*) have proposed that the time budget requirements of saddle-back tamarins mean that a pair could not feed enough to raise twins alone, and did not see simple pairs attempting to reproduce, simply *because* there were no pairs they had no data on breeding success of pairs compared to polyandrous trios. So although this is a plausible idea, it remains to be tested.

The benefits of helpers to breeding callitrichids

How do breeding marmosets and tamarins gain from a rearing system involving considerable investment in infant by non-parents? Several possible sources of benefit have been suggested for other taxa exhibiting communal rearing (see chapter 1), and in this section I will consider which of these might apply to cotton-top tamarins and to other callitrichids.

This study, and others, have suggested that a dual benefit might accrue to breeding cotton-top tamarins from having helpers:

(i) *Increased survival of infants in the current litter*.

There are several means by which additional helpers could improve offspring survival. Infant cotton-top tamarins in larger groups were carried more and received more food via sharing, although they were not suckled more (see also Feistner 1985; Feistner & Price 1990). By being carried longer they may be less exposed to predation. Food sharing may be particularly important not only in increasing the total amount of food infants receive, but in the acquisition of food items that are an important component of the diet but are difficult for young unskilled animals to acquire - insects, for example (Feistner 1985). Infants' skill in acquiring such resources increases with age in *Callithrix jacchus* (Chalmers & Locke-Haydon 1984), and it may therefore be some time before the complex skills necessary for finding, catching and processing animal prey are adequately developed.

In other callitrichid species too, infants in larger groups are carried more, at least in captivity (Pook 1976; Ingram 1977). The importance of other group members in helping infants to acquire animal prey has also been emphasised by Ferrari (1987*a*) for wild *Callithrix flaviceps*. Similar effects of group size in wild populations might well increase the infants' chances of survival, as has been suggested by Garber *et al.* (1984), but as yet additional confirmatory data from field studies are lacking.

Similarly, in numerous other taxa survival of offspring improves as more helpers become available: for example, grey-crowned babblers, *Pomatostomus temporalis* (Brown *et al.* 1982); Florida scrub jays, *Aphelocoma coerulescens* (Stallcup & Woolfenden 1978); African wild dogs, *Lycaon pictus* (Malcolm & Marten 1982); silverbacked jackals, *Canis mesomelas* (Moehlman 1979); dwarf mongooses, *Helogale parvula* (Rood 1990); and humans (Turke 1988). In some species, increased survival may be due to increased feeding rates, as in silverbacked jackals (Moehlman 1983), chestnut-bellied starlings, *Spreo pulcher* (Wilkinson & Brown 1984), and purple gallinules, *Porphyrula martinica* (Hunter 1987). However, in other species young in larger groups are not fed more, and alternative explanations such as improved predator avoidance may be more appropriate (e.g. grey-crowned babblers: Brown *et al.* 1978; coyotes, *Canis latrans*: Bekoff & Wells 1982).

So, on the basis of the available data, the benefits to be gained from helpers by callitrichid breeders seem very similar to those in other mammals and birds with communal rearing. If helpers are indeed beneficial to callitrichids in terms of infant survival, then the following predictions can be made:

(1) Infant survivorship will correlate positively with group size, at least up to a minimum size required for the successful rearing of twins. (Other possible factors are caretaking experience, parity, condition, etc.)

(2) Helpers (in the form of older offspring, other relatives, or immigrants) will be recruited by groups below the minimum size required.

(ii) *Reducing the costs of rearing the current litter.*

On average, each individual caretaker in larger families of cotton-top tamarins in the present study carried infants less and shared less food than caretakers in smaller families (see also Feistner 1985; Feistner & Price 1990). Although confirmatory data from studies of other species either in the wild or in captivity have yet to be obtained, this suggests that after a certain point, improved infant survival may not be the main benefit to be gained by callitrichid breeders from additional helpers - apart from isolated instances (e.g. *Saguinus oedipus*: N. Ellerton, pers. comm.; *Leontopithecus chrysomelas*: A. Feistner, pers. comm.), even in captivity triplet rearing without human assistance is extremely rare. As yet there is no information on the minimum number of helpers required to rear two infants in wild populations, but once this point is reached the primary benefit to breeders may be to reduce the costs of rearing the current litter. This appears to be the case in some other species - for example, increasing the number of helpers from one to two produces no additional effect on offspring survival in Florida scrub jays (Woolfenden & Fitzpatrick 1986). Rylands (1985) and Feistner (1985) have both suggested that breeding adults in callitrichid groups benefit from sharing care from helpers, in that the presence of helpers reduces the burden on parents, possibly leading to the breeders' improved future survival and reproductive success, as has been reported in dwarf mongooses (Rood 1990), Florida scrub jays (Stallcup & Woolfenden 1978), and the bicoloured wren, *Campylorhynchus griseus* (Austad & Rabenold 1986).

Because they have to bear the costs of gestation and lactation as well as carrying, breeding female callitrichids might be expected to benefit most from helpers in energetic terms, since freedom from carrying duties may allow them to feed and forage more, thus at least partially offsetting the costs of lactation. A similar hypothesis has been proposed for communally rearing carnivores (Oftedal & Gittleman 1989). However, because only females can provide for an infant's nutritional needs, I predicted that the contributions to care by cotton-top tamarin fathers would be more affected by group size than those of mothers. This prediction was borne out, but the almost complete absence of any effect of group size on maternal contributions to care was somewhat unexpected. Although similar results for captive cotton-top tamarins have been reported by Tardif *et al.* (1989*a*), and McGrew (1988) found that breeding male cotton-tops were affected by increases in family size relatively more than females, Cleveland & Snowdon (1984) found that cotton-top tamarin mothers' contributions to care did indeed decrease if older offspring were present, while male contributions stayed the same. Ingram (1977) reported the same effect in *Callithrix jacchus*. The reasons for these differences are unclear at present, and there is an obvious need for data on this point from wild populations.

Although the present study and others have suggested several ways in which the reproductive success of breeders may be improved, as yet there are no data on the survival and lifetime reproductive success of breeding callitrichids in the wild to confirm these possibilities, and comparative studies both in the field and in the laboratory are required.

Strategies of breeding callitrichids

Males and females have overlapping but not identical reproductive interests, and the mating and rearing systems shown by a particular group will therefore result from interactions between the individual interests of each sex (Wittenberger & Tilson 1980). This sort of sexual conflict may result in variable mating systems (Davies 1989). The most beneficial mating systems for female callitrichids are likely to be polyandry or monogamy, because their reproductive success is probably limited by time and energy constraints, and can be increased by male parental care. The reproductive success of males, on the other hand, is in principle limited largely by the number of females they can inseminate, and they should therefore attempt to be polygynous if by doing so they can increase the number of offspring they father (Wittenberger & Tilson 1980).

Emlen (1982*b*) has pointed out that since only the male suffers from shared paternity, occasions are likely to arise when the female is receptive to, or solicits, additional males, while the male attempts to prevent such interactions. In polyandrous groups of dunnocks (*Prunella modularis*), for instance, there is often fierce competition between males. One male is clearly dominant over the other (Davies 1985; Burke *et al*. 1989), and attempts to prevent him gaining access to the female. Males do not do better from polyandry in this species, but the female does; this explains why females encourage subordinate males, but dominant males attempt to drive them off. The fact that in the present study male and female cotton-top tamarins showed different patterns of investment in the pair relationship over time (females investing most during late pregnancy, males most during the post-partum period; see chapter 6), and that the polyandrous female described in chapter 7 showed no clear preference for a particular mate, suggests that some degree of conflict of interest between the sexes may also arise in cotton-top tamarins.

It was also interesting that female cotton-top tamarins rejected more mounting attempts by males when they were likely to conceive than when they were pregnant. The high costs of being simultaneously pregnant and lactating may mean that females would prefer to delay conception. Males, on the other hand, may want to impregnate the female as soon as possible, either because they could be in competition with other males in a polyandrous group, or because it might be in their interest to desert and mate with a second female as soon as they have impregnated the first one.

Given the benefits of communal rearing and the potential conflicts of interest between males and females, what strategies could breeding marmosets and tamarins adopt to make sure they maximise their benefits and minimise their costs?

Strategies of breeding females

Several strategies are available to a breeding female callitrichid to make sure that she receives the assistance she requires to maximise the number of infants she can rear successfully.

Sharing a male versus monopolising a male

Females appear highly unlikely to tolerate polygyny (see chapters 1 and 7), because since one female almost invariably loses her infants, reproductive effort is wasted. In captivity polygyny might be sustainable, especially if infants are not produced simultaneously, but in fact this appears to occur very rarely: although in the survey of cotton-top tamarin colonies conducted by Price & McGrew (in press *b*) two females in a group were sometimes seen mating and occasionally more than one became pregnant, no more than one female in any group ever successfully reared infants at any one time. The same was true of the group described in chapter 7. Similarly, although two females were found to be pregnant in a wild group of cotton-tops (Savage *et al.* 1989*a*), only one successfully reared her infants.

Polygyny also seems unlikely in the majority of other callitrichid species. Only one instance of polygyny in captivity in which infants were successfully reared by two females in one group has been reported: Rothe & König (1987) described a captive *Callithrix jacchus* group in which an unrelated male mated both with a mother and with her eldest daughter by a previous mate. The two females gave birth two weeks apart, and carried and suckled one another's infants. However, this group was not stable indefinitely: the day before the mother gave birth again, the daughter began to chase her and was therefore removed.

Particularly in wild populations of *Saguinus*, where seasonal food shortage means that breeding is limited to one part of the year (e.g. Goldizen *et al.* 1988), polygyny may not be possible (see chapter 7). Polygynandry may be stable if the number of males is great enough to allow the rearing of more than one set of infants, but this will depend in turn on the ability of the habitat to maintain larger groups. It is interesting that the only report of successful polygyny in wild callitrichids occurred in large groups (10-12 individuals) of *Leontopithecus rosalia* (A. Baker, cited in French *et al.* 1989).

Preventing other females from breeding

Excluding other females. The disadvantages of polygyny mean that a female may try to ensure that she is the only breeding female in the group. Consequently, aggression between females would be expected, and experimental introductions of unfamiliar adults in captivity suggest that females are unlikely to permit intruders to enter their group (e.g. *Leontopithecus rosalia*: French & Inglett 1989; *Saguinus fuscicollis*: Epple & Alveario 1985).

Aggression within groups might lead to subordinates having to leave. There are reports of severe aggression between female cotton-top tamarins in captivity (e.g. Hampton *et al.* 1966; McGrew & McLuckie 1986; McGrew, in press), although parent-offspring conflict is less common than aggression between siblings or unrelated females. Females may, however, adopt a strategy of allowing potential female helpers to remain in order to assist in infant care, but then evict them once their own offspring can act as helpers for later litters. In the polyandrous group described in chapter 7, the youngest female was immature when the new breeding female was first introduced into the group, and therefore presumably not a challenger for the breeding position. She was only evicted once the breeding female had given birth. A similar effect was reported by Price & McGrew (in press *b*): captive female cotton-top tamarins in polygynous or polygynandrous groups tended to evict rivals only after they had bred.

Aggression between females is also a feature of other callitrichids (e.g. Kleiman 1979; Inglett *et al.* 1989; Stevenson & Rylands 1988), but as in cotton-tops the timing of aggression may depend on the stage of the dominant female's breeding cycle: Abbott (1978, 1984) reported that in peer groups of *C. jacchus* the dominant female frequently attacked other females two or three months after her infants were born.

Fertility suppression. If a breeding female does allow other females to remain in the group, there appear to be several mechanisms by which she can prevent them from breeding, ranging from behavioural or physiological suppression of mating and breeding, to infanticide. The relationship between dominance and fertility amongst female primates in general is discussed by Harcourt (1987). Callitrichids appear to be extreme in the limitations imposed on female fertility (Abbott 1987). Physiological means of suppression include a delay in puberty, inhibition of ovulation, failure of embryo implantation, or spontaneous abortion (Abbott 1987). Some evidence for delayed maturation while in the natal family exists for female cotton-top tamarins (Tardif 1984) and saddle-back tamarins (Epple & Katz 1984), although Ziegler *et al.* (1987*b*) found that female cotton-tops still in their natal groups did show hormonal indications of puberty at 15-17 months, and begin ovarian cycling within days or weeks of being paired with a male.

Physiological suppression of ovulation has been described in some detail in *Saguinus oedipus* (French *et al.* 1984; Ziegler *et al.* 1987*b*; Savage *et al.* 1988; Heistermann *et al.* 1989; but see Tardif 1983, 1984). Recent work on cotton-top tamarins (Ziegler *et al.* 1987*b*; Widowski *et al.*, in press) has suggested that two factors may be involved: first, the presence of a dominant female induces complete physiological suppression; but in addition, the presence of an unrelated male may be necessary for the onset of regular cycling. If this is the case then it was very surprising that the daughter described in chapter 7 conceived at all. However, another recent paper (Heistermann *et al.* 1989) has challenged the notion that the presence of an unrelated male is necessary for the onset of ovarian cyclicity in cotton-top tamarins - daughters whose mothers had died began to cycle regularly whilst still living with the rest of their natal family. Nevertheless, the reasons for the onset of ovarian activity in the adult daughter in the present study while still in the presence of her mother remain unclear.

In *Callithrix jacchus* (Evans & Hodges 1984; Abbott 1984), physiological suppression of ovulation in subordinate females and adult daughters also appears to occur, though instances in which daughters have shown signs of ovarian activity while still in their natal families have occurred (Abbott 1984; Hubrecht 1989). However, in one callitrichid species, the golden lion tamarin *Leontopithecus rosalia*, ovulation may not be suppressed in any daughters (French & Stribley 1987; French *et al.* 1989). Intra-group aggression in this species is frequently severe, particularly between females (Kleiman 1979; Inglett *et al.* 1989), and daughters are not involved in sexual interactions. In this species, then, behavioural rather than physiological suppression appears to be in operation.

Occasional reports of (usually unsuccessful) polygyny in wild callitrichid groups (see chapters 1 and 7) have led A. Goldizen (pers. comm.) to suggest that in wild groups the greater distances between individuals might make the suppressive effect of the presence of a dominant female less strong. However, two captive studies have shown that suppression may occur without direct physical contact: Evans & Poole (1983) found that newly-paired female common marmosets took longer to conceive if housed near dominant relatives, and Savage *et al.* (1988) provided evidence that exposure to scent-marks from their natal families could delay the onset of breeding in newly-paired female cotton-top tamarins. In addition, French & Stribley (1987) found synchronous ovarian cycles in *Leontopithecus rosalia* females housed up to seven metres apart, providing further evidence that some form of communication (probably olfactory) capable of affecting breeding may operate at some distance.

Tardif (1984) has suggested that physiological inhibition of fertility may also occur at some other level than ovulation - for example, a subordinate female may be incapable of supporting a pregnancy or may lose her infants, and this is thought to occur in wolves (Zimen 1976; Packard *et al.* 1985) and in dwarf mongooses (Rasa 1973). As yet this possibility has not been investigated in any detail in callitrichids, because of the difficulty of detecting failures in early pregnancy (Abbott 1987).

Infanticide. Finally, breeding females could use infanticide to ensure that there is no rival drain on the group's resources for infant care. In all cases in which two females have become pregnant in a cotton-top tamarin group, at most one has successfully reared infants (see above). In two cases described by Price & McGrew (in press *b*) in which fertility suppression apparently failed in groups of cotton-top tamarins and a mother and daughter both gave birth, only one female's infants survived in each case. In one case a mother was seen to attack her daughter's infants, and in the other the daughter's infants were found mutilated. In the case of incest described in chapter 7, the daughter's infant, although stillborn, had been attacked, suggesting that it would not have survived.

Infanticide amongst primates has attracted most attention as a male strategy, typically practised by newcomers to a group, which functions to reduce the interval before a female ovulates again and thus increase reproductive success at the expense of that of other males (e.g. Hrdy 1979). In callitrichids, however, the killing of other females' offspring by dominant females could well be an adaptive strategy if help with infant care is a limited resource. It is possible that infanticide or behaviour that prevents a mother from taking care of her offspring may also occur in other callitrichid species (e.g. Roda & Roda 1987). S. Tardif (pers. comm.) described a *C. jacchus* group in which a mother and daughter both became pregnant. The mother gave birth to a single infant, but was prevented from approaching it by her daughter, and the infant died. Infanticide by dominant females of subordinates' young has also been observed in dwarf mongooses (Rood 1990), and in African wild dogs (van Lawick 1973, cited in Macdonald & Moehlman 1982).

Encouraging males to stay and help

A second important component of the reproductive strategies of female callitrichids is the ability to keep a male around when help is required with infant care. Females could adopt various means of ensuring this, including concealed ovulation; remaining sexually receptive during most or all of the breeding cycle; synchronising breeding with other females; investing more in their relationship with their mate shortly before infants are due; and soliciting the attentions of other males to encourage mate-guarding by the male.

Concealed ovulation. In many species of Old World monkey, and in chimpanzees, females have "sexual skin" in the anogenital area which undergoes cyclical changes in colouration and swelling. These changes are correlated with the stage of the reproductive cycle (Dixson 1983). In New World monkeys, on the other hand, similar indicators of a female's reproductive state have been reported only in one species of howler monkey, *Alouatta palliata* (Crockett & Eisenberg 1987) and in bearded sakis, *Chiropotes* (Robinson *et al*. 1987). In the monogamous genera *Aotus* (Dixson 1982; Robinson *et al*. 1987) and *Callicebus* (Robinson *et al*. 1987), there are no visible changes over the ovarian cycle. This also appears to be true of callitrichids. Although there was one early report of "sexual skin" in an unidentified marmoset species (Russell & Zuckerman 1935), this has not been confirmed by later and more detailed observations of several callitrichid species. Callitrichids do not menstruate and there are no changes in vaginal cytology over the ovarian cycle (Hampton *et al*. 1966; Hearn & Lunn 1975).

External signs of ovulation are therefore lacking in callitrichids. But there are other means by which males and others could detect ovulation - for example, changes in the composition of female scent-marks. However, Stribley *et al*. (1987) have proposed that little correlation exists between sociosexual behaviour and ovarian cycles in callitrichids, and have suggested two possible explanations. First, ovulation may be concealed in callitrichids, benefitting the female either by reducing the male's tendency to leave and thus increasing the chance that he will care for the infants, or by increasing the male's certainty of paternity: if other males cannot detect ovulation they will not mate with the female. This might again lead to increased paternal care or protection, or other benefits such as a reduction in the risk of male infanticide. Similar hypotheses have been proposed for humans (e.g. Turke 1984), as well as other primates (e.g. Andelman 1987; Hrdy 1979, 1988). There are several difficulties with this argument, however. It would, for example, be reasonable to put forward an alternative hypothesis that paternity certainty is *reduced*: this would clearly be the case in a polyandrous group, since the males could not be sure that they were mating when the female was likely to conceive.

However, the most serious difficulty with this hypothesis is that it is doubtful whether the lack of correlation between sociosexual behaviour and ovarian cycles is a genuine effect, at least in cotton-top tamarins. As discussed in detail in chapter 6, the majority of the evidence in favour of this hypothesis in cotton-tops has been obtained from new pairs (e.g. French 1982), and/or has used a limited-access paradigm that may seriously affect sexual activity (e.g. Brand & Martin 1983). In contrast, data presented in chapter 6 showed that male cotton-top tamarins in established pairs did appear to be sensitive to the female's reproductive state: females were quite clearly most attractive to males in the postpartum period. Furthermore, attractivity declined once a female became pregnant, while there was some indication (from frequencies of mounts) that it was maintained if she did not conceive.

In the other two species of callitrichid for which detailed observations have been made postpartum, similar results have been obtained. Dixson & Lunn (1987) found correlations between sexual activity and the stage of the ovarian cycle in *Callithrix jacchus*. The one established pair of *L. rosalia* in Stribley *et al.*'s (1987) study showed a similar pattern of maintenance of proximity to the cotton-top tamarins in the present study, with the male responsible for maintaining proximity only during the postpartum period. On the basis of the current evidence, the existence of concealed ovulation in at least these three callitrichid species seems unlikely.

An alternative hypothesis proposed by Stribley *et al.* (1987) to explain the lack of correlation between behavioural and hormonal measures in their study of *Leontopithecus rosalia* was that obvious signals indicating ovulation are unnecessary since the pair are close all the time. However, if males could detect ovulation there would be no point in wasting effort in mating when conception was unlikely. Peaks in mounting would therefore be expected around ovulation, and thus this hypothesis cannot explain the lack of such found in *L. rosalia* by Stribley *et al* (1987). Again, it also founders on the relatively poor quality of the data put forward in favour of a lack of correlation between sexual behaviour and ovulation. Considerably more research is therefore required in this area - probably the most fruitful approach would be to conduct concurrent hormonal and behavioural sampling during postpartum oestrus.

Continuous receptivity. Although it seems unlikely that the female's reproductive state is concealed from males, there was some evidence for female receptivity during most if not all of the breeding cycle in cotton-top tamarins (chapter 6). Muckenhirn (1967) also described a rise in sexual activity in late pregnancy in captive cotton-tops, and suggested that this may reflect increased attractiveness of the female, thus ensuring the male's help in infant care. The results of the present study (chapter 6), however, suggested that not only attractivity (measured by frequency of male mounts) but also female proceptivity (head-shaking, tongue-flicking and female mounting) and receptivity (acceptance of male mounts by the female) increased shortly before parturition. However, while attractivity increased after birth, proceptivity and receptivity declined. Brand (1984) found some indications that male interest in female cotton-top tamarins (measured by the frequency with which males sniffed the female's anogenital area) also varied over the ovarian cycle, and suggested that increases in proceptive behaviour by female cotton-top tamarins during troughs in the oestrogen cycle might be a method by which the female could maintain the male's interest when she was least attractive in hormonal terms. Interestingly, in Brand's study there was some evidence that pregnant and non-cycling females were the most proceptive but the least attractive; this agrees well with the results of the present study that pregnant females were more proceptive and receptive, but not so attractive to males (as measured by male approaching). Female cotton-top tamarins therefore appear to use sexual behaviour to maintain male interest when there is no possibility of conception.

In other callitrichid species, too, sexual behaviour is not confined to a rigid, periovulatory "oestrus" (e.g. Dixson & Lunn 1987, for *Callithrix jacchus*). Other studies of *C. jacchus* have found an increase in sexual activity in late pregnancy (e.g. Evans & Poole 1984). Sex during pregnancy has also been reported in other primates (e.g. chimpanzees, *Pan troglodytes*: Wallis 1982; vervets, *Cercopithecus aethiops*: Andelman 1987; for a review, see Hrdy & Whitten 1987), and in coyotes, *Canis latrans* (Gier 1975). Several authors (e.g. Kleiman & Mack 1977; Evans & Poole 1984) have suggested that sex during pregnancy may have an important function in maintaining the pair bond. However, it is not clear why a peak in *mid*-pregnancy, as reported by Kleiman & Mack (1977) in *L. rosalia*, should be important.

The changing patterns of proceptive and receptive behaviour over time observed in the present study have not previously been described in female callitrichids, and very little work has been done in other species on variations in the sociosexual behaviour (other than mounting) of breeding callitrichids over the breeding cycle. It is therefore difficult to assess the extent to which the different strategies adopted by male and female cotton-top tamarins are common to other marmosets and tamarins; this is clearly an area on which further research should be concentrated.

Postpartum oestrus. One particularly interesting facet of callitrichid reproduction is that females have a postpartum oestrus which is unaffected by lactation (*Callithrix jacchus*: Lunn & McNeilly 1982; *Saguinus oedipus*: French 1983; Ziegler *et al.* 1987*a*), and thus can conceive again within weeks of giving birth. This phenomenon appears to be extremely unusual amongst primates - typically, lactation affects the interbirth interval, either by increasing the time before cycling resumes, and/or by increasing the number of cycles to conception (Short

1987; Gomendio 1989). Amongst the other monogamous New World species that also have male parental care, a postpartum oestrus occurs in *Callimico* (Ziegler *et al.* 1989), but not in *Aotus* (Dixson 1982; Robinson *et al.* 1987) or in *Callicebus* (Robinson *et al.* 1987). A postpartum oestrus may have at least two possible functions: first, it might allow females to take advantage of variations in environmental conditions very quickly, by becoming pregnant again if conditions favour it. Amongst prosimians, species with a higher reproductive rate tend to live in unpredictable environments (Bearder 1987); this may also apply to callitrichids, and in particular to marmosets which live in unstable habitats (S. Ferrari, pers. comm.). Secondly, it may act as an encouragement to the male to stay nearby when the infants are still being carried most of the time. This may be particularly true of tamarins, which despite having a postpartum oestrus (at least in captivity) appear only to produce one litter a year on average in the wild (see chapter 1).

Reproductive synchrony. Another method open to callitrichid females to deter males from leaving them would be to synchronise their reproduction. Synchrony may occur on various time scales, for example at the level of the ovarian cycle, or by limiting births to a particular time of year (McClintock 1983; Lindburg 1987). Seasonality in wild tamarins is now well-established for many populations, including cotton-top tamarins (Neyman 1980). Although the proximate mechanism influencing this may be food availability (Goldizen *et al.* 1988), it may affect a male's ability to find and impregnate another female if he deserts his mate. Cotton-top tamarins, unlike the majority of callitrichids, maintain a birth peak in the spring even in captivity (Brand 1980). This also appears to occur in golden lion tamarins (Brand 1984). In addition, captive golden lion tamarins housed in auditory and olfactory contact gave birth at nearly the same time (Kleiman 1978*a*). Synchronising breeding in this way may reduce the benefit a male could gain from deserting and may therefore act as a strategy to increase male parental investment (Knowlton 1979).

Data presented by French & Stribley (1987) suggest that female golden lion tamarins may also have adopted strategies of synchronised ovulation, as well as birth, to limit breeding to one female, but whether this is true of cotton-top tamarins or of other species is not yet known.

Investment in the pair bond to obtain male assistance. In addition to using sexual behaviour to maintain a male's interest, female cotton-top tamarins in the present study also showed patterns of investment in their relationships with their mates that would be expected if their aim was to keep males nearby to help (chapter 6) - they groomed males more than they were groomed in return, and were responsible for maintaining proximity, particularly before they gave birth. As few other studies have investigated such changes in the relationships of breeding pairs over the breeding cycle, it is not yet clear whether this applies to other species. However, with only one exception (Savage *et al*. 1988), numerous other studies of captive cotton-top tamarins have also shown that, after the initial phase of pair formation, females groom males more than the reverse (Muckenhirn 1967; Wolters 1978; Welker & Lührmann 1978; Price & Hannah 1983). Even in Savage *et al*.'s (1988) study, males did not groom significantly more than females.

These results from cotton-top tamarins do not accord with Kleiman's (1977) hypothesis that, in contrast to the typical primate pattern, males in monogamous species tend to groom more than females. This was the case in a study of common marmosets (Evans 1986), in which males in established pairs groomed females more than vice versa during pregnancy. However, studies of several other callitrichid species in captivity have produced inconclusive results; some have found that males groom more than females (e.g. *Callithrix jacchus*: Evans & Poole 1983, 1984; *Leontopithecus rosalia*: Kleiman 1978*a*), others that females groom more (*Saguinus fuscicollis*: Vogt 1978*a*; *S. mystax*: Box & Morris 1980). Kinzey & Wright (1982) also found that males in wild monogamous *Callicebus torquatus* groomed no more than females did. If monogamy and polyandry are advantageous to females, then they might be expected to groom more, particularly once they have older offspring - once this point is reached, paternal care may be of less importance for successful reproduction, and there might therefore be more incentive for a male to desert.

Encouraging rival males. Finally, females may show interest in rival males, either in order to encourage mate-guarding by one male (and therefore increase the probability that he will not desert), or to encourage polyandry in order to obtain more assistance with infant care (Buchanan-Smith 1989). The female in the polyandrous group described in chapter 7 showed no clear preference for any particular male. In contrast, Kleiman (1978*a*) has suggested that the drop in scent-marking by *L. rosalia* females at oestrus indicates that they may not advertise their reproductive state when most receptive, thus preventing unattached males from interfering in the breeding of the bonded pair. It is not quite clear, however, how this would benefit the female, since it would presumably be to her benefit to *attract* additional males as she would then have more assistance with infant care. Finally, there is no reason to suppose that *frequency* of scent-marking is the important factor, if it is chemical signals in the scent-marks that convey the information (see, for example, Epple *et al.* (1988) for studies of the different types of information that may be contained in callitrichid scent-marks). Again, more detailed studies are required.

Anzenberger (1985, 1986) has also suggested that breeding female *Callithrix jacchus* are unlikely to take advantage of opportunities to mate with strange males, at least in captivity: they were aggressive to strange males and very little sexual behaviour was seen. Sexual interactions did occur, however, between males and subordinate females. Evans (1983*b*) and Sutcliffe & Poole (1984*a*) also found that when opposite-sexed marmosets were introduced, males solicited, but females did not respond. These results do not appear to accord with studies of polyandrous groups of tamarins. Several factors may account for this. First, the female common marmosets in these experiments were pregnant. Second, it is possible that once a female has established relationships with one or more males, new individuals may not be accepted - in the present study, the polyandrous female met all three males at the same time. Finally, the number of helpers already available to the female may affect her response: one study (French & Inglett 1989) found that the level of threats directed towards intruders by breeding golden lion tamarins was positively correlated with the number of sub-adult offspring present in the group. In the present study, the three males were the only helpers available to the polyandrous female, and it may therefore have been in her interest to maintain a sexual relationship with all of them.

Strategies of breeding males

Male marmosets and tamarins are presented with a parallel but rather different set of options to those of females. These options are: (1) whether or not to share breeding with other males; (2) when to stay with a single female, and when to desert and attempt to mate polygynously; (3) when and how much to invest in their relationships with females; and (4) how to best persuade females to accept them as mates.

Sharing a female versus monopolising a female

Preventing other males from breeding. Unlike subordinate females, subordinate male callitrichids do not appear to be physiologically incapable of breeding (Abbott & Hearn 1978; Abbott 1984, 1989; French *et al.* 1989), so when only one male in a multi-male group breeds, some sort of behavioural suppression must be operating. In the case of sons in their natal families, this may be incest avoidance (Carroll 1986). However, in the case of unrelated males, some other mechanism is likely. In order to increase his paternity certainty, a dominant male callitrichid could either (i) prevent access to the female by other males at all times, or (ii) prevent access to the females by other males only during oestrus, i.e. by mate-guarding.

(i) There is some evidence that captive male cotton-top tamarins defend access to a female regardless of her reproductive state (French & Snowdon 1981), and this may also occur in other species. Males are also particularly active participants in inter-group encounters in wild cotton-tops (Neyman 1980). French & Snowdon's (1981) experiment appeared to show that breeding male cotton-tops were more likely to be aggressive to intruders, particularly male intruders, than females were, suggesting that at least in this species, male-male aggression is well-developed and polyandry may be unlikely.

However, comparisons with other similar studies reveal strong and consistent species differences in responses to intruders (French 1986). In *Callithrix jacchus*, intra-sexual aggression is reported to be more common than inter-sexual aggression, but there is little evidence that one sex is more aggressive than the other (Epple 1967; Evans 1983*b*; Sutcliffe & Poole 1984*a*), although in one study male intruders received more aggression than females

(Evans 1983*b*). In *S. fuscicollis* (Epple 1978*a*; Epple & Alveario 1985) and *L. rosalia* (French & Inglett 1989), female-female aggression appears to be more pronounced than that between males (indeed, *Leontopithecus* males were rarely aggressive to intruders), and female intruders receive more aggression than male intruders. Studies of *S. labiatus* (Coates & Poole 1983; Buchanan-Smith 1989) produced little evidence of pronounced intra-sexual aggression.

The interpretation of such experiments is often difficult due to variations in experimental design and doubt as to the ecological validity of the paradigm (French 1986; Buchanan-Smith 1989); for example, as hardly anything is known of the process of group formation in the wild, experimental studies may not accurately reflect the process by which newcomers could be integrated into wild groups. French (1986) has pointed out several factors which may affect the results of such experiments, including context (both physical and social), the hormonal state of females, and the sex and status in their groups of the participants. The majority of these studies involved encounters between unfamiliar, unrelated, breeding adults. However, those studies which have compared responses to different categories of intruder have found that adults receive more aggression than sub-adults or juveniles (Epple 1967; Sutcliffe & Poole 1984*a*; French & Inglett 1989), and that socially familiar individuals are less aggressive to one another than strangers (Sutcliffe & Poole 1984*a*; Harrison & Tardif 1988). It may be possible to reconcile the relatively stable polyandry found in the present study with the results of French & Snowdon (1981), because the males in the present study were related, and two were immature when the group was established.

(ii) In order to prevent access to the female by other males when she is most likely to conceive, males must be able to detect changes in the female's reproductive state, and, as discussed above, there is some evidence that male callitrichids can do this. Although the monogamous male cotton-top tamarins in the present study were not under direct threat from other males, because incest avoidance meant that sons were unlikely to mate with their mothers, the increase in male following of females during the post-partum period (see chapter 6) might represent mate-guarding by males. It was also interesting that males showed their lowest levels of feeding and foraging during this period. "Consortships" have been observed in wild groups of saddle-backs containing more than one male (Terborgh & Goldizen 1985), but whether or not such consortships do represent mate-guarding and are effective in increasing a male's probability of paternity (as has been shown by Sherman (1989) in ground squirrels, *Spermophilus brunneus*) is not yet known. An ability to detect the likeliest time of conception predicts that males should show more intra-sexual aggression when their mates are cycling than when they are pregnant, and there are reports that aggression in captive groups is indeed related to the reproductive condition of the breeding female. Rothe (1975) for example, found that in *Callithrix jacchus*, the dominant male was more likely to harass other males when the female was in oestrus. Kleiman (1979) suggested that aggressive episodes in *L. rosalia* were related to the reproductive state of the breeding female, and Stribley *et al.* (1987) found that non-breeding males in their *L. rosalia* colony often showed aggression with approximately three-week periodicity, similar in length to the cycles in mating reported by Kleiman (1978*a*), and the ovarian cycle length of 19.6±1.4 days.

Sharing a female. In some cases, however, it may be impossible for callitrichid males to monopolise a female effectively, or it may in fact be to their advantage to share mating in order to breed successfully. In the polyandrous cotton-top group described in chapter 7, and in the polyandrous group of wild saddle-back tamarins studied by Goldizen (1989), there was no evidence of mate-guarding by any of the males involved. This contrasts with the results of captive studies of *L. rosalia* by Kleiman (1978*b*) and saddle-back tamarins by Epple (1972), who found that one male in two-male/one-female trios almost invariably had priority of access to the female.

The data from the polyandrous group presented in chapter 7 results resemble those of previous studies of other callitrichid species in that aggression was largely intra-sexual. Aggression between males occurred as soon as the new female was introduced, but the group then remained stable for long periods with two to three males, and there was no sign of mate-guarding during postpartum oestrus. Since polyandry results in a reduction in each male's probability of being the father of any resulting infants, initially each male may have been attempting to increase his chances of fathering offspring by expelling rivals before impregnation occurred, and thus reduce the probability that investment in infants was wasted on the offspring of others. Similarly, in four polyandrous or polygynandrous groups where male-male aggression and evictions occurred in Price & McGrew's (in press *b*) study of captive cotton-top tamarins, two males were eventually left in stable groups. If a single helper is sufficient for successful rearing of infants, two males can increase their chances of fathering infants by evicting surplus males, while still retaining one other male to help them in rearing. Two similar cases have been described in other species in captivity which support this hypothesis. Box (1977) reported that a young *C. jacchus* male housed with an unrelated family helped to care for two litters of infants, but was then attacked by the dominant male. Vogt *et al.* (1978) described a male *S. fuscicollis* who again helped to care for two sets of unrelated infants before being evicted from the group.

As discussed in chapters 1 and 7, there is little firm behavioural evidence of polyandry in wild callitrichids. However, relative testes size has been proposed as additional evidence in favour of polyandry. Harcourt *et al.* (1981) and Harvey & Harcourt (1984) found that *Saguinus geoffroyi* (which they reported as *Saguinus oedipus*) had larger testes in relation to body size than were expected for a monogamous primate: their testes size was more in line with those of multi-male species, while *Callithrix jacchus* came closer to the expected value for monogamy. However, for several reasons, considerably more data are required from other species before these results can be taken as evidence in favour of polyandry in tamarins. First of all, tamarins are more highly seasonal in breeding than marmosets (see chapter 1), and seasonal breeding is also associated with larger relative testes size because males must perform a large number of copulations in a short period (Harcourt *et al.* 1981; Martin & May 1981). Second, *Saguinus geoffroyi* is unusual in two respects: it shows considerably higher levels of inter-group movement than any other tamarin (see also chapter 1) and rarely rears more than one infant per litter (Dawson 1976, 1978; Rasmussen 1989), while other tamarins frequently rear two. However, Dixson (1987) has found that relative testes size in some marmoset species (*Cebuella pygmaea, Callithrix argentata*) is also larger than expected. This issue therefore remains to be resolved.

The prevalence and stability of polyandry in any callitrichid species, and how these vary with the local ecological conditions, are as yet unknown (Goldizen 1987*a*; Dunbar 1988). Garber *et al.* (1984) have suggested that males might tolerate multiple mating by the female if mating by higher ranking males was more likely to result in conception; if the sex ratio was biased towards males; or if males protect their investment by caring for young they are likely to have sired. Similar explanations have been proposed to account for "cooperative polyandry" in some bird species. In Galapagos hawks, the important factor appears to be the survivorship advantage gained from being in a group, as each male in a polyandrous group does no better from a reproductive point of view than monogamous males (Faaborg 1986). In Tasmanian native hens (Ridpath 1972; Maynard Smith & Ridpath 1972) the sex ratio is heavily skewed towards males. In dunnocks (Davies 1985; Burke *et al.* 1989), one male has priority of access; however, this is not true of Harris' hawk (*Parabuteo unicinctus*: Mader 1979), or Galapagos hawks (*Buteo galapagoensis*: Faaborg 1986). It is difficult to test Garber *et al.*'s (1984) hypotheses on the basis of the available data: there is little reason to suspect that sex ratios in callitrichid populations are heavily skewed towards males (see chapter 1), and also little evidence for priority of access by one male.

Dietz & Kleiman (1987) have recently presented data on canine size in wild *L. rosalia* groups suggesting that one of the males in potentially polyandrous groups (i.e. groups with more than one adult male) was always older than the other(s) and had longer canines. They proposed that this made it likely that multiple males were father and son(s), and concluded that monogamy was therefore a more probable mating system. The logic behind this argument, however, is not clear. First, the fact that two males are father and son does not mean that they cannot both mate unless the son's mother is still the breeding female, and even then incest cannot be entirely ruled out (for example, cases of mother-son copulations and pairings have been reported in gibbons: Chivers & Raemaekers 1980; Tilson 1981; Srikosamatara & Brockelman 1987). Evidence from Stirling (chapter 7; and personal observation of another group) suggests that a father and son may in fact be the most stable combination for a polyandrous group. The original father in the group described in chapter 7 was never involved in any aggression. Fathers in monogamous groups of callitrichids in captivity also rarely initiate aggression (*Saguinus oedipus*: McGrew, in press; *L. rosalia*: Inglett *et al.* 1989). Second, without knowledge of kin relationships there is no reason to assume automatically that different-aged males are father and son: they may be siblings, or they may even be unrelated.

However, it may well be beneficial for males in polyandrous groups to share mating with relatives, since this would reduce the costs of sharing paternity via kin selection (West Eberhard 1975). This appears to have been a major factor allowing the development of polyandry in Tasmanian native hens (*Tribonyx mortierii*), in which the males are frequently brothers (Maynard Smith & Ridpath 1972), and in human polyandrous societies in Tibet (Crook & Crook 1988), where again two brothers marry a single wife.

Goldizen (1987*a*) has recently proposed a hypothesis suggesting that the mating system of a tamarin group is primarily determined by the number of non-breeding helpers in a group, leading to the predictions that a pair with one or more helpers could be monogamous and raise twins; and second, that both members of a pair could potentially benefit from polyandry. The female clearly benefits, but males could also benefit if either there was a low chance of successfully reproducing in a monogamous group, or if the reproductive success of monogamous pairs was sufficiently low.

Consideration of these various factors leads to several predictions about the occurrence, reproductive success, and stability of polyandrous groups of callitrichids:

(1) Polyandrous trios will be more successful than monogamous pairs without helpers when the minimum group size required for successful rearing of infants is more than two (Goldizen 1987*a*).

(2) The maximum number of males in a polyandrous group will be governed by the number of individuals required for successful reproduction; in larger groups, surplus males will leave or be evicted.

(3) If a lone pair can raise a *single* offspring, polyandry should be less likely than monogamy as, while the *female* would benefit, the benefits to males of rearing twins in a polyandrous group would be no greater.

(4) Polyandry involving related males will be more stable than polyandry involving unrelated males as it reduces costs to males, such as copulatory competition, by inclusive fitness. The most stable combination may be a father and son.

(5) Given the advantages of fraternal polyandry, brothers will have stronger social bonds than those between sisters, or between brother and sister, even before they leave their natal group. However, fraternal bonds will have elements of competition as well as cooperation if inheritance of the natal territory is a possibility.

(6) Since polyandry seems more likely than polygyny (Price & McGrew, in press *b*; see also chapters 1 and 7), dominance relations will be less rigid among males than among females. Status will also affect who breeds in a particular group.

(7) Founding polyandrous males will emigrate, voluntarily or otherwise, as the benefits gained from polyandry decrease as increasing numbers of adult offspring become available to help, and groups will therefore tend towards monogamy.

Monogamy versus polygyny

A male has further options concerning whether to remain loyal to a single female, or attempt to mate polygynously. A male may initially need to be monogamous or share mating with another male in order to successfully rear any offspring he sires, but as the number of helpers increases, the benefits to males of monogamy are likely to be reduced much more than the benefits to females. For female mammmals there will always be a certain minimum investment required as only they are equipped to provide for an infant's nutritional needs. But for male breeders, there may come a point when their contribution is no longer necessary to rear infants successfully, and they may be able to desert without losing. This may explain why the male cotton-top tamarins in the present study showed more reduced levels of social interaction with other family members the longer they had been paired than did females. An alternative explanation (Kleiman 1977) is that there is a general decrease in the level of social interactions with time in monogamous species; however, this would not explain why the level of social interactions drops further in males than in females.

Dunbar (in prep.) has suggested that one important factor governing the decision a male callitrichid makes about whether or not to desert would be the *quality* of care that could be provided by helpers. If helpers could provide care equivalent to whatever the male provides, he should have no incentive to stay and instead should desert and attempt to mate polygynously. If, however, care by helpers is of poorer quality than that given by breeding males, it would be more likely to pay a male to stay with and help a single female. To test this, it would be necessary to compare the breeding success of a female who had the help of a male with that of a female in the absence of a male but in the presence of helpers. This would be difficult without performing removal experiments. However, it does seem likely that naive juveniles would be unable to provide adequate care - they are smaller than adults and thus the energetic costs of carrying are higher for them, and their inexperience may lead to them to behave inappropriately and thus jeopardise the safety of the infants. There was evidence from this study (chapter 4) that juveniles were more likely to reject infants than older siblings, and that other family members attempted to limit carrying by juveniles. This suggests that juveniles may indeed be less good caretakers. Effectiveness of helpers also increases with age in other species (e.g. brown jays, *Psilorhinus morio*: Lawton & Guindon 1981).

A male may therefore need to stay with a female until juveniles have had at least some experience with infant care. Furthermore, considerable investment of time is needed to establish a successfully reproducing pair or group, and it would therefore be unlikely that a male could manage to be polygynous - if he left he would have to go through the whole process again, and may initially not be as successful as in his previous group. Also, at least in *Saguinus fuscicollis* (Goldizen & Terborgh 1989) the available habitat appears to be saturated; a deserting male is therefore unlikely to be able to find a new territory.

Relationship with the breeding female

Changes in investment in the pair relationship over time. Like females, male cotton-top tamarins in the present study changed their levels of investment in pair-bond maintenance over time. They invested most in terms of affection and maintenance of proximity when the female had recently given birth, and was therefore likely to be able to conceive. This is readily explainable if males can detect changes in the female's reproductive state, and could therefore minimise wasting time and effort remaining close to a female when they were unlikely to be able to impregnate her.

Female dominance. It may also be to a male's advantage to ensure that the breeding female has preferential access to resources, particularly when she is pregnant or lactating, if by doing so he increases her ability to take on the energetic costs of reproduction. Very little aggression between pairs of cotton-top tamarins was seen in the present study (chapter 6), and there was no evidence that either the male or the female dominated the other. Although food-sharing was seen in only two of the five established pairs, food was transferred exclusively to females, suggesting that they may have priority of access to resources. Tardif & Richter (1981) also reported that breeding females in captive groups of cotton-top tamarins and common marmosets had priority of access to desirable foods and defended them aggressively against other family members.

Kleiman (1977) has suggested that there may be a general trend towards female dominance in monogamous mammals. Rood (1986), for example, reported that female dwarf mongooses, *Helogale parvula*, had priority of access to food. In the vast majority of primates, on the other hand, males have priority over females for desired food (Jolly 1984). Jolly (1984) suggests that the occurrence of female dominance over food in some species (for example, in the monogamous prosimian *Indri indri*; Pollock 1979), may have developed where for one reason or another female reproductive effort is particularly costly. This is very likely to be the explanation in marmosets and tamarins. Ferrari (1987*a*), for instance, found that the only adult in a group of wild *Callithrix flaviceps* to receive food from other group members was the breeding female, and this occurred only in a two-month period before and after she gave birth.

Female choice. Males may also need to consider the female's role in maintaining a relationship. Failed reproduction may lead to "divorce" in pair-bonding species: there is evidence from studies of birds and humans that reproductive failure is related to a greater chance that the members of a breeding pair will separate and seek new mates, although a causal relationship has not yet been proved (for a review, see Rasmussen 1981). In recent years there has been an increase in interest in the role of female choice amongst potential mates in primates (e.g. Smuts 1985, 1987). In species such as callitrichids in which male parental care is important, females might be expected to use infant care skills as one basis for assessing which males to mate with.

Infant carrying by males in other primates and other forms of affiliation with infants have been interpreted in several ways: as agonistic buffering (e.g. Deag 1980); as protection against infanticide (e.g. Busse & Gordon 1983); as a means of recruiting female aid (e.g. Dunbar 1984); and as a means of forming a relationship with the infant's mother and thus increasing the chance of mating with her in the future (e.g. Smuts 1985). The particular pattern of male care in callitrichids suggests that males may be using infants for the latter reason, as part of a "courtship" strategy. Even in larger groups, males in both wild and captive populations tend to *increase* their contributions to infant carrying over the first few weeks. In cotton-top tamarins, father's peak carrying times coincided with the most likely time of post-partum ovulation. There was also evidence from this study (chapter 4) that fathers competed with other family members to carry infants in this period, despite the presence of helpers. Why should breeding males be doing this?

One possible explanation is that they are using infants to "impress" the breeding female. By demonstrating that they are competent caretakers, they may be more likely to be able to persuade her to let them father her next infants. If male investment is important for reproductive success, it makes sense for females to make a choice between males on the basis of their skills as infant caretakers. It may therefore pay males to demonstrate to the breeding female that they are competent, and females may be more likely to mate with the male who impresses her most. This does not negate the importance of male parental investment for infant survival - on the contrary, it may be *because* paternal care is necessary that such tactics are expected to develop. This study provided evidence that male cotton-top tamarins used infant carrying as a courtship strategy (chapters 6 and 7), and there was some evidence that females were more likely to accept the mounts of a male who was carrying.

Infanticide by incoming males who are highly unlikely to be the fathers of any infants has been reported in several primate species (Hrdy 1979). The hypothesis that males may use infant carrying as a courtship strategy might provide an explanation for why this appears to be unknown in callitrichids - captive males of several species have been reported carrying infants who they definitely did not father (Epple 1975*b*; Box 1977; Vogt *et al*. 1978; McGrew, unpublished data). If by caring for a female's current litter these males ensure that she is more likely to mate with them, this strategy would not be as maladaptive as it might first appear.

The phenomenon of male use of infants as courtship has not previously been reported in callitrichids. Although such a strategy may not be very important for males living in captive monogamous groups with no competition from other males, the possibility of polyandry as an alternative mating system that some callitrichid groups can adopt make this observation of some relevance. I would therefore predict competition to carry infants between males in polyandrous groups.

In summary, one interesting way of looking at the different strategies of breeding cotton-top tamarins would be that females use sex to get help, but males use help to get sex.

Strategies of non-breeding callitrichids

Non-breeding callitrichids are also faced with decisions about the best strategies to adopt: should they stay in their natal territories as helpers, or leave? What benefits might be gained from helping that could influence this choice? If they disperse, where should they go and whom should they go with?

Benefits of helping

If helping younger sibs *is* beneficial, competition would be predicted in relationships amongst helpers. The occurrence of competition to carry infants among older siblings in captive families of cotton-top tamarins (chapter 4) suggests that helping behaviour is indeed cooperative rather than altruistic, i.e. that helpers as well as breeders benefit in some way. There was evidence from the present study that the distribution of infant carrying in cotton-top tamarin families was influenced not only by each individual's motivation to carry, but also by competition to carry infants, and by attempts by some individuals to control carrying by others (chapter 4). One other study (Pryce 1988) has shown that competition can affect the distribution of infant care in *S. labiatus*; however, the present study is the first to show that different age-sex classes of helper in callitrichids vary in the extent to which they compete for and control opportunities to carry infants. Carrying by adult daughters and juveniles appeared to be subject to control, most often by subadults and by adult sons. It therefore appeared that these last two age-sex classes were the most competitive.

Competition amongst helpers has also been reported in birds. Carlisle & Zahavi (1986) found that dominant helpers in Arabian babblers (*Turdoides squamiceps*) stole food from subordinate helpers and fed it to the nestlings themselves. They therefore suggested that helping might be a means of increasing status in this species, which may be important in establishing future cooperative relationships. Ligon & Ligon (1983) found that green woodhoopoe helpers also competed to feed the nestlings.

So, if tamarin helpers are competing to care for infants because they gain some benefit from helping, what might the source of this benefit be?

Developing useful relationships. Feistner & Chamove (1986) have suggested that one of the functions of caring for siblings in callitrichids may be to promote affiliative bonds with those sibs so that they will later assist the caretaker when it becomes a breeder. As yet, we have no idea whether in fact this sort of benefit occurs in callitrichids, although there is evidence of such reciprocal helping in some bird species. For example, Ligon & Ligon (1983) reported that older green woodhoopoes received help in acquiring and maintaining a territory and in rearing their offspring from younger, lower-ranking birds that the older individuals had previously helped to rear. This held true even if the participants were unrelated, and this might provide an explanation for why callitrichids have been reported to help with infants who are not related to them (e.g. Box 1977; Vogt *et al.* 1978).

Helping as "payment". Behaviour by a helper that increases the fitness of a breeder can reduce the risk of expulsion from the group (Emlen 1982*b*). Gaston (1978) has suggested that helping behaviour may therefore represent a form of "payment" for being tolerated on the parental territory. Helpers may be "rewarded" by eventual inheritance of the natal territory

(Woolfenden & Fitzpatrick 1978). These ideas have been applied to cotton-top tamarins by McGrew & McLuckie (1986) and McGrew (1987), who suggested that tamarin offspring carry infants more because this is somehow beneficial in increasing the likelihood of inheriting their parents' breeding position. More specifically, they suggest that an apparent (though slight) tendency for females to emigrate more often than males predicts that older males should carry more, and presented some data suggesting that sons in captive families of cotton-top tamarins did carry more than daughters.

However, this hypothesis has relatively little evidence in its favour. Just as some studies have been criticised for overemphasising the role of fathers in carrying infants, sex differences in infant care amongst callitrichid helpers have also been treated somewhat simplistically in the past. Although the results of the present study on infant carrying appeared to support McGrew & McLuckie's (1986) hypothesis, with oldest sons carrying most but older daughters relatively little (chapter 3), the effect did not carry over to another form of care, food-sharing. Moreover, there was evidence from behaviour during infant transfers that adult daughters were in fact *prevented* from carrying (chapter 4). Finally, there seems to be no clear reason why male rather than female cotton-top tamarins should benefit from inheritance (Dunbar 1988). A more sophisticated explanation is therefore likely to be required, one that takes into account not only an individual's own interests but its relationships with others.

If inheritance of the natal territory *is* a possibility, this permits us to predict that competition and therefore aggression between siblings will intensify as their parents age and the likelihood of a breeding vacancy increases. However, the high survival rates of adult tamarins in the wild makes it highly unlikely that such vacancies will occur very often, and thus very few individuals will be in a position to inherit their natal territory. Goldizen & Terborgh (1989) saw only two wild saddle-back tamarins (both females) breed in their natal groups, although whether they did so at the same time as their mother was not stated by Goldizen & Terborgh. Thus in this species at least, inheritance of a breeding position in the natal territory seems unlikely.

Finally, it has not yet been demonstrated that staying with parents assists young callitrichids to establish themselves in breeding positions, either by inheriting the natal territory, or by budding off a territory of their own once the group and its territory reaches a certain size. Parental assistance in acquiring territories has been reported in Kloss' gibbons, *Hylobates klossii* (Tenaza 1975; Tilson 1981); groups may expand their territory at the expense of their neighbours, allowing an offspring to establish itself in the new area; or parents may accompany offspring in contests over vacant territories - sub-adults accompanied by their parents won such contests. However, no similar occurrences have been described in callitrichids; in fact, in view of the considerable stability of marmoset and tamarin range boundaries under some conditions (see chapter 1), budding off seems extremely unlikely in these circumstances at least.

On the other hand, in callitrichid populations in which groups are not territorial but instead have overlapping home ranges, offspring may be able to establish themselves in a different area of the parental range. This appears to have occurred in Ferrari's (1987*b*) study group of *Callithrix flaviceps*: these groups were not territorial (Ferrari 1988), and Ferrari observed the formation of a new group composed of animals from two adjacent groups.

Benefits of living in a group. Scanlon *et al*. (1987) suggested that helpers in *Callithrix jacchus* benefit from obtaining group membership. These benefits might include decreased risks from predation, improved foraging efficiency, and so on. In coyotes, *Canis latrans*, for instance, juveniles who stayed at home had a better chance of surviving than those who dispersed (Bekoff & Wells 1982). Goldizen & Terborgh (1989) also suggest that dispersal may be risky for tamarins. However, this hypothesis remains to be tested with data on the survival of tamarins who disperse compared with those who are philopatric - there is as yet no evidence about whether staying in the natal territory leads to improved survival or future reproductive success in young callitrichids.

Experience. Finally, young callitrichids might benefit from obtaining experience in the care of younger siblings, and thus improve their chances of breeding successfully in the future. Inexperienced tamarins are frequently inept when they first begin to carry (personal observation), and experience with younger siblings appears to be important for the development of adequate parental behaviour (Ingram 1978*b*; Epple 1978*b*; Tardif *et al.* 1984*a*). However, Goldizen & Terborgh (1989) found no evidence that young wild saddle-back tamarins lacked the necessary parental skills: one-year-olds were seen to help substantially with infant care. It was also interesting that although juvenile and sub-adult female cotton-top tamarins did carry more than males of the same age (chapter 3), the present study found little evidence that immature tamarins *competed* to carry in order to gain as much experience as possible (chapter 4). In monogamous species such as *Aotus* and *Callicebus* in which sibling care is uncommon (Dixson 1982; Mendoza & Mason 1986), experience in infant care may not be so important to competent parental behaviour. For example, Mendoza & Mason (1986) reported that parental performance in captive *Callicebus moloch* was hardly affected at all by experience with siblings. There are as yet no data on the *amount* of experience that young callitrichids need in order to become competent parents.

Dispersal strategies

To stay or to go?. As yet, very little is known about the processes of dispersal, group formation, and the takeover of vacant breeding positions in callitrichids. Obviously, captive studies cannot assess the reasons why young callitrichids do not disperse. In wild populations, many individuals appear not to begin breeding until well past the age of sexual maturity (Neyman 1980; Goldizen & Terborgh 1989), but only one study (Goldizen & Terborgh 1989) has attempted to analyse the factors influencing delayed dispersal and breeding in a callitrichid population. In their study population of saddle-back tamarins, suitable habitat appeared to be saturated, and high annual survival rates for adults (88%) meant that there were few vacant breeding positions. The problems of coping successfully with an unpredictable environment have also been suggested as one reason why young animals might delay dispersal (see chapter 1), but there was no evidence from Goldizen & Terborgh's study that environmental variation caused tamarins to delay breeding.

Who goes? In primate groups composed of female kin, males tend to emigrate whilst females remain to breed in their natal groups, while the converse is true in species characterised by female dispersal (Pusey & Packer 1987). If polyandry, particularly fraternal polyandry, is likely, females might be expected to disperse more often; if monogamy is the modal mating system, then both sexes would be expected to disperse at equivalent rates. Although patterns of aggression in captive callitrichid groups have led some authors to suggest that females may indeed migrate more frequently than males (e.g. Kleiman 1979; McGrew & McLuckie 1986), and consequently that there should be differences in the behaviour of the two sexes prior to leaving (McGrew, in press), no tamarin population has yet been found to show a significant sex difference in the frequency of dispersal or the distance moved (e.g. Dawson 1976, 1978; Neyman 1978, 1980; Goldizen & Terborgh 1989). Other communally rearing mammals show variable patterns of sex-biased dispersal (e.g. in African wild dogs, females emigrate (Frame & Frame 1976), but in brown hyenas, *Hyaena brunnea* (Owens & Owens 1984), males do), while in birds, females fairly consistently disperse more often or further than males (see Brown 1987).

In addition, female intolerance may make it difficult for a female callitrichid to move between groups. However, Savage *et al*. (1988) have suggested that fertility suppression may provide a means by which migrating females could enter new groups. They argue that this would be beneficial to the female as she could acquire useful experience in infant care, and a non-breeding female might be perceived by a resident breeding female as a less serious threat. However, there are several difficulties with this: (a) a female could just as well stay at home and gain as much experience as she needed there, and would not be risking the dangers of dispersal by doing so; (b) although Savage *et al*. (1988) and Ziegler *et al*. (1987*b*) have argued that in cotton-top tamarins, ovarian cyclicity does not start immediately on departure from the natal group, and it is this factor that makes a transient female less threatening, in other species it does (e.g. *Callithrix jacchus*: Evans & Hodges 1984); (c) there is evidence of the onset of cyclicity in cotton-top tamarins without removal from the natal group, as long as the mother is absent (Heistermann *et al*. 1989).

However, there may be another reason why it would be to a female's advantage to transfer into a new group initially as a helper rather than a breeder. Wiley & Rabenold (1984) have suggested that "queueing" for a breeding position, in which participants are ranked by order of arrival, could be a beneficial strategy for helpers in communally rearing species. A similar hypothesis has been proposed by Rylands (1985) for female *Callithrix humeralifer*. This could be beneficial for females if there was a good enough chance of taking over a breeding position, and predicts that females would enter a group (a) if there were fewer other females ahead of her in the queue than in her original group, or (b) if the current breeding female was old.

Where to go to? Goldizen & Terborgh (1989) found that saddle-back tamarins tended to move from larger groups to smaller ones: there were strong trends towards a negative correlation between the number of immigrants and group size, and a positive correlation between the number of emigrants and group size.

Interestingly, in a study by Zack & Rabenold (1989), breeding vacancies in *larger* groups tended to be fought for by stripe-back wrens more strongly than vacancies in smaller groups, suggesting that in this example the number of available helpers was a crucial factor. Frame *et al*. (1979) found that breeding opportunities appeared to stimulate transfer in African wild dogs. It would therefore be an advantage for non-breeding callitrichids to monitor neighbouring groups so that they will be aware of (a) potential mates, and (b) breeding vacancies and potential helpers, and this has been suggested for cotton-top tamarins by Moore *et al*. (submitted for publication). Inter-group encounters, which have frequently been observed in the wild (e.g. Neyman 1980; Buchanan-Smith 1989) may well provide opportunities for appraising the situation in adjacent groups.

In order to minimise inbreeding, animals might be expected to move to a genetically unrelated group. But do they? In tamarins, as in other communally rearing species, emigration to a neighbouring territory is common. For example, 11 of 41 migrations in *Saguinus geoffroyi* (Dawson 1976) and 12 of 18 known destinations in *Saguinus fuscicollis* (Goldizen & Terborgh 1989) were to adjacent groups (see also chapter 1). Cheney & Seyfarth (1983) also noticed that vervet monkey males migrated to specific neighbouring groups, typically an adjacent group which had received members of its own group in the past. Cheney & Seyfarth suggest that the benefits of a reduced risk of predation from not having to go so far, and reduced risk of attack by residents, may well outweigh any costs of possible breeding with kin. Furthermore, it is possible they would have prior knowledge of neighbours from monitoring, and can therefore choose the most suitable group to move to and the best time to go. In other communally rearing species, young animals may make several temporary forays away from their natal groups in search of breeding opportunities (e.g. golden jackals, *Canis aureus*: Moehlman 1983; Florida scrub jays, *Aphelocoma coerulescens*: Woolfenden & Fitzpatrick 1986). This also appears to occur in callitrichids (e.g. Dawson 1976, 1978; Soini 1987*a*; see also chapter 1).

Close monitoring of the neighbours may give tamarins in adjacent groups an advantage in struggles over breeding vacancies. In a study of dispersal and the takover of vacant breeding positions in the communally rearing stripe-backed wren (*Campylorhynchus nuchalis*), Zack & Rabenold (1989) found that females from adjacent territories were more likely to win, and that this could not be explained simply on a "first-come, first-served" basis. Zack & Rabenold suggest that factors such as experience with the adjacent territory or group, or a previous relationship with members of the neighbouring group, may influence a female's ability to compete.

Several predictions can be made about the probability that a migrant callitrichid will be accepted into another group:

(1) As a group increases in size it will be less likely to accept immigrants.

(2) Groups will be *more* likely to accept immigrants if:

(a) the immigrant is genetically related to the group;

(b) the group has few or no adult helpers;

(c) the group has dependent infants;

(d) either the immigrant is male; or if the immigrant is not fertile if female (since an extra breeding female would place a considerable drain on the group's resources).

(3) Immigrants will seek to enter groups where the breeding individuals are old as there will be greater prospects of taking over the breeding positions. Similarly, adult offspring will be more likely to stay in their natal group if their

parents are old. Close monitoring of neighbouring groups would provide information on the breeding status and length of tenure of the current breeding individuals. As yet only one study has estimated tenure for breeding individuals in wild callitrichid groups: Goldizen & Terborgh (1989) found that male saddle-back tamarins may remain in breeding positions for four years or more, and females for at least five years.

(4) If a breeding adult in a monogamous group dies, the remaining partner will be expected either to emigrate to avoid inbreeding, or to try to recruit a new mate. The option chosen will depend on the sex of the remaining partner and the dispersal characteristics of the species. For example, if females migrate more than males, a widowed female might be less likely to be able to recruit a new mate than would a male in the same position, and might therefore choose to emigrate instead.

Alone or together? Should a callitrichid leave its natal family alone or in the company of others? There are several reports of members of communally rearing species dispersing in groups, usually with same-sex sibs (e.g. African wild dogs: Frame *et al*. 1979; dwarf mongooses: Rood 1983; for birds, see Brown 1987). In addition to reducing predation risk, dispersal in groups may have additional benefits - a group of individuals may be better able to contest a vacant territory or breeding position. In acorn woodpeckers (Hannon et al. 1985), the largest sib groups won power struggles over breeding vacancies. In view of this, it is interesting that at least two studies (Ferrari 1987*b*; Neyman 1980) have found that callitrichids may be more likely to disperse in groups.

Whom should young callitrichids disperse with? Not all possible partners may be equally advantageous for a young callitrichid to team up with when it leaves its natal family. Several predictions can be made about the most likely combinations:

(1) Male and female sibs would not be expected to join together since they presumably wish to avoid close inbreeding.

(2) Male sibs may well join together, particularly if polyandry is necessary in order to establish a successfully reproducing group. Males should join preferentially with sibs, rather than unrelated individuals.

(3) Females are unlikely to go together. However, fertility suppression or dominance might allow them to do so. Age-related dominance is well known in communally rearing species of bird (Ligon & Ligon 1983; Woolfenden & Fitzpatrick 1984), and may also occur in callitrichids (e.g. Evans & Hodges 1984; Heistermann *et al*. 1989). Thus if one female can suppress fertility in another, she

may allow the subordinate to stay with her and act as a helper.

(4) Individuals with a dominant/subordinate relationship would be more likely to emigrate together than those of equal rank, as this would reduce competition. However, to assess the probability of these last two predictions, considerably more information on status in callitrichids is required.

Breeder-helper relationships

If young adult callitrichids are to remain in their families instead of emigrating, their parents must tolerate them. Communally rearing species in general are characterised by a relaxation of the general rule of parental intolerance of offspring who could exist independently of them (Brown & Brown 1984; Brown 1987). It was interesting that in this study there was a notable absence of parent-offspring aggression even in polyandrous and polygynous groups (chapter 7). This would be consistent with a hypothesis that parents in callitrichid species, like breeders in other species with communal rearing, obtain some benefit from retaining older offspring as helpers. Similarly, callitrichid species appear to differ from other monogamous primates in the degree to which parents tolerate their offspring once they reach maturity. In gibbons and siamang, sub-adults, particularly males, are peripheralised by the parent of the same sex (Aldrich-Blake & Chivers 1973; Tilson 1981; Leighton 1987). Less evidence is available for the monogamous New World monkeys - Robinson *et al.* (1987) reported no signs of agonistic behaviour when sub-adult *Aotus* and *Callicebus* left their natal groups, although Aquino & Encarnación (1986) observed a fight in *Aotus nancymai* that could have been a peripheralisation, and Dixson (1982) reported occasional fights between parents and offspring in captive *Aotus*.

In most marmosets and tamarins, on the other hand, captive studies have shown that parents are rarely involved in "evicting" their offspring; instead, if forced departure occurs, it tends to result from aggression between sibs (Stevenson & Rylands 1988; K. Moore, unpublished data; personal observation). *Leontopithecus rosalia* appears to be an exception to this - aggression by breeding females towards juveniles occurs relatively often, although breeding males rarely initiate aggression (Kleiman 1979; Inglett *et al.* 1989).

As well as investing in the pair relationship, callitrichid breeders may need to invest in relationships with older offspring or other helpers in order to ensure their assistance. If parents *need* help in order to reproduce successfully, they would be expected to invest more time in establishing affilative relationships with offspring before birth; and those individuals who had had previously close relationships with their parents would subsequently be expected to carry more than those who did not. Alternatively, if helping is merely equivalent to "payment" to parents for "permission" to remain on their territory (Gaston 1978; McGrew & McLuckie 1986), parents might not be expected to invest a great deal in offspring.

Breeding cotton-top tamarins in this study invested relatively more time in relationships with offspring as group size increased. Established pairs in Savage *et al.*'s (1988) study also began to direct more attention towards their offspring. These results provide some support for the idea that it is beneficial for cotton-top tamarin parents to keep helpers, but considerably more research is required in this area, and population or species differences in the extent to which helpers are necessary may influence the pattern of relationships. Evans (1986), for example, found that captive breeding pairs of *Callithrix jacchus* spent more time in contact with and grooming their youngest offspring most, but received more grooming from their oldest offspring.

Even in communally rearing species, however, parental tolerance is likely to have limits. Callitrichids generally appear to be able to rear at most two infants from each litter. Helpers may allow a female to reduce her interbirth interval and have two litters a year, but although this may occur in marmosets it appears to be unusual in tamarins, possibly as a result of seasonal food shortages (e.g. Goldizen *et al*. 1988; Ferrari 1988). Furthermore, once breeding males are in a position to give up all infant care duties, and breeding females can limit their investment solely to suckling, their costs can be reduced no further. A ceiling effect is therefore likely, beyond which no further care is beneficial to breeders. At this point, surplus group members might be expected to leave, particularly if their major source of benefit is derived from inclusive fitness. If it would still be beneficial to the helper to stay, however, conflict between breeders and helpers would be expected, and as a result surplus individuals may be forced out ("evicted"). Peripheralisation of subordinate group members has been observed in wild *Cebuella pygmaea* (Soini 1988), and apparently forced dispersal in wild *Leontopithecus rosalia* (Baker 1987). It is of interest that in Stirling, evictions tend to occur only once a group has reached a certain size (mean = 9 individuals; K. Moore, unpublished data), although it is difficult to generalise from this as in captive situations overcrowding could also be a factor.

Several predictions can be made about the degree of tolerance that breeders should show towards helpers:

(1) As groups increase in size as offspring reach adulthood, they will become less stable as the net benefit provided by additional helpers reaches an asymptote.

(2) Maximum group size will be based on the trade-off between the benefits that can be derived from tolerating helpers and the costs of sharing a territory, though this will vary with such factors as habitat quality. For example, Reyer (1980) found that breeding pied kingfishers (*Ceryle rudis*) tolerated non-offspring helpers (as opposed to helpers who were older offspring) only in poor environmental conditions.

(3) "Extra" males will be better tolerated than extra females, as each female is a potential draw on the group's infant care resources.

Flexibility: variation between species, populations, and groups

As more accurate data become available on the reproductive parameters of callitrichids it is becoming clear that their reproductive strategies appear to be characterised by a considerable degree of flexibility. The purpose of this section is to consider some possible explanations for this variability.

Interspecific variation

There are some notable differences in the rearing strategies of different callitrichid species. The most obvious of these is the apparently exclusively maternal care shown by *Leontopithecus* during the first two to three weeks after birth (Hoage 1978), compared to other tamarins and the marmosets, in which carrying by other family members is common from the first day (see chapter 3). Attempts have been made to explain these different patterns using the ratio between litter weight at birth and maternal weight as an indicator of the energetic burden that females must bear. For example, Kleiman (1977) suggests that there is a correlation between the weight ratio and the onset of paternal care in callitrichids. Table 8.1 lists adult weights, infant weights at birth, approximate litter/maternal weight ratios, and gestation periods for members of each of the four callitrichid genera, and for the Goeldi's monkey. Amongst the callitrichid examples, *Leontopithecus rosalia* has the lowest weight ratio, and therefore mothers may be able to afford to carry for longer; however, it is not markedly lower than those of the other species. Furthermore, analysis of litter/maternal weight ratios is extremely difficult for several reasons. First, data on weights of wild populations are lacking; for neonatal infants in particular there are almost no data. Consequently, most estimates have been made from captive populations, and the relevance of these is questionable. Lastly, weights of individual infants vary considerably according to litter size (e.g. Wolfe *et al.* 1975), and therefore it is difficult to determine a "mean" neonatal weight. It is therefore difficult to explain the very different pattern of infant care in *L. rosalia* compared to other callitrichids solely on the basis of weight ratios.

However, *L. rosalia* also has by far the shortest gestation period among callitrichid species so far studied. In combination with the weight ratio, this suggests that female lion tamarins may be investing less during pregnancy than other tamarins and marmosets, and can therefore afford to invest more post-partum. It may therefore be possible to develop a more sophisticated model of maternal investment to relate to the observed pattern of non-maternal care on the basis of patterns of investment both pre- and post-partum; for this, we will need accurate and complete weight data, preferably from wild populations, and also information on the energetics of reproduction.

There are several further differences between *L. rosalia* and the other callitrichid genera, which appear to tie in with a reduced need for non-maternal care: (1) there may be a lack of physiological suppression (French *et al.* 1989); (2) mother-daughter conflict may be more frequent than in other species (Inglett *et al.* 1989); (3) aggression appears to occur at smaller group sizes in captivity (Inglett *et al.* 1989), and only in this species has forced emigration been observed in the wild (Baker 1987); (4) successful polygyny has been seen in the wild (A. Baker, cited in French *et al.* 1989); and (8) sexual dimorphism in canine size has been reported, with males having larger canines than females (Dietz & Kleiman 1987).

TABLE 8.1. Reproductive and physical parameters of selected species of callitrichid and the Goeldi's monkey.

Species	*Average adult weight (g)*[a]	*Average weight of single infant (g)*[a]	*Litter/ maternal weight ratio*[b]	*Gestation period (days)*[c]	*Sources*
Cebuella pygmaea	119 (W)	13-15 (W)	0.22-0.25	137 (B)	1
Callithrix jacchus	300 (C)	30 (C)	0.21	148 (H)	2,3,4,5
Saguinus oedipus	410 (W) 450-550 (C)	45-50 (C)	0.16-0.24	184 (H)	6,7,8,9, 10
Leontopithecus rosalia	710 (C)	60 (C)	0.17	128 (B)	11,12
Callimico goeldii	570 (C)	44 (C)	0.08	149 (H)	13,14,15

a. W = based on data from wild-caught animals; C = based on data from captive animals.

b. Based on a modal litter size of two for callitrichids, and one for *Callimico*. Approximate values only (see text).

c. B = based on observations of sexual behaviour; H = based on hormonal analysis.

Sources:

1. Soini 1988; 2. Hearn & Lunn 1975; 3. Lunn 1983; 4. Abbott & Hearn 1978; 5. Küster 1983; 6. Ziegler *et al*. 1987*a*; 7. Dronzek *et al*. 1986; 8. Pook 1976; 9. this study (see chapters 2 and 5); 10. Neyman 1980; 11. Kleiman 1978; 12. Hoage 1982; 13. Ziegler *et al*. 1989; 14. Pook 1978; 15. Pook 1975.

Why do mothers in *L. rosalia* not just go on carrying past week 3? Possibly by this age, the infants' weight combined with the steadily increasing costs of lactation (see chapter 6) means she cannot continue alone. Therefore, although successful polygyny may be possible, presumably it is still advantageous for a female to be monogamous and therefore competition between females may be intense. As a result a breeding female is likely to attempt to evict rivals.

Saguinus geoffroyi also appears to be anomalous in some respects, notably in the extremely high level of inter-group movements found in wild populations, and in the fact that most wild groups appear able to rear only one infant at a time (Dawson 1976, 1978; Rasmussen 1989). It is possible that these two features are related: a high level of inter-group movement may lead to decreased paternity confidence on the part of males, and therefore to less paternal investment.

The highest neonatal-maternal weight ratio is shown by *Cebuella*. Soini (1988) has found that recently-formed pairs of *Cebuella* have relatively low reproductive success, and incipient or established couples may be accompanied by a third individual, sometimes a younger sib of one of the adults. *Cebuella* groups also tend to have fewer adults than other callitrichids, and more younger individuals. Soini (1988) also noticed that wild *Cebuella* infants were carried continuously only for the first one or two weeks of life; they were then left in specific, relatively protected places for increasing periods. This is reminiscent of "parking" in prosimians, and could perhaps be explained by the relatively high infant weight in comparison with that of other species.

It is not always easy to develop convincing explanations for species differences. Tardif & Harrison (1986) and Tardif *et al*. (1986*b*) have argued that the fact that since marmoset infants are carried for a shorter period of time than tamarins, rearing infants may be less energetically demanding for marmosets. Gum-feeding may mean that marmoset groups have less need to move far and as a result can reject their infants earlier. Tardif & Harrison (1986) also argue that the small range of neonatal/maternal weight ratios is not sufficient to explain these different rearing strategies. Nevertheless, it does appear (table 8.1) that weight ratios are higher in marmosets, and as yet we have no information on how an increase in relative litter weight is reflected in the energetic costs of carrying. It could therefore also be argued that marmoset infants are relatively *more* expensive to rear, and that this is the reason for earlier rejection. In the present study, and in that by Tardif *et al.* (1986*b*), it was clear that cotton-top tamarin infants, unlike common marmosets, initiate their own independence to begin with, rather than being rejected by caretakers. This suggests that caretakers are willing to provide more care than infants seek, at least in the early stages of the development of infant independence, lending some support to the view that rearing *is* more energetically expensive for marmosets.

Interspecific variation in mating and rearing systems is also a feature of one of the other mammalian groups in which communal rearing is common, the Canidae (Moehlman 1986, 1989). Small canid species have a tendency towards polygyny and often have female helpers (e.g. red foxes); medium-size canids tend to be strictly monogamous and have equal numbers of helpers of each sex; while large species are monogamous and occasionally polyandrous (e.g. African wild dogs), with a higher proportion of male helpers. The reason for this probably lies in the fact that larger canids tend to have relatively more altricial young, leading to the need for more postpartum investment. If the available care were to be shared among more than one female's offspring, successful rearing would be unlikely, and so females in these species could not afford to tolerate polygyny.

In conclusion, given that callitrichid species differ from one another in many ways (e.g. dispersal characteristics, inter-birth interval, number of infants reared per litter, rearing system, range size, group size, and so on) it is highly unlikely to be useful to attempt to apply a single characterisation to the reproductive strategies of all callitrichids.

Intraspecific flexibility

Kleiman (1977, p. 40) has pointed out that "a species may stray from what is considered to be its modal social system in an optimum habitat. Thus, some species considered to be basically monogamous might, under some conditions, exhibit polygamy". Brown (1987) has also pointed out that variable mating systems amongst communally rearing birds are common. Davies (1985), for example, observed monogamous, polyandrous, polygynous and polygynandrous groups in a single population of dunnocks (*Prunella modularis*). Strahl & Brown (1987) have reported geographic variation in the communal rearing system of the Mexican jay (*Aphelocoma ultramarina*), with one population exhibiting plural breeding, and another singular breeding. Moehlman (1989) has described several species of canid in which mating and rearing systems vary, often influenced by ecological conditions: for example, African wild dogs may be monogamous or polyandrous; red foxes (Macdonald 1979) may be monogamous or polygynous. Even in some species of gibbon and Old World monkeys in which monogamy has been reported, there is evidence of polygyny in some populations (e.g. gibbons: Srikosamatara & Brockelman 1987; *Cercopithecus neglectus*: Brennan 1985, Leutenegger & Lubach 1987; *Simias concolor*: Watanabe 1981).

Several authors (Garber *et al.* 1984; Rylands 1985; Goldizen 1987*a*) have recently begun to emphasise the flexibility of callitrichid social organisation. Intraspecific variability can be understood if it represents decisions taken according to the prevailing conditions. Monogamous and polyandrous mating systems, perhaps even polygyny, and associated rearing systems could be seen as part of a continuum of strategies available to a callitrichid monkey, the choice of which will depend on its circumstances, such as how many helpers are needed to rear twins successfully, and how many helpers are available. Variation across or within species, either in the energetic costs of feeding and carrying infants, or in activity budgets due to variations in habitat and diet, could affect the number of helpers needed (Goldizen 1987*a*). This could affect the probability of each type of system occurring in a given population and the frequency with which it does so. Many of these possibilities have already been considered in this discussion, and it is easy to see how flexibility could arise within species, populations, groups or individuals over time. The probability of intraspecific variation renders even more questionable the validity of applying a single definition to an entire family of primates.

Callimico

It is interesting to compare the regularly-twinning callitrichids with their closest relative, *Callimico goeldii*, the Goeldi's monkey. The only member of the family Callimiconidae, *Callimico*, like the callitrichids, has often been considered to be monogamous. Very little is known of the species in the wild: it appears to be sparsely distributed (Moynihan 1976; Terborgh 1983), occurring at very low densities in localised areas, frequently with wide separation between localities in which it is found (Heltne *et al.* 1981; Pook & Pook 1981). Group sizes are often reported to be small (e.g. 2-3: Terborgh 1983; less than five: Izawa 1979, cited in Heltne *et al.* 1981), but larger groups have been seen: Pook & Pook (1981) estimated that group size averaged about six, while their main study group comprised eight individuals.

Although approximately the same size as a tamarin (adult weight 570g, see table 8.1), the Goeldi's monkey typically produces only a single infant. Altmann *et al.* (1988) recorded four twin litters (2%) in 192 pregnancies in one captive colony; however, in no case was more than one infant successfully reared by its parents, even when the parents were experienced and competent. A recent series of papers has revealed that the endocrinology of reproduction in captive *Callimico* is very similar to that of callitrichids. Ovarian cycle length is about 24-28 days (Carroll *et al.* 1989; Christen *et al.* 1989), and a postpartum ovulation occurs within a month of birth which usually (five out of six cycles recorded) results in conception (Ziegler *et al.* 1989). Oestrus is accompanied by a marked increase in sexual behaviour (Lorenz 1972; Heltne *et al.* 1981; Masataka 1981*a*). Therefore, like all the callitrichids so far studied, *Callimico* females may be simultaneously pregnant and lactating. An understanding of *Callimico*'s social organisation might therefore provide a model of how monogamy could have arisen in the related callitrichids before the development of twinning.

Why does *Callimico* not twin? Altmann *et al.* (1988) have suggested that a *Callimico* mother producing twins would at the time of birth already have invested more than a tamarin mother, as neonate size and gestation are greater in *Callimico*. However, this does not appear to be the case: firstly, Pook (1975) reported that captive-born *Callimico* infants weighed about 44g at birth - larger than marmosets, but about the same size as tamarin infants (see table 8.1). Furthermore, a recent paper by Ziegler *et al.* (1989) has shown that gestation in *Callimico* is about 149 days, a figure which, although greater than *Leontopithecus* (Kleiman 1978*a*), is very similar to that of common marmosets (Hearn & Lunn 1975), and substantially shorter than that of cotton-top tamarins (Ziegler *et al*. 1987*a*) (see table 8.1).

An additional factor proposed by Altmann *et al*. (1988) is that since a *Callimico* mother cares for her infant exclusively for the first few weeks, the additional nutritional stress may be intolerable even in captivity. As in *L. rosalia* (Hoage 1978), *Callimico* mothers do all the infant carrying until infants reach the age of 2-3 weeks, both in captivity (Heltne *et al*. 1973, 1981; Pook 1975, 1978; Carroll 1987*b*), and in the wild (a provisioned group studied by Masataka (1981*a*)). However, since other marmosets and tamarins have developed early non-maternal care, and *Callimico* fathers do carry their offspring for considerable periods after infants reach the age of about three weeks, there seems no reason why *Callimico* should not have adopted a similar rearing strategy and thus been able to take advantage of twinning if it occurred.

We must therefore look elsewhere for an explanation of the differences between *Callimico* and the callitrichids. Two field studies have provided evidence which, although not conclusive, suggest that Goeldi's monkeys may adopt polygyny under some circumstances. Masataka (1981*a, b*) saw two females in one group produce infants about one month apart. The breeding male mated with each female during her post-partum period. The two breeding females, along with other group members, helped to take care of one anothers' infants. Although this group was provisioned, and therefore may have represented a situation in which two females could occupy the same area without deleterious competition over resources, Masataka (1981*a*) also observed a wild (non-provisioned) group with two infants apparently born about the same time. In addition, Pook & Pook's (1981) study group contained two immature individuals about 12 months old. This might suggest that more than one female was breeding, although it could also be explained by immigration.

Following from these observations, Carroll (1988) has predicted that female *Callimico* should be more tolerant of other females, and there is some evidence of this in captivity. Carroll (1987*a*, 1988) studied three one-male/two-female trios of *Callimico* in captivity. In each case, the females were unrelated, and were about 1-5 months apart in age. Two trios were stable for almost a year, and in these groups both females conceived. In one, the females gave birth about a month apart, and both infants were successfully reared. In the second, the females gave birth three months apart, but both infants died, one apparently killed during fighting between the females. In the remaining trio, one female was acyclic; this female lost the fight that resulted in the break-up of the trio after only six weeks. The remaining trios were also eventually broken up following aggression between the females. Although the stability of these groups and successful reproduction in one is in marked contrast to results from both wild and captive callitrichids groups with more than one breeding female (Price & McGrew, in press *b*; see also chapters 1 and 7), the male in each group showed a much closer association with one female, and the females interacted little.

The possibility of polygyny, the lack of twinning, and the reduced role of older offspring in infant care suggest that the energetic costs of infant care in *Callimico* are likely to be less than in callitrichids, and therefore that helpers are not required to the same extent. Comparative studies are therefore essential to understand the different reproductive strategies of *Callimico* and callitrichids. In a discussion of *Callimico* rearing systems compared to callitrichids, Pook (1978) suggested that since all species with marked paternal care are monogamous, paternal care might be the *result* of the adoption of a system that tended towards monogamy, rather than have evolved to meet a twinning female's need for help. Twinning could evolve once male care was established. Pook suggested that one possible reason why *Callimico* could not adopt twinning was if the male could not help until week 3, but there is no obvious reason *why* males could not help from birth onwards, however.

Carroll (1988) has suggested that more effective exploitation of the territory and enhanced predator avoidance may mean that a small group with more than one breeding female may be more successful than a single pair. Pook & Pook (1981) reported that intergroup encounters were infrequent, and therefore that opportunities for sub-adults to meet potential mates were limited. As a result, multi-female groups may be advantageous. So, if polygyny was an advantage in some circumstances, male parental investment would be less likely, and therefore twinning would not be favoured.

Testing the predictions

In order to investigate adequately the factors influencing callitrichid reproductive strategies, nothing can take the place of systematic, long-term field studies in which individuals can be followed as they move between groups and begin to breed. To fully understand relationships in multi-male groups of callitrichids, three lines of evidence will be needed in future studies: (i) detailed behavioural observations to determine sexual access and status relationships; (ii) hormonal data so that mating can be related to probability of conception; and (iii) genetic analyses to determine paternity. Until recently, techniques were not available for accurately determining paternity in callitrichids, because of the mixing of twins' blood supply *in utero* (Wislocki 1932). The recent development of DNA fingerprinting techniques promises to considerably advance understanding in this area (Burke 1989). Such techniques have already been successfully applied to birds with variable mating systems (e.g. Burke *et al.* 1989). Recently, the results of preliminary studies on captive marmosets have been published (Dixson *et al.* 1988), and analysis of samples from wild *Callithrix jacchus* is underway (A. Dixson, pers. comm.).

Evidence of marrow chimerism has been found in *Cebuella, Callithrix jacchus, Saguinus oedipus, S. nigricollis* and *L. rosalia* (Benirschke & Brownhill 1962; Soares *et al.* 1982), but there is apparently no chimerism in other tissues (Benirschke & Brownhill 1962). The fact that chimerism is confined to blood provides an easy means of identifying twins whilst being able to use other tissues to detect other relationships: DNA fingerprints obtained from the blood of twins are virtually identical. It will therefore be possible to tell whether or not individuals of the same age are from the same litter. Samples of other tissue (e.g. skin biopsies) will allow the separation of twins and the possibility of detecting multiple paternity in the same or different litters. These methods will be very important for understanding relationships within groups: for example, whether siblings migrate together, whether polyandrous males are related, and so on.

It might also be possible to test some ideas in captivity. Examples of this include the work of Epple (1972) and Kleiman (1978) on polyandrous trios of saddle-back and golden lion tamarins, and McGrew & McLuckie's (1986) simulation of dispersal in cotton-top tamarins. In the laboratory it is easier to investigate sexual behaviour in relation to oestrus and conception. For example, concurrent hormonal and behavioural sampling of polyandrous trios should reveal if multiple paternity could occur (confirmed by DNA fingerprinting), and if so, how it works. Systematic investigation should unravel the possible factors that influence the likelihood and stability of non-monogamous groups: status, group composition, emigration and immigration, effects of group size and sex ratio on reproductive success and stability. The energetic costs of infant care need to be specified in order to refine models of the costs and benefits of communal rearing. Thus, along with more extensive data on the strategies used by wild marmosets and tamarins, captive studies can make important contributions to the understanding of callitrichid mating, breeding and rearing systems.

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Appendix A. Changes in the compositions of the cotton-top tamarin groups at Stirling during the study period (January 1987-August 1989).

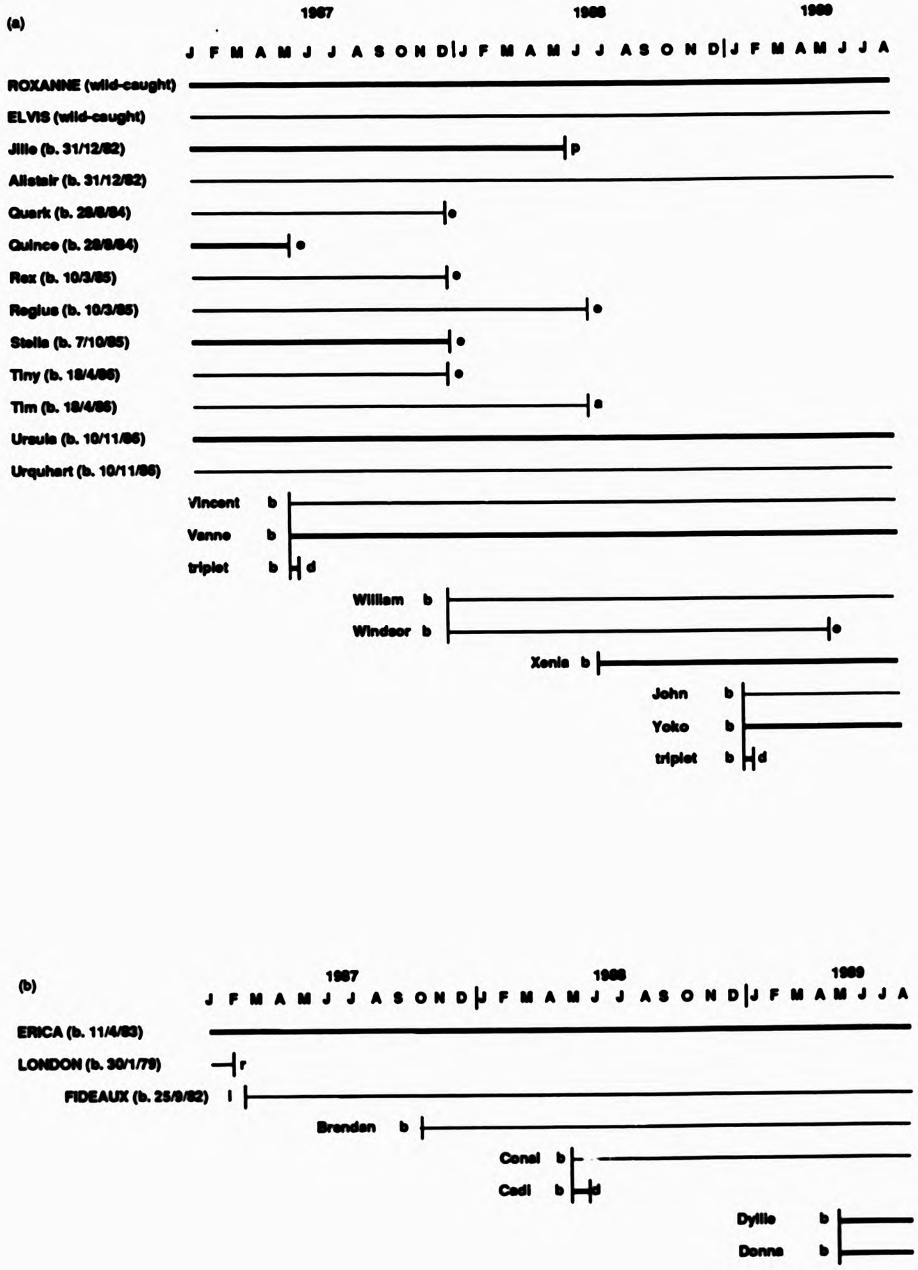
(a) Roxanne's group
(b) Erica's group
(c) Elsa's group
(d) Delaware's group
(e) Sioux's group/Shoshone's group
(f) Hopi's group
(g) Genevieve's group
(h) Pixie's group/Jille's group
(i) Alpha's group
(j) Viva's group

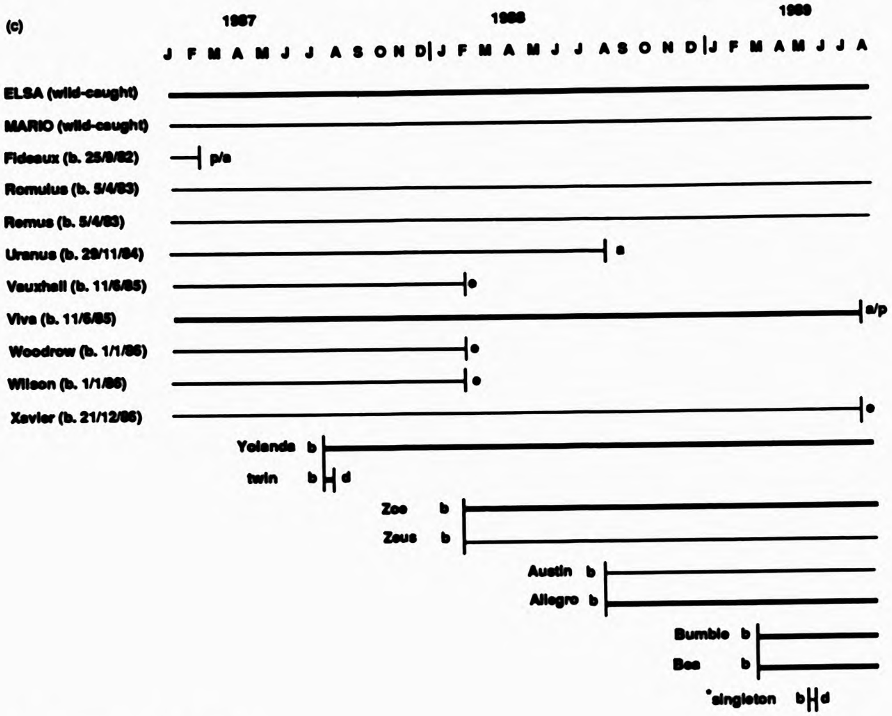
Key

Females are represented by broad lines, males by narrow lines. Names in capitals indicate breeding individuals.

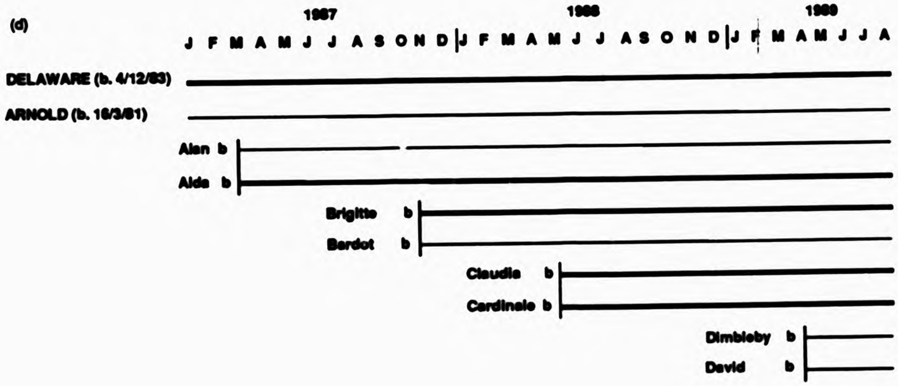
────	present in group
├───	arrives in group
───┤	leaves group
├─── ├───	siblings from same litter

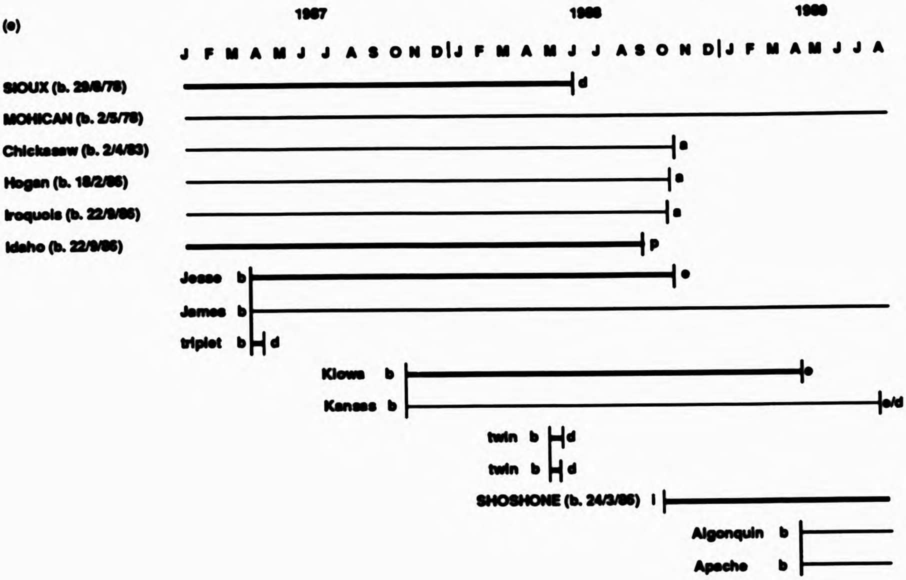
b	born
d	died
i	introduced into group as adult
p	removed for pairing
e	evicted after aggression from other family members(s)
a	removed after aggression towards other family members(s)
r	removed for any other reason

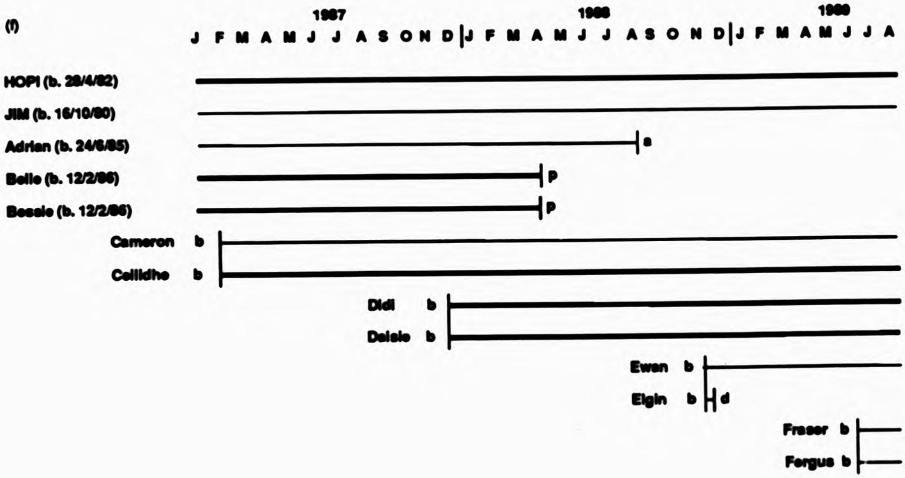
(a)
1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
ROXANNE (wild-caught)
ELVIS (wild-caught)
Jille (b. 31/12/82)
p
Alistair (b. 31/12/82)
Quark (b. 28/8/84)
Quince (b. 28/8/84)
Rex (b. 10/3/85)
Regius (b. 10/3/85)
Stella (b. 7/10/85)
Tiny (b. 18/4/86)
Tim (b. 18/4/86)
Ursula (b. 10/11/86)
Urquhart (b. 10/11/86)
Vincent b
Vanne b
triplet b d
William b
Windsor b
Xenia b
John b
Yoko b
triplet b d
(b)
1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
ERICA (b. 11/4/83)
LONDON (b. 30/1/79) r
FIDEAUX (b. 25/9/82) i
Brendan b
Conal b
Cadi b d
Dyllie b
Donna b



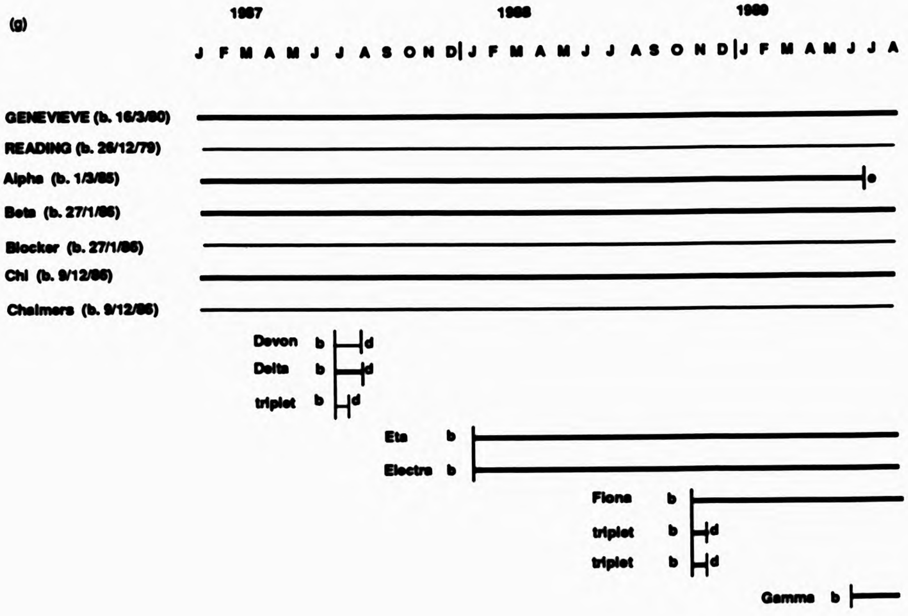
* *Singleton infant born to Viva*



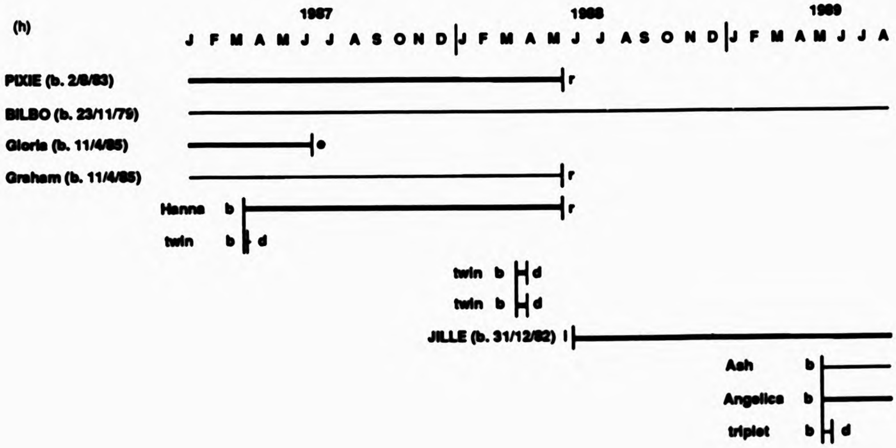

(e)
1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
SIOUX (b. 29/8/78)
d
MOHICAN (b. 2/5/78)
Chickasaw (b. 2/4/83)
e
Hogan (b. 18/2/86)
e
Iroquois (b. 22/9/86)
e
Idaho (b. 22/9/86)
p
Jesse b
e
James b
triplet b
d
Kiowa b
e
Kansas b
e/d
twin b
d
twin b
d
SHOSHONE (b. 24/3/86) I
Algonquin b
Apache b


(f)
1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
HOPI (b. 28/4/82)
JIM (b. 16/10/80)
Adrian (b. 24/6/85)
e
Belle (b. 12/2/86)
p
Bessie (b. 12/2/86)
p
Cameron b
Ceilidhe b
Didi b
Daisie b
Ewan b
Elgin b
d
Fraser b
Fergus b

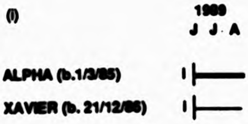
(g)


1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
GENEVIEVE (b. 16/3/80)
READING (b. 26/12/79)
Alpha (b. 1/3/85)
e
Beta (b. 27/1/86)
Blocker (b. 27/1/86)
Chi (b. 9/12/86)
Chalmers (b. 9/12/86)
Devon b d
Delta b d
triplet b d
Eta b
Electra b
Fiona b
triplet b d
triplet b d
Gamma b

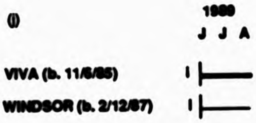
(h)


1987
1988
1989
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
PIXIE (b. 2/8/83)
r
BILBO (b. 23/11/79)
Gloria (b. 11/4/85)
e
Graham (b. 11/4/85)
r
Hanna b
r
twin b d
twin b d
twin b d
JILLE (b. 31/12/82) I
Ash b
Angelica b
triplet b d

(i)


1989
J J A
ALPHA (b.1/3/85)
I
XAVIER (b. 21/12/86)
I

(j)


1989
J J A
VIVA (b. 11/6/85)
I
WINDSOR (b. 2/12/87)
I

Appendix B. Details of reliability tests

TABLE B.1. Actual scores obtained by two observers (EP and AH) for nine behavioural categories in ten adult observation sessions, and the associated coefficients of reliability (r).[1]

Subject		*Sit*	*Move*	*Feed*	*Forage*	*Groom*	*Other*	*Scratch*	*Scent mark*	*Genital rub*
		Behavioural category								
Males										
Bilbo (1)	EP	50	1	2	6	0	1	13	0	0
	AH	52	0	2	5	0	1	14	0	0
	r	0.96	0	1.00	0.83	-	1.00	0.93	-	-
Bilbo (2)	EP	33	5	15	7	0	0	4	0	0
	AH	36	5	14	5	0	0	5	0	0
	r	0.92	1.00	0.93	0.71	-	-	0.80	-	-
Fideaux	EP	32	1	10	16	0	1	3	0	0
	AH	27	1	12	20	0	0	1	0	0
	r	0.84	1.00	0.83	0.80	-	0	0.33	-	-
Graham	EP	46	0	12	2	0	0	0	0	0
	AH	43	0	13	3	0	0	0	0	0
	r	0.93	-	0.92	0.67	-	-	-	-	-
Jim	EP	56	1	0	0	0	3	0	0	0
	AH	53	1	0	0	0	3	0	0	0
	r	0.94	1.00	-	-	-	1.00	-	-	-
Females										
Pixie	EP	46	2	7	3	0	0	2	0	0
	AH	45	2	6	4	0	0	2	0	0
	r	0.98	1.00	0.86	0.75	-	-	1.00	-	-
Jille	EP	53	6	0	1	0	0	10	4	9
	AH	50	9	0	1	0	0	8	2	5
	r	0.94	0.67	-	1.00	-	-	0.80	0.50	0.55
Erica	EP	36	2	15	6	1	0	4	7	4
	AH	40	0	15	5	0	0	2	5	3
	r	0.90	0	1.00	0.83	0	-	0.50	0.71	0.75
Delaware	EP	40	2	10	4	4	0	3	0	0
	AH	39	2	8	3	4	0	3	0	0
	r	0.98	1.00	0.80	0.75	1.00	-	1.00	-	-
Hopi	EP	58	1	0	0	1	0	12	11	4
	AH	55	1	0	0	0	0	6	11	0
	r	0.95	1.00	-	-	0	-	0.50	1.00	0

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained by the two observers, and D = the difference between the two scores.

TABLE B.2. Number of agreements (A) and disagreements (D) obtained by two observers for six behavioural categories in ten adult observation sessions, and the associated coefficients of reliability (r).[1]

		Behavioural category					
Subject		*Overall activity*	*Spatial relationship*	*Approach*	*Leave*	*Groom*	*Affection*
Males							
Bilbo (1)	A	59	57	5	6	-	-
	D	1	3	3	2	-	-
	r	0.93	0.95	0.63	0.75	-	-
Bilbo (2)	A	51	59	5	4	-	-
	D	9	1	1	2	-	-
	r	0.85	0.98	0.83	0.67	-	-
Fideaux	A	49	57	14	14	-	-
	D	11	3	5	6	-	-
	r	0.82	0.95	0.74	0.70	-	-
Graham	A	57	50	8	9	1	0
	D	3	10	12	10	0	2
	r	0.95	0.83	0.40	0.47	1.00	0
Jim	A	53	46	16	16	-	-
	D	7	14	12	10	-	-
	r	0.88	0.77	0.57	0.62	-	-
Females							
Pixie	A	54	59	10	9	0	-
	D	6	1	6	7	1	-
	r	0.90	0.98	0.63	0.56	0	-
Jille	A	57	58	5	5	-	-
	D	3	2	0	0	-	-
	r	0.95	0.97	1.00	1.00	-	-
Erica	A	49	56	13	15	-	0
	D	11	4	7	5	-	2
	r	0.82	0.93	0.65	0.75	-	0
Delaware	A	52	45	17	15	6	0
	D	8	15	12	13	0	1
	r	0.97	0.75	0.59	0.54	1.00	0
Hopi	A	54	46	22	17	1	-
	D	6	14	9	16	2	-
	r	0.90	0.77	0.71	0.52	0.33	-

---

[1] Coefficients of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

TABLE B.3. Actual scores obtained by two observers (EP and KM) for five behavioural categories in four infant observation sessions, and the associated coefficients of reliability (r).[1]

					Behavioural category				
Infant	*Sex*	*Status*	*Age (weeks)*		*Number of carry bouts (focal inf)*	*Number of carry bouts (other inf)*	*Number of bouts off (focal inf)*	*Number of bouts off (other inf)*	*Number of bouts suckle (focal inf)*
Austin	Male	Twin	8	EP	2	4	2	2	1
				KM	2	4	2	2	1
				r	1.00	1.00	1.00	1.00	1.00
Allegro	Female	Twin	8	EP	5	2	5	2	0
				KM	5	2	5	2	0
				r	1.00	1.00	1.00	1.00	-
Ewan	Male	Single	4	EP	1	-	0	-	0
				KM	1	-	0	-	0
				r	1.00	-	-	-	-
Fiona	Female	Single	5	EP	6	-	0	-	2
				KM	6	-	0	-	2
				r	1.00	-	-	-	1.00

---

1. Coefficents of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained by the two observers, and D = the difference between the two scores.

TABLE B.4. Number of agreements (A) and disagreements (D) obtained by two observers for five behavioural categories in four infant observation sessions, and the associated coefficients of reliability (r).[1]

					Behavioural category				
Infant	*Sex*	*Status*	*Age (weeks)*		*Carrier of focal infant*	*Carrier of other infant*	*Suckle*	*Spatial relations (if infant off)*	*Food-sharing*
Austin	Male	Twin	8	A	117	117	37	28	-
				D	3	3	0	12	-
				r	0.98	0.98	1.00	0.70	-
Allegro	Female	Twin	8	A	119	120	0	74	8
				D	1	0	0	27	3
				r	0.99	1.00	-	0.73	0.73
Ewan	Male	Single	4	A	120	-	0	-	-
				D	0	-	0	-	-
				r	1.00	-	-	-	-
Fiona	Female	Single	5	A	120	-	16	-	-
				D	0	-	0	-	-
				r	1.00	-	1.00	-	-

---

1. Coefficents of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

TABLE B.5. Actual scores obtained by one observer (EP) for nine behavioural categories in repeated viewings (sessions 1 and 2) of eight adult observation sessions, and the associated coefficients of reliability (r).[1]

Subject		*Sit*	*Move*	*Feed*	*Forage*	*Groom*	*Other*	*Scratch*	*Scent mark*	*Genital rub*
		Behavioural category								
Males										
Bilbo	1	59	1	0	0	0	0	6	0	0
	2	59	1	0	0	0	0	7	0	0
	r	1.00	1.00	-	-	-	-	0.86	-	-
Fideaux	1	44	3	0	13	0	0	13	0	0
	2	46	3	0	11	0	0	14	0	0
	r	0.96	1.00	-	0.85	-	-	0.93	-	-
Arnold	1	44	3	4	8	1	0	21	0	0
	2	45	4	4	6	1	0	20	0	0
	r	0.98	0.75	1.00	0.75	1.00	-	0.95	-	-
Jim	1	41	5	2	6	5	1	6	2	0
	2	42	5	2	5	5	1	6	2	0
	r	0.98	1.00	1.00	0.83	1.00	1.00	1.00	1.00	-
Females										
Jille	1	14	9	34	3	0	0	3	3	10
	2	14	8	35	3	0	0	2	3	9
	r	1.00	0.89	0.97	1.00	-	-	0.67	1.00	0.90
Erica	1	49	6	0	2	1	2	8	0	1
	2	48	7	0	2	1	2	8	0	1
	r	0.698	0.86	-	1.00	1.00	1.00	1.00	-	1.00
Delaware	1	48	3	6	2	0	1	1	4	0
	2	46	3	8	2	0	1	1	3	0
	r	0.96	1.00	0.75	1.00	-	1.00	1.00	0.75	-
Hopi	1	35	4	8	12	0	1	1	4	4
	2	33	6	8	12	0	1	1	4	6
	r	0.94	0.67	1.00	1.00	-	1.00	1.00	1.00	0.67

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1. Coefficients of reliability calculated from the formula A/(A+D), where A = the lower of the two scores obtained by the two observers, and D = the difference between the two scores.

TABLE B.6. Number of agreements (A) and disagreements (D) obtained by one observer for six behavioural categories in repeated viewings of eight adult observation sessions, and the associated coefficients of reliability (r).[1]

		Behavioural category					
Subject		*Overall activity*	*Spatial relationship*	*Approach*	*Leave*	*Groom*	*Affection*
Males							
Bilbo	A	60	57	3	3	-	1
	D	0	3	1	1	-	0
	r	1.00	0.95	0.75	0.75	-	1.00
Fideaux	A	57	59	7	7	-	-
	D	3	1	0	0	-	-
	r	0.95	0.98	1.00	1.00	-	-
Arnold	A	59	57	14	15	4	0
	D	1	3	1	0	1	3
	r	0.98	0.95	0.93	1.00	0.80	0
Jim	A	57	55	17	17	10	-
	D	3	5	1	1	1	-
	r	0.95	0.92	0.94	0.94	0.91	-
Females							
Jille	A	59	60	1	1	-	1
	D	1	0	0	0	-	0
	r	0.98	1.00	1.00	1.00	-	1.00
Erica	A	56	60	10	10	2	-
	D	4	0	1	1	0	-
	r	0.93	1.00	0.91	0.91	1.00	-
Delaware	A	58	49	21	21	4	1
	D	2	11	7	8	0	0
	r	0.97	0.82	0.75	0.72	1.00	1.00
Hopi	A	58	60	8	8	-	-
	D	2	0	3	3	-	-
	r	0.97	1.00	0.73	0.73	-	-

---

1. Coefficients of reliability calculated from the formula A/(A+D), where A = the number of agreements obtained on individual occurrences, and D = the number of disagreements.

Appendix C. Results of statistical tests in chapters 3 and 4.

ANOVAs and ANCOVAs unless otherwise stated
Results prefixed by • indicate results of ANCOVA

CHAPTER 3

Sample sizes

	Singletons	*Twins*
Mothers	7	7
Fathers	7	7
Adult sons	6	10
Adult daughters	3	4
Sub-adult sons	7	8
Sub-adult daughters	5	4
Juvenile sons	4	3
Juvenile daughters	4	6

Carrying index	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.00	1,76	0.986	
Age class of caretaker	13.96	3,76	0.000	
Litter size	4.00	1,76	0.049	
Sex x age class	1.87	3,76	0.142	
Sex x litter size	0.31	1,76	0.580	
Age class x litter size	1.63	3,76	0.190	
Sex x age class x litter size	0.07	3,76	0.977	
• Group size	23.60	1,75	0.000	-32.87
• Sex of caretaker	0.14	1,75	0.711	
• Age class of caretaker	13.41	3,75	0.000	
• Litter size	7.56	1,75	0.008	
• Sex x age class	2.63	3,75	0.057	
• Sex x litter size	0.44	1,75	0.508	
• Age class x litter size	2.21	3,75	0.094	
• Sex x age class x litter size	0.02	3,75	0.995	

Frequency of positive responses to infant begs	*d.f.*	*p*	*Regression coefficient*	
Sex of caretaker	3.58	1,76	0.062	
Age class of caretaker	10.68	3,76	0.000	
Litter size	13.27	1,76	0.0005	
Sex x age class	1.70	3,76	0.175	
Sex x litter size	0.00	1,76	0.982	
Age class x litter size	0.27	3,76	0.850	
Sex x age class x litter size	1.46	3,76	0.231	
• *Group size*	1.16	1,75	0.284	-0.2286
• *Sex of caretaker*	3.87	1,75	0.053	
• *Age class of caretaker*	8.51	3,75	0.0001	
• *Litter size*	13.96	1,75	0.0004	
• *Sex x age class*	1.64	3,75	0.187	
• *Sex x litter size*	0.00	1,75	0.988	
• *Age class x litter size*	0.25	3,75	0.860	
• *Sex x age class x litter size*	1.40	3,75	0.250	

Frequency of resistance to infant begs	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.34	1,76	0.564	
Age class of caretaker	5.58	3,76	0.002	
Litter size	14.57	1,76	0.0003	
Sex x age class	1.19	3,76	0.318	
Sex x litter size	0.45	1,76	0.507	
Age class x litter size	0.22	3,76	0.879	
Sex x age class x litter size	1.33	3,76	0.272	
• *Group size*	9.24	1,75	0.003	-0.5035
• *Sex of caretaker*	0.69	1,75	0.410	
• *Age class of caretaker*	2.82	3,75	0.045	
• *Litter size*	18.50	1,75	0.0001	
• *Sex x age class*	1.48	3,75	0.228	
• *Sex x litter size*	0.46	1,75	0.498	
• *Age class x litter size*	0.22	3,75	0.884	
• *Sex x age class x litter size*	1.49	3,75	0.225	

Total number of food items shared	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	2.39	1,76	0.126	
Age class of caretaker	12.37	3,76	0.000	
Litter size	17.87	1,76	0.0001	
Sex x age class	1.45	3,76	0.235	
Sex x litter size	0.01	1,76	0.915	
Age class x litter size	0.64	3,76	0.593	
Sex x age class x litter size	2.08	3,76	0.110	
• *Group size*	2.25	1,75	0.138	-0.3440
• *Sex of caretaker*	2.77	1,75	0.100	
• *Age class of caretaker*	9.89	3,75	0.000	
• *Litter size*	19.27	1,75	0.000	
• *Sex x age class*	1.38	3,75	0.257	
• *Sex x litter size*	0.01	1,75	0.923	
• *Age class x litter size*	0.59	3,75	0.622	
• *Sex x age class x litter size*	2.03	3,75	0.116	

Proportion of positive responses to infant begs	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	3.77	1,76	0.056	
Age class of caretaker	5.72	3,76	0.001	
Litter size	0.12	1,76	0.731	
Sex x age class	1.11	3,76	0.352	
Sex x litter size	1.16	1,76	0.284	
Age class x litter size	0.36	3,76	0.784	
Sex x age class x litter size	0.65	3,76	0.582	
• *Group size*	3.66	1,75	0.060	2.0125
• *Sex of caretaker*	3.44	1,75	0.068	
• *Age class of caretaker*	6.49	3,75	0.001	
• *Litter size*	0.02	1,75	0.888	
• *Sex x age class*	1.23	3,75	0.306	
• *Sex x litter size*	1.28	1,75	0.262	
• *Age class x litter size*	0.44	3,75	0.722	
• *Sex x age class x litter size*	0.84	3,75	0.474	

Frequency of offers

Effects of litter size (Mann-Whitney U-test)	$U = 843.5$	$z = -1.764$	$p = 0.078$
Effects of age class (Kruskal-Wallis one-way ANOVA)	$\chi^2 = 18.99$	d.f. = 3	$p = 0.0003$

Sex differences (Mann-Whitney U-tests)

Parents:	$U = 88$	$z = -0.482$	$p = 0.630$
Adults:	$U = 41.5$	$z = -1.022$	$p = 0.307$
Sub-adults:	$U = 66$	$z = -0.107$	$p = 0.915$
Juveniles:	$U = 28.5$	$z = -0.853$	$p = 0.394$

Proportion of items shared that were offers

Effects of litter size (Mann-Whitney U-test)	$U = 716$	$z = -1.790$	$p = 0.073$
Effects of age class (Kruskal-Wallis one-way ANOVA)	$\chi^2 = 9.35$	d.f. = 3	$p = 0.025$

Sex differences (Mann-Whitney U-tests)

Parents:	$U = 82$	$z = -0.739$	$p = 0.460$
Adults:	$U = 20$	$z = -2.138$	$p = 0.032$
Sub-adults:	$U = 60.5$	$z = -0.185$	$p = 0.853$
Juveniles:	$U = 17.5$	$z = -0.448$	$p = 0.654$

CHAPTER 4

Measures of transfers according to sex and status of infant

Male singletons: n = 3; Female singletons: n = 4; Male twins: n = 6; Female twins: n = 8

(a) Total number of transfers	*F*	*d.f.*	*p*	*Regression coefficient*
Sex	1.04	1,17	0.323	
Status	0.02	1,17	0.889	
Sex x status	1.09	1,17	0.310	
• *Group size*	8.03	1,16	0.012	20.67
• *Sex*	0.02	1,16	0.897	
• *Status*	0.53	1,16	0.476	
• *Sex x status*	0.03	1,16	0.873	

(b) No. of completed transfers	*F*	*d.f.*	*p*	*Regression coefficient*
Sex	1.29	1,17	0.272	
Status	0.05	1,17	0.828	
Sex x status	1.15	1,17	0.299	
• *Group size*	6.68	1,16	0.020	17.55
• *Sex*	0.10	1,16	0.757	
• *Status*	0.07	1,16	0.795	
• *Sex x status*	0.06	1,16	0.810	

(c) No. of attempted transfers	*F*	*d.f.*	*p*	*Regression coefficient*
Sex	0.00	1,17	0.962	
Status	3.64	1,17	0.074	
Sex x status	0.19	1,17	0.740	
• *Group size*	4.95	1,16	0.041	3.115
• *Sex*	0.70	1,16	0.415	
• *Status*	6.34	1,16	0.023	
• *Sex x status*	0.11	1,16	0.740	

(d) No. of interventions	*F*	*d.f.*	*p*	*Regression coefficient*
Sex	0.27	1,17	0.607	
Status	0.09	1,17	0.768	
Sex x status	0.19	1,17	0.671	
• *Group size*	3.03	1,16	0.101	0.854
• *Sex*	0.01	1,16	0.925	
• *Status*	0.00	1,16	0.973	
• *Sex x status*	0.09	1,16	0.764	

Effect of infant sex on behaviour of infants towards takers

Active	*F*	*d.f.*	*p*
Sex of infant	0.10	1,10	0.758
Category of caretaker	5.74	3,30	0.003
Sex x category	0.20	3,30	0.896

Passive	*F*	*d.f.*	*p*
Sex of infant	1.84	1,10	0.205
Category of caretaker	6.11	3,30	0.002
Sex x category	0.63	3,30	0.601

Resistance	*F*	*d.f.*	*p*
Sex of infant	0.29	1,10	0.604
Category of caretaker	2.49	3,30	0.079
Sex x category	0.75	3,30	0.533

Effect of infant sex on behaviour of infants towards carriers

Active	*F*	*d.f.*	*p*
Sex of infant	0.05	1,10	0.824
Category of caretaker	4.05	3,30	0.016
Sex x category	0.12	3,30	0.946

Passive	*F*	*d.f.*	*p*
Sex of infant	0.59	1,10	0.461
Category of caretaker	7.35	3,30	0.001
Sex x category	0.67	3,30	0.577

Resistance	*F*	*d.f.*	*p*
Sex of infant	0.05	1,10	0.827
Category of caretaker	5.71	3,30	0.003
Sex x category	0.28	3,30	0.837

Behaviour of carriers according to sex of infant

Active	*F*	*d.f.*	*p*
Sex of infant	0.20	1,31	0.661
Category of caretaker	9.14	3,31	0.0002
Sex x category	0.39	3,31	0.759

Passive	*F*	*d.f.*	*p*
Sex of infant	0.07	1,31	0.789
Category of caretaker	1.97	3,31	0.140
Sex x category	3.63	3,31	0.024

Resistance	*F*	*d.f.*	*p*
Sex of infant	0.00	1,31	0.999
Category of caretaker	2.62	3,31	0.068
Sex x category	1.12	3,31	0.354

Behaviour of takers according to sex of infant

Active	*F*	*d.f.*	*p*
Sex of infant	0.38	1,31	0.543
Category of caretaker	2.16	3,31	0.113
Sex x category	1.36	3,31	0.272

Passive	*F*	*d.f.*	*p*
Sex of infant	0.09	1,31	0.761
Category of caretaker	2.77	3,31	0.058
Sex x category	0.62	3,31	0.608

Resistance	*F*	*d.f.*	*p*
Sex of infant	0.19	1,31	0.664
Category of caretaker	7.10	3,31	0.001
Sex x category	0.50	3,31	0.683

Behaviour of caretakers in infant transfers

For sample sizes, see results for chapter 3

Number of transfers involved in as carrier	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.17	1,76	0.682	
Age class of caretaker	7.42	3,76	0.0002	
Litter size	5.23	1,76	0.025	
Sex x age class	3.03	3,76	0.035	
Sex x litter size	0.01	1,76	0.916	
Age class x litter size	0.49	3,76	0.688	
Sex x age class x litter size	0.41	3,76	0.747	
• *Group size*	14.20	1,75	0.0003	-2.1027
• *Sex of caretaker*	0.51	1,75	0.476	
• *Age class of caretaker*	7.53	3,75	0.0002	
• *Litter size*	4.37	1,75	0.040	
• *Sex x age class*	3.58	3,75	0.018	
• *Sex x litter size*	0.01	1,75	0.929	
• *Age class x litter size*	0.62	3,75	0.602	
• *Sex x age class x litter size*	0.43	3,75	0.730	

Proportion of completed transfers when carrier	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.88	1,76	0.352	
Age class of caretaker	1.02	3,76	0.390	
Litter size	0.29	1,76	0.590	
Sex x age class	0.21	3,76	0.887	
Sex x litter size	0.34	1,76	0.560	
Age class x litter size	1.73	3,76	0.168	
Sex x age class x litter size	1.33	3,76	0.272	
• *Group size*	0.00	1,75	0.948	0.0392
• *Sex of caretaker*	0.87	1,75	0.354	
• *Age class of caretaker*	0.95	3,75	0.420	
• *Litter size*	0.29	1,75	0.590	
• *Sex x age class*	0.21	3,75	0.889	
• *Sex x litter size*	0.34	1,75	0.563	
• *Age class x litter size*	1.70	3,75	0.174	
• *Sex x age class x litter size*	1.31	3,75	0.277	

Behaviour of carriers

Active	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	1.11	1,76	0.295	
Age class of caretaker	11.01	3,76	0.000	
Litter size	5.40	1,76	0.023	
Sex x age class	0.76	3,76	0.523	
Sex x litter size	0.00	1,76	0.974	
Age class x litter size	0.69	3,76	0.564	
Sex x age class x litter size	1.55	3,76	0.208	
• *Group size*	0.07	1,75	0.790	-0.0122
• *Sex of caretaker*	1.05	1,75	0.308	
• *Age class of caretaker*	10.34	3,75	0.000	
• *Litter size*	5.40	1,75	0.023	
• *Sex x age class*	0.76	3,75	0.520	
• *Sex x litter size*	0.00	1,75	0.973	
• *Age class x litter size*	0.68	3,75	0.568	
• *Sex x age class x litter size*	1.54	3,75	0.212	

Passive	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	1.07	1,76	0.304	
Age class of caretaker	10.11	3,76	0.000	
Litter size	4.61	1,76	0.035	
Sex x age class	0.33	3,76	0.802	
Sex x litter size	0.06	1,76	0.810	
Age class x litter size	0.37	3,76	0.772	
Sex x age class x litter size	1.87	3,76	0.142	
• *Group size*	0.01	1,75	0.914	0.0009
• *Sex of caretaker*	1.07	1,75	0.305	
• *Age class of caretaker*	9.77	3,75	0.000	
• *Litter size*	4.46	1,75	0.038	
• *Sex x age class*	0.32	3,75	0.808	
• *Sex x litter size*	0.06	1,75	0.811	
• *Age class x litter size*	0.37	3,75	0.776	
• *Sex x age class x litter size*	1.84	3,75	0.147	

Resistance	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.00	1,76	0.957	
Age class of caretaker	0.77	3,76	0.513	
Litter size	0.23	1,76	0.635	
Sex x age class	0.94	3,76	0.426	
Sex x litter size	0.31	1,76	0.580	
Age class x litter size	0.40	3,76	0.757	
Sex x age class x litter size	0.45	3,76	0.716	
• *Group size*	1.01	1,75	0.318	0.0031
• *Sex of caretaker*	0.00	1,75	0.985	
• *Age class of caretaker*	0.54	3,75	0.656	
• *Litter size*	0.33	1,75	0.567	
• *Sex x age class*	1.01	3,75	0.394	
• *Sex x litter size*	0.30	1,75	0.584	
• *Age class x litter size*	0.42	3,75	0.741	
• *Sex x age class x litter size*	0.50	3,75	0.681	

Number of transfers involved in as taker	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.06	1,76	0.811	
Age class of caretaker	10.14	3,76	0.000	
Litter size	6.98	1,76	0.010	
Sex x age class	4.04	3,76	0.010	
Sex x litter size	0.11	1,76	0.738	
Age class x litter size	1.88	3,76	0.140	
Sex x age class x litter size	0.10	3,76	0.962	
• *Group size*	10.80	1,75	0.002	-1.7094
• *Sex of caretaker*	0.00	1,75	0.987	
• *Age class of caretaker*	10.41	3,75	0.000	
• *Litter size*	6.08	1,75	0.016	
• *Sex x age class*	4.70	3,75	0.005	
• *Sex x litter size*	0.14	1,75	0.706	
• *Age class x litter size*	2.30	3,75	0.084	
• *Sex x age class x litter size*	0.13	3,75	0.939	

Proportion of completed transfers when taker	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.21	1,76	0.650	
Age class of caretaker	0.34	3,76	0.799	
Litter size	1.07	1,76	0.303	
Sex x age class	0.47	3,76	0.706	
Sex x litter size	0.13	1,76	0.724	
Age class x litter size	3.83	3,76	0.013	
Sex x age class x litter size	0.83	3,76	0.481	
• *Group size*	0.17	1,75	0.684	-0.2497
• *Sex of caretaker*	0.18	1,75	0.674	
• *Age class of caretaker*	0.37	3,75	0.778	
• *Litter size*	0.97	1,75	0.328	
• *Sex x age class*	0.47	3,75	0.705	
• *Sex x litter size*	0.12	1,75	0.727	
• *Age class x litter size*	3.77	3,75	0.014	
• *Sex x age class x litter size*	0.78	3,75	0.506	

Behaviour of takers

Active	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	1.32	1,76	0.255	
Age class of caretaker	1.15	3,76	0.335	
Litter size	0.88	1,76	0.352	
Sex x age class	0.39	3,76	0.762	
Sex x litter size	0.18	1,76	0.669	
Age class x litter size	0.31	3,76	0.817	
Sex x age class x litter size	0.36	3,76	0.783	
• *Group size*	4.14	1,75	0.045	0.0222
• *Sex of caretaker*	1.04	1,75	0.312	
• *Age class of caretaker*	1.18	3,75	0.324	
• *Litter size*	1.33	1,75	0.253	
• *Sex x age class*	0.38	3,75	0.769	
• *Sex x litter size*	0.18	1,75	0.672	
• *Age class x litter size*	0.23	3,75	0.877	
• *Sex x age class x litter size*	0.28	3,75	0.839	

Passive	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.21	1,76	0.650	
Age class of caretaker	1.36	3,76	0.261	
Litter size	0.00	1,76	0.977	
Sex x age class	0.28	3,76	0.837	
Sex x litter size	0.12	1,76	0.729	
Age class x litter size	0.83	3,76	0.479	
Sex x age class x litter size	0.26	3,76	0.853	
• *Group size*	0.83	1,75	0.364	-0.0093
• *Sex of caretaker*	0.15	1,75	0.699	
• *Age class of caretaker*	1.55	3,75	0.210	
• *Litter size*	0.01	1,75	0.905	
• *Sex x age class*	0.29	3,75	0.836	
• *Sex x litter size*	0.12	1,75	0.734	
• *Age class x litter size*	0.79	3,75	0.505	
• *Sex x age class x litter size*	0.22	3,75	0.882	

Resistance	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	2.00	1,76	0.162	
Age class of caretaker	4.44	3,76	0.006	
Litter size	3.09	1,76	0.083	
Sex x age class	0.56	3,76	0.645	
Sex x litter size	0.05	1,76	0.830	
Age class x litter size	1.08	3,76	0.364	
Sex x age class x litter size	0.38	3,76	0.770	
• *Group size*	5.32	1,75	0.024	-0.0129
• *Sex of caretaker*	1.64	1,75	0.204	
• *Age class of caretaker*	3.39	3,75	0.023	
• *Litter size*	4.11	1,75	0.046	
• *Sex x age class*	0.52	3,75	0.667	
• *Sex x litter size*	0.04	1,75	0.837	
• *Age class x litter size*	1.12	3,75	0.346	
• *Sex x age class x litter size*	0.37	3,75	0.773	

Behaviour of carriers according to the identity of the taker

Active	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	12.37	1,75	0.001	
Age class of caretaker	1.32	3,75	0.276	
Litter size	0.98	1,75	0.326	
Sex x age class	2.39	3,75	0.075	
Sex x litter size	0.13	1,75	0.715	
Age class x litter size	0.64	3,75	0.589	
Sex x age class x litter size	1.00	3,75	0.397	
• *Group size*	0.06	1,74	0.803	0.0019
• *Sex of caretaker*	12.13	1,74	0.001	
• *Age class of caretaker*	1.32	3,74	0.275	
• *Litter size*	0.92	1,74	0.340	
• *Sex x age class*	2.31	3,74	0.083	
• *Sex x litter size*	0.13	1,74	0.722	
• *Age class x litter size*	0.62	3,74	0.606	
• *Sex x age class x litter size*	1.00	3,74	0.396	

Passive	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	6.16	1,75	0.015	
Age class of caretaker	0.53	3,75	0.664	
Litter size	2.43	1,75	0.123	
Sex x age class	2.46	3,75	0.069	
Sex x litter size	0.00	1,75	0.955	
Age class x litter size	0.74	3,75	0.531	
Sex x age class x litter size	0.96	3,75	0.416	
• *Group size*	0.18	1,74	0.672	-0.0037
• *Sex of caretaker*	5.83	1,74	0.018	
• *Age class of caretaker*	0.36	3,74	0.779	
• *Litter size*	2.28	1,74	0.135	
• *Sex x age class*	2.43	3,74	0.072	
• *Sex x litter size*	0.00	1,74	0.946	
• *Age class x litter size*	0.74	3,74	0.530	
• *Sex x age class x litter size*	0.99	3,74	0.404	

Resistance	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.73	1,75	0.394	
Age class of caretaker	2.45	3,75	0.070	
Litter size	0.91	1,75	0.343	
Sex x age class	2.63	3,75	0.056	
Sex x litter size	0.27	1,75	0.605	
Age class x litter size	1.39	3,75	0.252	
Sex x age class x litter size	1.01	3,75	0.394	
• *Group size*	0.08	1,74	0.778	0.0018
• *Sex of caretaker*	0.76	1,74	0.385	
• *Age class of caretaker*	1.98	3,74	0.124	
• *Litter size*	0.85	1,74	0.358	
• *Sex x age class*	2.62	3,74	0.057	
• *Sex x litter size*	0.28	1,74	0.602	
• *Age class x litter size*	1.40	3,74	0.255	
• *Sex x age class x litter size*	1.00	3,74	0.396	

Behaviour of the taker according to the identity of the carrier

Active

Effects of litter size (Mann-Whitney U-test)	$U = 1053.5$	$z = 0.546$	$p > 0.05$
Effects of age class (Kruskal-Wallis one-way ANOVA)	$\chi^2 = 7.80$	d.f. = 3	$p = 0.050$

Sex differences (Mann-Whitney U-tests)

Parents:	$U = 114.5$	$p > 0.05$
Adults:	$U = 69$	$p > 0.05$
Sub-adults:	$U = 50.5$	$p > 0.05$
Juveniles:	$U = 19.5$	$p > 0.05$

Passive

Effects of litter size (Mann-Whitney U-test)	$U = 961$	$z = -0.214$	$p > 0.05$
Effects of age class (Kruskal-Wallis one-way ANOVA)	$\chi^2 = 7.50$	d.f. = 3	$p = 0.058$

Sex differences (Mann-Whitney U-tests)

Parents:	$U = 104$	$p > 0.05$
Adults:	$U = 48$	$p > 0.05$
Sub-adults:	$U = 80$	$p > 0.05$
Juveniles:	$U = 36.5$	$p > 0.05$

Resistance

Effects of litter size (Mann-Whitney U-test)	$U = 1026.5$	$z = 0.538$	$p > 0.05$
Effects of age class (Kruskal-Wallis one-way ANOVA)	$\chi^2 = 5.65$	d.f. = 3	$p = 0.130$

Sex differences (Mann-Whitney U-tests)

Parents:	$U = 130$	$p > 0.05$
Adults:	$U = 78$	$p > 0.05$
Sub-adults:	$U = 85.5$	$p > 0.05$
Juveniles:	$U = 28.5$	$p > 0.05$

Behaviour of infants according to the identity of the carrier

Active	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.43	1,76	0.515	
Age class of caretaker	3.44	3,76	0.021	
Litter size	1.03	1,76	0.312	
Sex x age class	0.18	3,76	0.907	
Sex x litter size	0.04	1,76	0.845	
Age class x litter size	0.42	3,76	0.741	
Sex x age class x litter size	0.48	3,76	0.697	
• *Group size*	0.10	1,75	0.750	-0.0032
• *Sex of caretaker*	0.45	1,75	0.504	
• *Age class of caretaker*	3.27	3,75	0.026	
• *Litter size*	0.95	1,75	0.333	
• *Sex x age class*	0.17	3,75	0.915	
• *Sex x litter size*	0.04	1,75	0.848	
• *Age class x litter size*	0.42	3,75	0.743	
• *Sex x age class x litter size*	0.47	3,75	0.701	

Passive	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.17	1,76	0.684	
Age class of caretaker	1.96	3,76	0.127	
Litter size	1.72	1,76	0.193	
Sex x age class	0.13	3,76	0.944	
Sex x litter size	0.19	1,76	0.663	
Age class x litter size	2.84	3,76	0.043	
Sex x age class x litter size	0.12	3,76	0.948	
• *Group size*	2.34	1,75	0.131	0.0125
• *Sex of caretaker*	0.27	1,75	0.604	
• *Age class of caretaker*	2.59	3,75	0.059	
• *Litter size*	2.16	1,75	0.146	
• *Sex x age class*	0.09	3,75	0.965	
• *Sex x litter size*	0.20	1,75	0.652	
• *Age class x litter size*	2.83	3,75	0.044	
• *Sex x age class x litter size*	0.15	3,75	0.932	

Resistance	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.20	1,76	0.657	
Age class of caretaker	5.28	3,76	0.002	
Litter size	9.15	1,76	0.003	
Sex x age class	0.08	3,76	0.968	
Sex x litter size	0.65	1,76	0.424	
Age class x litter size	3.95	3,76	0.011	
Sex x age class x litter size	1.06	3,76	0.370	
• *Group size*	1.86	1,75	0.177	-0.0093
• *Sex of caretaker*	0.12	1,75	0.729	
• *Age class of caretaker*	4.76	3,75	0.004	
• *Litter size*	10.00	1,75	0.002	
• *Sex x age class*	0.10	3,75	0.959	
• *Sex x litter size*	0.67	1,75	0.416	
• *Age class x litter size*	3.92	3,75	0.012	
• *Sex x age class x litter size*	1.10	3,75	0.356	

Behaviour of infants according to the identity of the taker

Active	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	1.51	1,76	0.224	
Age class of caretaker	2.42	3,76	0.072	
Litter size	0.47	1,76	0.494	
Sex x age class	1.44	3,76	0.237	
Sex x litter size	0.98	1,76	0.326	
Age class x litter size	1.09	3,76	0.357	
Sex x age class x litter size	1.14	3,76	0.337	
• Group size	1.52	1,75	0.221	-0.0120
• Sex of caretaker	1.30	1,75	0.258	
• Age class of caretaker	1.81	3,75	0.152	
• Litter size	0.32	1,75	0.574	
• Sex x age class	1.51	3,75	0.219	
• Sex x litter size	0.97	1,75	0.328	
• Age class x litter size	1.01	3,75	0.392	
• Sex x age class x litter size	1.03	3,75	0.384	

Passive	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	0.68	1,76	0.413	
Age class of caretaker	2.08	3,76	0.110	
Litter size	0.07	1,76	0.786	
Sex x age class	1.17	3,76	0.329	
Sex x litter size	1.85	1,76	0.177	
Age class x litter size	0.25	3,76	0.863	
Sex x age class x litter size	0.53	3,76	0.664	
• Group size	1.28	1,75	0.261	0.0091
• Sex of caretaker	0.55	1,75	0.461	
• Age class of caretaker	1.89	3,75	0.138	
• Litter size	0.15	1,75	0.702	
• Sex x age class	1.23	3,75	0.306	
• Sex x litter size	1.84	1,75	0.179	
• Age class x litter size	0.21	3,75	0.891	
• Sex x age class x litter size	0.45	3,75	0.716	

Resistance	*F*	*d.f.*	*p*	*Regression coefficient*
Sex of caretaker	1.36	1,76	0.247	
Age class of caretaker	2.82	3,76	0.044	
Litter size	3.72	1,76	0.057	
Sex x age class	0.74	3,76	0.529	
Sex x litter size	0.07	1,76	0.788	
Age class x litter size	2.36	3,76	0.078	
Sex x age class x litter size	1.30	3,76	0.281	
• Group size	0.41	1,75	0.524	0.0030
• Sex of caretaker	1.24	1,75	0.269	
• Age class of caretaker	2.17	3,75	0.099	
• Litter size	3.42	1,75	0.068	
• Sex x age class	0.75	3,75	0.528	
• Sex x litter size	0.07	1,75	0.786	
• Age class x litter size	2.28	3,75	0.086	
• Sex x age class x litter size	1.23	3,75	0.305	