The Captive Behaviour and Reproduction of Goeldi's Monkey *Callimico goeldii*

Thesis

How to cite:

Carroll, John Bryan (1992). The Captive Behaviour and Reproduction of Goeldi's Monkey Callimico goeldii. PhD thesis. The Open University.

UNRESTRICTED.

THE CAPTIVE BEHAVIOUR AND REPRODUCTION OF GOELDI'S MONKEY *CALLIMICO GOELDII*

John Bryan Carroll BSc(Hons)

Submitted for the degree of Doctor of Philosophy

Biology Department, The Open University

October 1st 1992

Submission date: 7 October 1992
Award date: 21 December 1992

ABSTRACT

Behaviour and reproduction of Goeldi's monkey *Callimico goeldii* were studied over a 5-year period at the Jersey Wildlife Preservation Trust. The investigation comprised a study of female reproductive hormones during pregnancy and the non-pregnant phase; a study of pair bonding in newly-established pairs, long-established pairs and breeding pairs rearing infants; a study of bonding in experimentally established male-female-female trios; and a study of infant rearing.

The major urinary oestrogen metabolite was oestrone-3-glucuronide, and it was a good indicator of ovarian cycles and pregnancy. Ovarian cycle length was 24.1 ± 0.9 days. Gestation length was 145-152 days. Female proceptive behaviour was significantly elevated during ovulatory periods, but no significant change in male sexual behaviour was found across the female cycle, possibly indicating that ovulation was 'hidden' from the male. In two of the three male-female-female trios both females conceived, but infants were reared in only one trio. In the third trio, reproductive suppression of the subordinate female occurred. All three trios were disbanded following serious fights between the females.

Bond-promoting behaviour was primarily performed by the male and was reduced significantly in established pairs compared to new pairs. During the first six weeks of infant rearing bond-promoting behaviours were elevated almost to those of new pairs, although the infant, rather than the female, may have been the focus of the male's attention. There was little evidence for a lasting pair bond. In the male-female-female trios, the male associated with one female more than the other as measured by approaches, time in proximity and grooming. The preferred female was not necessarily the 'winner' of the fight between the two females.

The female was the predominant infant caretaker, undertaking exclusive care for three to seven weeks. Even after extra-maternal care began, the female remained the major caretaker. Use of maternal time-budget modelling suggested that seven weeks may be the maximum time that a female can rear the infant unaided, coinciding with the approximate time of doubling of infant body mass. There was no evidence of competition among carers to carry the infant and most transfers were infant-initiated. The benefits of extra-maternal care were discussed.

Allometric analysis of New World monkeys showed that *Callimico* may be unique in having a single relatively small infant. The other species considered have either a relatively large single infant, or two relatively small infants. Theories concerning the evolution of twinning among the Platyrrhini were discussed.

Acknowledgements

This research work, having been carried out on a part-time basis, has taken rather more years to complete than the usual PhD study. Accordingly, a great many people have helped along the way, both directly and indirectly, and I apologise now if anyone is omitted from these acknowledgements.

This study was only made possible through the Jersey Wildlife Preservation Trust. I am particularly grateful to Jeremy Mallinson, for giving permission for the *Callimico* colony to be the subject of the research and for his constant support over the years. I would also like to thank the members of the Council, the Board of Management and the Scientific Advisory Committee of JWPT for their understanding of the problems involved in carrying out the research part time, and for their continued support. Both Jersey Wildlife Preservation Trust and Wildlife Preservation Trust International supported aspects of the projects financially.

I would like to thank my Supervisor, Bob Martin, for his considerable support and guidance throughout this study. He not only supervised the project, he also wholeheartedly endorsed the idea that a zoo keeper should pursue a higher degree while working as a keeper. I would also like to thank him for his support as Chairman of the Scientific Advisory Committee of JWPT and as a Council member of JWPT. I hope that I may have at least stimulated and added to his interest in *Callimico*.

I am grateful to my Open University Internal Supervisors, Neil Chalmers -who saw the research through its early years - and, more recently, Tim Halliday, who both supported the project through many years and several extensions of the period of registration.

I am also grateful to David Abbott for his help, supervision and collaboration on the investigation of the reproductive physiology of *Callimico*. Lynn George taught me the assay techniques, somehow making them comprehensible, and carried out those I was unable to perform myself through lack of time. The assay work was supported financially through grants from the Association for the Study of Animal Behaviour and from the Nuffield Foundation.

Several people have read part or all of earlier drafts of the thesis. I am especially grateful to Bob Martin and Anna Feistner who made comments on the entire thesis, sometimes several times over and often in spite of a heavy workload. Eluned Price commented on early drafts of most of the thesis. Chris Pryce made some extremely helpful suggestions on the chapter on reproductive physiology. David Waugh kindly did a great job proof reading the thesis at a time when he was already very busy.

I would like to thank Phillip Coffey and Karen Mc Donnell for their assistance with the computer generation of some of the figures, and Phillip Coffey for the use of some of his photographs.

Many people have assisted with the project, both directly or indirectly, knowingly or unknowingly through friendship, advice or enthusiasm. Maggie Redshaw encouraged my first tentative steps into zoo research and Anna Omedes encouraged

my interest in small New World monkeys. Anna Feistner gave considerable advice during writing up. Simon Tonge, Quentin Bloxam, Chris West, Karen Hayes, June Manning, Bob Rattner, Diane Rattner, Eluned Price and Anna Feistner are among those who gave support when the going was tough. Helen Shaw recently gave valuable advice on aspects of the reproductive physiology work.

Several people helped with the husbandry of the *Callimico* colony throughout the study. My thanks go especially to Nick Lindsay, Chris West and Gary Clarke.

June Manning and Rachael Moore both typed some parts of the thesis.

Lastly, I would like to thank my wife, Christine, for her constant help, support, understanding and above all patience. She didn't let me give up when I felt I should have done so, but didn't really want to. This thesis would not have been completed without her.

CONTENTS

Chapter 5 Bonding in multi-female social groups

Chapter 6 Infant care in *Callimico goeldii*

Chapter 7 General discussion

CHAPTER 1 INTRODUCTION

The small, clawed New World primates have been a focus of particular attention for over two decades. This group contains the four marmoset and tamarin genera: *Cebuella, Callithrix, Saguinus* and *Leontopithecus* that comprise the family Callitrichidae, and the monospecific genus *Callimico* (Goeldi's monkey) that has variously been assigned to the Cebidae (*e.g.* Simpson 1945, Martin 1990), the Callitrichidae (e.g. Hill 1959, Napier and Napier 1967), or to the monospecific family Callimiconidae (*e.g.* Hershkovitz 1977). Much of this attention was sparked originally by the potential of these animals as laboratory primates (*e.g.* Wolfe *et al.* 1972, Kingston 1969, 1975, Hiddleston, 1977), followed by a growing concern about the conservation status of some species, particularly the lion tamarins (*e.g.* Bridgewater 1972, Coimbra-Filho and Mittermeier 1973, Hernandez-Camacho and Cooper 1976).

The attention that has followed has revealed that this is a remarkable group of mammals. Unusually for such small-bodied primates, they are diurnal rather than nocturnal (Martin 1990). It is now generally accepted that they are dwarf forms, derived from a large-bodied ancestral stock (Ford 1980, Leutenegger 1980, Martin 1990, 1992), although this is not universally accepted (see Hershkovitz, 1977).

While *Callimico* has a single infant, the genera *Cebuella, Callithrix, Saguinus* and *Leontopithecus* are unique among simian primates in typically having twin offspring (*e.g.* Hershkovitz 1977, Martin 1990). The developing foetuses share a single bidiscoidal placenta and are carried within the same amniotic sac, yet are heterozygotic (Luckett 1974, Hershkovitz 1977). Infant care is shared among group members although there is usually only a single breeding female, breeding by other females typically being suppressed (Hershkovitz 1977, Abbott 1984).

The social group structure and reproductive strategy have been the subjects of considerable research over the last 15 years. Although all members of the Callitrichidae were once thought to be strictly monogamous (see Kleiman 1977), it has emerged that their social and reproductive strategy may embrace not only monogamy but polyandry, polygynandry and more rarely polygyny [see a recent review by Ferrari and Lopes Ferrari (1989)]. Within a single species, the saddleback tamarin *Saguinus fuscicollis*, all four of the above mating systems have been seen (Goldizen 1988).

The complex relationship between twinning, infant care patterns, and social group structure has attracted a good deal of attention as well. The production of twins by the marmosets and tamarins has considerable consequences for the mother, who must not only sustain a double burden during pregnancy, but also subsequently rear the twins to independence (Hershkovitz 1977, Dunbar 1988). In *Callithrix*, the female may be pregnant during rearing as there is no period of lactational anoestrus in the species studied to date. Further, unlike *Saguinus*, *Callithrix* species are not seasonal breeders (Ferrari and Lopes Ferrari 1989). As social group structure and communal rearing patterns have probably evolved to ensure that twins are reared, twinning is at the hub of most theories regarding their evolution. The evolution of twinning itself has also been the subject of some debate. Leutenegger (1973) and Ford (1980) have suggested that twinning is a direct result of the progressively increasing neonate:mother weight ratio associated with decreased body size (dwarfism). Martin (1992), on the other hand, argues that twinning is more likely to have evolved as a response to some ecological selective factor favouring the production of large litters to increase reproductive capacity.

Goeldi's monkey, *Callimico goeldii*, the subject of this thesis, is extremely important in testing these theories about twinning. *Callimico* is a small-bodied primate closely related to the marmosets and tamarins. Its body weight of between 550g-600g [data from captive animals, (Carroll, 1982)] falls within the weight range spanned by the marmosets and tamarins [*i.e.* 120g in the pygmy marmoset, *Cebuella pygmaea*, to 650g in the golden lion tamarin *Leontopithecus rosalia* (Hershkovitz 1977, Soini 1988, J. Dietz pers. comm.)]. It occupies a similar ecological niche, being diurnal, arboreal, frugivorous and insectivorous. It lives in small social groups of six to eight animals (Izawa 1979, Pook and Pook 1979a, Buchanan-Smith 1991) and displays many similarities to the social group patterns and infant care patterns shown by the marmosets and tamarins. However, as it produces only a single infant [just five incidences of twinning have been reported in over 25 years of captive breeding spanning several hundred births (Hill 1966, Rettberg 1986, Warneke 1988, Altmann *et al.* 1988)], *Callimico goeldii* is of particular significance for testing and re-evaluating theories concerning the evolution of twinning among the Callitrichidae.

This thesis reports on a study of reproduction and of the social behaviour of *Callimico goeldii* in captivity, and provides a comparison with the marmosets and tamarins. This first chapter contains a description of Goeldi's monkey and a review of its taxonomic and phylogenetic affinities, followed by an account of the species both in the wild and in captivity. Thereafter, subsequent to a review of the reproductive biology of the marmosets and tamarins, the aims of the study are described.

Throughout the thesis, higher taxonomic categories as defined by Hershkovitz (1977) will be adopted. The family Callitrichidae refers exclusively to the extant genera *Cebuella*, *Callithrix*, *Saguinus*, and *Leontopithecus*. The family Callimiconidae refers only to the monospecific genus *Callimico*, while the family Cebidae contains the other extant platyrrhines. This does not imply acceptance of Hershkovitz's (1977) view concerning evolutionary relationships among the New World monkeys, nor is it meant as a judgement on the relative validity of arguments concerning the taxonomic status of *Callimico*. These points are discussed further below (section 1.2).

Common names will be used in the thesis in the following way: 'Marmoset' refers to the genera *Cebuella* and *Callithrix*. 'Tamarin' refers to the genera *Saguinus* and *Leontopithecus*. Following Martin (1990), the term 'clawed New World monkeys' refers to the marmosets, tamarins and *Callimico* together, while the other platyrrhine genera are referred to as the 'true New World monkeys'. Use of specific names follows Mittermeier *et al.* (1988). As the genus *Callimico* is monospecific, the species will henceforth be referred to by the generic name only.

1.1 The research subject

Goeldi's monkey, *Callimico goeldii* (Thomas 1904), is a small-bodied South American primate with a mean body weight in captivity of 581.5g (range 553g - 610g, n=6) (Carroll 1982). The genus *Callimico* is generally regarded as monospecific and no subspecies variation has been reported. The fur is typically uniformly black, with some flecking of brown around the thighs and lower back, particularly in older specimens (see plate 1). Such flecking arises from a band of lighter colouring at the tips of hairs, which are otherwise black. Some specimens, including the type specimen, also have some areas of white hair, although this is atypical. In captivity, white hair is occasionally seen on neonates on the lower torso (see plate 2), and is usually moulted out by the age of six to nine months to be replaced by normally-coloured black hair (Carroll 1982). It has been suggested that these areas of white hair are caused by a prenatal nutritional deficiency (A. F. Coimbra-Filho pers. comm.). In adults, it is thought to be most frequently caused by injury, which results in a temporary loss of melanin in the scar tissue and hence in the new hair. Again, such white hair is usually replaced with normal black hair following a moult.

The face is bare, apart from some short, sparse hairs on the chin and lips, and the exposed facial skin is black. The ears are also bare and black, but are partially hidden behind a ruff of hair which extends erect over the crown of the head, giving a distinctive characteristic appearance to the adults of the species. The palms of the hands and soles of the feet are also black, but the skin beneath the hair is white, as is the skin of the abdomen, which is only sparsely haired. Neonates and juveniles are similar in appearance except that the hair on the head is longer and more flattened than that of the adults (see plate 3). Like the marmosets and tamarins, *Callimico* has claws on all the digits except the hallux, which bears a flattened nail.

Both sexes have scent gland fields in the circumgenital, perineal, abdominal, and sternal areas (Epple and Lorenz 1967, Hershkovitz 1977). Heltne *et al.* (1982) also distinguish two further fields, the manubrial at the apex of the sternum, and

Plate 1.1 An adult Goeldi's monkey *Callimico goeldii*.

Fig. 1.1 Distribution of *Callimico goeldii* in South America

the suprapubic, just anterior to the genitals. Scent marking is performed either by rubbing the scent glands directly on the substrate, or by coiling the tail and rubbing it vigorously against the glands.

In spite of the superficial similarity of *Callimico* to the Callitrichidae, the species also has some features characteristic of the Cebidae. Firstly, it has the cebid dental formula (36 teeth), having retained the third molars which the callitrichids have lost. Secondly, like the cebids, it produces a single infant rather than twins. The main characteristics distinguishing the families Callitrichidae and Cebidae are presented in table 1.1.

Table 1.1 The major features distinguishing the Callitrichidae and the Cebidae

Cebidae	Callitrichidae
Third molar present	Third molar absent
Quadritubercular upper molars	Tritubercular upper molars
Adult weight 650g - 15000g	Adult weight 120g - 650g
Flattened nails on all digits	Claws on all digits except hallux
Single infants	Twin infants

The apparent intermediacy of *Callimico* between the two main platyrrhine families has led to considerable discussion of evolutionary relationships within the group. The taxonomic history and likely phylogenetic affinities of *Callimico* are reviewed below.

1.2 A brief taxonomic and systematic history of *Callimico.*

The species was first described in 1904 by Oldfield Thomas of the British Museum of Natural History (Thomas, 1904), from a skin provided by Emilio Goeldi, the Swiss zoologist who founded the Goeldi Museum at Parà in Belem at the mouth of the River Amazon. The characteristics of the specimen led Thomas to believe that this was a new species of the genus *Hapale* (= *Callithrix*) and he initially gave the species the name of its discoverer, *Hapale goeldii* (Thomas, cited in Goeldi and Hagmann 1904). When the description of the species was actually published, it was given the name *Midas (= Saguinus) goeldii* (Thomas,1904). Seven years later, Thomas was sent the type specimen of a new genus and species subsequently named as *Callimico snethlageri* by Miranda Ribeiro (1912). He immediately recognised this as being the same species as his *Midas goeldii*. Ribeiro had sent him the intact skin and skeleton of *Callimico snethlageri*, and from the skull of the specimen Thomas noted an important difference between this species and the genus *Midas*, *viz*. that the new specimen had 36 teeth, unlike *Midas* which has 32. Thomas upheld the generic name *Callimico*, but due to the precedence of the specific name *goeldii*, the species became *Callimico goeldii*, the sole representative of the subfamily Callimiconinae (Thomas, 1913). Thomas described the intermediate nature of *Callimico* between the Cebidae and the Callitrichidae, but, on the basis of the dental formula, he ascribed the new sub-family to the Cebidae. Since that time, the genus has been assigned to the monospecific subfamily Callimiconinae within either the Cebidae (*e.g.* Simpson 1945, Martin 1990) or the Callitrichidae (*e.g.* Pocock 1920, Hill 1959, Ford 1980), or alternatively allocated to a monospecific family, the Callimiconidae (*e.g.* Dollman 1937, Hershkovitz 1977, Coimbra-Filho 1990).

This variation in the higher taxonomic status accorded to *Callimico* reflects a variety of opinion on evolutionary relationships within the Platyrrhini, partly reflecting the relative weight given to certain characters. As long ago as 1917, Pocock first suggested that the claws of callitrichids were a derived feature [a view later supported by Thorndike (1968) and Ford (1980)] associated with the animal's smallness of size, also a derived feature. Later, he wrote that he considered *Callimico* to be a primitive callitrichid (Pocock, 1925). This view has been supported by many authorities since, *e.g.* Miranda Ribeiro (1941), Remane (1956), Osman Hill (1959), Dutrillaux *et al.* (1988), and Martin (1990).

An opposing view has been taken by Hershkovitz (1977), who does not consider the Callitrichidae to be a derived group. Instead, he considers that claws, small size, tritubercular upper molars and twinning are retained primitive features, and that the Cebidae are hence the more advanced group. He does not view *Callimico* as being necessarily an evolutionary intermediate between the two families either, arguing that their intermediate grade status may have been independently evolved. Hershkovitz advanced the theory that the Callitrichidae are an early derivative from primitive platyrrhine stock, while *Callimico* and the Cebidae diverged at a later date from this stock. Accordingly, he proposes that *Callimico* should have separate family status, being one of three major lines from a basal stock.

The balance of the evidence for and against these viewpoints weighs strongly in favour of the interpretation that the main features of the clawed New World monkeys are derived and has recently been summarised by Martin (1990, 1992). Strong evidence suggests that the claws are derived, rather than primitive (Thorndike 1968). Luckett (1974) has shown that the placental structure is clearly derived. Ford (1980), using various skeletal features, has also provided strong evidence that the clawed New World monkeys are derived not primitive. Karyological work by Dutrillaux and co-workers (Dutrillaux *et al.* 1988) provided confirmation that chromosomal evolution among the group follows the path suggested by Hill (1957), based on the morphology of *Callimico*. Given the cumulative weight of this evidence, it is now widely accepted that the clawed New World monkeys belong to a dwarf lineage, and the evidence also supports Pocock (1925) in his suggestion that *Callimico* is a primitive offshoot of the lineage leading to the marmosets and tamarins.

It should perhaps be pointed out here that electrophoretic and immunological studies have not been helpful in demonstrating relationships within the clawed New World monkeys. Studies of albumins and transferrins by Scheffrahn and Glaser (1977) and Cronin and Sarich (1978) both suggested that the genus *Callimico* was more closely related to *Callithrix* than to *Saguinus*. Cronin and Sarich (*op. cit.*) placed *Callimico*, *Cebuella* and *Callithrix* in a single lineage with *Saguinus* and *Leontopithecus* each in separate lineages. A similar phylogenetic arrangement was also proposed by Seuánez *et al.* (1989) based on a study of middle repetitive (LINE-1) DNA sequences of *Callimico* and eight other New World monkeys. This is most unlikely, however, as all other evidence suggests that the marmosets and tamarins form a monophyletic group to the exclusion of *Callimico*. The phylogenetic scheme of Cronin and Sarich (1978) and Seuánez *et al.* (1989) has one major problem. It requires twinning to evolve on three separate occasions, and on each occasion to be accompanied by the loss of M_3, while *Callimico* retains M_3 and does not evolve twinning. The alternative scheme requires *Callimico* to revert to a single infant from a twinning ancestor, and to regain the third molar lost in the ancestral form.

As a final note, mention should be made of the taxonomic scheme first proposed by Rosenberger (1977) and followed by Szalay and Delson (1979). This places the clawed New World monkeys in the family Cebidae along with the genera *Cebus* and *Saimiri*. The other New World monkeys are placed in the family Atelidae. This is designed to reflect an inferred dichotomy within the 'true' New World monkeys. The scheme is controversial as it is based on limited evidence, mainly dental morphology, and is not supported by other morphological, anatomical, or karyological evidence (Martin 1990).

1.3 *Callimico* in the wild

There have been four field studies of *Callimico* in which the species was the main focus of attention. These were carried out in 1978 by George and Gillian Pook (Pook and Pook 1979a, 1979b, 1980), in 1979 by Masataka (1981a, 1981b, 1982), in 1987 by an undergraduate expedition from Oxford University (Cameron *et al.* 1987), and in 1991 by Christen (Christen and Geissman in prep.). All these were relatively short term, the longest being Masataka's (6 months) while the Pooks' and Christen's studies were slightly shorter (5 months). Cameron's study took place over a 6-week period. In addition to these field studies, observations have been published on *Callimico* in the wild by Moynihan (1976) and by Izawa (1979), who carried out surveys of the primates in the western Amazon Basin. More recently, the species was observed by Buchanan-Smith (1989, 1991) during her field study of the red-bellied tamarin *Saguinus labiatus* in Bolivia.

The Pook, Cameron and Christen expeditions were all essentially ecological surveys in the Pando region of northern Bolivia focussing on *Callimico*. Pook and Pook also habituated a *Callimico* group to their presence and made observations on the social and ranging behaviour of the group as well as making detailed notes on their diet. Masataka's study was on a habituated group that was trained to come to a baited site. At this site, social behaviour and the vocal repertoire of the species were studied.

The information presented below on *Callimico* is summarised mainly from Pook and Pook (1979a), Izawa (1979), Masataka (1981a, 1981b), Cameron *et al.* (1987) and Christen and Geissman (in press). The major work in all of these studies was carried out in northern Bolivia. *Callimico* also occurs in Manu National Park in Peru, but has been seen only rarely within the study area of Cocha Cashu where Terborgh and co-workers have studied the primate community for several years, and has not been the focus of any study there (Terborgh, 1983).

Distribution and conservation status

Very little is known about the status of *Callimico* in the wild. It occurs over a very large area of the western Amazon basin, from southern Colombia, south through eastern Peru and western Brazil into northern Bolivia (see fig. 1.1). It may also occur in eastern Ecuador. However, while the distribution map provided by Wolfheim (1982) shows the species as present in Ecuador, it has not actually been recorded from there (Hershkovitz, 1977). The northern boundary of the range appears to be the Rio Caqueta and the southern boundary the Rio Orthon-Rio Munuripi, encompassing a north-south distance of some 1500-2000 km around the upper Amazon basin (Izawa, 1979). Most of the information about the distribution comes from the location records of specimens held in museums. This is supplemented, particularly in Peru and northern Bolivia, by a small number of sight records (Hershkovitz 1977).

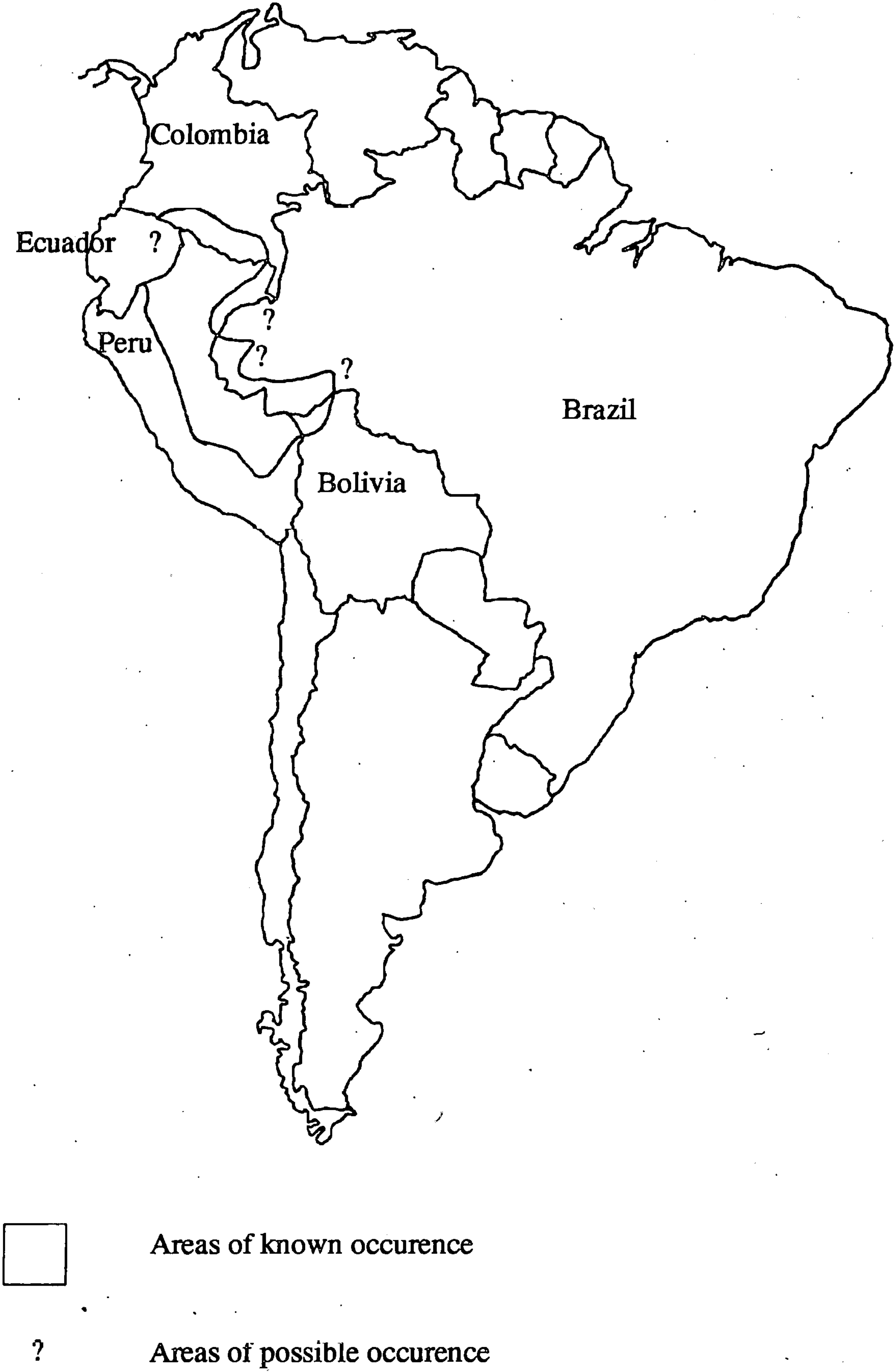


Fig. 1.1 Distribution of *Callimico goeldii* in South America

Callimico goeldii is listed in the IUCN Red Data Book as "Rare" (IUCN 1990). This is perhaps rather surprising in view of its extremely extensive range in the western Amazon basin. It would seem, however, that within its geographical range of probably hundreds of thousands of km^2, it is very sparsely distributed. Where the species does occur and has been studied, it occurs at very low densities (Moynihan 1976, Hershkovitz 1977, Izawa 1979, Pook and Pook 1979a). The Pooks, for instance, calculated a density of 1.5 animals per km^2. Cameron *et al.* (1987), by contrast, calculated a density of 9.6 animals per km^2 , an estimate that they are sure represents accurately the population in their census areas. This is probably a reflection of their choice of census site, which was made on the basis of reports of high primate density and diversity in those areas, rather than just reports of the presence of *Callimico* which the Pooks used for their choice of study site. Evidence for low population density comes from the paucity of museum specimens, as well as from the direct experience of field biologists (Heltne *et al.* 1981). The information given by Moynihan (1976), Hernandez-Camacho and Cooper (1976), and Hershkovitz (1977) suggests that small *Callimico* groups are widely spaced. This is supported by unpublished accounts cited by Izawa (1979), by his own field work and by that of Pook and Pook (1979a). Christen and Geissman (in prep.), on the other hand, report finding groups in adjacent home ranges.

It has been suggested by both Izawa (1979) and Pook and Pook (1979a) that the reason for the very scattered distribution of *Callimico* within its range is related to the rather specialised habitat it exploits. These authors report that *Callimico* is dependent on a dense scrub understorey, which is not found in primary forest with an unbroken canopy or in forest subject to seasonal flooding. Izawa (1979) suggests that this habitat was historically more widespread, and that the species originally had a more continuous distribution within its range, although he does not say what factors may have reduced the habitat.

Further fragmentation of the distribution of *Callimico* may have resulted from competition with *Saguinus* species, notably *S. fuscicollis*, which Izawa (1979) considers to be a "good" competitor of *Callimico*. Not only might *Saguinus* species compete for food and other resources, but, as they give birth to twins as opposed to *Callimico*'s single infant, they have potentially double the recruitment rate to the population. If *Saguinus* do compete with *Callimico*, their higher birth rate would be expected to give them a considerable advantage. Ross (1991), however, has shown - using data from captive populations - that *Callimico*'s intrinsic rate of population increase (r_{max}) is higher than expected from the litter size. Because it has an earlier age of first reproduction, the r_{max} of *Callimico* is close to, although still lower than, that of *Saguinus*. *S. fuscicollis* is certainly a very successful species. It is found everywhere in the western Amazon basin and, to date, 13 subspecies have been described, none of which is rare or threatened (Hershkovitz 1977, R. Mittermeier pers. comm.). It must be pointed out, however, that - although some competition may occur between these species - *Callimico* forms mixed species associations and co-exists apparently amicably not only with *S. fuscicollis* but also with *S. labiatus* as well. These tamarins may not, therefore, be serious competitors of *Callimico*.

It may also be, of course, that *Callimico* is actually present in larger numbers where suitable habitat occurs. Several authors cite areas where local people were unaware of the presence of this primate in their vicinity (Neville *et al.* 1976, Hernandez-Camacho and Cooper 1976, Pook and Pook 1979a). It inhabits dense scrub, is black in colour, and very shy. It would therefore not be unexpected for short-term surveys to fail to detect animals and hence to record reduced numbers or complete absence. Izawa (1979) gives two locations, one in Peru and one in Bolivia, where *Callimico* occurs at quite high densities; but in his opinion these are exceptional. All the evidence to date, except that of Cameron *et al.* (1987), points to the species existing at very low densities.

The low density of the natural population renders the species very vulnerable to any factor that may cause a decline in numbers. It has been estimated that each *Callimico* group may be separated from its neighbours by as much as 2 km (Pook and Pook 1979a). Thus migrations between groups would be considerably curtailed and groups may become effectively isolated. Given that reproductive suppression of offspring occurs within families in captivity, the loss of a breeding animal would have dire consequences for the group, with perhaps none of the young animals attaining breeding status (Beck *et al.* 1982, Carroll 1982, 1986). In the *Callimico* colony at Jersey Wildlife Preservation Trust, a father-daughter dyad cohabited for over a year following the death of the breeding female, with no reproduction occurring between them (pers. obs.). Thus, a trapping programme or even minor changes to the habitat may have a disastrous effect on the viability of the local *Callimico* population.

So far, human settlement within the range of *Callimico* is at relatively low densities, much of the area being undeveloped forest inhabited only by indigenous indians. As the upper Amazon basin becomes increasingly settled by people of European descent, they will inevitably change local land-use practices and increase the pressures on the land. Much of the habitat suitable for *Callimico* is found bordering smaller rivers with a width of "several tens of metres at most" (Izawa, 1979 p. 8). As the river system is the main highway of the Amazon basin, the river fringes are the first areas to become settled and then remain so.

A further threat comes from gold prospecting in the upper Amazon. This usually involves panning river silt and material from the river banks, often using mercury to extract the gold. This affects the river system by altering patterns of silting as well as through the disastrous effects of increased mercury levels in the water.

Human population pressure will undoubtably increase in the upper Amazon. The states of Rôndonia and Acre in Brazil are being actively settled. Land is given away by the Federal government on the understanding that it be "developed" in some way. This inevitably means that the land is deforested either for agriculture or for timber. Any land which is not used in some way brings tax penalties for the owner. Although such active encouragement to develop the land is not offered in Colombia, Peru, or Bolivia, the human population in those countries is, nevertheless, rising and more and more land suitable for settlement is sought. The Bolivian government, for instance, was reported by Pook and Pook (1979b) to be seeking to encourage impoverished upland indians to resettle in the Pando region. It is inevitable, therefore, that the total area of suitable habitat available for *Callimico* will continue to decline and the population become even more fragmented. It will perhaps, in time, lead to a real danger of extinction for the species.

Habitat

The information available from most studies on *Callimico* in the wild indicates that, in the areas of study at least, it does not inhabit primary forest, but rather what has been described by Izawa (1979 p.7) as "shabby" forest. This is mixed, degraded or secondary forest, bamboo forest, or forest with an open canopy and well developed scrub (Moynihan 1976, Izawa 1979, Pook and Pook 1979a, Cameron *et al.* 1987). These forests may arise from shifting agricultural practices or from natural events. *Callimico* uses the scrub stratum most frequently, and does not inhabit forest that does not have a scrub layer, such as that which is subject to seasonal flooding. Christen (pers. comm.), on the other hand, reports seeing *Callimico* in both primary and secondary forest, even in areas of primary forest without a dense scrub layer.

The species has been said to favour the lower 5m of the forest strata for travel, which is accomplished mainly by leaping between vertical supports, rather than the quadrupedal running exhibited by the *Saguinus* species with which *Callimico* co-exists (Izawa 1979, Pook and Pook 1979a). Christen reported that quadrupedal running was the main mode of locomotion of the *Callimico* in her study area (Christen and Geissman in prep.). *Callimico* has been seen to descend to the forest floor either when alarmed (Moynihan 1976, Izawa 1979, D. Wormell, pers. comm.) or to capture insects when feeding (Pook and Pook 1979a).

Diet

There are few observations of feeding in the wild. They indicate, however, that the diet includes berries and larger fruit (Moynihan 1976, Hernandez-Camacho and Cooper 1976, Izawa 1979, Pook and Pook 1979a). The only sap that they have been seen to eat was that exuding from the sticky pods of *Parakia legumae* (Pook and Pook 1979). Many researchers have also noted that *Callimico* feeds on arthropods, both insects and spiders (Moynihan 1976, Izawa 1979, Pook and Pook 1979a). Pook and Pook (1979a) described *Callimico* jumping to the ground to capture large grasshoppers, a hunting strategy that was unique among the clawed primate species in their study area. Izawa (1979) has also reported seeing *Callimico* search the joints and bases of epiphytes, presumably for insects or small vertebrates such as tree frogs. Captive *Callimico* in Louisiana captured and ate snakes and lizards that entered their cages (Lorenz 1972).

Social behaviour in the wild

As with diet, there is little information on social behaviour in the wild. Groups of *Callimico* are reported to contain between one and nine individuals. Moynihan (1976) thought that three was the usual group size. Izawa (1979) estimated that groups comprised five or fewer individuals, while Christen and Geissman (in press) saw groups of between three and five individuals. Cameron *et al.* (1987) report four single individuals, two groups of three and one group of six. Pook and Pook's (1979a) study group was of eight individuals, while Masataka's (1981a) contained nine. Masataka's study group, however, included three captive males, supposedly originating from the group, that were released and subsequently reintegrated into it during his study. Buchanan-Smith (1991) also reported a group of nine or possibly ten animals. Even larger groups have been recorded. A report is cited by Hershkovitz (1977) of groups of up to 70 *Callimico* in Acre in Brazil, although both he and Heltne *et al.* (1982) doubt the accuracy of this report.

Group composition is poorly reported, although Pook and Pook (1979a) and

Masataka (1981a, 1981b) both report the presence of two breeding females in their study groups. The Pooks' group contained two adult females and two juveniles that appeared too similar in size to belong to consecutive litters from the same female. Masataka, on the other hand, saw two females nursing infants in his group at the same time. Masataka's group consisted of two males and four females as well as the three males integrated into it. The group was baited to an observation position and it is possible that the use of bait attracted two groups that temporarily associated. Masataka's own data from the end of his study suggest that his "group" split into two smaller sub-groups, each containing one of the breeding females.

Callimico appear to be active from about 0600 hrs until about 1700 hrs (Izawa 1979, Pook and Pook 1979a). The Pooks' group generally fed in the early morning and travelled up to 0.5 km by late morning. The rest of the day was usually spent feeding and resting interspersed with short bouts of travelling. A daily travel distance of up to 1 km was recorded for this group (Pook and Pook 1979a).

Few social behaviours have been reported from the wild. Allogrooming is frequently seen during rest periods (Pook and Pook 1979a, Masataka 1982). Scent marking has also been recorded in the wild, both by rubbing the tail against the scent gland fields and by marking directly onto substrates (Pook and Pook 1979a).

Mixed species associations

Callimico has been seen in the wild to associate with other primate species, particularly with callitrichids. Moynihan (1976) reported it associating with saddleback tamarins (*Saguinus fuscicollis*) and squirrel monkeys (*Saimiri* sp.). Hernandez-Camacho and Cooper (1976) and Masataka (1981a) also report it being seen with *S. fuscicollis*. Pook and Pook (1979a) reported *Callimico* in association with *S. fuscicollis, S. labiatus*, and a single titi monkey (*Callicebus moloch*). Cameron *et al.* (1987) also report an association with *Callicebus* and the two tamarin species. Unlike the associations between *S. fuscicollis* and *S. imperator* in Peru (Terborgh 1983), there have been no reports of cooperative territorial defence involving *Callimico.*

1.4 *Callimico* in captivity

The first record of a captive *Callimico* is that of the type specimen of the genus. Prior to the mid 1970s, the species was seen only rarely in captivity, but at that time small numbers were imported into the United States and Europe from Bolivia. Those wild-caught animals form the founder stock of the current captive population, which numbered 352 in 1988 (Warneke, 1988).

Material published on captive *Callimico* prior to 1980 was mainly based on anecdotal observations. Much of it concerned husbandry, but it also contained a considerable body of observations on behaviour and reproductive biology (*e.g.* Lorenz 1969, 1970, 1971, 1972, Heinemann 1970, Pook 1975). Subsequent to 1980, in addition to husbandry reviews (Beck *et al.* 1982, Carroll 1982), publications have mainly been concerned with behaviour (Carroll 1985, 1988), and with reproductive physiology (Carroll *et al.* 1989, 1990, Christen *et al.* 1989, Ziegler *et al.* 1989, 1990). The vocal repertoire was studied by Masataka (1983).

Husbandry

Callimico has been kept most successfully following husbandry techniques similar to those used for the marmosets and tamarins (Heinemann 1970, Lorenz 1972, Pook 1975, Beck *et al.* 1982, Carroll 1982). They are kept as nuclear family groups comprising a monogamous pair and their offspring. Like the marmosets and tamarins, reproductive suppression seems to prevent the offspring breeding even when sexually mature (Carroll 1982, 1986). When kept in this way, family groups have contained as many as nine individuals and remained stable. Individual groups are ideally maintained without visual contact with other conspecific groups, as territorial integrity is evidently an important consideration. Visual contact between conspecific groups leads to elevated levels of scent marking, aggressive displays and vocalisations, which reflect high levels of stress (Lorenz 1972).

Social behaviour

An ethogram for the species was published by Heltne *et al.* (1982). In many respects, the behaviour of *Callimico* is similar to that of the callitrichids, although Omedes and Carroll (1980) noted a relatively low frequency of interactions between the members of monogamous *Callimico* pairs as compared with four callitrichid species housed under identical conditions.

Two behaviours exhibited by *Callimico* are not seen among callitrichids studied to date. One of these is 'arch bristle leap', ABL, a mobbing display during which the animals piloerect, stare at and approach the addressee while leaping from support to support (Omedes and Carroll 1980). An open-mouth vocalisation accompanies the display. ABL may be equivalent to the 'quadrupedal threat-attack stance' described by Heltne *et al.* (1982), although they do not mention the locomotor component that is a striking feature of ABL.

The other behaviour unique to *Callimico* is that of scent marking the tail by coiling it between the legs and rubbing it against the ventral scent-gland fields. This behaviour is named 'tail mark' by Heltne *et al.* (1982), but is referred to as 'tail anoint' in this thesis to reflect the moistening of the tail with urine as well as scent gland secretion. Hershkovitz (1977) interpreted this behaviour as masturbation.

Literature dealing with quantitative studies of the behaviour of the species in captivity is sparse. Masataka (1983) published an account of the vocal repertoire of *Callimico* in captivity. Infant-carrying behaviour is described by Heltne *et al.* (1973). Pair-bonding behaviour is described by Carroll (1985) on the basis of data presented in this thesis. This aspect of behaviour is discussed fully in Chapter 4.

Reproductive Biology

Observations of captive animals have contributed almost everything that is known about the reproductive biology of *Callimico* to date. Lorenz (1969, 1972) and Heinemann (1970) confirmed that *Callimico* typically has only a single infant. Only five incidences of twins have been reported in the literature (Hill 1966, Altmann *et al.* 1988). Unlike the infant care pattern seen in most callitrichids, in which the father and other group members may participate in infant care from the day of birth, extra-maternal care in *Callimico* is not seen until the infant is two to three weeks old (Lorenz 1972, Heltne *et al.* 1973, Pook 1978). In this respect, *Callimico* has been said to be similar to *Leontopithecus*, in which the male may not actively care for the infants until they are two weeks old (Hoage 1977). In *Leontopithecus*, however, the age at which the infant receives extra-maternal care is much more variable than it is in *Callimico*. *Leontopithecus* may exhibit this from as early as day 1 or 2 following a birth, while in *Callimico* the infant has not been reported to be carried by another group member before it is two weeks old (Kleiman *et al.* 1988).

Observations on matings and interbirth intervals have led to a gestation estimate of 149-159 days (Lorenz 1972) and a range of 150-170 days (Heltne *et al.* 1973). These estimates have been confirmed by hormonal studies reviewed below (Carroll *et al.* 1989, Ziegler *et al.* 1989). Interbirth intervals of between 160 and 170 days are not uncommon, with 155 days being the shortest published interbirth interval (Lorenz 1972, Heltne *et al.* 1981, Beck *et al.* 1982, Carroll 1982).

Lorenz (1972) observed behavioural changes in his *Callimico* groups and estimated as a result of these that oestrous cycle length is 21-24 days with a mean of 22 days. On the basis of behavioural changes, Lorenz (1972) and Hershkovitz (1977) indicate the existence of a post-partum oestrus occurring approximately 10 days after parturition. Hormonal studies have also confirmed the accuracy of these estimates (Carroll *et al.* 1989, Christen *et al.* 1989, Ziegler *et al.* 1989).

Reproductive physiology

Recent hormonal studies have been carried out on the species to determine the physiological control of reproduction and to confirm the estimation of gestation length, oestrous cycle length and the occurrence of a post-partum oestrus. One of those studies forms part of this thesis and this aspect of the reproductive biology of *Callimico* is discussed fully in Chapter 3. Ziegler *et al.* (1989, 1990) studied the endocrinology of conception and pregnancy; Christen *et al.* (1989) reported on oestrous cycles, while Carroll *et al.* (1989, 1990, this study Chapter 3) investigated the endocrinology of oestrous cycles, conception, and pregnancy.

1.5 The reproductive strategy of the Callitrichidae

Reproduction among the marmosets and tamarins has received a great deal of attention over recent years. This is reviewed below.

Social group structure and breeding strategies

Until recently, the callitrichids were assumed to be monogamous, a relatively rare reproductive strategy among mammals (Kleiman 1977), with nuclear families based on a monogamous pair being the most stable social group structure in captivity (*e.g.* Kingston 1969, Epple 1970, 1977, Mallinson 1975, Kleiman 1978). In these captive groups, sons and daughters are reproductively suppressed, through either physiological or behavioural mechanisms (*e.g.* Abbott 1984, French and Stribley 1987), and the exclusive breeding status of the pair is thus maintained.

More recent evidence, however, indicates that callitrichids are much more flexible in their social group structure and mating patterns than previously thought. In the wild, groups with more than one adult of either or both sexes have been recorded in several species *e.g.* *Saguinus geoffroyi* (Dawson 1977), *S. oedipus* (Neymann 1977), *Callithrix jacchus* (Hubrecht 1984), *C. humeralifer* (Rylands 1981), *S. mystax* (Soini and Soini 1982, Garber *et al.* 1984). Accordingly, following the terminology of Brown (1987), monogamy (mating between one male and one female), polyandry (mating between one female and more than one male), polygyny (mating between one male and more than one female), and polygynandry (mating between more than one male and more than one female) have all been described among the callitrichids.

Care must be taken, however, to distinguish between social group structure and mating relationships when discussing reproductive strategies. The presence in a group of more than one adult of either sex does not necessarily indicate that they are all reproductively active. They may, for instance, be non-reproductive mature offspring of the breeding male or female. In captivity, mature offspring may remain in a stable group and yet not enter a breeding relationship with their parents or siblings, as they are reproductively suppressed. The fact that a female may mate with more than one male is also not conclusive evidence of a polyandrous <u>breeding</u> system, although it is obviously suggestive of this. Only when paternity of offspring can be established will the breeding system be understood.

In fact, in spite of the many reports of group structure indicating that there may be more than one breeding pair in a wild callitrichid group, only a few studies have actually reported seeing females mated by more than one male. These are in *C. jacchus* (Hubrecht 1984), *C. humeralifer* (Rylands 1987), *S. fuscicollis* (Goldizen 1988) and *L. rosalia* (A. Baker pers. comm.). Even fewer studies have reported more than one breeding female in a social group at the same time. These are in *S. fuscicollis* (Terborgh and Goldizen 1985), *L. rosalia* (A. Baker pers. comm.) and possibly *C. jacchus* (Scanlon *et al.* 1988).

It is, however, not surprising that there is a paucity of data from wild groups. As Goldizen (1990) has pointed out, the marmosets and tamarins are small, difficult to habituate to the presence of observers, and mating may last only a few seconds. Goldizen's studies have shown, however, that even within a species (*S. fuscicollis*) the reproductive strategy may vary. She found groups to be monogamous, polyandrous, polygynous, and polygynandrous in their mating system at least. She suggested that this variability is related to demographic effects and the need for helpers to rear offspring successfully (Goldizen 1990). Infant rearing is discussed more fully below.

<u>Reproductive suppression</u>

Reproductive suppression of subordinate females among captive callitrichid groups is a well-documented phenomenon (*e.g. C. jacchus*, Epple 1972a, 1977, Abbott and Hearn 1978, Abbott 1984; *S. fuscicollis*, Epple and Katz 1984; *S. oedipus*, Ziegler *et al.* 1987, Savage *et al.* 1988). In *C. jacchus*, hormonal studies of females in peer groups have shown that the behaviourally dominant female is the only female to undergo normal ovulatory cycles (Abbott and Hearn 1978). In nuclear family groups, it has also been shown that daughters do not exhibit ovulatory cycles and are therefore also suppressed in the three species *C. jacchus*, *S. fuscicollis*, and *S. oedipus* (Abbott *et al.* 1981, Epple and Katz 1984, Savage *et al.* 1988). In the last two species, daughters show no evidence of ovulating, but in *C. jacchus* some daughters do ovulate (although they do not cycle regularly) while still in their natal group (Abbott 1984). In *Leontopithecus rosalia*, on the other hand, French and Stribley (1985) have shown that daughters do undergo normal ovulatory cycles within their natal groups. Young females are often subject to severe aggression from their mother when they mature (Kleiman 1979) and are thus prevented from breeding through behavioural rather than physiological means.

Physiological suppression of female cycles is by no means absolute. There are several instances of breakdown of suppression in the literature (*e.g.* Abbott 1984, Carroll 1986, Price and McGrew 1991). Daughters among several species ovulate in the presence of their mothers if they are both housed with an unfamiliar male. This has led Abbott (1984) and Carroll (1987) to suggest that something other than dominance is operating to maintain reproductive suppression of daughters within their natal groups and effectively acts as an inbreeding avoidance mechanism.

Twinning

The marmosets and tamarins are unique among simians in their habit of twinning. While single infants and triplets are not uncommon among marmosets and tamarins, the most frequent litter size is two (Hershkovitz 1977). Occasionally, quadruplet births have occurred, but there are no reports of all four infants being born alive. The incidence of triplets has been reported to increase with time in captive colonies of *C. jacchus* and may relate to a high protein diet in captivity

(Hiddleston 1977). It is unusual for all three infants of a triplet litter to be parent-reared in captivity (pers. obs.). Recently, evidence from DNA studies has provided good evidence that triplets have been reared to independence in a wild group of *C. jacchus* (Dixson *et al.* 1992).

Callitrichid twins are dizygotic and share the same placenta and amniotic sac. Some considerable discussion has centred around whether twinning is a primitive feature that has been retained, or a derived feature. Hershkovitz (1977) maintained that twinning was a primitive feature, while most other authorities have considered it derived, citing the highly specialised placentation, simplex uterus, and number of teats as evidence (*e.g.* Ford 1980, Martin 1990, 1992).

There has also been some discussion about the selection pressure leading to the evolution of twinning. Leutenegger (1973, 1980) suggested that twinning in callitrichids evolved as a result of dwarfism. He argued that, as maternal body size decreases, the relative size of an infant increases. Eventually, the single infant is so large in relation to the mother that a high incidence of obstetric problems occur and he cites reports of obstetric problems in *Saimiri* as supporting evidence. In order to reduce these problems, selection favours females that produce two smaller, rather than one larger, infant. Martin (1992), on the other hand, argued that - while dwarfism might lead to selection favouring the production of smaller infants - it would not necessarily lead to an increase in litter size. He puts forward the alternative hypothesis that twinning has evolved in order to maintain a maximum intrinsic rate of population increase (r_{max}) that is predicted by the body weight range exhibited by the callitrichids. Citing data from Ross (1988), Martin suggested that *Callimico*, which has only a single infant, achieves its r_{max} by breeding at an earlier age than the marmosets and tamarins.

Infant care patterns among the Callitrichidae

It has been suggested that twinning has major consequences for the breeding female among the Callitrichidae. Not only must the female carry twin foetuses through pregnancy, she must also rear them to independence. Kirkwood and Underwood (1984) showed that in captive cotton-top tamarins, *Saguinus oedipus*, energy intake by the female increased during lactation. Price (1990) showed in the same species that, when lactating, feeding rates of females increased to a peak during the second month following birth, and only declined when infants began to receive food from other group members. Dunbar (1988), has used models developed by Altmann (1980, 1983) to predict the costs of twinning to tamarin mothers. His predictions suggested that a callitrichid mother could rear twins only if she did not have to carry them as well. In short, the female needs help if she is to rear both twins successfully. Several researchers have suggested that this is the reason for the communal or cooperative pattern of infant care seen among the callitrichids in which several, if not all, group members are involved in infant carriage and provision of food (*e.g.* Kleiman 1977, Sussman and Garber 1987, Dunbar 1988, Goldizen 1990). This will be discussed further in Chapter 6.

Recent reviewers of the social and reproductive systems of the marmosets and tamarins have attempted to interpret the inter-relationship between the sex ratio of wild groups, the mating systems that they exhibit and the rôle of helpers providing extra-maternal care of the offspring. These communal breeding systems have been referred to as 'cooperative polyandry' (Goldizen and Terborgh, 1986), 'facultative polyandry' (Goldizen 1987), or 'functional polyandry' (Sussman and Garber 1987). These reviewers have pointed to parallels with the social and reproductive sytems of some bird species. It has been shown, for instance, that among Florida scrub jays (*Aphelocoma coerulescens*) and grey-crowned babblers (*Pomatostomus temporalis*) breeding pairs with helpers rear more infants than pairs without helpers (Brown 1987). Florida scrub jay helpers are usually offspring from previous clutches that may stay with the breeding pair over several breeding seasons rather than leave to establish a breeding territory of their own. This is generally thought to relate to the availability of territories of suitable quality in which to breed, and it is proposed that the helpers gain through 'inclusive fitness' (Emlen 1984). Birds that exhibit polyandrous mating patterns include dunnocks (*Prunella modularis*), Tasmanian native hens (*Tribonyx morteirii*) and acorn woodpeckers (*Melanerpes formicivorous*) (Goldizen 1990). Sussman and Garber

(1987) consider that the social system of the acorn woodpecker is closest to that of the callitrichids, as it includes a promiscuous mating system resulting in functional polyandry (as only one female breeds) and the presence of helpers at the nest. The variability shown both within and between callitrichid breeding systems is, however, becoming increasingly apparent. For instance, differences have already been highlighted between breeding systems of the marmosets and tamarins that probably relate to fundamental differences in their ecology (Ferrari and Lopes Ferrari 1989). It is unlikely, therefore, that such generalisations about the callitrichid breeding systems will be sustainable in the future.

1.6 Aims of the study

The above review outlines the importance of *Callimico* both in its evolutionary uniqueness and as a tool for testing and evaluating theories of callitrichid reproductive strategies. The aim of the research was, therefore, to investigate the reproduction and social behaviour of *Callimico*, particularly in the following areas.

1. What is the physiological background to reproduction in the species - how is reproduction hormonally controlled among females?
    - what is the oestrous cycle length?
    - what is the gestation period?
    - does the species have a post-partum oestrus?
    - what are the major hormones of the oestrous cycle and pregnancy?

2. What is the behaviour of breeding pairs
    - do they form pair bonds?
    - is such a bond measurable?
    - how does their relationship change with time?
    - how does their relationship change when rearing infants?

3. Are polygynous social groups stable in captivity?
    - what are the social relationships within polygynous groups?
    - does reproductive suppression of subordinates occur among females in polygynous groups?
    - will successful breeding occur in polygynous groups?

4. What is the infant care pattern shown by the species - how does it relate to the single infant?
    - which animals are the major care givers?
    - how do caregiver patterns change with time?
    - what is the infant care pattern when the female does not have exclusive access to helpers in polygynous groups?
    - how do infant care patterns differ from the those of the marmosets and tamarins?

From the work outlined above, comment will be made on the interrelationship between twinning and social group structure, infant care patterns, and the rôle of caretakers. The effect of twinning on callitrichid social and breeding systems will be reassessed. These aspects of the biology of *Callimico* will be discussed in the light of current knowledge of evolutionary relationships within the Platyrrhini.

CHAPTER 2 MATERIALS AND METHODS

2.1 Subjects

The subjects of the study were contained in the colony of Goeldi's monkey *Callimico goeldii* maintained at the Jersey Wildlife Preservation Trust (JWPT). This colony was established in 1975 from three pairs of wild-caught animals, reported by the supplier to have originated in Bolivia. Since that time, careful group management combined with the introduction of new stock has minimised inbreeding. Following accepted guidelines for the husbandry of marmosets, tamarins and Goeldi's monkeys, husbandry methods have been based on a policy of minimal interference with the animals (*e.g.* Epple 1970, Lorenz 1972, Mallinson 1975). For instance, animal handling has been kept to a minimum, groups are allowed to expand through breeding from the starting point of a heterosexual pair, and young are not usually removed from their natal group unless they become peripheralised. Thus, the husbandry policy allows the undisturbed development of social relations, resulting in stable groups within the captive environment. Further details of the captive husbandry methods used in the colony are provided elsewhere (Carroll 1982).

When the study began, there were six breeding groups in the colony, each comprising an adult pair and their offspring. These breeding groups and their progeny were the subjects of the study. During the study, the colony was expanded by the establishment of new pairs and male-female-female trios that were included in the behavioural research.

The research project had two major components, a study of the reproductive physiology of breeding females, and a study of behaviour within the captive groups.

1. Reproductive physiology

An investigation of the endocrinology of reproduction in *Callimico* was carried out. The subjects were six adult females that were either pregnant or were presumed to be undergoing ovulatory cycles. They were all parous, in good health and physically mature. Details of these females are provided in Chapter 3, Table 3.1.

2. Behavioural study

Pair bonding

This study compared the social behaviour of adult *Callimico* in newly established pairs (early bonding), in pairs that were cohabiting with two independent offspring (established pair bonds) and in pairs cohabiting with two independent offspring while rearing a dependent infant (bonding during infant rearing).

This part of the study took place between September 1983 and February 1988. The subjects in the early pair-bonding study were all aged between 18 and 40 months and had not previously been housed with an unrelated member of the opposite sex. Table 2.1 lists the identities, ages and the dates of first pairing for the subjects involved. Study of bonding in new pairs began on the first day of introduction. Tables 2.2 and 2.3 give the compositions of the groups involved in the studies on established pairs and on bonding during infant rearing, along with the dates of commencement of study. In order to eliminate variability due to differences in group size, the decision was made to restrict observations to groups comprising the breeding pair and two surviving independent offspring. The possibility of variability due to sex and age of the offspring in the groups remained, but restricted availability of animals and the limitations of zoo conditions precluded control of these factors.

Study of Trios

This study examined bonding in male-female-female trios, and is reported in Chapter 5. Details of the composition of the study groups is given in Table 2.4.

Study of Infant Rearing

A study of infant rearing was carried out, as reported in Chapter 6. The subjects were the infants born into the groups used in the bonding study, detailed in Table 2.3. The date of commencement of the study was the date of birth of the infant.

Table 2.1 Subjects of the early pair-bonding study

		i.d.	**Age when introduced** (months)	**Date when introduced**
Pair 1	♂	M728	21 mo	05/09/1983
	♀	M696	38 mo	
Pair 2	♂	M751	40 mo	05/12/1983
	♀	M850	25 mo	
Pair 3	♂	M941	UNK*	07/03/1984
	♀	M577	36 mo	
Pair 4	♂	M800	35 mo	03/04/1984
	♀	M820	18 mo	
Pair 5	♂	M697	26 mo	03/07/1984
	♀	M777	24 mo	
Pair 6	♂	M1062	23 mo	15/08/1985
	♀	M440	37 mo	

* This male was bred in captivity at Stuttgart Zoo. His date of birth is unknown.

Table 2.2 Group composition in the study of established pairs

		i.d.	Age at start of study (months)	Date of start of study
Group 1	♂	M437	121 mo*	05/02/1983
	♀	M438	121 mo*	
	♂	M782	15 mo	
	♀	M817	9 mo	
Group 2	♂	M579	74 mo	11/06/1984
	♀	M521	89 mo	
	♂	M814	25 mo	
	♀	M922	9 mo	
Group 3	♂	M549	110 mo	05/03/1987
	♀	M509	117 mo	
	♂	M974	20 mo	
	♀	M1093	7 mo	
Group 4	♂	M941	72 mo*	25/08/1986
	♀	M577	101 mo	
	♂	M993	24 mo	
	♀	M1179	3 mo	
Group 5	♂	M705	72 mo	19/10/1986
	♀	M786	48 mo	
	♀	M1040	24 mo	
	♂	M1186	3 mo	
Group 6	♂	M627	102 mo	10/12/1987
	♀	M761	108 mo	
	♀	M1208	11 mo	
	♂	M1255	4 mo	

* based on estimated age when imported into the colony

Table 2.3 Group composition in the study of bonding during infant rearing (date of commencement of the study coincides with the date of birth of an infant).

		i.d.	**Age at start of study** (months)	**Date of start of study**
Group 1	♂	M437	123 mo*	07/03/1983
	♀	M438	123 mo*	
	♂	M782	17 mo	
	♀	M817	11 mo	
Group 2	♂	M941	68 mo*	16/04/1986
	♀	M577	98 mo	
	♂	M993	20 mo	
	♂	M1080	7 mo	
Group 3	♂	M549	103 mo	18/08/1986
	♀	M509	111 mo	
	♂	M974	12 mo	
	♂	M1022	10 mo	
Group 4	♂	M705	75 mo	31/12/1986
	♀	M786	51 mo	
	♀	M1040	27 mo	
	♂	M1186	6 mo	
Group 5	♂	M627	99 mo	03/08/1987
	♀	M761	105 mo	
	♀	M1190	16 mo	
	♀	M1208	8 mo	

* based on age estimated when imported into the colony

Animal I.D.	**Sex**	**Age at introduction to trio**	**Date ♀♀ introduced**	**Date ♂♂ introduced**	**Date trio disbanded**	**Comments**
Trio 1						
M705	♂	3 years 11 months	16.04.84	05.09.84	22.07.85	Trio stable 320 days. Infants born 8.3.85 and 3.4.85. Both infants reared. ♀1 dominant following fight July 1985.
M786	♀1	2 years 4 months				
M817	♀2	1 years 11 months				
Trio 2						
M904	♂	2 years 1 month	15.05.85	16.06.85	12.05.86	Trio stable 326 days. Infants born 14.2.86 and 5.5.86. Both died 3 days old. ♀2 dominant following fight May 1986.
M866	♀1	2 years 2 months				
M872	♀2	2 years 1 month				
Trio 3						
M878	♂	2 years 7 months	20.07.85	03.11.85	19.12.85	Trio stable 46 days. Neither female pregnant. ♀2 dominant following fight December 1985.
M922	♀1	1 year 9 months				
M947	♀2	1 year 8 months				

Table 2.4 Summary of the history of each of the three trios of Goeldi's monkeys.

2.2 Housing and husbandry regime

The subjects of the pair-bonding study were housed within the two marmoset complexes at Jersey Wildlife Preservation Trust. These buildings, each housing 10 breeding groups of marmosets, tamarins and Goeldi's monkeys, were designed specifically to house the Trust's collection of callitrichids and have been fully described by Mallinson (1975a, 1975b). Briefly, the first building constructed (the Miller range) has 16 inside cages, each measuring 122cm (width) x 91cm (depth) x 152cm (height). The floor of each cage is 76cm above the floor of the room to facilitate daily cleaning, which is accomplished by hosing the cage floors with water. There are 10 outside cages. Six of these are each linked to two inside cages while the remaining four are each connected to a single inside cage. The outside cages vary in height from 210-261 cm and in floor area from 6.7 m^2 to 8.9 m^2. Fig 2.1 shows a plan of the building.

The second building (the Eric Young range) has 10 inside cages each measuring 183cm (width) x 91cm (depth) x 152cm (height) and each being linked with an outside cage *via* a short tunnel. The outside cages are similar in size to those in the Miller range.

In both buildings, the inside cages are furnished simply with two horizontal wooden bars as perches, a ladder, a corner shelf, two feeding platforms and a nest box (see plate 2.1). The nest box is a simple wooden box measuring 30cm (width) x 23cm (depth) x 28cm (height). The animals gain access to the box through a hole 15cm in diameter which can be closed from outside the cage. The nest box is situated at the front of the cage in the top left hand corner. Although the marmosets and tamarins in the colony sleep in the box and use it as a refuge, *Callimico* rarely enter the box except during play chases.

Access to the inside cage areas is restricted to a small number of the Zoo's keeping staff, whereas the outside cages are on public display.

The subjects in the study of trios were housed either in the Behavioural Research Unit (BRU) (Trios 1 and 3) or in a similar unit in the Zoo (Trio 2). Oliver (1983) provided details of the construction of the BRU. The cages in the

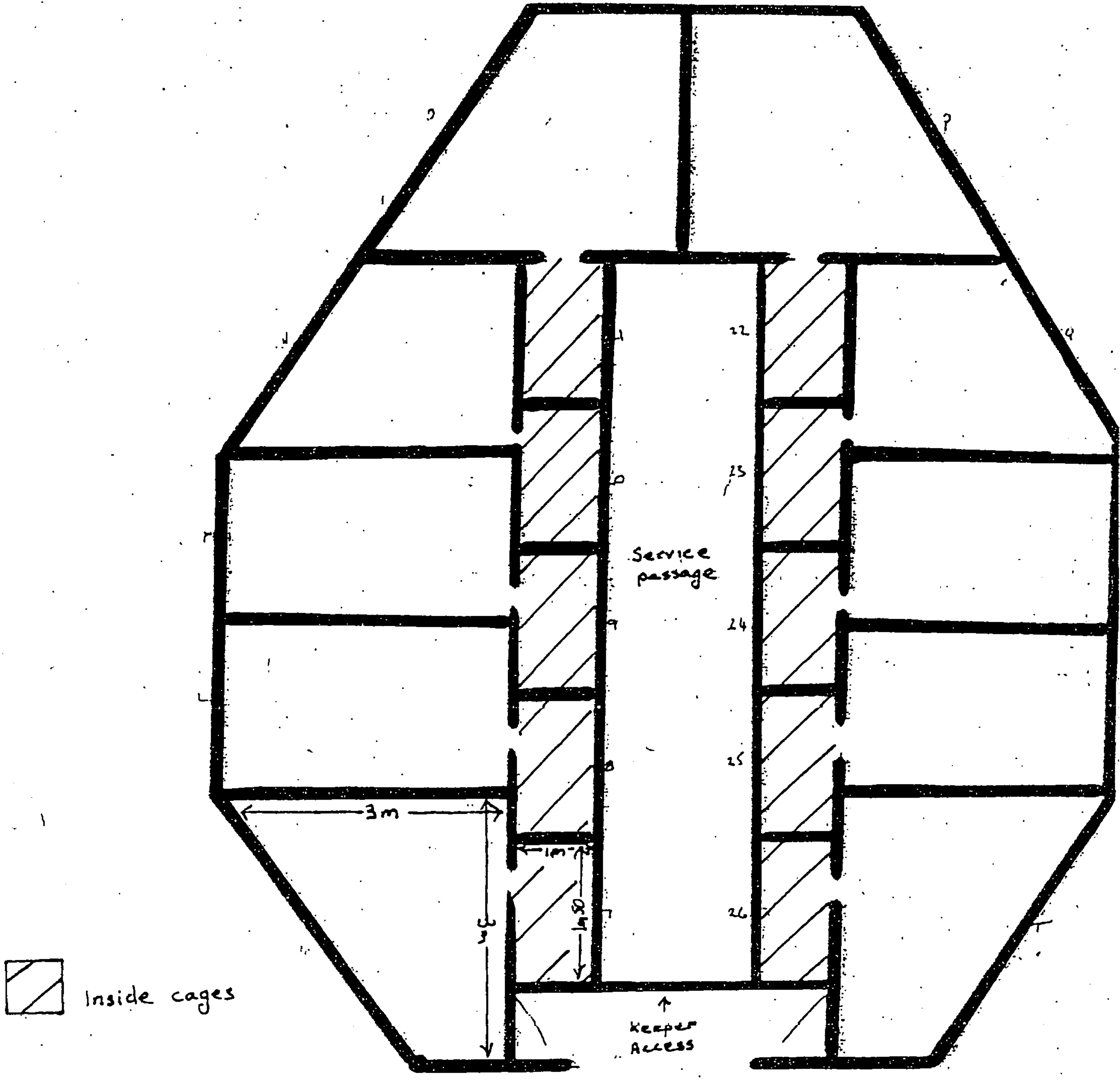


Fig 2.1 A ground plan of one of the Goeldi's monkey houses at JWPT

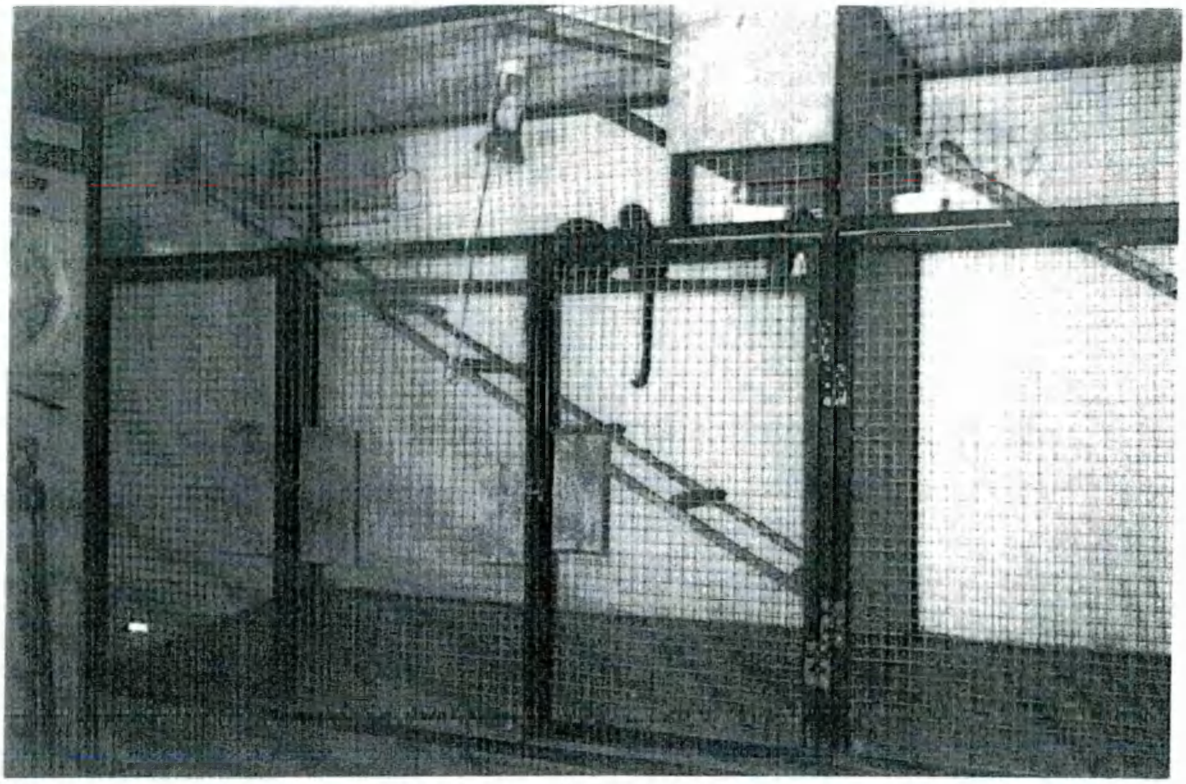


Plate 2.1 An off-exhibit cage for Goeldi's monkeys at Jersey Wildlife Preservation Trust.

BRU are not on display and comprise an indoor cage measuring 1.5m (width) x 2m (depth) x 3m (height) and a large outside cage measuring 6m (width) x 4m (depth) x 4m (height). Both inside and outside cages were furnished with natural branches. The inside cages also had a shelf, a nest box and a feeding platform. The outside cages were planted with shrubs and had a grass floor.

The dietary regime for the *Callimico* at JWPT has been specified elsewhere (Carroll 1982, Allchurch 1985). In common with the marmosets and tamarins in the colony, they are fed three times daily, all food being presented in the inside cages. The first feed, a commercial primate diet, follows morning cleaning at around 09.30 hrs. The second feed contains a variety of chopped fruit and a high-protein item, such as commercial cat food or hard boiled eggs, and is presented at midday. The third feed consists of small high-protein items, such as insects or freshly killed young mice (3-6 days old), and is provided at about 16.00 hrs.

The daily cleaning routine begins at 08.00 hrs. The cage floors are hosed clean and the feeding platforms wiped with warm water and detergent. Once monthly, each cage is thoroughly cleaned, the walls, wire, and perches being scrubbed with warm water and detergent and then rinsed. Nest boxes are cleaned twice yearly. They are rarely soiled with faeces and the accumulation of scent mark secretions helps to reinforce the inside cage area as the most secure part of the group's territory.

Groups are housed in such a way that they do not have visual contact with conspecifics; nor are conspecifics housed in adjacent cages even in the absence of visual contact.

This husbandry regime gives the animals a varied environment, with the inside cages providing a secure refuge from the weather and from the effects of being on public display. In the inside cages, a policy of non-interference with the animals reduces stress and encourages expression of a wide variety of social behaviours.

2.3 Data collection

1. Reproductive Physiology

In order to monitor changes in the levels of hormones over time, it is necessary to take samples at regular intervals. Either blood or urine can be used, as it has been shown with callitrichids and small cebids that reproductive hormones can be detected in both (e.g. Hodges *et al.* 1981, Abbott 1984). Collection of blood samples requires invasive techniques, but circulating hormone levels in the blood are most relevant to physiological events taking place in the body. The use of urine sampling, by contrast, permits a non-invasive investigation, but measurement and interpretation of hormone levels in urine introduces certain problems. Oestrogens and progestagens are typically eliminated from the body as metabolites rather than as free hormones, and the levels in the urine may not accurately or immediately reflect levels in the blood. In spite of these potential drawbacks, the overriding factor in the present study was the need for a non-invasive sampling technique and urine sampling was therefore chosen as the appropriate approach. This has subsequently been shown to be a valid approach, as researchers in the Anthropological Institute of the University of Zürich have recently validated urinary hormone levels as a reliable indicator of circulating hormone levels in the plasma (C. Pryce, pers. comm.).

The technique of radioimmunoassay has proved to be extremely useful for measuring the levels of steroid hormones and their metabolites in urine samples. Radioimmunoassay is a method of indirect measurement using a radioactively-labelled form of the hormone to be measured, the basic assumption being that the labelled hormone will act in exactly the same way as the unlabelled form. The principle behind the technique is that a specific antibody to a given hormone metabolite is raised. A measured amount of the antibody, an excess of labelled hormone metabolite, and the sample containing the unlabelled hormone metabolite that is to be measured are mixed, and the antibody-antigen reaction is allowed to reach equilibrium. At this stage, the labelled and unlabelled hormone are bound to the antibody in proportions equal to that in which they are present in the reaction mixture. Unbound hormone metabolite (both labelled and unlabelled) is then removed from the sample and the amount of radioactivity remaining is measured. Comparison of the amount of radioactivity with a standard curve then allows estimation of the amount of hormone metabolite present in the original sample. Further details of the methodology used during the study of reproductive hormones are given in Chapter 3.

2. Behavioural study

Identification of animals

Individual Goeldi's monkeys do not often have obvious distinguishing characteristics and can be difficult to distinguish from one another without practice. Familiarity with the study groups, acquired by working with them over several years prior to the study, allowed accurate identification of individuals to be made on the basis of minor differences in size and pelage. For instance, the amount of brown flecking on the thighs, the height of the erect crest of hair on the head and the shape of the face are all variable. Such distinguishing characteristics were used during the study as aids to recognition. In addition, where there was a possibility of confusing individuals because of their physical similarity, a 2cm band of hair was clipped from the tail of some animals. Varying the position of the clipped region on the tail allowed up to three animals to be clipped in a group, with the fourth left unmarked.

These methods of recognition proved quite satisfactory, and obviated the need for dye-marking of individuals or the use of coloured medallions. Any use of such methods would have conflicted with the aim of displaying the colony to the public under simulated naturalistic conditions.

Ethogram

An ethogram for *Callimico* was published by Heltne *et al.* (1981) describing 38 behaviours, including nine vocalisations. Although some of these behaviours are unique to *Callimico*, many are also performed by the callitrichids or by other primates and had been described previously (e.g. by Stevenson and Poole 1976). Some of the behaviours unique to *Callimico* had also been defined previously (Omedes and Carroll 1980). In order to maintain consistency with previous published work on callitrichid social behaviour, the terminology used here follows that of Stevenson and Poole (1976). A previous behavioural study of *Callimico* (Omedes and Carroll 1980) provided the basis for the choice of categories of behaviour used in this research. A brief description of the behavioural categories is given below. Where the behavioural category has an alternative name, this is also given. The names of behavioural categories are given in bold type.

Non-social behaviour

Feed included manipulating and searching for food (foraging), as well as eating. Thus an animal searching through the contents of a food dish was recorded as feeding. Drinking was not recorded.

Autogroom was scored when the subject groomed itself for more than three seconds. This category did not include scratching, which was not recorded.

Locomotion involved the spatial displacement of the subject by at least 10 cm. Changes of position during resting or grooming were thus not recorded as locomotion.

Spatial relationships

Proximity and **contact** were recorded. **Proximity** was scored whenever the torsos of the subjects were less than 15 cm apart but not touching, and **contact** was scored when the subjects were touching. An **approach** was scored when one animal moved to within 15 cm of another and stayed within that distance for at least three seconds. A **leave** was scored when an individual moved out of proximity or contact (*i.e.* more than 15 cm away) for more than three seconds.

Social behaviour

In all social behaviour, both the recipient and performer of the behaviour were recorded.

Allogrooming - the subject groomed another individual by parting the fur manually. The mouth and tongue were used to clean the groomee. Allogrooming may be solicited by a **sprawl.** The addressor approaches the addressee and presents its head and shoulders to be groomed (= grooming solicit crouch, Heltne *et al.* 1981).

Play included all playful behaviours such as play chasing, rough-and-tumble play and play wrestling.

All agonistic behaviour shown between members of the pair was lumped into the one category of **aggression. Aggression** included physical contact such as pushing and cuffing (= 'fight' in Heltne *et al.* 1981). Frequently, **aggression** toward another individual was indicated by a stare, lowering the brows, and approaching the addressee, who would retreat. No fighting occurred during the observation periods.

Arch bristle leap (ABL) is a mobbing behaviour performed as a response to threat. It may be directed both toward non-group *Callimico* and to other species. The behaviour is rarely performed by a single animal. Usually, several group members perform ABL simultaneously. The performers piloerect and leap from perch to perch, holding an arch posture for up to a second before leaping from one perch to another. While pausing between leaps, the addressee is stared at, and an open mouth call may be given. The animals may leap within inches of the addressee. In the wild, this has been observed as a mobbing response to ground predators (Pook 1979a, Heltne *et al.* 1981). It is broadly similar to, but a more direct threat than, the 'arch bristle movement' described by Stevenson and Poole (1976) for the common marmoset. This behaviour is frequently seen in the colony at JWPT, but was not included in the ethogram of Heltne *et al.* (1981). The bipedal guard stance and bipedal threat, both static threat displays described by Heltne *et al.* (1981), were not seen. The only bipedal posture was seen in the context of sexual behaviour (see below).

Scent marking

Tail anoint - the tail is coiled between the legs, moistened with urine and rubbed against the scent gland fields of the anogenital region and sometimes along the mid-line of the ventrum to the sternal scent gland (= tail mark, Heltne *et al.* 1981).

Nose rub - the muzzle and chin are rubbed against the substrate, sometimes accompanied by sneezing. Heltne *et al.* (1981) considered this to be a scent-marking activity and not merely a means of cleaning the face. Although not previously recognised as a scent-gland field in primates, Heymann *et al.* (1989) have recently demonstrated histologically the presence of scent glands around the muzzle of *Saguinus mystax*. Unfortunately, the action performed in the nose-rub scent mark is also shown in cleaning the muzzle. Rubbing the nose and mouth against the substrate is seen frequently if an animal has a nasal discharge, or if food adheres around the mouth. It is thus impossible to distinguish scent marking from hygiene; accordingly, nose rub was considered separately from the other scent mark categories in analysis.

Anogenital - the scent glands of the perineal and subcaudal areas are rubbed against the substrate (= anal rub, Heltne *et al.* 1981).

Suprapubic/sternal - the scent-gland fields of the ventrum are rubbed against the substrate. In callitrichids, sternal scent marks are easily distinguishable from suprapubic marks, but in *Callimico* they are not. In contrast to the callitrichids, which have separate sternal and suprapubic scent gland fields, the glands of *Callimico* extend along the ventral mid-line from the genitalia to the sternum. During a mark, many or all of these fields may be rubbed against the substrate (= ventral rubs, Heltne *et al.* 1981).

Sexual behaviours

Bipedal stance - the female approaches the male and stands bipedally with her sternum close to the male's face and her arms held at right angles to her body. This behaviour was only seen to be performed by females and is presumably a sexual solicitation behaviour. It was seen most frequently accompanying **presenting.**

Present - the female stands quadrupedally in front of the male, facing away from him, and frequently looks over her shoulder at him. She will sometimes reach back towards the male with one of her hands and may walk backwards towards him (= solicit mounting, Heltne *et al.* 1981). Bipedal stance and present were together regarded as **proceptive behaviour.**

Sniff genitals - olfactory investigation of the partner's genital region, sometimes accompanied by licking; usually performed by the male (= scent licking, Heltne *et al.* 1981).

Mount refers to typical primate mounting. The male holds the female around the ribs while attempting to manoeuvre into a position for intromission. Where **thrusting** accompanied a mount, intromission was assumed to have been attained. There was no indication of ejaculation, although semen was occasionally seen on the male's penis during post-copulatory grooming. It was presumed that all mounts accompanied by thrusting resulted in ejaculation, as the male invariably did not attempt to mount the female again immediately, grooming his genitals instead.

Tongue flick - the tongue is rhythmically protruded about three millimetres through the lips, usually when the addressor approaches another individual.

Infant care

Carrying is a major component of infant care. An infant was scored as carried if its weight was supported by the carrier. If it was not carried by this definition, it was recorded as **off.**

In the breeding groups, infants were carried by several group members. A **transfer** was recorded when an infant moved from one carrier to another. Transfers commonly occurred as a result of the carrier rubbing the infant against the substrate, and another coming to take it in response to the infants calls. They also occurred as a result of an animal approaching the carrier and taking the infant, or as a result of the infant moving independently from one carrier to another. Transfers were therefore recorded as **carrier-initiated, receiver-initiated,** or **infant-initiated**. Unsuccessful transfers were recorded as **attempted transfers.**

Suckling was recorded when the infant's head was under the mother's armpit where the nipple is located. Usually, a mother is alert and in a sitting position when suckling the infant.

Food sharing was recorded when an item of food was transferred from one individual to another. This was usually, but not exclusively, from an older animal to an infant in response to begging by the infant. On one occasion, an animal was seen to offer food to an infant. The infant approached the adult in response to the adult reaching towards the infant with food in its outstretched hand. The offering of food to infants by adults has been reported for several species of marmoset and tamarin as well as for Goeldi's monkey (Feistner and Price 1990, 1991).

Observation procedures

All observations were made while the subjects were confined to the inside cages. This allowed continuous monitoring of behaviour, as the animals were always in view. It also removed a possible source of variation in the data, as inside cages are all furnished in a similar way, while the outside cages vary considerably in the arrangement of branches as well as in the amount and nature of natural vegetation they contain. Further, the animal's use of outside areas is subject to seasonal variation and day-to-day variation in the weather conditions.

During data collection, the observer sat in the passage in front of the cage in view of the occupants. All the animals had been previously habituated to the presence of an observer in the building, and in every observation session a settling period of five minutes was allowed between the arrival of the observer and recording of data. An electronic timing device emitting an audible tone (a 'bleeper') was used to indicate time intervals. The tone was audible only to the observer *via* an earpiece.

Observations were made between 12.00 hrs and 15.00 hrs, at least 30 minutes after the midday feed had been presented. Observations could only be made during this period in order to take account of the husbandry routine and duties of the animal keepers, including those of the researcher. Restricting observations to this period may have had the effect of reducing the range of behaviours seen. On the other hand, it reduced the effect of variation of behaviour through observing at different times of day. Observation periods were 30 minutes long and one hour of data was collected on each observation day.

Data were collected on checksheets. Previous familiarisation with the checksheet had taken place during an earlier study on the callitrichid colony (Omedes and Carroll 1980).

Focal animal sampling was chosen as the method for sampling behaviour (Altmann 1974). In the pair-bonding study, both the male and female subjects were sampled simultaneously. This was possible because both the subjects were continuously visible and clearly identifiable. In the trios study, all three subjects were sampled simultaneously.

Behaviours of longer duration - *viz.* locomotion, feeding, autogrooming, allogrooming, infant carrying, as well as proximity data - were recorded using instantaneous sampling at 15 second intervals. The 15-second time interval has been used previously for studies of callitrichid behaviour and was therefore felt to be appropriate for *Callimico* (e.g. Omedes and Carroll 1980, Evans 1981). In her study of cotton-top tamarins, Price (1990) compared actual frequencies with data obtained by instantaneous sampling at several time intervals. She found that the 5, 10 and 15 second time intervals were equally good at estimating durations of behaviour, while 30 and 60 second intervals were less efficient.

Instantaneous sampling is not an appropriate method, however, for recording behaviours of short duration such as approaches, leaves, scent marking, *etc.*. All events of behaviours other than locomotion, grooming, feeding and infant carrying were therefore recorded.

2.4 Statistical tests

All statistical tests carried out are described by Siegel (1956) and Sokal and Rohlf (1981). Non-parametric tests were used throughout the analysis, as it was difficult to be certain that the conditions necessary for parametric tests had been met. Firstly, the sample sizes were small (*e.g.* $N=5$ in the infant rearing study, and $N=6$ in the pair-bonding study), and hence the distribution of the data was difficult to assess. Secondly, in within-pair comparisons over time it is unlikely that the data are independent, as the behaviour of one member of the group affects that of other members, and behaviour on one day may affect that on the next day.

The tests were performed either by hand or by using the MS-DOS versions 5.1 and 6.1 of Minitab statistical software (Cle. Com. Ltd, 97, Vincent Drive, Edgbaston, Birmingham B15 2SQ) on an IBM PC/XT, or IBM AT. All tests were two-tailed and $p<0.05$ was used as the level of significance.

2.5 Problems of studying under zoo conditions

Study of animals in the zoo environment poses certain problems peculiar to that situation which deserve mention here, as they affect both the scope of the research, and the methods used in it..

The primary aim of a zoo is either to display animals for entertainment or education, or to hold breeding colonies for conservation reasons. These aims must be met before the needs of research, and they inevitably restrict the options for any research programme that relies on manipulation of the subjects in order to test hypotheses.

Whatever the ultimate aim, zoo colonies of primates tend to be small, usually comprising only one or two groups. This results in a small number of subjects being available. In this study, a core of six breeding groups was available for study and, while offspring of those groups could be used to make new breeding pairs, cage space was limited by the need to house other species. As well as limiting the number of breeding groups available for study, this also limited the length of time that new pairs could be held for the pair-bonding study. As a result, observation on any new pair was limited to a period of one month.

The *Callimico* in this study were part of a primate colony which has the primary purpose of captive breeding for conservation. Accordingly, the colony is managed in such a way as to maintain optimum conditions for reproduction, which generally means maintaining a quiet and stress-free environment, conditions that are held to be vital for successful reproduction of small New World primates (Lorenz 1972, Mallinson 1975, Beck *et al.* 1982, Carroll 1982, in press). This necessarily results in a serious constraint to the amount of manipulation that can be carried out within the colony. For instance, if a pair is to be used for breeding purposes, it is not compatible to use it to study the effects of separation on the relationship between members of the pair. Similarly, the effects of an intruder may undermine the territorial security that a pair enjoy, and hence an intruder study may not be desirable. At the time that this study was designed, Goeldi's monkeys were relatively uncommon in captivity and the need for continued successful captive breeding in the colony was paramount.

The animals in this study were part of a public display that had to continue throughout the study. This also limited the options for manipulation of the subjects and the times at which behavioural observations could be made. In particular, the needs of public display increase the husbandry time needed to maintain a clean environment. The display cages must not only <u>be</u> wholesome and healthy, they must also <u>look</u> so. Therefore, the times of least disturbance to both the animals and the colony routine had to be chosen for observation. In this study, this meant limiting the times of observation to a 4-hour period in the middle of the day.

These constraints mean that the zoo environment is not as conducive to manipulative research as is the research laboratory. While rare species are kept primarily or exclusively in such breeding colonies, however, these limitations must be accepted as a precondition for essential research.

CHAPTER 3 URINARY OESTROGEN EXCRETION DURING THE OVARIAN CYCLE AND PREGNANCY IN GOELDI'S MONKEY (*Callimico goeldii*)

3.1 Introduction

In mammals, the physiology of reproduction is controlled by a suite of interacting hormonal mechanisms. These have been well studied in many species, including the higher primates (*e.g.* in apes - Martin *et al.* 1975, Kingsley 1980, Czekela *et al.* 1988, Masters and Markham 1991; Old World monkeys - Townsley 1974, Ando *et al.* 1976, Abbott *et al.* 1986; New World monkeys - Bonney *et al.* 1979, Nagle *et al.* 1979, Abbott 1984, Epple and Katz 1984, Heistermann *et al.* 1987, Pryce *et al.* 1988).

The marmosets and tamarins have been, and continue to be, of particular interest to researchers in this field for several reasons:

1. The importance of captive breeding of callitrichids both as laboratory primates and for conservation reasons.
2. Their tendency to form monogamous groups in captivity which led to the belief that the species in the group were exclusively monogamous.
3. The reproductive suppression of non-breeding females in both family groups and peer groups.
4. Their unique habit (among the higher primates) of twinning.
5. Communal rearing of infants.
6. The relationship between reproductive hormones and behaviour.

Endocrinological studies have provided basic information on the reproductive biology of a growing number of callitrichid species; the common marmoset *Callithrix jacchus* (*e.g.* Abbott 1977, Abbott *et al.* 1987, Eastmann *et al.* 1984, Hearn 1977, Hearn and Lunn 1975, Hodges *et al.* 1981), the pygmy marmoset *Cebuella pygmaea* (Ziegler *et al.* 1990), the saddle-back tamarin *Saguinus fuscicollis* (Epple and Katz 1984), the cotton-top tamarin *S. oedipus* (Brand 1981, French *et al.* 1984, Heistermann *et al.* 1989, Ziegler *et al.* 1987), the red-bellied tamarin *S. labiatus* (Pryce *et al.* 1988) and the pied tamarin *S. b. bicolor* (Heistermann *et al.* 1987). Information on basic features such as ovarian cycle length and gestation length for these species allows interpretation of social behaviour to be made against a background of the underlying physiological status of the female. Studies of reproductive suppression among females have been useful in interpreting social group structure and intrasexual behaviour within groups.

In common with the marmosets and tamarins studied to date, Goeldi's monkeys do not demonstrate any overt signs of their reproductive status, such as menstruation or a change in sex skin swelling or coloration. Monitoring of hormonal changes, therefore, represents the only reliable way to detect ovulation and pregnancy. Measurement of urinary oestrogens has proved particularly informative as regards ovarian cyclicity and pregnancy in New World primates (*e.g.* Brand 1981, Eastman *et al.* 1984, Epple and Katz 1984, French *et al.* 1984, Hodges and Eastman 1984, Hodges *et al.* 1979, 1981, Lunn 1978, Pryce *et al.* 1988). The collection of voided urine allows studies to be carried out in a non-invasive way, in contrast to collection of serial blood samples, which may lead to considerable stress for the animal and which may itself affect ovarian function.

In spite of similarities between the callitrichids and *Callimico* under captive conditions (*e.g.* stability of monogamous groups, lack of breeding by mature daughters in family groups), the differences between them (*e.g.* birth of single infants, the possibility of naturally occurring polygynous groups in the wild in *Callimico*) suggest that there are likely to be differences in their reproductive physiology. Most particularly, observations of polygynous groups in the wild suggest that there is no reproductive suppression of subordinates in groups containing more than one unrelated female.

No studies of the reproductive physiology of Goeldi's monkey had been carried out prior to the present investigation, although other studies on ovarian function (Christen *et al.* 1989) and on pregnancy (Ziegler *et al.* 1989, 1990) were conducted elsewhere after the project was initiated.

The aims of this study were to:

(i) identify the major oestrogen metabolites excreted in the urine of Goeldi's monkeys during the ovarian cycle and pregnancy from a representative number of females

(ii) demonstrate that the measurement of the principal urinary oestrogen metabolite provided a reliable marker of ovarian cyclicity and pregnancy

(iii) establish ovarian cycle length and gestation length through measurement of hormonal metabolites

(iv) determine whether ovarian cycles are suppressed in socially subordinate female Goeldi's monkey

A concurrent behavioural study examined changes in sexual behaviour changes across the ovarian cycle to ascertain whether a peak in sexual activity coincided approximately with the time of ovulation as indicated by the endocrine parameters.

3.2 Methods

Study subjects

Six adult female Goeldi's monkeys were used in this study. Table 3.1 gives details of the animals and the dates of investigation. The females were housed as described in Chapter 2 and were studied under three conditions:

(i) In male-female pairs (n=2 females)

(ii) In male-female-female trios (n=4 females)

(iii) Three of the above females were also studied prior to the introduction of a male (in one pair and one trio).

Urine sample collection

Urine samples were collected either by using a syringe to remove urine from the floor of the cage of an isolated female, or by using a cup to catch the first morning urine as it was voided. In the former situation, samples were collected between 07.30hrs and 11.00hrs, whereas in the latter case they were collected shortly after the room lights were switched on at 07.30hrs. Samples were normally collected at intervals of 1-3 days over periods of between 1.5 and 5.5 months (see Table 3.1 for details). Directly after collection, urine samples were stored at -30°C until assayed.

Table 3.1 List of female Goeldi's monkeys used in the study groups, showing times of male introduction, urine sampling and behavioural observation

Female	Group	Period of urine sampling	Period of behavioural sampling
M440	Single	12 June - 16 August 1985	-
M440	Paired with male on 17 August 1985	17 August - 26 November 1985	17 August - 16 September 1985
M820	Paired with male on 3 July 1984	27 June - 7 August 1984	3 July - 2 August 1984
M947	Single	12 June - 20 July 1985	-
M947 M922	Trio (No 3) Male introduced on 3 November 1985	24 October - 27 February 1986	3 November - 5 December 1985
M866 M872	Trio (No 2) Male introduced on 16 June 1985	17 February - 21 April 1986	-

Creatinine determination

When measuring levels of hormone in urine, it is necessary to control for variations in the volume and concentration of voided urine. This is achieved by determining the creatinine content of the urine as this urinary product is excreted at a virtually constant rate. Urinary hormone concentrations were hence expressed as mass/mg creatinine (mgCr). The following methodology, as used by Brand (1981), was used to determine the creatinine content of each urine sample.

Reagents

Alkaline triton X-100
Saturated picric acid
Deionised distilled water (DIDW)

Procedure

1. The alkaline triton was freshly prepared by adding 12.5 ml 1N NaOH to 4.2 ml triton X-100 followed by the addition of 66.0 ml DIDW.
2. The alkaline triton was then used to prepare the working picrate reagent by mixing one volume of alkaline triton with one volume of saturated picric acid and four volumes of DIDW.
3. Urine samples were thawed and two 25 μl aliquots taken from each sample and dispensed into light-path plastic cuvettes.
4. 3.0 ml picrate reagent was added to each cuvette, then left for 1½-2 hours away from direct light.
5. The absorbance of each sample was then determined at a wavelength of 520 nm in a colorimeter.

A standard curve was prepared for each assay session using triplicate standard dilutions of creatinine at 0 to 3.0 mg creatinine/ml. The colorimeter was zeroed using the 0 mg/ml standard, while the 3.0 mg/ml standard was used to set the top of the scale. Creatinine content of each sample was determined by comparison with the standard curve.

Immunoreactive oestrogens

a) Hydrolysis of oestrogen conjugates

Mammals generally excrete high proportions of oestrogen in a conjugated form, including glucuronides, sulphates and other, unidentified conjugates in order to be rendered soluble in urine (Hodges *et al.* 1979, 1983, Hodges and Eastman 1984). It is necessary to determine the most abundant form in which oestrogens are excreted for two reasons. Firstly, the most abundant form is more likely to reflect hormonal levels in the blood and secondly, small changes in concentrations can be monitored. Oestrogens may be excreted as oestrone or oestradiol in the glucuronide or sulphate forms, or as some other unidentified conjugate. To determine the most abundant urinary oestrogen metabolite during the follicular and luteal phases of the ovarian cycle and during early pregnancy, sequential enzyme and acid hydrolysis was carried out on urine samples from study females and the liberated oestrogens measured by specific radioimmunoassay. In this process, the amount of free oestrogen in the urine is measured first. This is followed by the use specific enzymes to separate the conjugate from the oestrogen, and the amount of free oestrogen liberated is measured. This is carried out firstly with a glucuronidase, to remove the glucuronide fraction, followed by a sulphatase, to remove the sulphate fraction. This is followed by acid hydrolysis, or solvolysis (Hawkins and Oakey 1974), a stringent procedure that liberates oestrogen from all known conjugates (Eastman *et al.* 1984, Hodges and Eastman 1984). These procedures were carried out by Dr D. Abbott and L. George, while I was in attendance.

Enzyme hydrolysis was performed sequentially (Eastman *et al.* 1984) on urine samples from three females in the follicular phase of the ovarian cycle, three females in the luteal phase and one female during the early stages of pregnancy. Hydrolysis began with β-glucuronidase (Sigma Chemical Co., Poole, Dorset; activity 600,000 Fishman units/g: 300 Fishman units being added per tube to 50 μl aliquots of Goeldi's monkey urine diluted 1:20), was followed by sulphatase (Sigma Chemical Co.; 20,000 Fishman units/g: 20 Fishman units being added per tube), and concluded with acid hydrolysis. The amounts of oestrone and oestradiol released by each procedure were measured by specific radioimmunoassay (Eastman *et al.* 1984) and are expressed as μg/mg Cr in Table 3.2. Oestrone accounted for 90-97% of the urinary oestrogen measured. Between 85-96% of the urinary oestrone measured was released by β-glucuronidase enzyme hydrolysis (glucuronide fraction in Table 2), indicating oestrone glucuronide as the principal urinary oestrogen metabolite at all stages of the reproductive cycle.

Procedural losses during extraction were estimated in triplicate by the addition of tracer amounts (2000 c.p.m./20 μl) of [^{3}H] oestrone (spec. act. 91 Ci/mmol) to 50 μl of a diluted urine pool. Mean recovery was 86.0 ± 1.8% (mean ± s.e.m., n = 5). These values relate to the recovery of unconjugated fractions in Table 3.2.

The efficiency of each hydrolysis step was determined by hydrolysing trace amounts of [^{3}H] oestrone-3-glucuronide (spec. act. 53 Ci/mmol) and [^{3}H] oestrone-3-sulphate (spec. act. 60 Ci/mmol) to oestrone in 50 μl diluted urine. The recoveries obtained were as follows:

1. β-glucuronidase
   Recovery from oestrone-3-glucuronide was 68.9 ± 10.4% (n = 5) and from oestrone-3-sulphate, 3.5 ± 0.4% (n = 5). These values relate to the glucuronide fraction in Table 3.2.

2. sulphatase
   Recoveries were 75.9 ± 6.3% (n = 4) and 69.4 ± 9.7% (n = 5) from the glucuronide and sulphate forms respectively. These values relate to the sulphate fraction in Table 3.2.

3. acid hydrolysis
   Recoveries were 79.2 ± 2.4% (n = 5) and 65.7 ± 6.5% (n = 5) from the glucuronide and sulphate forms, respectively. These values relate to the residual fraction in Table 3.2.

These results confirmed the specificity of β-glucuronidase in cleaving glucuronide conjugates (Eastman *et al.* 1984).

Table 3.2 Urinary oestrogen conjugates during the ovarian cycle and one conception cycle in Goeldi's monkey

		OESTRONE (μg/mg Cr)				OESTRADIOL (μg/mg Cr)			
		Unconjugated fraction	Glucuronide fraction	Sulphate fraction	Residual fraction§	Unconjugated fraction	Glucuronide fraction	Sulphate fraction	Residual fraction§
<u>Ovarian cycle</u> Follicular phase*	Mean conc. (± s.e.m.)	0.02 ± 0.01	1.00 ± 0.34	0.07 ± 0.02	0.02 ± 0.01	-	0.07 ± 0.02	0.02 ± 0.01	0.01 ± 0.01
	Mean % of $E_1 + E_2$	2.1¶	81.8	5.6	2.5	-	6.1	1.6	1.0
Luteal Phase†	Mean conc. (± s.e.m.)	0.25 ± 0.06	8.73 ± 0.93	0.74 ± 0.11	0.11 ± 0.02	0.04 ± 0.01	0.88 ± 0.08	0.22 ± 0.03	0.01 ± 0.01
	Mean % of $E_1 + E_2$	2.3	79.5	6.7	1.0	0.4	8.0	2.0	0.1
<u>Conception cycle</u> 1-14 days after conception‡	Mean conc. (± s.e.m.)	0.15 ± 0.03	10.30 ± 2.42	1.50 ± 0.36	0.08 ± 0.01	-	0.20 ± 0.02	0.07 ± 0.03	0.01 ± 0.01
	Mean % of $E_1 + E_2$	1.3	82.8	12.0	0.6	-	2.1	0.9	0.1

* 14 samples from 3 females
† 9 samples from 3 females
‡ 5 samples from 1 female
§ Oestrogen liberated by solvolysis after enzyme hydrolysis
¶ Mean percentage of all oestrogen measured ($E_1 + E_2$): E_1 = oestrone; E_2 = Oestradiol

b) Radioimmunoassay for oestrone conjugates

On the basis of the above data, oestrogen in the urine from study females was monitored by a direct, non-extraction radioimmunoassay for oestrone-3-glucuronide (Hodges and Eastman, 1984; Hodges *et al.* 1984). Duplicate aliquots (5-20 μl) of urine were taken for assay. The antiserum used in the assay was raised in a rabbit against oestrone-3-glucuronide-BSA and showed the following cross-reactivities: 120% for oestrone, 62% for oestrone-3-sulphate, 2.0% for oestradiol-3-sulphate, <0.1% for oestradiol-17-sulphate, oestradiol-17-glucuronide and oestriol-16-glucuronide.

Using a biological system as an assay method requires close quality control. For that reason, the following quality controls are carried out: Each assay includes three standards of high, medium and low concentrations to assess interassay variability. In addition, the use of 10 replicates of the standards in occasional assays provides a measure of intra-assay variability. The accuracy of the assay is measured by addition of a known amount of hormone to a low concentration urine pool and the percentage recovery estimated. Assay precision is examined by measuring the standard deviation of the difference between duplicates from their mean ($d^2/2n$, where d = difference between the duplicates and n = number of duplicates considered). As non-specific binding (NSB) occurs (*i.e.* labelled hormone binds non-specifically to the antibody), an assessment of total NSB is required. This is achieved by addition of buffer to labelled hormone without the antibody present and the recovery of labelled hormone measured. It is also necessary to assess whether non-hormonal factors are interfering with the assay, and hence causing a reduction in the amount of radioactive hormone binding to the antibody. This is achieved by including a 'zero binding' assessment, where no sample is included in the assay tube. Lastly, in order to keep a check on % binding at the zero point of the standard curve, the total counts added to the antibody are assessed by running triplicate tubes containing only buffer and labelled hormone.

Assay protocol

1. Reagents

Reference standard - oestrone-β-D-glucuronide (Sigma No E1752)

Sodium phosphate buffer
Radioactive oestrone-3-sulphate (labelled with ^{3}H)
Antiserum - raised in a rabbit against oestrone-3-glucuronide-BSA
Dextran-coated charcoal suspension
Quality controls (QC) - low and high concentrations

2. Procedure

The assay tubes were set up as follows:

3 x total counts	(800μl buffer + 100μl tracer)
3 x NSB	(600μl buffer + 100μl tracer)
2 x zero binding	(500μl buffer + 100μl tracer + 100μl antiserum)
3 x standards	(500μl standard + 100μl tracer + 100μl antiserum)
2 x zero binding	as above
2 x QC	(500μl QC + 100μl tracer + 100μl antiserum)
2 x samples	(500μl sample + 100μl tracer + 100μl antiserum)
2 x QC	as above
2 x zero binding	as above
3 x total counts	as above

All the tubes were mixed in a vortexer and incubated at 4°C overnight. Following incubation, tubes were placed on ice for 15 minutes prior to charcoal addition. The Dextran-charcoal suspension was stirred and 200μl added to each assay tube (excluding 'total counts'). Tubes were vortexed, incubated for 15 minutes and centrifuged at 2400 rpm for 10 minutes at 4°C. The supernatant was then decanted and added to 8ml scintillation vials each containing 2ml scintillant, then shaken. After equilibration for at least two hours, vials were loaded into a liquid scintillation spectrometer (Model 3255 Packard Tricarb) and the beta-radioactivity measured.

Serial dilutions of Goeldi's monkey urine (0.1 - 10 μl) from two females in the luteal phase of the ovarian cycle and one pregnant female gave displacement curves parallel to that obtained with oestrone glucuronide standards. The mean ± s.e.m. recovery of unlabelled oestrone-3-glucuronide added to a Goeldi's monkey urine pool was 100.5 ± 6.9% (n = 7) over the standard curve range of 31.3-2000 pg/tube. The sensitivity limit of the assay at 90% binding was 6.1 pg/tube. Inter-assay precision was

10.6% with a urine pool of 10.0 ± 0.4 μg/mg creatinine (8 assays). Intra-assay precision was 4.0% with a urine pool of 3.89 ± 0.03 μg/mg creatinine (n = 24).

As the cross-reactivities with oestrone and oestrone-3-sulphate were so high, the assay was actually measuring free oestrone and oestrone sulphate as well as oestrone glucuronide. Accordingly, the results are expressed here as 'oestrone conjugates' (E_1C).

Ovarian cycle length and the estimated time of ovulation

All but one ovarian cycle length was estimated from the time of the rapid and sustained fall in urinary concentrations of oestrone-3-glucuronide to 5 μg/mg Cr and below, at the end of one cycle, until the next sustained fall in oestrone-3-glucuronide values to this level. The one exception was estimated from the time between the onset of two periods of sustained elevations of oestrone-3-glucuronide values above 5 μg/mg Cr. Thus, sustained elevations of urinary oestrone conjugates above 5 μg/mg Cr until the time of rapid and sustained fall in urinary oestrone conjugate values below 5 μg/mg Cr were designated as from the luteal phase of the cycle. The follicular phase then continued until urinary oestrone conjugate concentrations rose above 5 μg/mg Cr again. Ziegler *et al.* (1989) have shown that, during the *post-partum* ovulatory period, the urinary LH peak occurred at the time of the onset of the rise in concentrations of urinary oestrone conjugates. More recently, C. Pryce (pers. comm.) has found that there is a good correlation between urinary oestrone conjugates and plasma oestrone conjugates with the rapid rise in their concentration coinciding with the surge in plasma progesterone that accompanies ovulation. An estimated time of ovulation was, therefore, taken as the day before urinary oestrone conjugate concentrations reached 5 μg/mg Cr. This estimate may be inaccurate by 1-2 days, but this potential source of error is sufficiently limited for the purpose of this study.

Behavioural observations

Four of the six females were observed in their home cages for one month following the introduction of a male (two pairs and one trio: Table 1). Each pair or trio was observed for one hour every two days, between 1100-1530 hrs, as described in Chapter 2. Quantitative behavioural measurements were recorded on to check-sheets and the following behavioural categories were scored:

(i) female proceptive behaviour (sexual solicitation of the male by the female as previously described in Chapter 2).
(ii) mount
(iii) copulation (mount with thrusting)
(iv) sniff genitals
(v) approach
(vi) leave
(vii) time in proximity
(viii) allogroom
(ix) anogenital, suprapubic/sternal and tail anoint scent marking

Approach and leave data were used to calculate the Hinde Index, a measure of responsibility for maintaining contact and proximity (Hinde and Spencer Booth 1967, Hinde and Atkinson 1970), where I = % 'approach' by the male - % 'leave' by the male. If the index is positive, the male is more responsible than the female for maintaining proximity, and if the index is negative, the female is more responsible. This measure was also compared with the stages in the ovulatory cycle.

Statistical analysis of behavioural data was conducted using the Kruskal-Wallis one-way analysis of variance to detect differences in the levels of these behaviours between the follicular, periovulatory and luteal phases of the cycle. For the purposes of these behavioural analyses, the follicular phase of the cycle was taken as Days -11 to -3 from the estimated day of ovulation (Day 0), the peri-ovulatory period was taken as Days -2 to 2 and the luteal phase was taken as Days 3-12. Where a significant difference was indicated within the three phases of the cycle, *post-hoc* pair-wise Mann-Whitney 'U' tests were performed to indicate where the differences lay.

3.3 Results

Ovarian cycle

Four of the study females were found to be undergoing ovarian cycles. The mean ovarian cycle length was estimated to be 24.1 ± 0.9 days (mean ± sem; n=9 cycles). Fig. 3.1 illustrates the mean (± sem) values of urinary oestrone conjugates across the 24-day cycle. Measurement of urinary oestrone conjugates gave a clear indication of ovarian cyclicity, with values obviously elevated during the luteal phase. Mean urinary concentrations of E_1C were 1.18 ± 0.17 μg/mgCr during the presumed follicular phase (days -11 to -1), and 11.79 ± 1.02 μg/mgCr during the presumed luteal phase (days 1 to 12). Fig. 3.2 shows the hormonal profile of oestrone conjugates during three ovarian cycles in a typical female (M440), housed alone prior to the introduction of a mate.

Pregnancy

Concentrations of urinary oestrone conjugates were consistently elevated following conception in three females that were sampled through a conception cycle (M947, M440 and M866). Fig. 3.3 shows data from these three conception cycles. The fourth pregnant female in the study (M872) was sampled during the period -11 to -2 weeks prior to parturition. In this female, urinary oestrone concentrations were 130 ± 7 μg/mgCr (range: 71.6-224 μg/mgCr) during the sampling period (fig. 3.4). Two to three weeks following conception, urinary oestrone conjugate concentrations frequently exceeded the maximum value of 61.3 μg/mgCr found during the luteal phase of non-fertile cycles. In the only female (M866) to be sampled across the *post-partum* period, urinary oestrone conjugate concentrations fell from 130 μg/mgCr on the day after parturition to 1.17 μg/mgCr four days later. Values then remained low until after the *post-partum* conception occurred, approximately 15 days following parturition. The only two pregnancies which went to term (females M866 and M947) and were monitored for urinary oestrone conjugate concentrations at the time of

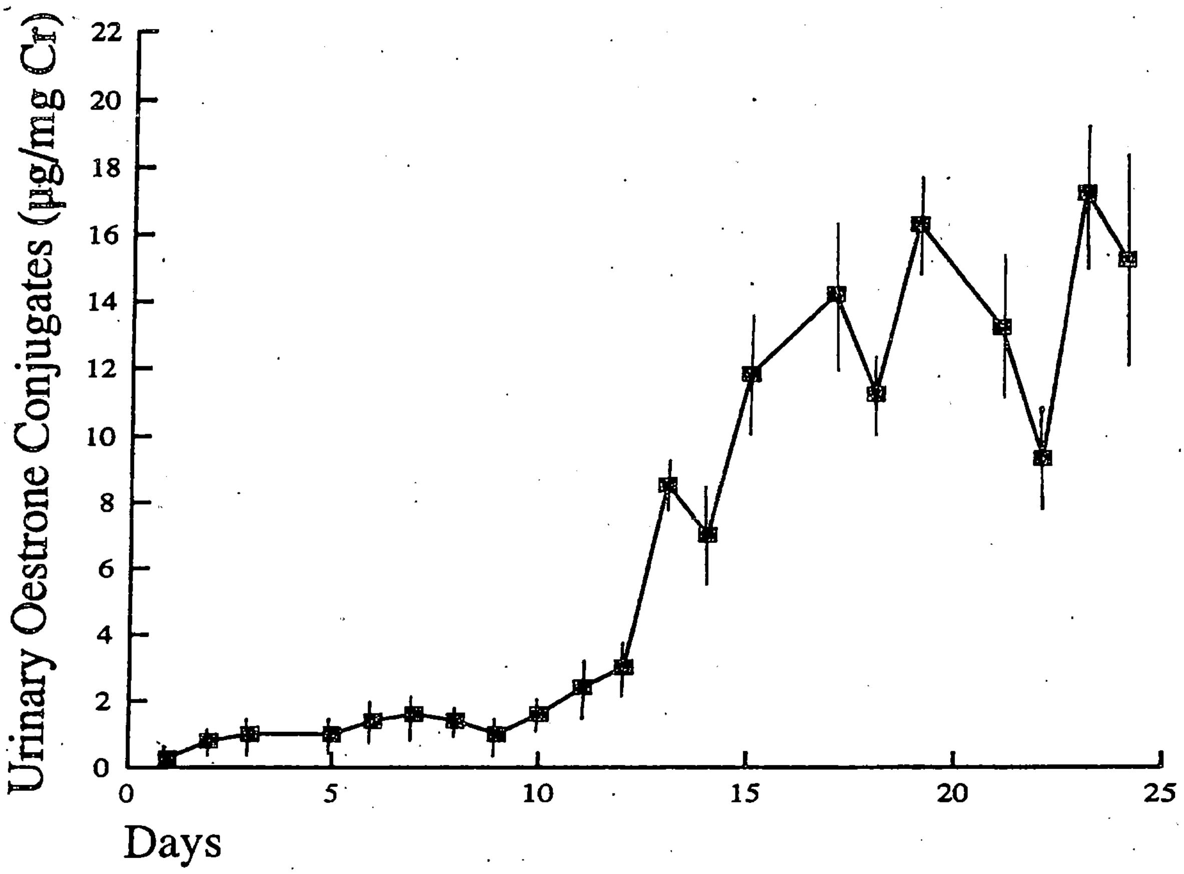


Fig. 3.1 Mean ± sem urinary concentrations of oestrone conjugates across the ovarian cycle in female Goeldi's monkeys (9 cycles from 4 females). The estimated time of ovulation is taken as the day before urinary oestrone conjugates rose above 5µg/mg Cr.

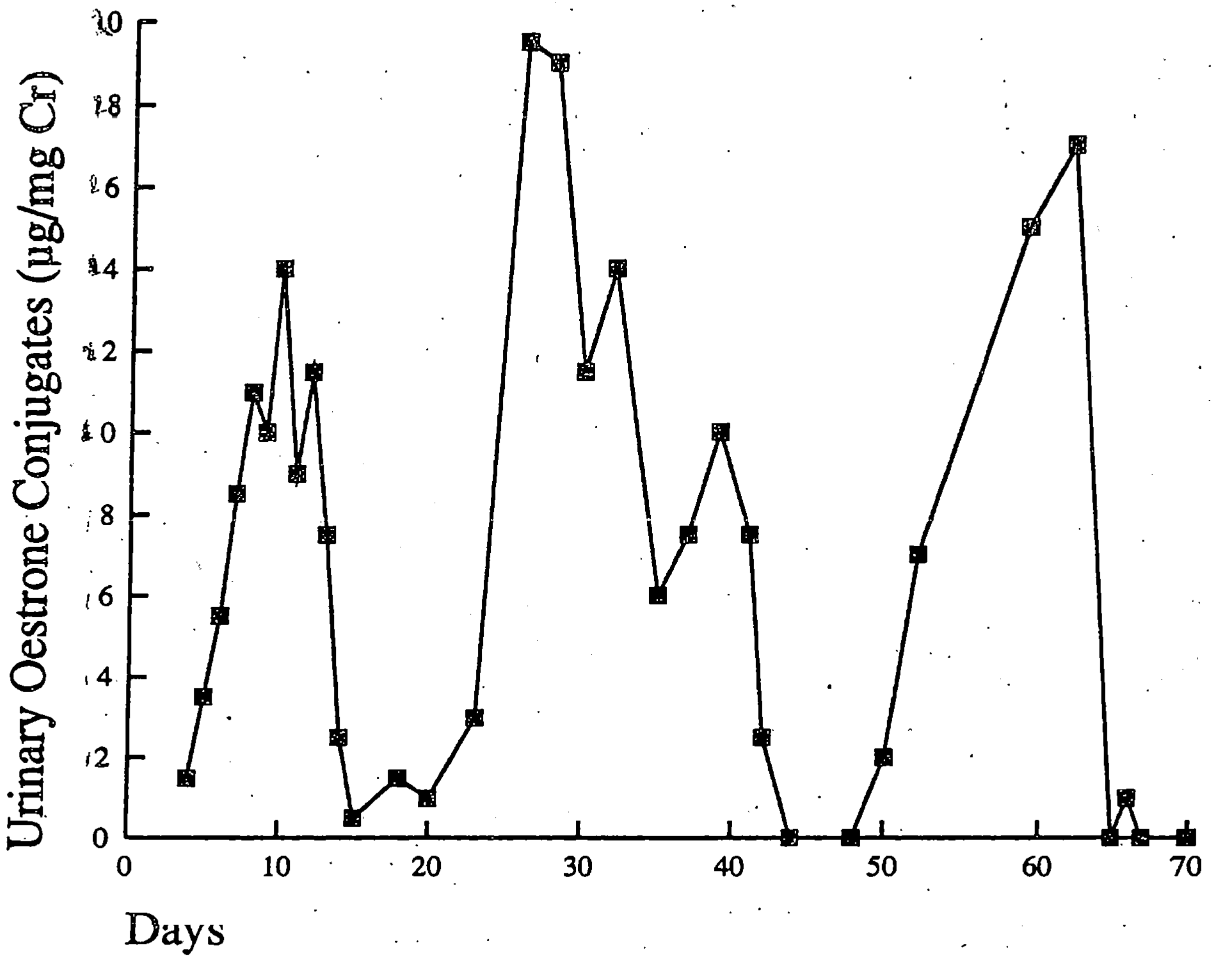


Fig. 3.2 The typical patterns of urinary concentration of oestrone conjugates across individual ovarian cycles in female Goeldi's monkey M440. Day 1 of the sample period was 12th June 1985

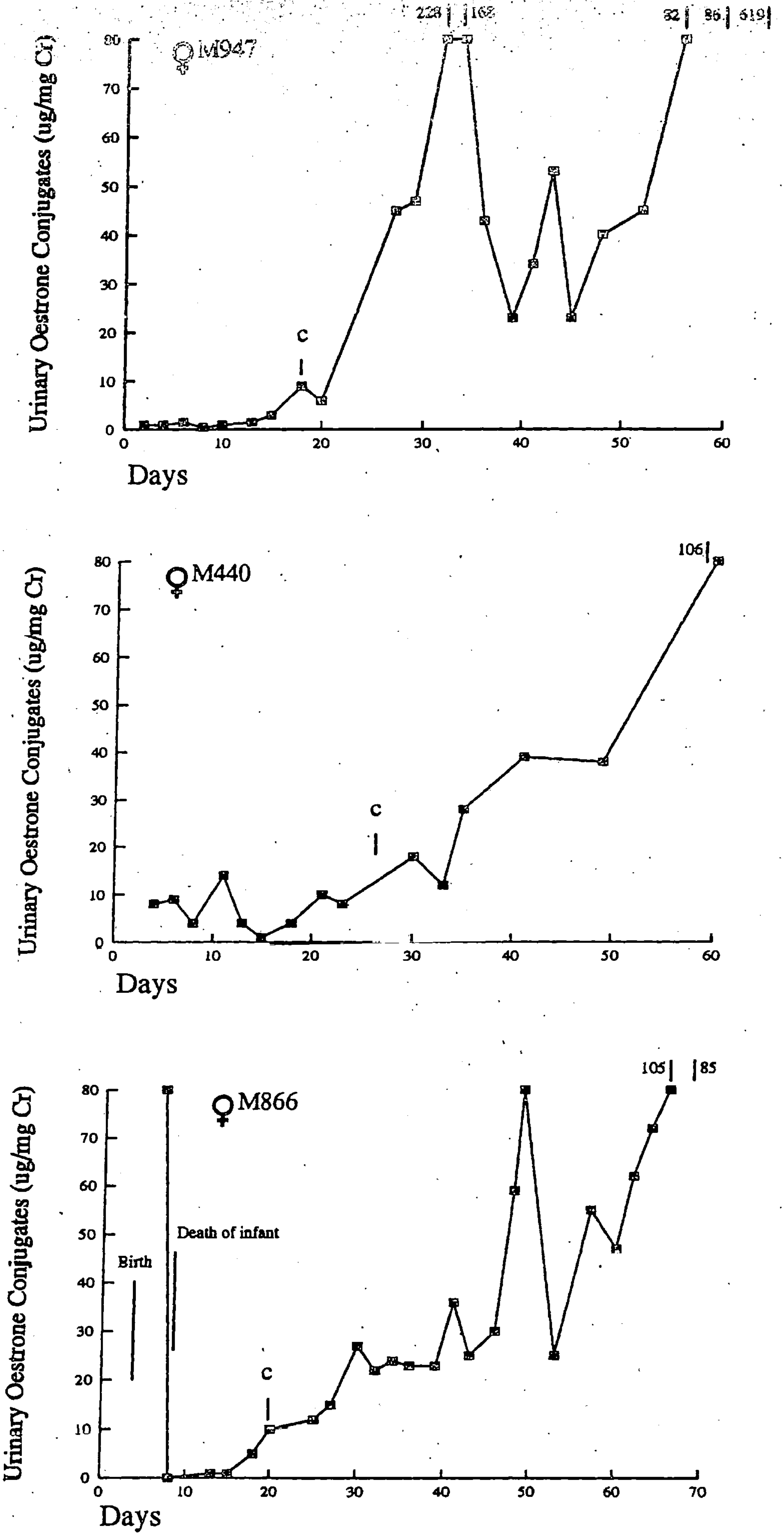


Fig. 3.3 Levels of urinary oestrone conjugates through conception and early pregnancy in three female Goeldi's monkeys

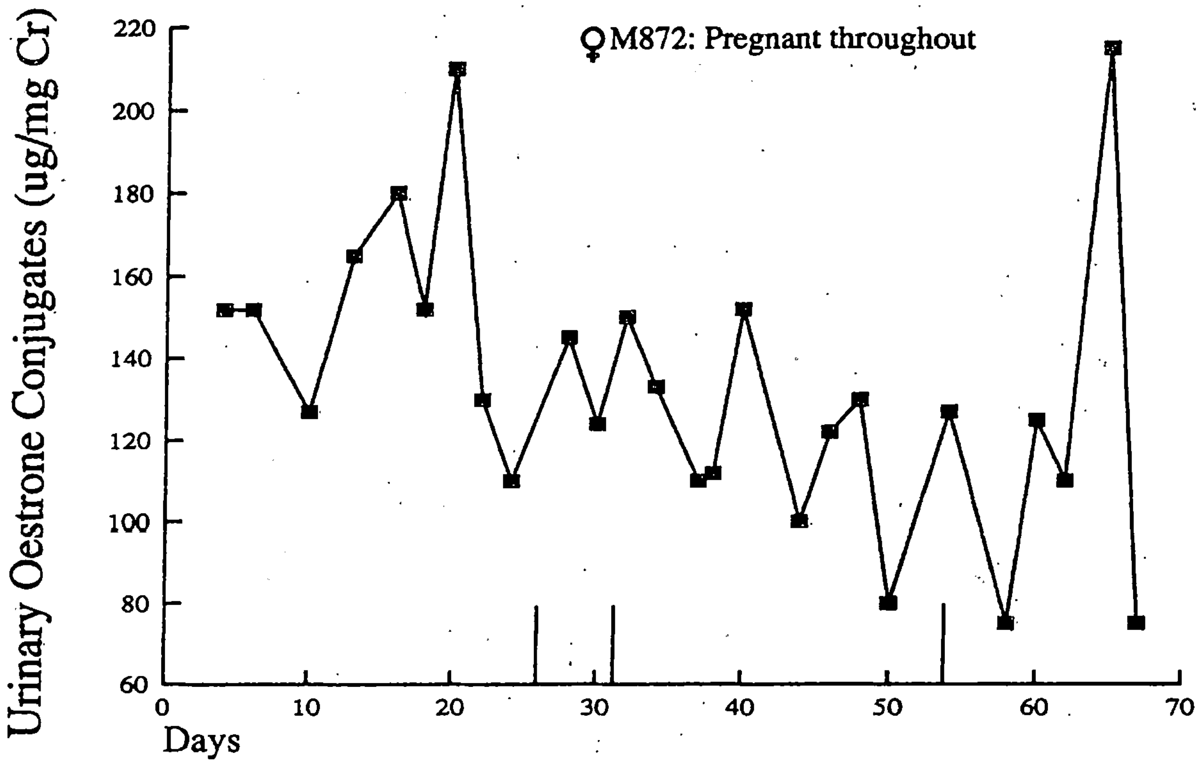


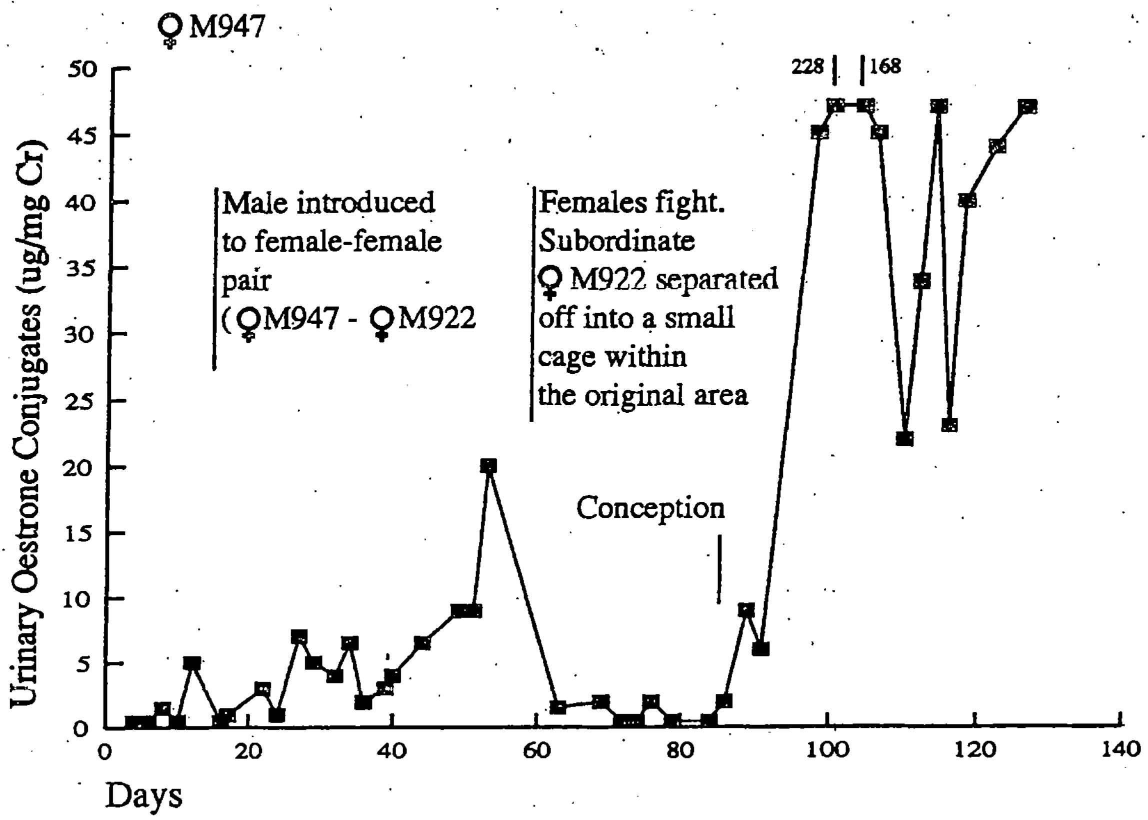
Fig. 3.4 Urinary concentration of oestrone conjugates during mid-to-late pregnancy. Day 1 of the sample period was 17th February 1986. The sample period finished 22nd April 1986. Birth occurred on 5th May 1986.

conception had gestation lengths of approximately 144 and 155 days, respectively. Following the present study, female M866 was housed singly, except for three separate occasions when she was housed for one day with an adult male 294, 160 and 48 days before giving birth. This gives a further gestation period estimate of 160 days. This range of gestation length (144-160 days) is approximately ± 6%.

Reproductive suppression

In two out of three trios, each of which was established with two females and one male (Table 1), both females became pregnant and gave birth. In trio 1, both females reared their infants whereas, neither did in trio 2. In the latter trio, the infant of the dominant female died at four days old while the subordinate female's infant died at three days old. In both trios, the dominant female gave birth first, the subordinate females giving birth 25 and 80 days later, respectively. 325 and 326 days, respectively, after the two trios had been established, the subordinate females had to be removed because of aggression received from the dominant female. Both dominant females subsequently proved to be pregnant at the time when the subordinates were removed. Neither subordinate female proved to be pregnant at that time.

In the third trio, no offspring were produced. At the time of the introduction of the male, the dominant female (M947) apparently underwent premature curtailment of the luteal phase of a cycle (fig. 3.5). However, she then proceeded through a normal cycle shortly thereafter. Neither cycle was included in the aggregate hormonal profiles shown on fig 3.1, because urinary oestrone conjugate concentrations did not clearly delineate the luteal phases. Subsequent assays of urinary progesterone and pregnanediol glucuronide concentrations proved useful in demonstrating cyclicity and were used as indicators of ovarian function in this single instance (Carroll *et al.* 1990). The profiles of the subordinate female (M922), on the other hand, suggest that, when the male was introduced, she was in the follicular phase of a cycle, having shown a decline in E_1C levels compatible with the end of the luteal phase of a cycle four days earlier. She then apparently stopped showing ovarian cyclicity following the introduction of the male (fig. 3.5). This acyclic state persisted until after the two females fought, 46 days after the introduction of the male. Immediately after the



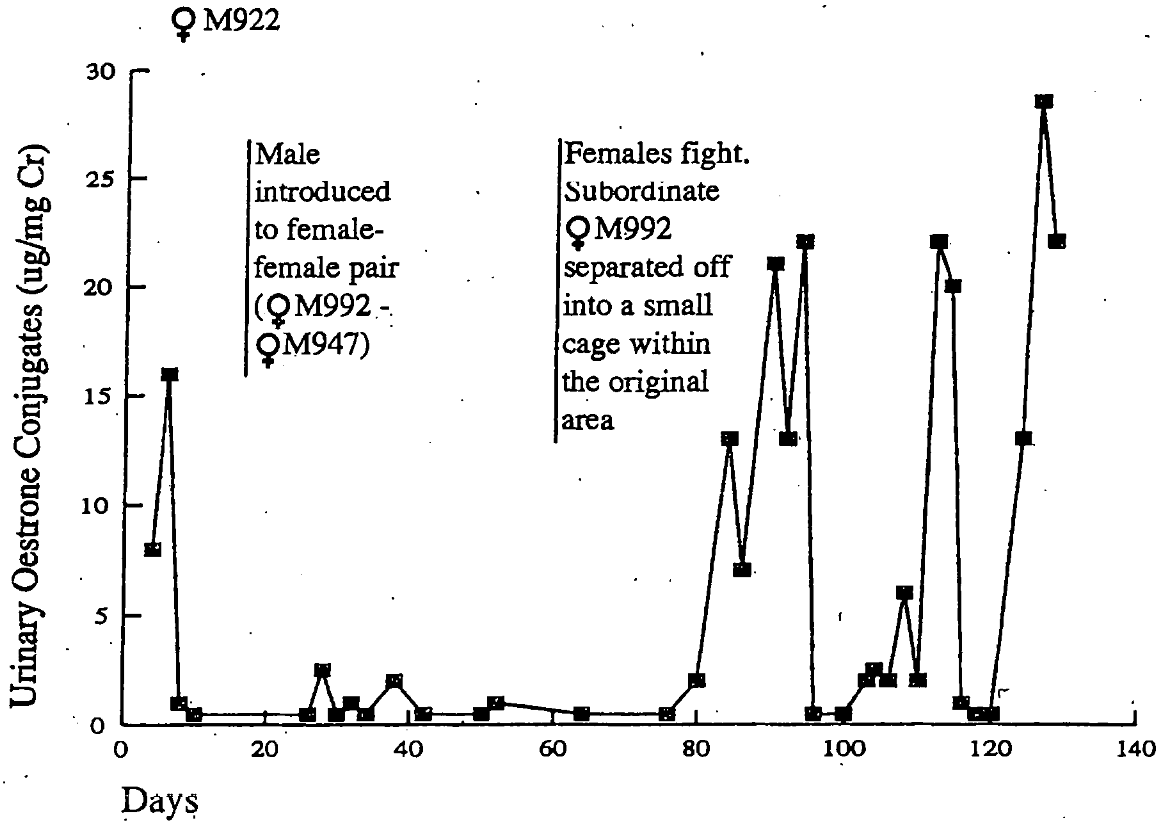


Fig. 3.5 Urinary concentrations of oestrone conjugates in two cohabiting founder Goeldi's monkeys. Day 1 of the sample period was 24th October 1985. The sample period ended on 24th February 1986

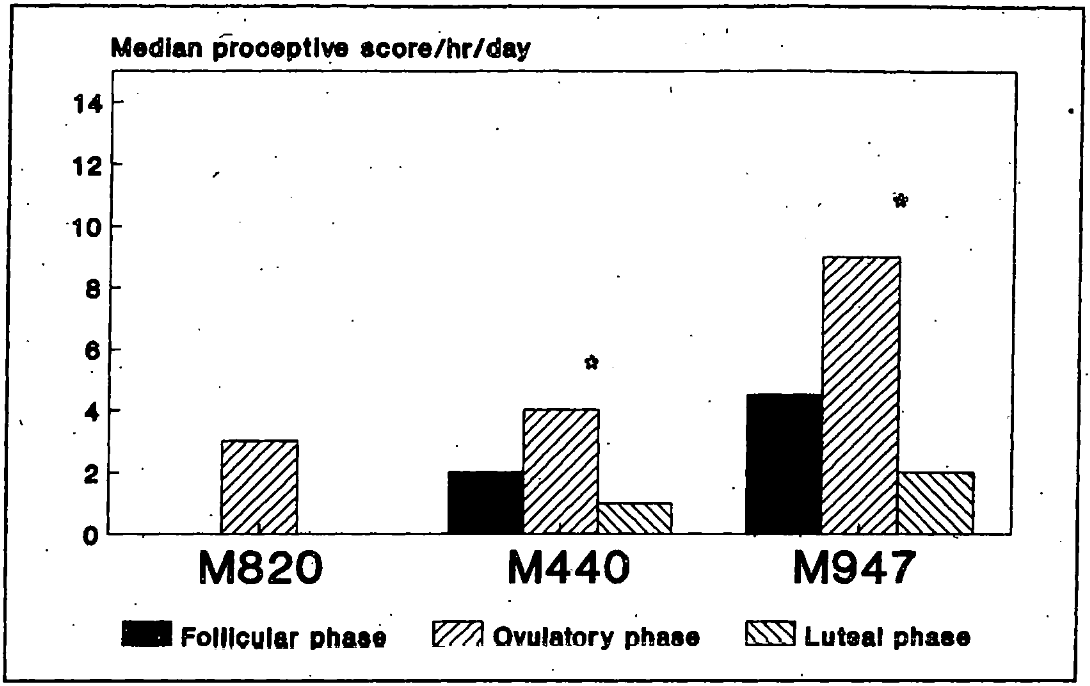


Fig 3.6 Median number of proceptive behaviours/hour/day scored for each female during the follicular, ovulatory and luteal phases of the ovulatory cycle.
* indicates a significant difference between the ovulatory and luteal phases ($p < 0.05$, Mann-Whitney 'U' test).

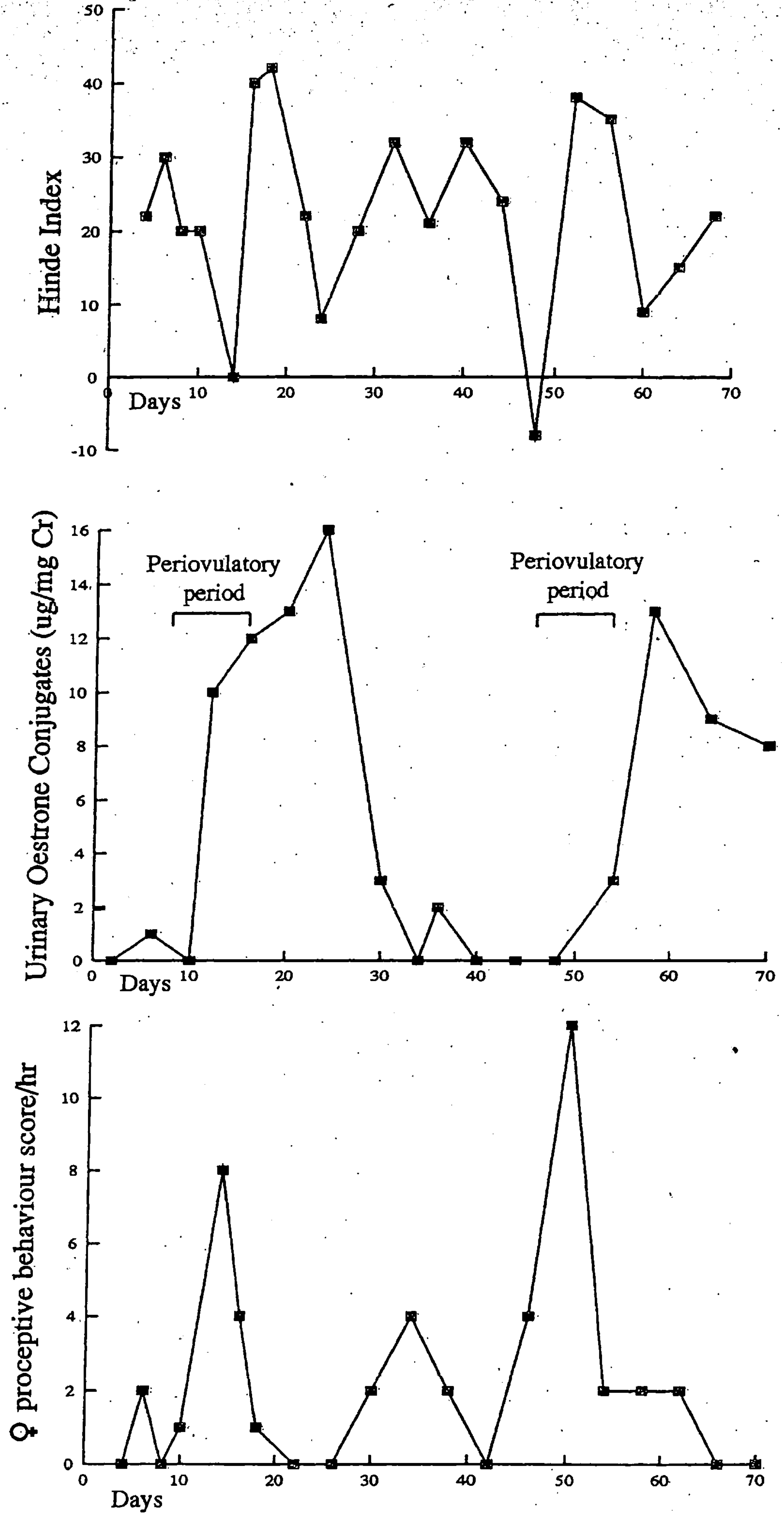


Fig. 3.7 Daily changes in Hinde Index and ♀ proceptive behaviour across two ovulatory cycles in a Goeld's monkey (M440). The sample period began 17th August 1985

fight, subordinate female M922 was partitioned off within the enclosure containing the dominant female (M947) and the male, such that she remained in visual, olfactory and auditory contact of the pair. The subordinate female's ovarian cyclicity re-commenced within 2-3 weeks of this separation (fig. 3.5).

Sexual behaviour

Three out of the four females observed (Table 3.1) exhibited proceptive behaviour to males (fig. 3.6). In two of the three females, these sexual solicitations were demonstrated significantly more frequently during the periovulatory period than during the luteal phase ($p < 0.05$; Kruskal-Wallis ANOVA followed by *post-hoc* Mann Whitney U test). In one female (M440) the periovulatory period was accompanied by a rise in female proceptive behaviours and a change in the Hinde Index (fig 3.7). During the periovulatory period the Hinde Index approaches zero or is negative, indicating that the female is more responsible for contact maintenance than the male. At other times, the male is more responsible for contact maintenance.

Copulation was rarely observed. With female M947, copulations were seen on day -5 of the follicular phase and day 11 of the luteal phase. With female M440, a single copulation was observed on day 8 of the luteal phase, while with female M820 a single copulation was seen on day -2 of the follicular phase. With the latter female, the copulation coincided with the periovulatory period of increased proceptive behaviour. None of these copulations was followed by pregnancy.

No significant differences between the follicular, periovulatory and luteal stages of the cycle were found for any other behaviour of either the male or female.

3.4 Discussion

Oestrone-3-glucuronide was the most abundant urinary oestrogen detected, throughout both the ovarian cycle and early pregnancy in Goeldi's monkey. Measurement of urinary oestrone conjugates, using a radioimmunoassay for oestrone glucuronide, provided a reliable indicator of ovarian cyclicity and pregnancy in Goeldi's monkey. These results compared well with limited data from other New World primates. Most studies have similarly shown that conjugated oestrone is the predominant form of oestrogen in urine during the ovarian cycle or pregnancy: owl monkey *Aotus trivirgatus* (Bonney *et al.* 1979); cotton-top tamarin *S. oedipus*: (French *et al.* 1983); saddle-back tamarin, *S. fuscicollis* (Epple and Katz 1984); pied bare-face tamarin *Saguinus b. bicolor* (Heistermann *et al.* 1987); golden lion tamarin *Leontopithecus rosalia* (French and Stribley 1985).

Two exceptions to this rule are the female common marmoset *C. jacchus* (Eastman *et al*, 1984) and the pregnant female red-bellied tamarin *S. labiatus* (Pryce *et al*, 1988), in which conjugated oestradiol was the most abundant urinary oestrogen. In a variety of Old World primates, oestrone has been found to be the principal urinary oestrogen metabolite (Lasley *et al.* 1981).

The pattern of sustained elevations in concentrations of urinary oestrone conjugates during the non-pregnant cycle in female Goeldi's monkeys were subsequently found to parallel those found in measurements of urinary progesterone and pregnanediol glucuronide, suggesting that the sustained periods of elevated urinary oestrone conjugate excretion reflected the post-ovulatory luteal phase of the ovarian cycle and not the pre-ovulatory follicular phase (Carroll *et al.* 1990). The heightened frequency of sexual solicitations by females at the approximate time of increasing urinary oestrone conjugate levels also suggested the occurence of an ovulatory event at this time. Further evidence for the post-ovulatory nature of increased urinary oestrone conjugate excretion in female Goeldi's monkeys was provided by Ziegler and colleagues (1989, 1990), as the pre-ovulatory urinary LH peak associated with a *post-partum* ovulation occurred coincident with the onset of sustained elevations of urinary oestrone conjugate concentrations. An investigation of the LH concentrations in the urine samples in this study was carried out by D. Abbott and colleagues, but similar confirmatory LH data were not found. This may have been due to the failure to stabilise bioactive LH in the urine samples because no glycerol was added prior to freezing (Ziegler *et al.* 1987b). Alternatively, the LH surge may not have been apparent because samples were not collected frequently enough. It is necessary to take daily samples in order to be sure of detecting the ovulatory LH peak. Further, investigators at the University of Zürich have since found that plasma LH is elevated throughout the luteal phase of the cycle in Goeldi's monkey (C. Pryce pers. comm.). Post-ovulatory elevations in concentrations of urinary oestrone conjugates in Goeldi's monkeys clearly resembled the pattern of urinary oestrogen excretion found in marmoset and tamarin monkeys (Eastman *et al.* 1984, French and Stribley 1987, French *et al.* 1984, Heistermann *et al.* 1987, Hodges and Eastman 1984, Ziegler *et al.* 1987b). Such a pattern of urinary oestrogen excretion is distinct from that found with one cebid monkey, the capuchin *Cebus albifrons* (Hodges *et al.* 1979), in which the urinary oestrogen profile clearly identified a pre-ovulatory oestrogen rise preceding or coincident with the urinary LH peak. However, since another cebid monkey (the owl monkey, *Aotus trivirgatus*) showed only luteal phase elevations in urinary oestrogen concentrations (Bonney *et al* 1979, Dixson 1983), these urinary hormonal differences may simply reflect the idiosyncracies of steroid hormone excretion in individual species rather than true differences in hormone metabolism and excretion between the Callitrichidae and the Cebidae. Care must be taken, however, in making such comparisons with the studies on the two cebids mentioned above. These studies did not identify the major oestrogen metabolite in the urine and therefore may not have been measuring the metabolite most likely to yield information.

The ovarian cycle length of approximately 24 days determined for *Callimico* compares well with previous behavioural and endocrinological estimates made for Goeldi's monkey (Beck *et al.* 1982, Christen *et al.* 1989, Lorenz 1972) and for most other New World primates with the exception of the squirrel monkey *Saimiri sciureus* (French *et al.* 1983, Harlow *et al.* 1983). *Saimiri* undergoes cycles that may be as short as eight days, although the cycle length appears to vary under different conditions and may be as long as 20 days (Baldwin and Baldwin 1981). The gestation lengths of 144 and 155 days determined in this study, based on concentrations of urinary oestrone conjugates as estimates of the day of conception, agree well with gestation estimates ranging from 144 to 157 days (mean ± S.D. 148.8 ± 5.2 days, n=6) made by Ziegler *et al.* (1989, 1990) from the day of the pre-ovulatory urinary LH peak to parturition.

Normally, mature daughters do not breed in captive monogamous family groups of *Callimico* (Carroll 1982). It is not yet known whether ovulation is suppressed in the non-breeding daughters. A similar pattern of suppression is seen within the natal groups of callitrichids (*e.g.* Abbott 1984, Hodges *et al.* 1981). In the common marmoset, it has been found that when unrelated females cohabit, the subordinate female is suppressed by the dominant (Abbott and Hearn 1978, Abbott 1984). It is often assumed that the same is true of other callitrichids, but this has not been tested in other species, with the exception of the golden lion tamarin. In this species, cohabiting unrelated females are not suppressed, regardless of dominance relationships. The golden lion tamarin is also unique among callitrichids studied to date as daughters are not suppressed in their natal groups. Rather, they show hormonal profiles typical of ovulatory cycles. It is interesting that golden lion tamarin females, unlike other callitrichid species, are extremely intolerant of other physically mature females. When mature females cohabit, even within the same family, their relationship is likely to result in extreme aggressive combat, resulting in severe injury, or death, for one of the females. It is possible that two different strategies exist within the Callitrichidae relating to reproductive suppression. Either a female is suppressed physiologically by the dominant or by her mother, or she is attacked and driven from the group or killed. Among *Callimico*, it appears that reproductive suppression of daughters occurs within family groups, while suppression does not necessarily take place among cohabiting unrelated females. In this study, only one female in three male-female-female trios was suppressed.

It is, perhaps, surprising that the two trios in which there was no physiological suppression remained stable for so long. If suppression occurs because females are competing for a male to ensure the presence of a helper at a subsequent birth, it would be predicted that either the first to conceive would then drive out other females, or alternatively would kill any other infants born into the group either prior to, or subsequent to, the birth of her infant. In this study, this happened in Trio 2, when two females gave birth a week apart in the same group. The female that had given birth first attacked the other female two days after she gave birth. In the attack, the second female sustained severe injury and her infant was killed. In the other trio in which both females bred, both reared their infants, although eventually the females in this group had to be separated following severe aggression between them.

All callitrichids appear to benefit from the presence of non-breeding helpers which aid in caring for the young of the dominant female, and this might explain why these primates demonstrate such extreme suppression of subordinate female reproduction. Non-breeding helpers also help raise the offspring of the dominant female in captive groups of Goeldi's monkeys. However, in contrast to callitrichids, Goeldi's monkey mothers care for their infants exclusively until the infants reach about three weeks of age, at which time typical callitrichid infant-sharing among the group members commences (Carroll, 1982). Perhaps there is a less extreme form of female reproductive suppression in Goeldi's monkeys because non-breeding helpers are less important in raising the offspring of the dominant female. Further research is required to determine whether this is really the case.

This study showed a periovulatory increase in proceptive behaviour by the female. It is surprising that this was not accompanied by an increase in male sexual behaviour such as genital sniffing or mounting, or even in contact promoting behaviours such as approach or groom. If sexual behaviour at the periovulatory period is elevated solely as a result of an increase in female proceptive behaviour, rather than through changes in the male's behaviour, this suggests that the timing of ovulation is hidden from the male. Females are clearly receptive to the male outside the ovulatory period, as demonstrated in this study, and may also mate during pregnancy (pers. obs.). This may be a strategy to reduce the likelihood of desertion by the male. Price (1990) suggested that a period of female receptivity prior to parturition in cotton-top tamarins was part of a strategy to ensure that a helper was present after parturition. If a *Callimico* male cannot detect an ovulatory period or pregnancy in the female, he may be induced into staying with the female through other periods of receptivity.

SUMMARY

1. A non-invasive study of urinary hormones in 6 captive female Goeldi's monkeys provided accurate information on patterns during the non-pregnant cycle and pregnancy.

2. Conjugated oestrone (essentially oestrone glucuronide) accounted for 80-85% of the urinary oestrone and oestradiol measured.

3. Measurements of conjugated oestrone provided a reliable indicator of cyclic ovarian function. Mean cycle length was 24.1 ± 0.9 days; n=9, gestation length 145-155 days; n=2.

4. Female sexual solicitations of males were maximal when oestrone conjugate concentrations rose, indicating a peri-ovulatory period. No other significant changes in levels of behaviour at the inferred time of ovulation were detected.

5. Three male-female-female trios were established. Ovulation was suppressed in only one of the three subordinate females in those groups. In the other two, both females conceived and carried pregnancies to term, but in only one trio were the infants reared to independence.

CHAPTER 4 BONDING IN HETEROSEXUAL PAIRS

Introduction

The Pair Bond

The term 'pair bond' has been extensively used in describing the relationship between the two members of a heterosexual pair. It has been used particularly frequently in situations where a monogamous relationship is supposed to exist, wherein the individuals are described as a 'bonded pair'. The general concept that this term embodies may seem sufficiently self-evident as to warrant no further elaboration. However, it is apparent that the term 'pair bond' can be used in different ways to describe different aspects of behaviour, and hence, to make different predictions about social relationships.

The concept of the 'pair bond' has been attributed to Konrad Lorenz. In his 'Studies in Animal Behaviour, Vol I' (1970), Lorenz discussed pair formation and used the term 'pair bond' to describe a relationship that persists over 'several seasons'. Subsequent use of the term has not been consistent. Lack (1968), for instance, has been quoted by Kleiman (1977) as referring to a pair bond being maintained over a single breeding season. This is further confused by Lack's (*op. cit.*) use of the term to describe the mating system of birds, referring to a polygynous or monogamous pair bond without concern for the social relationships between the animals. For this reason, care must be taken to distinguish between the mating system of a species, its social group structure and the qualitative description of the social dynamics of the group under consideration. Most authors use the term 'pair bond' to describe the last of these, the social relationships within a group or between a pair of animals. When used to describe a relationship within a group, 'pair bond' generally refers to the relationship between a breeding pair (e.g. Mason 1974, Kleiman 1977a, Kummer 1978, Immelman 1980, Poole 1985), although Wilson (1975) refers to a 'pair bond' forming in a polygynous mating system and does not refer to it in a monogamous mating system. Within the context of social relationships, however, most authors have failed to define their use of the term even at the most elementary level. The few that do so use it in different ways. Immelman (1980), for instance, referred to the pair bond as a long-term heterosexual bond between the male and female of a pair that persists for years. At the other extreme, Wittenberger and Tilson (1980) say that a pair bond may exist for only one day in some brood-parasitic birds. Poole (1985) referred to the pair bond as being an attraction between the male and female outside the fertile period.

It is clear that a satisfactory definition of the term 'pair bond' is needed and an attempt to provide one is given in what follows.

The Collins English Dictionary defines a bond as 'something that binds, fastens or holds together'. As such, the term must mean that the existence of the bond reduces the likelihood of the bound parts becoming separated. In the framework of social behaviour, the 'bond' must be a cohesive force within a social relationship.

Thus, a 'bond' is an attribute of a social relationship, a relationship being defined by Hinde (1982) as a series of interactions between two individuals that are known to each other. However, not all relationships are bonds. A relationship that is agonistic or perhaps even only one of tolerance cannot be described as a 'bond'. In social behaviour, the term implies that there is a positive relationship between all the individuals involved. In this respect, there must be an attraction between the individuals to maintain physical proximity and thus interact positively. It may be predicted that the attraction would probably be to some extent reciprocal. If one member of a dyad was always responsible for making contact, while the other always terminated contact, it might be difficult to demonstrate the existence of a bond. The word 'attraction' is used here to mean only "a bringing together", i.e. an attraction in terms of proximity in time and space. In its more general sense, however, 'attraction' carries considerable connotations for a relationship as it is frequently used loosely in describing human emotions. Care must be taken, therefore, to avoid anthropomorphic use of the term.

It is usually implicitly accepted, but not necessarily a prerequisite, that all the partners involved contribute to the maintenance of the bond. Kummer (1978) referred to 'long-term investments' by the participants in the bond. Poole (1985) defined a pair bond as a reciprocal social bond.

Qualification of the term 'bond' to 'pair bond' must refer to a heterosexual pair. Other qualifications of 'bond' are used to describe other relationships, e.g. mother-infant bond, sibling bond etc. It is generally accepted that the term 'pair bond' embraces a breeding relationship and thus applies to a mated pair.

When does a 'relationship' become a bond?

Within the context of breeding relationships, a distinction must be made between a relationship that forms solely for mating and one that persists through and beyond infant rearing. The former may occur without any positive social interaction other than perhaps the rituals of courtship, but may also involve aspects of mating behaviour such as mate guarding. In the latter case, where the members of the pair continue to associate through infant rearing, biparental investment - either direct or indirect - would be a feature of such a relationship, as it is difficult to envisage a relationship between a male and female that persists through infant care but which does not have at least elements of indirect paternal contribution to infant rearing. In this respect, after 'attraction', 'cohesion' is the second key element in the bond if it is to persist over time. The mere physical proximity of a partner, however, is not sufficient to constitute a 'bond' as the term implies some positive social interaction. For example, elephant shrews have a mating system of facultative (Type I) monogamy (Kleiman 1977, 1981) in which males and females rarely meet outside the female's fertile period. When they do, the meetings are characterised by aggression [Rathbun, quoted in Kleiman (1977)]. In this situation, no positive social 'bond' can be said to exist.

Thus, a 'pair bond' refers to:

1. A relationship between a male and female.
2. A relationship that encompasses, but goes beyond the fertile period.
3. A reciprocal relationship, contributed to by both members of the dyad.
4. A cohesive force within the pair.

Although there may be an obvious point at which one might conclude that a bond exists within a pair, *e.g.* following the rearing of an infant, it would not be correct to suggest that this is the point at which the pair bond is formed. Buchanan-Smith (1989), however, suggested that the criterion of infant rearing by a pair should be used to define the existence of the pair bond. By the time the infant is reared, the bond has been in existence for some time, perhaps since courtship was concluded and the female conceived. Indeed, in species where males make a contribution to infant rearing, the bond must have formed by the time of birth, otherwise the male may desert the female, leaving her to rear the infant(s) alone and risking loss of his fitness through their deaths. Where species have a prolonged period of courtship and association, and where discreet courtship displays are not a feature of their reproductive behaviour, there will be no clearly identifiable point at which a pair bond forms.

We may therefore qualify Poole's (1985) discussion of a 'pair bond' and define it as a cohesion between a mated male and female that encompasses and persists beyond the fertile period.

This definition is not restricted by the length of time the relationship lasts. It may encompass the rearing of a single brood, clutch or litter, or it may last a lifetime. Similarly, it is not restricted by the mating system of the species. Pair bonds may be formed between males and females in polygynous species with harem or multimale/multifemale societies as well as in those species with monogamous mating systems, although the nature of the pair bond will be rather different under different social systems and different mating systems.

It must also be noted that this definition says nothing about fidelity within the pair and should not be taken to imply mating exclusivity, even in pair bonds within monogamous mating systems. The existence of a pair bond may reduce, or in some species exclude, the likelihood of mating infidelity, but it does not necessarily preclude it.

Pair Bonding and Monogamy in Primates

Within any social group, some relationships are very close (e.g. mother-infant), while others are less so. The pair bond is often thought of as being a product of, or at least a reflection of, the social group structure and mating system of the species. For this reason, study of the nature and strength of the pair bond will tell us something about the underlying features of the reproductive strategy of the species. Mason (1974, 1975) and Anzenberger *et al.* (1986) have shown that differences in the social relationship between males and females in squirrel monkeys, *Saimiri sciureus*, and titi monkeys, *Callicebus moloch*, reflect differences in social organisation and mating strategy. These differences are indicated through differences in grooming relationships, proximity relationships, choice of associates and differential response between the sexes to intruders. Thus, the direction and relative contribution to the pair bond varies between species and their social organisations and these differences can be measured.

In her review of monogamy in mammals, Kleiman (1977) has indicated the features by which monogamy may be recognised in mammals. These are:

1. Close proximity of the pair both during and outside the mating season.
2. Strong mating preferences.
3. Absence of unrelated adult conspecifics from the pair's territory.
4. Breeding by only one adult pair within the group.

Several workers have suggested features that should theoretically characterise monogamy. These include features that relate to social interaction between the members of the breeding pair. They are detailed below and then discussed critically.

There should be a reduction in sexual dimorphism both behaviourally and morphologically (Kleiman 1977, Clutton-Brock and Harvey 1977). Behaviourally, this should include territorial behaviours such as scent marking, vocalisations and aggression towards intruders (Kleiman 1977, 1981). There should be a tendency for females to be aggressive to their mates, leading to female dominance (Kleiman 1977a). The two members of the pair should synchronise behaviours such as foraging, feeding, resting and territoriality (Kleiman 1981). The pair should exhibit strong bonds characterised by spending a considerable amount of time in close proximity or contact, and in primates by having a close allogrooming relationship. Kleiman (1977) also suggested that males should initiate grooming more frequently than females and that males should groom females more than the reverse. This may relate to the dominance relationship of the pair, wherein females may be dominant to males. Lastly, once bonds between the male and female have been established, courtship should be reduced, as there is no advantage or necessity in prolonging courtship beyond the initial bonding phase of the relationship (Parker 1974).

These predictions have often been used as the basis of pair bond studies, but several of them involve behaviours that are not <u>characteristic</u> of monogamy or appear to be flawed on closer examination, particularly when considered in the light of the pair bond encompassing a period of infant rearing.

1. Behavioural dimorphism need not be reduced. A relationship that involves mutual investment does not necessarily mean identical roles for the sexes. Different roles during gestation and infant rearing are inevitable in mammals and it is unlikely that differences in behaviour are confined to these periods.

Even in the early bonding period, before pregnancy occurs, behaviour is unlikely to be similar between the sexes. If the relationship is a lasting one, i.e. encompassing infant rearing, it is in the interests of both males and females to choose partners that will maximise their breeding success. It may be predicted, therefore, that sexual dimorphism in behaviour would be at least as pronounced during the early bonding phase as during infant rearing itself, and that the differences would follow the same pattern and direction.

2. The prediction that there should be a tendency toward female dominance is made on the basis that a bonded male can maximise his fitness by mating a second female and that the bonded female will use a dominance relationship to curb this. In fact, there is no evidence to support this among marmosets and tamarins. All callitrichid species studied to date suppress extra-pair mating, in captivity at least, through intrasexual mechanisms, by either physiological or behavioural suppression

(Abbott 1984, 1988, Epple and Katz 1984, French and Stribley 1985).

Given that the pair bond is a relationship involving mutual investment, unless the investment by one sex is considerably more than that by the other, codominance would be predicted to occur.

3. The prediction that the two members of the pair should synchronise activity could be made about any cohesive dyad or indeed any cohesive social group. The degree of synchrony may give an indication of the strength of a bond but cannot be used to characterise a pair bond. It may, for instance, be advantageous for the members of a pair not to synchronise behaviour. It has been shown in klipspringers *Oreotragus oreotragus*, for instance, that one member of the pair remains vigilant while the other feeds (Dunbar and Dunbar 1980).

4. The same comments may be applied to proximity and contact as evidence of a strong bond between the pair members. They may indeed indicate a strong bond but cannot be used to characterise a pair bond.

5. Prediction 5 concerning the reduction in sociosexual interactions after the initial bonding phase is usually made on the basis of Parker's (1974) observation that courtship should not be prolonged beyond the initial bonding phase. The logical extension of this is that sexual behaviour should be reduced over time, but that this will not necessarily apply to other bond-promoting behaviours unless there is a 'cost' to the animal in terms of fitness. Thus, behaviours such as resting in contact and allogrooming would be expected to increase to a plateau during the bonding phase and remain at that level as long as the bond exists, while behaviours such as approaches and following, and sexually related behaviour such as genital sniffing, mounting and presenting should all decline with time.

This prediction leaves us with the problem that sociosexual behaviours may vary for reasons other than the amount of time that a bond has been in existence. Particularly, they will vary with changes in the reproductive cycle. Unless the fertile period is hidden, and there is some evidence to suggest that this is the case in at least one callitrichid (Stribley *et al.*, 1987), changes will occur across the ovulatory cycle and while the female is pregnant. In *Leontopithecus*, a peak in mating activity occurs during mid-pregnancy (Kleiman and Mack 1977), suggesting that other factors also govern sociosexual behaviour. Changes in roles of the sexes may also occur following a birth which may have repercussions on sociosexual behaviour. In *Callimico* for instance, where the female carries the infant exclusively for up to three weeks post-partum, the male may assume increased vigilance or guarding behaviour, which may in turn affect his proximity relationship with the female.

Changes in the pair relationship will also be affected by changes in group size and structure with time. As group size increases, the time available for interaction with the breeding partner will decrease.

Lastly, a decrease in the level of sociosexual interaction may occur because the attraction within the pair bond is diminishing, rather than because the bond exists. The obvious way to test this experimentally would be to provide an animal with the opportunity to desert its partner. Other indications, however, may be the level of behaviours mentioned such as allogrooming and time spent in proximity that would indicate the strength of the pair bond.

Thus, while few behaviours can be used to prove the existence of the pair bond, measurement of levels of proximity, synchronised behaviour and allogrooming can be used to show that a positive relationship exists between the members of a pair. Measurement of variables such as responsibility for making contact and maintaining contact will be useful in determining the relative contribution made by the partners to the bond. Measurement of variables such as territorial behaviours will be useful in determining the roles of males and females in the group context, which will reflect overall social structure of the species but will not necessarily be useful in measuring the pair bond.

In the wild, pair bonds may help to maintain group stability and thus help maintain the advantages of group life, such as increased predator avoidance, more efficient foraging and better territorial defence. They may also convey possible reproductive advantages to both the male and female, such as mating exclusivity or assistance with infant rearing. It must be remembered, however, that social conditions in the wild may be quite different from those in captivity. Wild groups have natural emigrations and immigrations. There is an abundance of space in which individuals may associate and disassociate. Both emigrating and immigrating individuals may, for instance, remain peripheral to the group for some time before finally moving in or away. Captive groups, on the other hand, are usually closely managed. Pair formation is imposed by the researcher and no spontaneous migration in or out of the group can occur. The behavioural manifestations of pair bonding in captivity may accordingly be different to those in the wild. Mason (1975), however, has shown that - in *Callicebus* and *Saimiri* at least - captive behaviour reflects real differences in natural social structure between the two taxa.

Passive study through observation of captive groups may be useful in describing certain features of the pair bond, but the real test of whether or not a bond exists, and how strong the bond is, comes when the animals are given either an opportunity to desert the bonded partner, or a choice of partners with which to interact. Few studies of monogamous primates have been made under these conditions. Several intruder studies have been carried out where members of the pair were visually exposed to an intruder for a short time and the differential responses of the male and female recorded (*e.g.* Mason 1975, French and Snowdon 1981, Evans 1983, Anzenberger 1985, 1988, Buchanan-Smith 1989). These studies did not allow an opportunity to desert or to interact with the intruder beyond territorial reactions to its presence. Among studies on callitrichids, only Epple (1972, 1977, 1981), Kleiman (1978), Buchanan-Smith (1989) and Price (1990) report on experimental situations in which a choice of partners is available. These studies provide a great deal of information about the pair bond, although caution must be used when extrapolating these findings from captive studies to social behaviour in the wild.

Bonding among heterosexual pairs of marmosets and tamarins has been widely studied in captivity (*e.g.* Epple 1977, 1978, Evans 1983, Kleiman 1977, 1978, Poole 1978). The results of these studies have been interpreted against the background of the often firmly held belief that all members of the Callitrichidae are strictly monogamous. Indeed, the results of many studies support this hypothesis quite strongly. In captivity, at least, it is very difficult to maintain callitrichids in social groups with more than one unrelated male or more than one unrelated female (Epple

1972b, Mallinson 1975a, Kleiman 1977, 1978, Carroll in press). Such social groups are characterised by intrasexual aggression that is often very violent, usually resulting in at least reproductive suppression of subordinates and often necessitating the removal of the subordinate animal for its own safety (Abbott 1978, 1984, Epple 1972b, Hearn 1978, Kleiman 1978). In some cases, deaths have resulted from the injuries sustained during these aggressive encounters (Kleiman, 1979).

Studies of heterosexual pairs of marmosets and tamarins have shown that, contrary to predictions by Kleiman (1977, 1981), sexual dimorphism in the behaviour of the pair is quite pronounced. Male common marmosets, *Callithrix jacchus*, for example, are more responsible for making contact with the female when first paired than *vice versa*. They also allogroom significantly less than the female (Evans 1983, Evans and Poole 1984). Female cotton-top tamarins, *S. oedipus*, have been shown to scent mark more than males and to have correspondingly larger scent-gland fields (French and Cleveland 1984). In saddleback tamarins, *S. fuscicollis*, females show more aggressive behaviour than males and higher scent-marking frequencies (Epple 1977, 1981).

It has also been shown that dimorphism in behaviour is not consistent over time. Evans and Poole (1984) showed that, after the first week of cohabitation, male and female common marmosets were equally responsible for making contact, whereas males made significantly more approaches to the female than *vice versa* during the first week of cohabitation and during late pregnancy.

Studies comparing behaviour during early pair bonding and in well-established pairs have shown that the levels of most socio-sexual behaviours are elevated in newly established pairs as compared with levels of behaviour later on when the bond is presumed to have been established. This may be a feature either of bond establishment or of the reproductive status of the female, as few studies have controlled for this. Price (1990) has, in fact, demonstrated that changes in responsibility for making contact in pairs of cotton-top tamarins depends on the reproductive status of the female. In her study, males were responsible for making contact during the early bonding phase when the female was not pregnant and also shortly after birth, while females were responsible for making contact during the latter half of pregnancy.

Like marmosets and tamarins, *Callimico* has been found to form very stable and reproductively viable monogamous groups in captivity (Beck *et al.* 1982, Carroll 1982, Lorenz 1972). There have, however, been no quantitative studies published of the behaviour of this species in captivity. Evidence from field studies suggests that large groups of wild *Callimico* may contain more than one breeding female (Pook and Pook 1979a, 1979b, Masataka 1981a, 1981b). Other studies have found smaller groups although the composition of these smaller wild groups is unknown (Moynihan 1976, Izawa 1979, Cameron *et al.* 1987, Christen and Geissman in prep.). Izawa's study group of nine individuals apparently contained only one adult male. The number of adult males in the Pooks' group is not known, although it contained six adults. It is possible, therefore, that the group contained more than one breeding male.

If *Callimico* is flexible enough in its breeding strategy to embrace polygyny and polygynandry, it might be expected that this would be reflected in the nature of the pair bond between the male and female. It could be predicted that the male and female would spend less time in proximity and allogrooming than occurs among marmosets and tamarins. Likewise, less change in the level of socio-sexual interaction over time would be predicted. Outside ovulatory periods, the male would not be responsible for making contact or maintaining proximity, and low levels of behavioural synchrony should be seen.

The study reported in this chapter concerns an investigation of the formation and maintenance of the pair bond in *Callimico*. The findings will be compared with those from studies on bonding behaviour in callitrichids as well as with theoretical predictions of the characteristics of monogamous relationships.

The behaviour of heterosexual pairs of *Callimico* was studied under three different conditions:

1. The early period of cohabitation following the introduction of a male to a female, for a period of 28 days.

2. Established pairs that had been cohabiting for at least two years and had reared at least two offspring.

3. Established pairs that were rearing an infant, over a period of six weeks starting from the day of birth.

The study was carried out to test the predictions outlined in this chapter that:

(i) behavioural sexual dimorphism during the early bonding period should follow the pattern exhibited during infant rearing

(ii) there should be no indication of dominance between the male and female

(iii) outside ovulatory periods, the male should not be responsible for making or maintaining contact

(iv) behaviour of the male and female should be synchronised

(v) allogrooming and time spent in proximity with the partner should be seen frequently and should increase with time but when the 'bond' is formed should remain at a steady rate

(vi) sociosexual interactions should decrease with time

Study 4.1

The behaviour of newly established pairs

4.1.1 Aims

This study was designed to examine the behaviour of the male and female during the first four weeks of co-habitation in order:

1. To examine differences between the sexes and their roles within the relationship

with regard to:

a) bond formation and maintenance
b) territorial behaviour
c) reproductive behaviour

2. To examine changes in the relationship over the first four weeks of co-habitation particularly with respect to the predictions stated above.

4.1.2 **Methods**

The study methodology followed the procedures given in chapter 2.

Six pairs were studied for a month following the introduction of the male to the female. Details of the pairs are given in Chapter 2, table 2.1. In Pair 4, the female became ill on day 22 following pairing and had to be removed for veterinary treatment. No signs of illness were exhibited before that time, so data prior to her illness are included here.

4.1.3 **Results**

The behavioural categories of 'activity', 'feed', 'autogroom' and 'allogroom' were scored most frequently. By their nature, these behaviours occur in obvious bouts thus accounting for a far greater percentage of total observation time than brief behavioural activities scored as events.

Locomotor activity

Fig 4.1 shows the mean number per hour of 15 second scans in which each animal moved. It is the behaviour seen most frequently during the observation periods. In all but two pairs, males showed more locomotion than females; but over the six pairs there was no significant difference between the sexes ($p > 0.05$, Wilcoxon test).

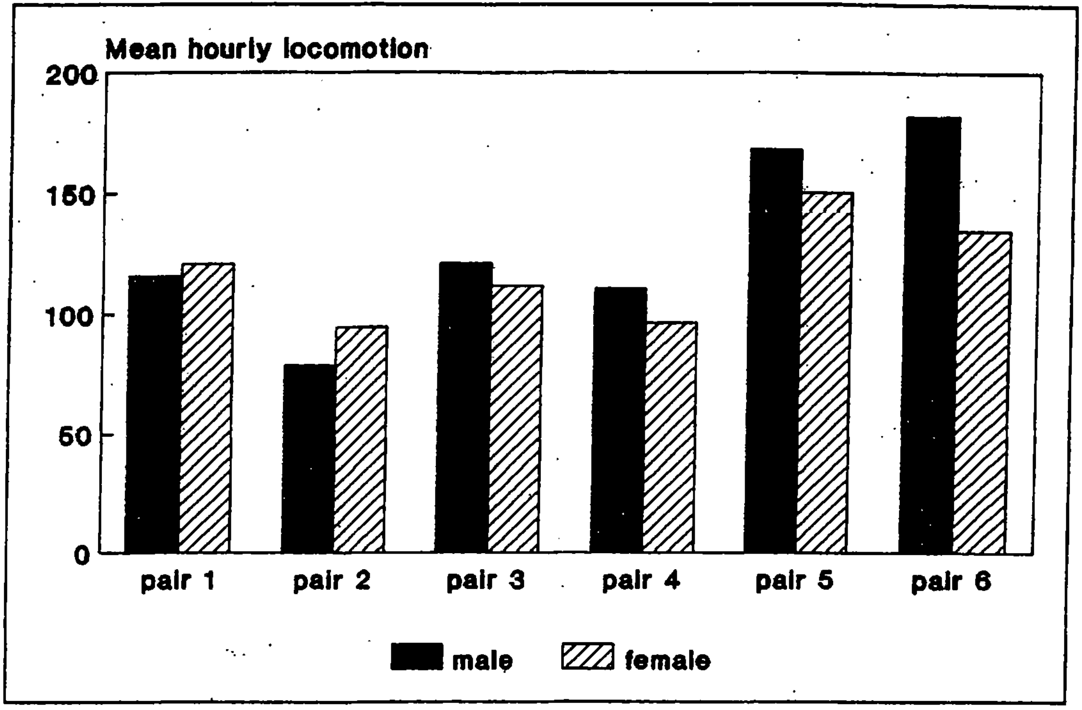


Fig 4.1 Mean number of scans per hour in which locomotion was scored in pairs of Goeldi's monkey during the first four weeks of cohabitation.

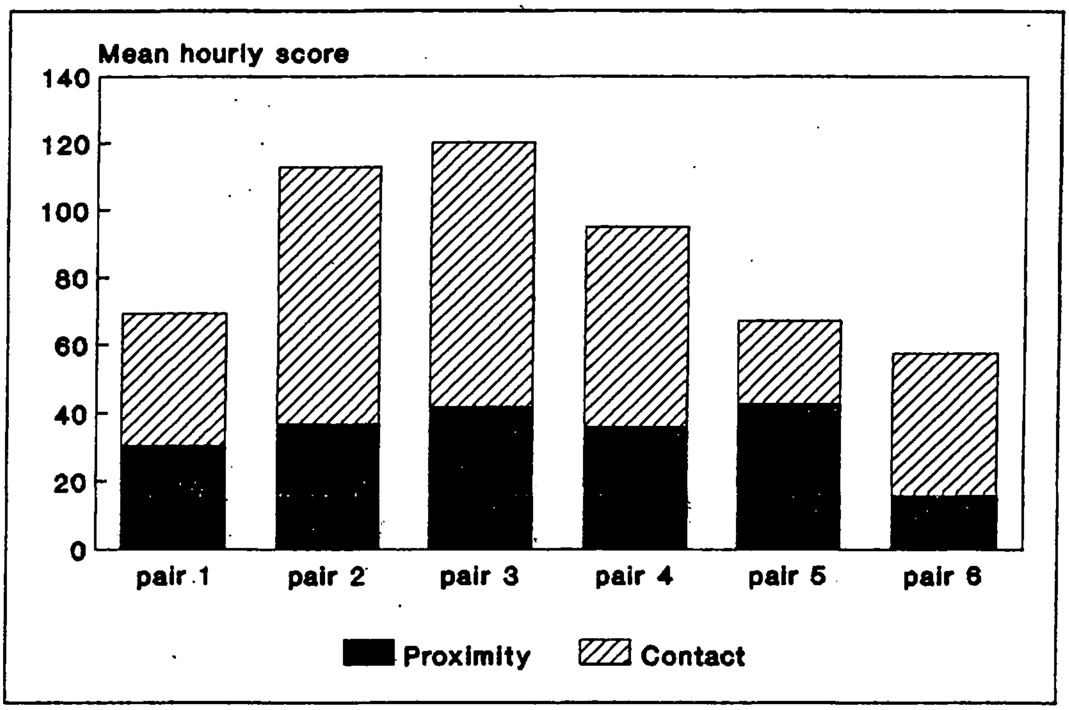


Fig 4.2 Mean number of scans per hour in which 'proximity' (< 15cm) and 'contact' were scored in the study pairs during the first four weeks of cohabitation.

Grooming

Results for autogrooming and allogrooming are shown in table 4.1. In all six pairs, females autogroomed more than did males and this difference was significant ($p<0.05$, Wilcoxon test).

By contrast, in three pairs males groomed their partners more than *vice versa*. Overall, mean male allogrooming score was 12.0 per hour compared with 10.7 per hour for females. This difference was not significant.

Spatial relationships

(i) Time spent in proximity

Consideration of all six pairs indicated that, overall, 20.0% of the time was spent with the partners in 'contact' while 14.9% of the time was spent in 'proximity'. Since about 50% of the time was spent stationary, on average, the time spent in 'contact' or 'proximity' accounted for about two-thirds of time spent immobile. Fig. 4.2 shows the times for each pair. In all pairs except pair 5, more time was spent in 'contact' than in 'proximity'.

(ii) Making and breaking contact

Table 4.2 shows the mean hourly score for 'approach' and 'leave' by the male and female partners of each pair.

Wilcoxon tests were carried out on the scores for male and female within each pair. Where a significant difference ($p<0.05$) was found, it is indicated in the table by an asterisk. It can be seen that the male made significantly more approaches than the female in all six pairs and that in pair 6 the male scored significantly more 'leaves'.

Table 4.1 Mean hourly auto- and allogroom scores in newly paired dyads of *Callimico*

	Autogroom		Allogroom	
	♂	♀	♂	♀
Pair 1	8.2	10.6	16.6	9.2
Pair 2	8.2	13.2	15.1	18.3
Pair 3	10.1	11.5	15.6	13.6
Pair 4	10.3	15.1	18.8	4.2
Pair 5	5.5	10.1	1.9	10.9
Pair 6	11.8	14.2	3.9	8.2

Table 4.2 Mean hourly approach, leave and Hinde Index scores in new pairs

* denotes a significantly higher score than that of the partner

	Approach		Leave		Hinde Index
	♂	♀	♂	♀	
PAIR 1	17.5 *	9.6	14.3	12.8	11.8
2	16.3 *	10.3	8.9	16.7 *	25.1
3	29.1 *	11.5	15.7	22.2 *	30.2
4	20.9 *	8.0	14.6	14.4	22.0
5	23.9 *	11.9	17.3	17.3	16.8
6	44.2 *	6.8	33.6 *	17.9	20.9

In pairs 2 and 3, the female left significantly more than the males. Overall, combining the data for the six pairs, males 'approached' significantly more than females ($p < 0.05$ Wilcoxon test), but there was no significant difference in 'leave' frequencies.

(iii) Maintaining proximity

The Hinde Index (I) was calculated for each observation day. This measures which of the two animals is more responsible for maintaining contact by comparing the percentage of 'approach' scores made by a particular animal with the percentage of 'leave' scores. (Hinde and Spencer-Booth 1967, Hinde and Atkinson 1970):

I = % 'approach' by male - % 'leave' by male

If the index is positive, the male is more responsible for contact maintenance and if it is negative, the female is more responsible. Fig 4.3 shows the changes in the Hinde index over the study period for each pair. It shows that, for all pairs, the male was more responsible for contact maintenance than the female except for very brief occasional periods. In some of these periods, this was due to a reduction in the percentage of 'approach' scores of the male (either by the male approaching less, or the female more), and in others to an increase in the percentage of 'leave' scores by the male (again either by the male leaving more or the female leaving less).

In those pairs that exhibited a switch to female regulation of proximity twice during the study period, the intervals between those times were as follows: 18 days (pair 1), 10 days (pair 2), 17 days (pair 3), 8 and 12 days (pair 5), 20 days (pair 6). The mean interval was 14.2 days (± s.e. 4.8 days). This is shorter than the estimated oestrous cycle length of 21 days (see Chapter 3). If, however, only those pairs showing a clear shift in proximity regulation are considered (i.e. pairs 1, 3, and 6), the interval between days when females were responsible for proximity maintenance was 18 days, 17 days and 20 days, respectively. For these three pairs, this shift is compatible with estimated oestrous cycle length and may be related to it in some way. In M440, (Pair 6), the only female in this study for which physiological data are available, the changes in Hinde Index have been shown earlier (Chapter 2) to occur during peri-ovulatory periods, and coincident with a rise in proceptive behaviour.

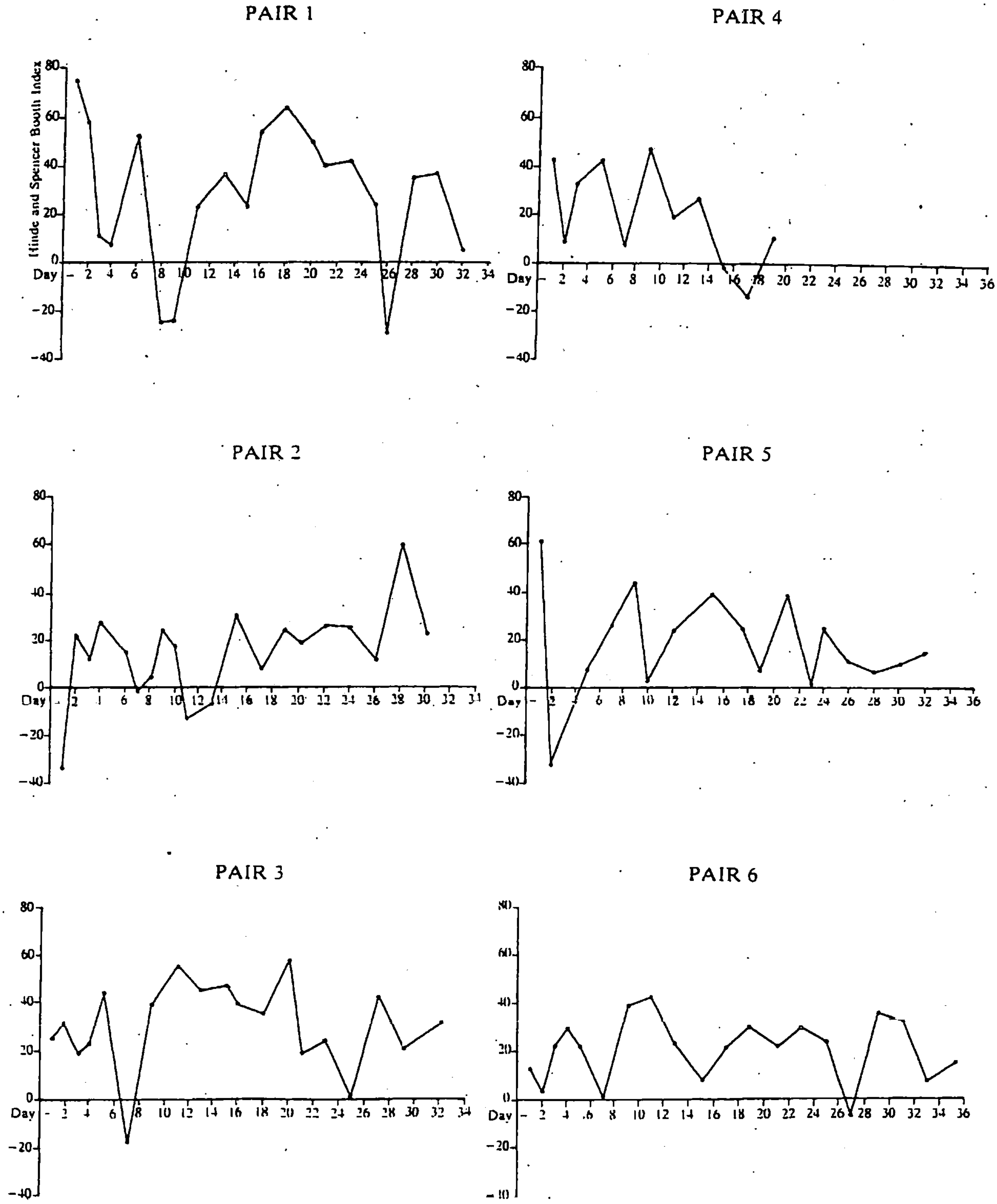


Fig. 4.3 Daily Hinde and Spencer Booth Indices for each of the six study pairs (positive values indicate the male is responsible for contact maintenance).

Table 4.2 includes the Hinde Index for each pair over the study period derived from calculations of total approach and leave scores for the total of 20 hours of observation. As there were high positive values in all cases, the males were clearly responsible overall for maintaining contact.

Sexual behaviour

Sexual behaviour was rarely seen, even in these newly-paired animals. Four behaviour categories relate directly to sexual behaviour, 'sniff genitals', 'present', 'mount' and 'mount with thrust'. Table 4.3 shows the mean hourly score for each pair in each of the above categories.

Pair 3 exhibited extremely high levels of mounting by the male and presenting by the female. No reason could be seen for this. Pair 6 did not show the behaviour 'sniff genitals' and mounting occurred relatively rarely.

Spearman rank correlation coefficients were used to test for correlation between sexual behaviours and other affiliative parameters, *viz*, proximity, contact, male and female approaches, Hinde Index and allogrooming. No significant correlations were found.

Scent marking

Scent marking was frequently observed. The mean hourly numbers of scent-mark scores are given in Table 4.4.

Table 4.4 indicates that tail anointing was the most frequently seen type of scent mark, accounting for over 75% of the marks seen. Nose rubbing and anogenital scent marking accounted for a further 13% and 11% respectively, while ventral marking was less than 1% of the total marking score.

Wilcoxon signed-rank matched-pairs tests were performed on the scent-mark scores. No significant difference was found between the levels of male and female scent marking for any of the three more frequently scored scent-mark categories, nor

TABLE 4.3 Mean hourly scores for sexually orientated behaviours during the study

PAIR	SNIFF GENITALS		PRESENT		MOUNT		MOUNT AND THRUST	
	♂	♀	♂	♀	♂	♀	♂	♀
1	0.8	0.1	0	0	1.1	0	0.5	0
2	1.7	0.1	0	0.1	1.2	0	0.4	0
3	1.0	0.1	0	1.3	6.7	0	0.5	0
4	0.7	0	0	1.5	1.8	0	0	0
5	0.4	0	0	0.9	0.2	0	0.1	0
6	0	0	0	0.8	0.1	0	0	0

TABLE 4.4 Mean number per hour of each type of scent mark in each study pair

PAIR	TAIL ANOINT		NOSE RUB		ANOGENITAL		VENTRAL	
	♂	♀	♂	♀	♂	♀	♂	♀
1	7.95	3.35	0.45	1.05	1.25	1.25	0	0
2	6.65	4.05	1.0	0.95	0.65	0.6	0	0
3	11.21	5.58	2.26	1.37	0.95	0.37	0	0
4	6.36	11.36	0.73	1.82	0.91	1.55	0.27	0.09
5	3.22	7.94	0.56	0.17	0.39	1.0	0	0.28
6	4.9	3.4	0.35	2.1	0.35	1.7	0.4	0

for the total scent-mark scores. Within some pairs, however, significant differences were found. In pairs 1 and 3, males tail anointed significantly more than females, while in pair 5 the female did so. In pair 6, the female nose rubbed significantly more than her male partner, while in pair 5 the female anogenitally scent marked significantly more than the male. The total scent mark scores for each pair showed significant differences for pairs 3, 4 and 5, the male scent marking more in pair 3 and the female more in pairs 4 and 5.

When expressed graphically, scent mark frequency showed clear daily fluctuations, but no regular fluctuations that could be indicative of, for instance, oestrus. Spearman rank correlation coefficients were calculated to test for any correlations within pairs between the scent mark levels of each sex and the activity scores, numbers of approaches by each sex or time spent in proximity and contact. The results of these tests are shown in table 4.5. In pairs 1, 2, 5 and 6, there was a negative correlation between male scent marking and male activity, while in pairs 1, 5 and 6 a significant negative correlation between male scent marking and male approach was found. Male scent marking totals also correlated positively with time spent in contact and proximity in three pairs: 1, 4 and 5.

Across all six pairs, no significant correlation was found between scent-marking levels and any of the categories mentioned above. However, the value of Spearman's rank correlation coefficient for total male scent marking versus time spent in contact and proximity (a negative correlation) and for male versus total female scent marking (a positive correlation) was close to significance ($r=0.77$ in both cases; 0.83 is the critical value for $p=0.05$).

Agonistic behaviour

Agonism between partners was extremely rare. For instance, in Pair 6 one event of brief mutual chastisement, in the form of vocalisation and teeth baring, was the only case noted in 20 hours of observation. Aggressive behaviour was, however,

TABLE 4.5 Results of Spearman's rank correlations of total scent mark scores (SM) with activity (ACT), approach scores (AP), and time spent in proximity and contact (P+T)

\+ indicates a significant positive correlation ($p < 0.05$)
\- indicates a significant negative correlation ($p < 0.05$)

PAIR	♂SM/♂ACT	♂SM/♀ACT	♂SM/♂AP	♂SM/♀AP	♂SM/P+T	♀SM/♂ACT	♀SM/♀ACT	♀SM/♂AP	♀SM/♀AP	♀SM/P+T
1	-	-	-	ns	+	ns	ns	ns	ns	ns
2	-	ns	ns	ns	ns	ns	ns	ns	ns	ns
3	ns	ns	ns	ns	ns	+	ns	ns	ns	ns
4	ns	ns	ns	ns	+	ns	ns	ns	ns	ns
5	-	ns	-	ns	+	-	ns	ns	ns	+
6	-	ns	-	ns	ns	ns	ns	ns	ns	ns
ALL	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

TABLE 4.6 Mean number of 15 sec scans per hour in which Arch Bristle Leaping was scored in new pairs of *Callimico goeldii*

	♂	♀
Pair 1	5.8	4.4
Pair 2	1.7	1.3
Pair 3	5.2	4.9
Pair 4	0.2	0.2
Pair 5	0.1	0
Pair 6	6.0	4.2

Table 4.7 Results of binomial tests for synchronised behaviour among new pairs of *Callimico goeldii*

Pair	* Simultaneous score observed	expected	** Z	Probability
1	6.6	9.7	-1.3	ns
2	12.0	7.1	2.6	$0.001<P<0.01$
3	9.6	1.8	-	-
4	7.2	4.3	1.4	ns
5	5.9	11.2	-2.2	$0.01<P<0.05$
6	12.2	5.0	3.13	$P<0.001$

* Simultaneous score is the mean number of scores per hour in which both individuals performed the same behaviour.

** Z test statistic

NB. For pair 3, the expected scores were too small to perform the test validly.

however, directed towards the observer as 'arch bristle leaping' (ABL). This occurred as a cooperative behaviour, both male and female frequently displaying simultaneously. The simultaneous nature of the display was apparent from day 2 onwards in all pairs. Only pair 1 exhibited ABL on day 1 and the behaviour was performed only by the male. Males appeared to initiate the display and usually displayed for slightly longer than the females. Overall, males displayed more than females, although the difference was not quite significant (p=0.059, Wilcoxon test). Table 4.6 shows the mean number of ABL scores per hour for each pair.

Synchrony of behaviour

The degree of synchrony of behaviour within the pair was assessed by examining the frequency with which the same behaviour was scored for both members of the pair in a scan. The behaviours 'feed', 'groom' and 'ABL' were examined in this analysis. The behaviours recorded as events were too short in duration for them to be performed simultaneously with any great frequency and the method of data collection would not have recorded them as such, only as having been performed in the same 15-second period. Allogrooming was not included because, by definition, this behaviour requires the participation of both members of the pair, but they do not perform the same behaviour.

The degree to which the members of the pair synchronised their behaviour varied greatly between pairs. For instance the male of pair 3 performed over 50% of feeding, grooming and ABL at the same time as the female, while the female of pair 5 performed less than 10% in synchrony with the male. In all but pair 6, a greater percentage of the male's time spent performing these behaviours was spent in synchrony with the female than *vice versa*.

Table 4.7 shows the mean hourly number of scans during which simultaneously performed behaviours were scored and the expected scores based on the frequency that the pair performed the behaviours, calculated using the method proposed by Sutcliffe and Poole (1978). Table 4.7 also shows the results of binomial tests used to determine whether the incidence of simultaneous scores was higher than predicted by chance. The test could not be performed on the scores for pair 3, as the value of

NPQ (N = total number of scans, P = probability of the behaviour being performed simultaneously due to chance, Q = 1-P) was less than 9, which is the minimum value required for the test. Of the other pairs, pairs 2, 5 and 6 were demonstrated to have a simultaneous score significantly different from the expected value. In pairs 2 and 6, the score was significantly higher than expected, while in pair 5 the score was significantly lower than expected.

The sign test was carried out across all six pairs to test whether the divergence between observed and expected values was significant. It was not (p=0.34).

Apart from ABL, for which the male initiates performance of the behaviour by the female, there was no clear pattern regarding which sex performed the behaviour first and which joined in to perform it simultaneously. There was often quite a long period when one animal performed the behaviour alone before the second followed suit. Behaviours often appeared to be performed in overlapping bouts rather than in simultaneous bouts.

Changes in the pair relationship over the first four weeks

In order to identify any changes in behaviour over time, the data were collapsed into four 1-week blocks and the hourly mean per week for each behaviour calculated. These means were then analysed using Friedman's 2-way analysis of variance to test for significant differences in the weekly means. Data for Pair 4 were omitted, as only three weeks of observations were conducted on this pair, and Friedman's ANOVA is not valid for unbalanced data.

No significant differences were found between the weekly means for any of the behavioural parameters measured. Some pairs showed clear trends in the level of certain behaviours with time, while other pairs showed the opposite trend, or no trend at all. Thus, overall, no significant differences were found. The data for male approaches were typical and are given in table 4.8 for illustration.

TABLE 4.8 Mean number of approaches per hour made by the male to the female over the first 4 weeks of cohabitation. The data for each pair are ranked in ascending order, the ranks being indicated in bold parentheses.

	WEEK 1	WEEK 2	WEEK 3	WEEK 4
PAIR 1	23.8 **(4)**	15.2 **(2)**	16.0 **(3)**	13.7 **(1)**
PAIR 2	23.4 **(4)**	18.3 **(3)**	11.8 **(2)**	10.0 **(1)**
PAIR 3	11.8 **(1)**	27.0 **(2)**	33.5 **(3)**	47.8 **(4)**
PAIR 5	16.4 **(1)**	27.3 **(3)**	33.5 **(4)**	25.0 **(2)**
PAIR 6	54.5 **(4)**	242.7 **(3)**	40.8 **(2)**	32.7 **(1)**

It can be seen that the male in pairs 2 and 6 made most approaches to the female in week 1 and thereafter the number of approaches steadily declined. In pair 3, the fewest approaches were made in week 1 and thereafter increased. Pairs 1 and 5 showed no particular trend. The male of pair 1 made most approaches in the first week, while that of pair 5 made most approaches in week 3 and fewest in week 1.

It may be that the variability in the data reflects a dichotomy of response to removal from the natal group to a novel environment and exposure to a strange conspecific. The data for males show that, during week 1, approaches were either highest (ranked 4), or lowest (ranked 1). This pattern is only apparent in week 1 and is also seen at this time in male locomotion and time spent within 15 cm of the partner. The data for male locomotion exactly mirrored those for male approaches, with males of pairs 1, 2 and 6 being most active in week 1 while the males of pairs 3 and 5 were most sedentary. The data for resting within 15 cm of the partner, however, reveal that pairs 1, 3 and 5 showed this most during week 1, while pairs 2 and 6 showed it least.

Female proceptive behaviours (pilostand, bipedal stand and present) appeared to show a trend in that, in five of the six pairs, proceptivity was higher in week 2 than in week 1. The exception was pair 3, which showed a very high rate of sexual activity overall and particularly in week 1. The data for proceptive behaviours are shown in

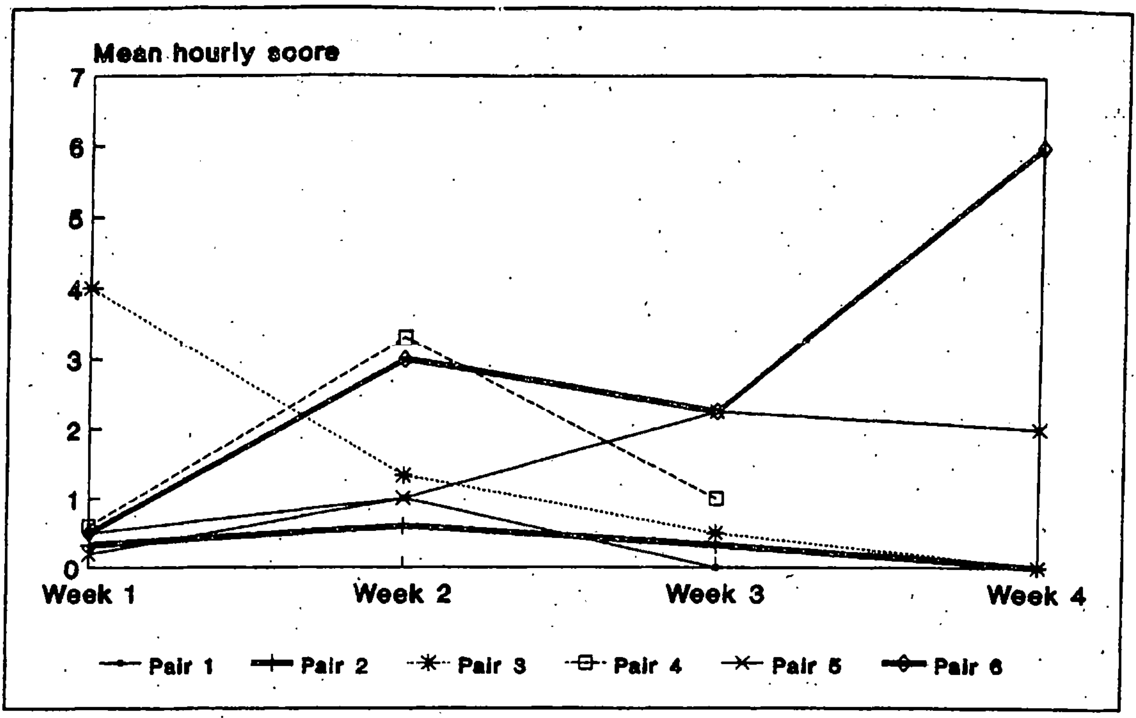


Fig 4.4 Mean hourly scores for female proceptive behaviour per week for each of the first four weeks of cohabitation.

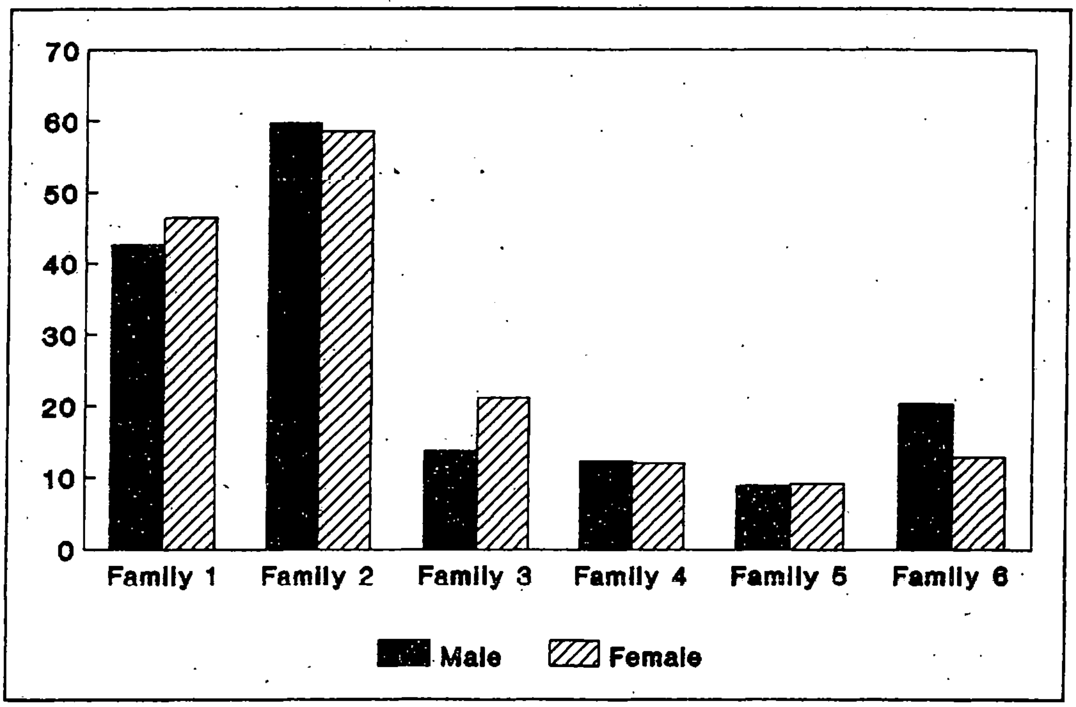


Fig 4.5 Mean number of scans per hour in which locomotion by the adult male and female was scored in established breeding groups.

fig. 4.4.

4.1.4 DISCUSSION

These findings show that the relationship between newly-paired male and female *Callimico* is strikingly amicable, even during the first week of cohabitation. Agonism was rarely seen, while affiliative behaviours such as allogrooming or resting in proximity or contact were seen frequently. About 60% of the time that an animal was stationary was spent within 15 cm of its partner, and over half of that time was spent in contact with the partner. Allogrooming was seen frequently, accounting for over 10% of the time budget. Outside the study periods, the animals fed together and slept together in close contact on a shelf or perch.

Differences in the rôles of the sexes

The only social behaviours that showed significant differences between the sexes across all six pairs were approaches and ABL. Males consistently performed both of these behaviours more than females. The Hinde Index also showed that males were responsible for maintenance (or regulation) of proximity in all six pairs, except for occasional days when females regulated proximity or showed the same degree of regulation as the males (*i.e.* the Index was either negative or close to zero).

In one of the study pairs, the days that the female regulated proximity corresponded with ovulatory periods indicated by measurement of physiological parameters (see Chapter 3). As no change in male behaviour was seen at these times, this suggests that *Callimico* has a concealed ovulation and that the female indicates sexual receptivity at this time through changes in her behaviour rather than the male detecting the peri-ovulatory period through olfaction.

Scent marking

No significant differences between the sexes were seen in the level of scent marking, and no changes were seen over time. This is perhaps surprising, as Epple (1970, 1986) suggested that scent marking in callitrichids serves the function of intragroup communication rather than inter-group communication, such as territorial marking. The lack of apparent sexual dimorphism would suggest that information communicated via scent marks is dependent on qualitative variation (*i.e.* through chemical changes in the scent mark constituents) rather than on changes in the frequency of marking.

Synchrony

The data showed some evidence of synchrony of behaviours, but with considerable variation among pairs. Only one pair was demonstrated to synchronise behaviour significantly more than expected by chance and one was shown to synchronise significantly less than expected. The sign test failed to reveal evidence of synchrony across the six pairs, with two of them showing simultaneous behaviour less frequently than expected.

It is quite possible that synchrony may have been underestimated because behaviour was sampled for only one hour per day in two half-hour blocks. Sampling for longer periods might reveal synchrony, which would only become apparent when the activity budget over the day is revealed.

Arch bristle leaping

ABL was the only agonistic behaviour seen. As males initiated the display and continued to perform it after the female had ceased, this may represent a form of mate-guarding. It may also be an aspect of territorial behaviour. If its function were solely a mobbing display toward predators, one might expect both sexes to perform it equally, particularly during the early phase of establishment of a pair relationship in which the male does not yet have an 'investment' to protect. In a 'bonded' pair, the female may be pregnant or carrying an infant and thus be more vulnerable to attack, in which case the male would be expected to perform ABL more. Conversely, if it is a form of mate-guarding, the behaviour should be performed more frequently by the male during the early bonding period, as it is in his interests to prevent other males from gaining access to the female. This could only be tested by means of intruder studies in which study pairs are given visual or physical access to a conspecific intruder and their response studied.

Because ABL is the only behaviour that is clearly performed in synchrony by the partners, the degree of synchrony shown in this behaviour might potentially be used to assess the 'pair bond'. This seems unpromising, however, as no variation in the performance of the behaviour over time was recorded. Within the first two days of cohabitation, all pairs were seen to perform the behaviour simultaneously. If it is a reflection of the strength of the 'pair bond', the bond must form very rapidly.

Changes over time

It had been predicted that measurable changes in certain behaviours should occur over time. In fact, the analysis did not reveal any statistically significant changes with time. The only trend was in female proceptivity, with higher scores in the second week than in the first in five of the six study pairs.

Changes in the Hinde index seen in the six pairs were shown in one of them to be related to underlying changes in the ovulatory cycle. In this respect, sexual behaviour appears to be driven by the female's behaviour and not by that of the male. No changes in male behaviour, for example in approaches, following, genital sniffing, etc., were detected. Changes in the Hinde index due to changes in the female reproductive cycle may well have masked any changes due to pair bond formation, as it is likely that the females were at different stages of the ovulatory cycle when first introduced to the males. In order to control for these effects when studying pair bond formation, hormonal monitoring of the female would be necessary to establish the ovulatory cycle and hence to ensure that all introductions took place at the same stage in the cycle.

Study 4.2
The behaviour of breeding pairs in established breeding groups.

4.2.1 Aims

This study was designed to examine the relationship of the male and female in breeding groups of *Callimico* in which the pair had cohabited for at least two years and had reared at least two offspring.

4.2.2. Methods

The breeding pair of each of six long-established groups was studied, following the study methodology described in Chapter 2. Each group comprised the breeding pair and two of their offspring. The age/sex structure of these groups is detailed in Table 2.2. 20 hours of observation were carried out on each breeding pair within the group over a period of three months. All the breeding females were pregnant throughout the study.

4.2.3. Results

Locomotion

Fig 4.5 shows the mean hourly locomotion score for the males and females in all six breeding pairs. Locomotion was infrequent in some pairs and no significant difference was found in the amount of locomotion performed by the two sexes (Wilcoxon test $p > 0.05$).

Allogrooming

Fig 4.6 shows allogrooming scores for the breeding pair in each of the six

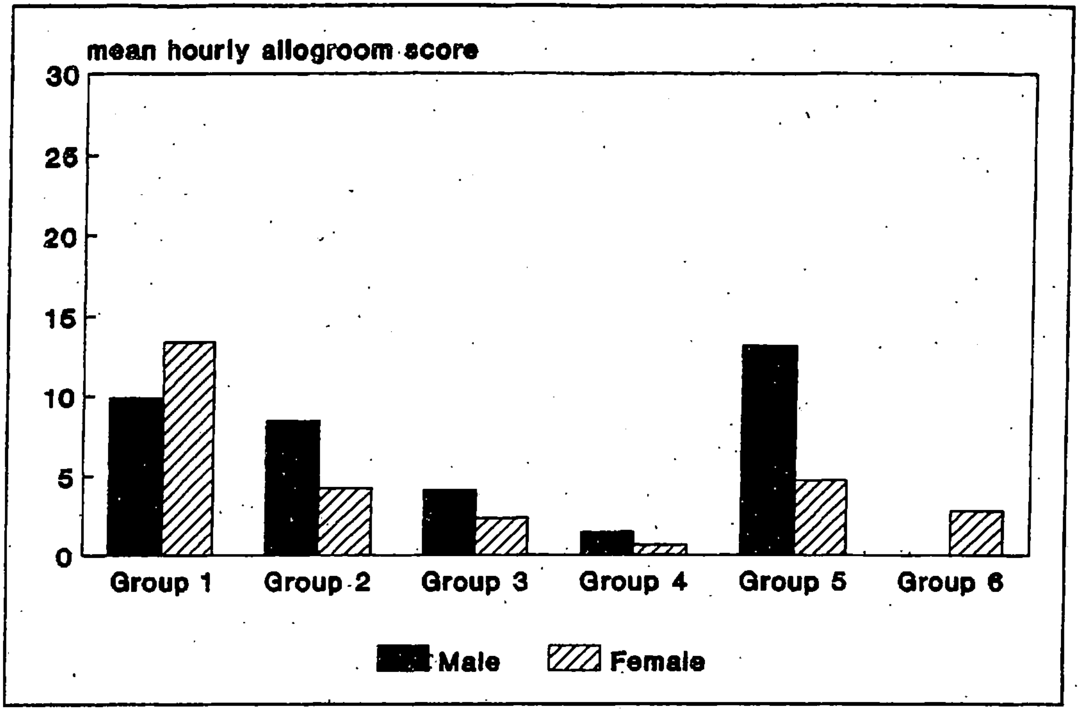


Fig 4.6 Mean number of scans per hour in which one member of the breeding pair was scored allogrooming the other.

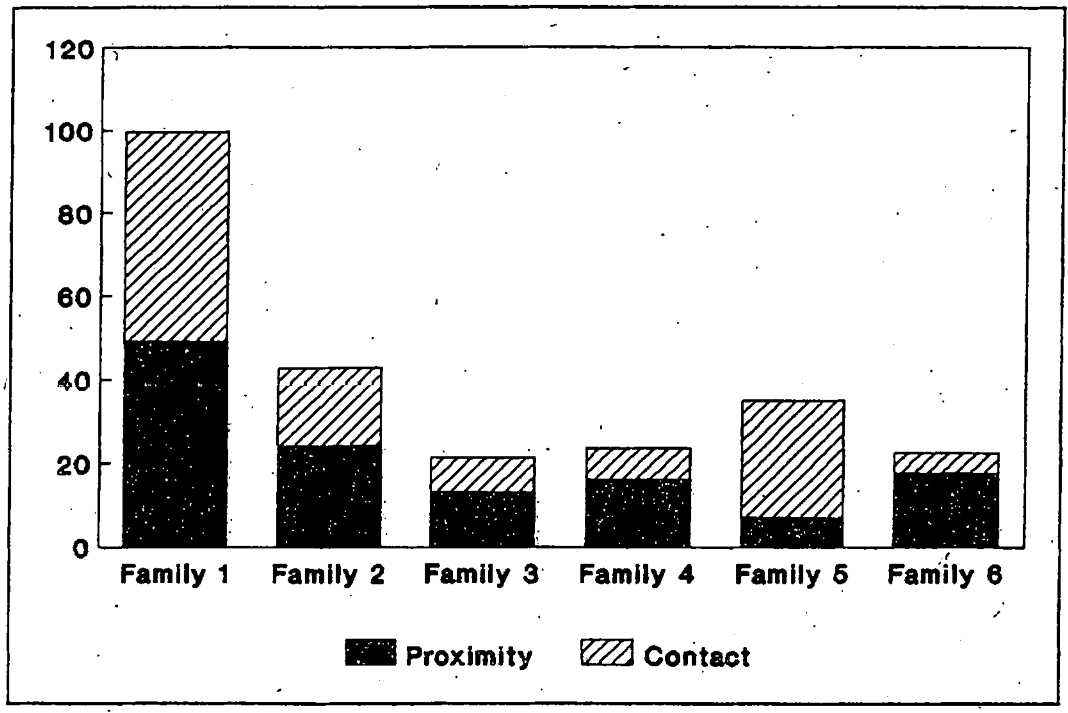


Fig 4.7 Mean number of scans per hour in which the partners of the breeding pair in established *Callimico* groups were scored in proximity (< 15cm) and contact.

groups. No significant differences were found between male and female allogrooming scores (Wilcoxon test $p > 0.05$).

Spatial Relationships

(i) Proximity

Time spent in proximity and contact is shown in Fig. 4.7. In breeding pairs 3, 4 and 6, less than 10% of their time was spent within 15 cm of the partner. This amounts to less than 5% of resting time for some pairs. The male and female of pair 1, on the other hand, spent almost half their time within 15 cm of each other and around half that time in contact.

(ii) Making and breaking contact

In all groups but one (group 5), the male approached the female more than *vice versa*. The difference was close to significance ($p = 0.059$, Wilcoxon test). No significant difference in the number of times one partner left the other was found. Approach and leave data are given in Table 4.9.

Hinde Index values for each breeding pair are shown in Table 4.9. In five of the six groups, males were responsible for maintaining contact. In the sixth, the index was -0.49, indicating that the female was marginally more responsible for proximity regulation than the male.

Sexual behaviour

Proceptive behaviour was observed with only one of the six study females. In pair 2, the female presented once in 20 hours of observation. In three of the six pairs, the male was observed to sniff the female's genitals, but at very low frequencies (means were 0.45, 0.35 and 0.1 per hour in pairs 2, 3 and 5, respectively). No copulations, mounts or attempted mounts were seen.

Table 4.9 Mean hourly approach, leave and Hinde Index scores of breeding pairs in established groups

	Approach		Leave		Hinde Index
	♂	♀	♂	♀	
PAIR 1	9.7	7.6	4.6	9.6	23.5
2	8.0	4.1	7.7	4.6	40.9
3	7.8	4.9	3.3	9.6	36.1
4	4.3	2.6	2.2	4.9	36.1
5	4.6	4.9	4.5	4.6	-0.5
6	10.2	5.1	8.0	7.2	14.1

Table 4.10 Mean hourly scent mark scores in the breeding pair in established family groups of *Callimico goeldii*

Family	Tail anoint		Nose rub		Anogenital		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
1	3.4	1.1	0.5	1.1	1.3	1.3	9.7	5.7
2	1.7	4.3	1.0	1.0	0.7	0.6	8.3	5.6
3	1.2	2.4	2.3	1.4	1.0	0.4	14.4	7.3
4	2.3	2.3	0.7	1.8	0.9	1.5	8.0	14.7
5	2.7	4.9	0.6	0.2	0.4	1.0	4.2	9.1
6	10.3	1.0	0.4	2.1	0.8	1.7	6.1	7.1

Scent marking

Scent marking scores are shown in Table 4.10. Tail anointing was the most frequently-observed marking activity, while ventral marking was least frequently seen. No significant differences in scent-marking frequency were seen between the male and female.

Agonistic behaviour

In a total of 120 hours of observation, no agonistic interactions were seen between the breeding male and female in any of the study groups. In five of the six pairs, arch bristle leaping was performed more by males than females. In Pair 6, the ABL scores were identical for male and female (see fig 4.8). Overall, the males did not perform this behaviour significantly more than did the females, but the difference approaches significance ($p = 0.059$, Wilcoxon test).

Synchrony

Table 4.11 shows the results of binomial tests used to determine whether the incidence of simultaneous scores was higher than predicted by chance. The test could not be performed on the scores for pairs 2 and 5 as the value of NPQ (N=total number of scans, P=probability of the behaviour being performed simultaneously due to chance, $Q = 1\text{-}P$) was less than 9, the minimum value for the test. Of the other pairs, only pair 3 was demonstrated to have a simultaneous score significantly higher than expected.

The sign test was carried out across all six pairs to test whether the divergence between observed and expected values was significant. It was not ($p=0.344$).

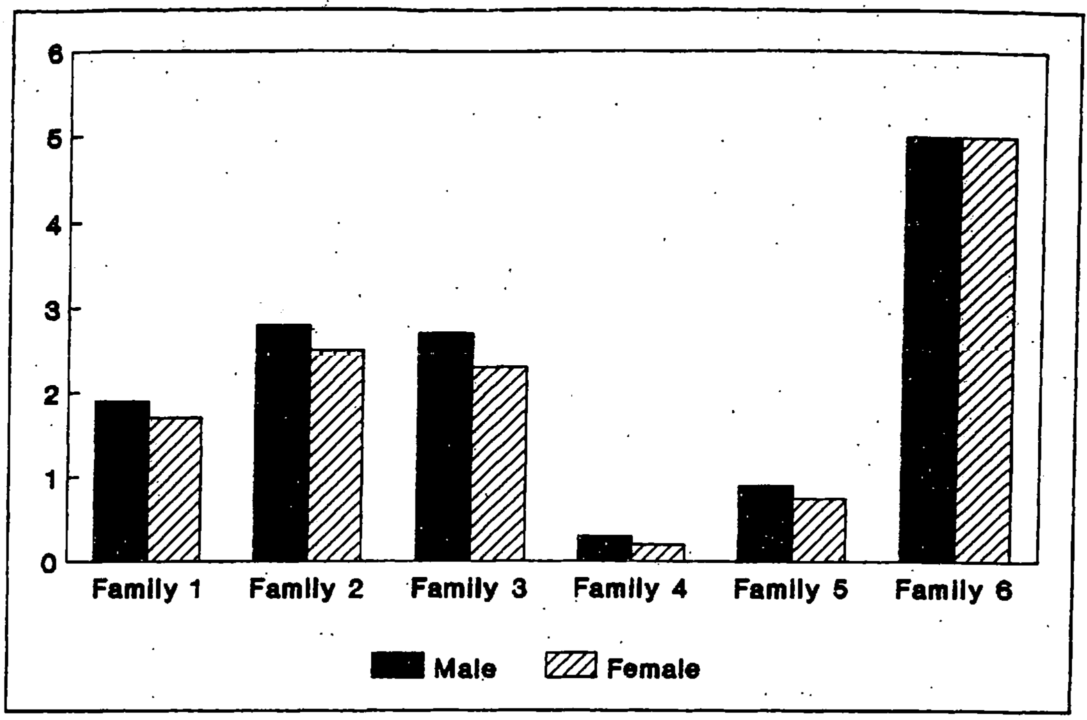


Fig 4.8 Mean number of times per hour that ABL was performed by the breeding male and female in each of the six study groups.

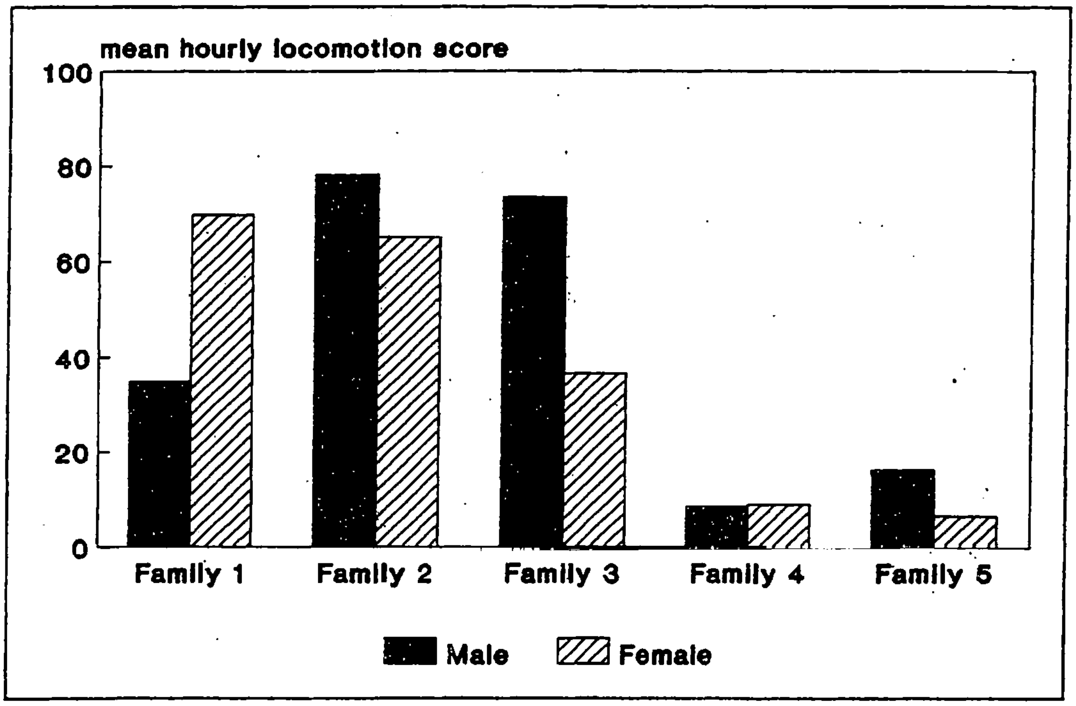


Fig 4.9 Mean number of scans per hour in which locomotion by the breeding male and female was scored in families of Goeldi's monkey during the infant-rearing study period.

Table 4.11 Results of binomial tests for synchronised behaviour among the breeding pairs in established groups of *Callimico goeldii*

Pair	* Simultaneous score observed	 expected	** Z	Probability
1	3.5	4.7	0.717	ns
2	4.3	1.7	-	-
3	12.2	4.4	4.47	P<0.001
4	4.3	6.1	0.877	ns
5	8.3	1.7	-	-
6	8.3	6.7	0.75	ns

* Simultaneous score is the mean number of scores per hour in which both individuals performed the same behaviour.

** Z=test statistic

NB. For pairs 2 and 5, the expected scores were too small to validly perform the test.

4.2.4 Discussion

The relationship of the adult male and female in the established group seemed to be one of mutual tolerance rather than a close "bonded" relationship. Locomotion was infrequent in some breeding pairs, reflecting low approach and leave scores. For pair 4, for instance, just 5% of the observation time was spent moving, while 25% of the time was spent moving in pair 2. Approaches averaged between 17 per hour and only 5 per hour. This reflects little time spent within 15 cm of the partner. Apart from the pair in group 1, the partners of which spent about 40% of their time within 15 cm of each other, the breeding pairs of the other five groups spent less than half that time in proximity or contact. Once again, the males made more approaches than the females and the difference in approach scores was close to significance. Also, males were responsible for maintaining contact in all breeding pairs except pair 5, in which the Hinde Index was close to zero.

Sexual behaviour was very rarely seen. This may be a reflection of the existence of a 'pair bond' (following Parker's (1974) predictions concerning frequency of courtship). It may also be due to the females being pregnant and therefore not sexually receptive. This may be particularly important if the females are primarily responsible for promoting sexual interactions and physical proximity during oestrus. Copulations have been seen during pregnancy (pers. obs.) but detailed monitoring throughout pregnancy would be necessary to determine the frequency of sexual behaviour. It may be that it occurs without any particular pattern, but there may also be a peak of sexual activity, as has been recorded in several species. In *Leontopithecus rosalia*, for instance, a peak of sexual behaviour is seen in mid-pregnancy (Kleiman and Mack, 1977). Similar findings have been reported in *C. jacchus*, (Evans and Poole, 1984), *S. labiatus*, (Coates and Poole, 1983), and *S. oedipus*, (Price, 1990). At other times during pregnancy, little sexual activity is seen in these species. Sexual activity during pregnancy may help to maintain a cohesive group. In *Callimico*, a female can probably rear her single infant unaided, so males might be expected to desert a female once she is pregnant and then mate with another female. By maintaining intermittent sexual activity during pregnancy, a female may be able to conceal her reproductive status from her mate and thereby ensure his continued presence up to the birth of the infant, through the post-partum oestrus to the point where the male does become directly involved in infant rearing as a carrier.

As in the newly-established pairs, no differences in scent-marking frequencies were seen between the pairs. Arch Bristle Leaping was performed by males more frequently than by females, but this was a highly synchronised activity with females usually taking part in the display whenever the male initiated it. Apart from ABL, little synchrony was seen in behaviours.

Overall, there is little to suggest that any 'bond' exists between the male and the female. If anything, the behaviour of the breeding pair in the established group is characterised by a lack of interaction. Such mutual disinterest may well reflect a lack of social bond, particularly as neither the male nor the female spend much time resting in proximity or allogrooming.

Study 4.3

Male-female interaction during infant rearing

4.3.1. Aims

This study was designed to examine the relationship between the members of the breeding pair in groups of *Callimico* following the birth of an infant. There were two aims to this investigation:

1. Assessment of differences in rôles within the "pair bond" relationship.
2. Assessment of changes in the relationship during infant rearing.

4.3.2. Methods

Five groups were studied, as outlined in Chapter 2 (see Table 2.3). Observation on each group started on the day of birth and continued until the infant spent 50% of an observation period uncarried. This point was reached at different times between week 7 and week 9 following birth, so this study focuses on the first six weeks post partum, for which data are complete for all five pairs.

4.3.3. Results

Locomotion

Fig 4.9 shows the mean hourly locomotion scores for the breeding male and female of each pair. In pairs 4 and 5, locomotion is very limited, whereas in the other pairs it is more frequent. In some pairs, the males show more locomotion than the females (pairs 2, 3 and 5), while in the others the converse is the case. No significant difference was found overall between males and females for locomotion ($p>0.05$, Wilcoxon test).

Table 4.12 Mean hourly approach, leave and Hinde Index scores of breeding pairs rearing an infant in established groups

	Approach		Leave		Hinde Index
	♂	♀	♂	♀	
PAIR 1	9.6	5.7	2.3	11.7	46.4
2	8.6	3.6	5.3	6.5	25.5
3	11.0	1.2	6.9	5.0	32.3
4	7.4	2.0	2.9	6.2	46.1
5	9.4	1.3	7.6	2.6	10.8

Table 4.13 Mean hourly scent mark scores performed by the breeding pair when rearing an infant in *Callimico goeldii*

Pair	Tail anoint		Nose rub		Anogenital		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
1	1.4	2.0	1.0	2.3	0.3	1.3	2.8	5.6
2	4.4	1.9	1.7	1.3	0.6	1.1	6.7	4.4
3	5.3	4.0	1.6	1.4	0.1	0.6	7.0	6.1
4	4.5	3.5	2.1	1.2	0.2	0.7	6.9	5.4
5	3.6	2.0	0.9	0.8	0.8	0.6	4.6	3.4

Allogrooming

The mean allogrooming scores per hour are shown graphically in fig 4.10 for the male and female in each dyad. In every group, the male allogroomed more than the female. The difference in scores approached significance ($p=0.059$, Wilcoxon test). In four of the five groups, the male groomed the female more than twice as much as she groomed him.

Spatial relationships

(i) Proximity

Fig 4.11 shows the time spent by the male and female within 15 cm, expressed as the mean number of 15-second scans per hour in which proximity or contact was scored. This ranges from about 16% of the time in group 2 to about 43% of the time in group 1. Interestingly a low proximity score was recorded in pair 4, despite the fact that the male and female were also extremely inactive. For 84% of the time this pair spent resting, the male and female were apart. This contrasts markedly with pair 1, in which the male spent around 60% of the female's resting time within 15cm of her.

(ii) Making and breaking contact

Approach, leave and Hinde index scores are presented in table 4.12.

In all five groups, the breeding male approached the female more than *vice versa*. Overall, this difference is close to significance ($p = 0.059$, Wilcoxon test). There was no significant difference in the number of times each member of the dyad broke contact ($p = 0.79$, Wilcoxon test). The Hinde Index is positive in all five groups, indicating that the males were responsible for proximity regulation.

Table 4.14 Results of binomial tests for synchronised behaviour among the breeding pairs rearing an infant in groups of *Callimico goeldii*

Pair	* Simultaneous score		** Z	Probability
	observed	expected		
1	11.7	2.54	-	-
2	7.3	4.14	1.47	ns
3	7.6	2.3	-	-
4	2.1	5.48	- 1.9	$0.02 < P < 0.05$
5	11.1	6.6	2.3	$0.001 < P < 0.01$

* Simultaneous score is the mean number of scores per hour in which both individuals performed the same behaviour.

** Z=test statistic

NB. For pairs 1 and 3, the expected scores were too small to validly perform the test.

Table 4.15 Weekly mean number of female leaves per hour in each group rearing an infant during the first six weeks following the birth. The weekly scores for each group are ranked and the rank is indicated in bold type.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Group 1	13.3 **4**	16.8 **6**	10.3 **2**	8.8 **1**	14.3 **5**	10.8 **3**
Group 2	4.5 **1**	7.5 **5**	14.3 **6**	5.0 **2**	6.7 **4**	6.0 **3**
Group 3	6.2 **4**	11.0 **6**	8.3 **5**	3.3 **1**	3.4 **2**	3.7 **3**
Group 4	3.8 **2**	10.1 **6**	2.7 **1**	10.0 **5**	6.3 **4**	6.0 **3**
Group 5	2.5 **2**	3.7 **6**	3.0 **5**	2.0 **1**	2.7 **3**	2.8 **4**

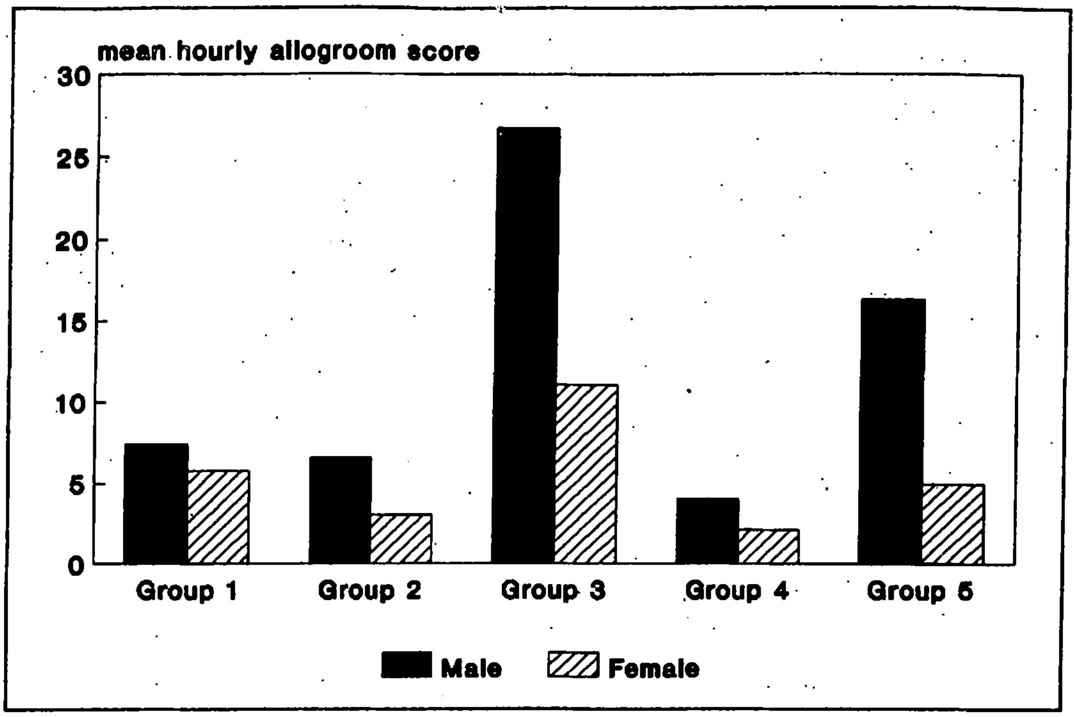


Fig 4.10 Mean hourly allogroom score for each breeding pair in the five study families during infant rearing.

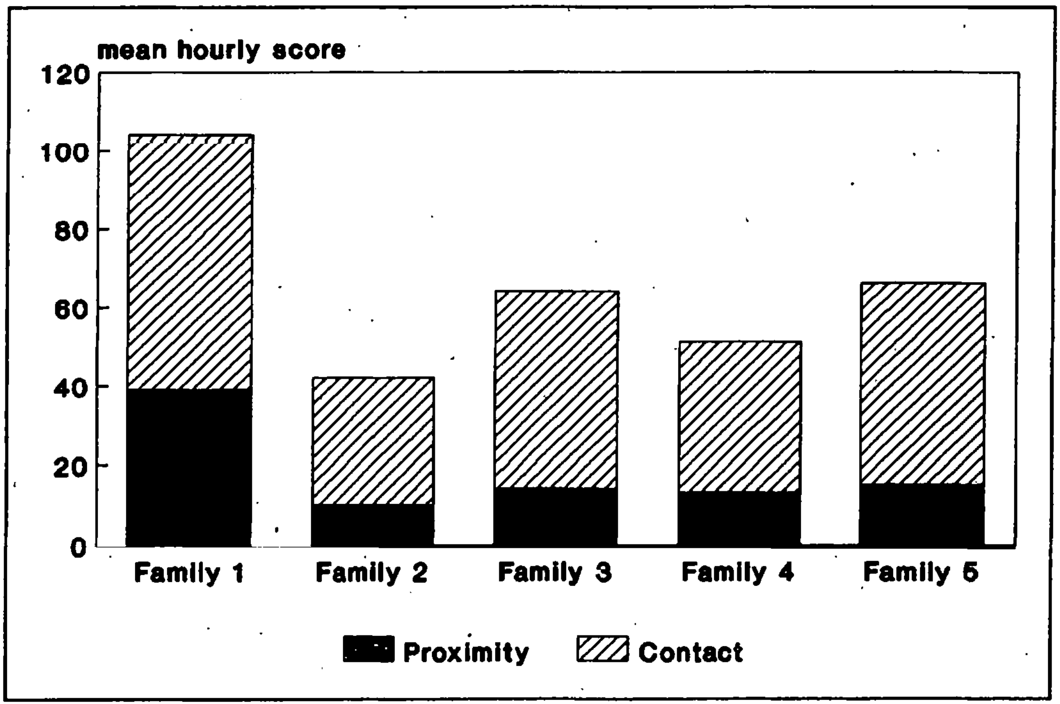


Fig 4.11 Mean number of scans per hour in which the members of the breeding pair were scored in proximity (<15cm) or contact with each other during the infant rearing study period.

Sexual behaviour

Sexual behaviour was infrequent. None was noted in group 1. In the other pairs, the male sniffed the female's genitals less than once an hour on average, while females presented to the males less than once every two hours of observation. No mating was seen.

Scent marking

Scent-marking scores are given in Table 4.13. Tail anoints were the most frequent type of marking seen. In four of the five groups, the male tail anointed more frequently than did the females, but the difference was not significant ($p = 0.1$, Wilcoxon test). Females marked anogenitally more than did males and this difference was close to significance ($p = 0.059$, Wilcoxon test). No significant difference was found between male and female total scent-marking scores ($p = 0.59$, Wilcoxon test).

Agonistic behaviours

Agonism was again very low. No agonistic interaction occurred between the breeding male and female in any of the study periods. Mean ABL scores per hour are given in fig 4.12. Males performed the behaviour more frequently than females in every group. The difference was not quite significant ($p=0.059$, Wilcoxon test). In group 3, the female performed very little ABL, while the male performed almost twice as much as any other male. In group 4, on the other hand, there was very little ABL, with the female not performing any.

Synchrony

Table 4.14 shows the observed and expected frequencies of simultaneous behaviour. In two groups, 1 and 3, the expected frequencies were too low to allow the test to be performed. Among the remainder, the score of two groups differed significantly from the expected. The pair of group 4 behaved simultaneously significantly less than expected, while that of group 5 did so significantly more than expected.

Table 4.16 Weekly mean Hinde Index in each group rearing an infant over the six weeks following a birth in the group. The weekly scores for each group are ranked and the rank is indicated in bold type.

	week 1	week 2	week 3	week 4	week 5	week 6
group 1	36.6 **2**	63.0 **6**	16.5 **1**	37.3 **3**	50.4 **4**	60.1 **5**
group 2	28.4 **4**	45.5 **5**	58.7 **6**	11.4 **2**	8.2 **1**	11.9 **3**
group 3	32.3 **3**	53.9 **5**	64.4 **6**	27.4 **2**	8.5 **1**	37.9 **4**
group 4	24.3 1	60.5 **5**	35.8 **4**	27.0 **2**	27.3 **3**	63.9 **6**
group 5	15.2 **3**	19.9 **5**	26.2 **6**	5.6 **1**	10.8 **2**	16.9 **4**

Table 4.17 Mean hourly female tail anoint score for each week following the birth of an infant in each of the five study groups.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Group 1	3.3	3.5	0.3	1.0	0.7	0.3
Group 2	3.7	1.7	1.7	3.0	0	1.0
Group 3	4.6	2.5	2.7	3.7	4.3	3.0
Group 4	5.7	1.3	5.0	11.7	0.8	0
Group 5	1.8	2.3	2.3	2.7	2.0	1.7

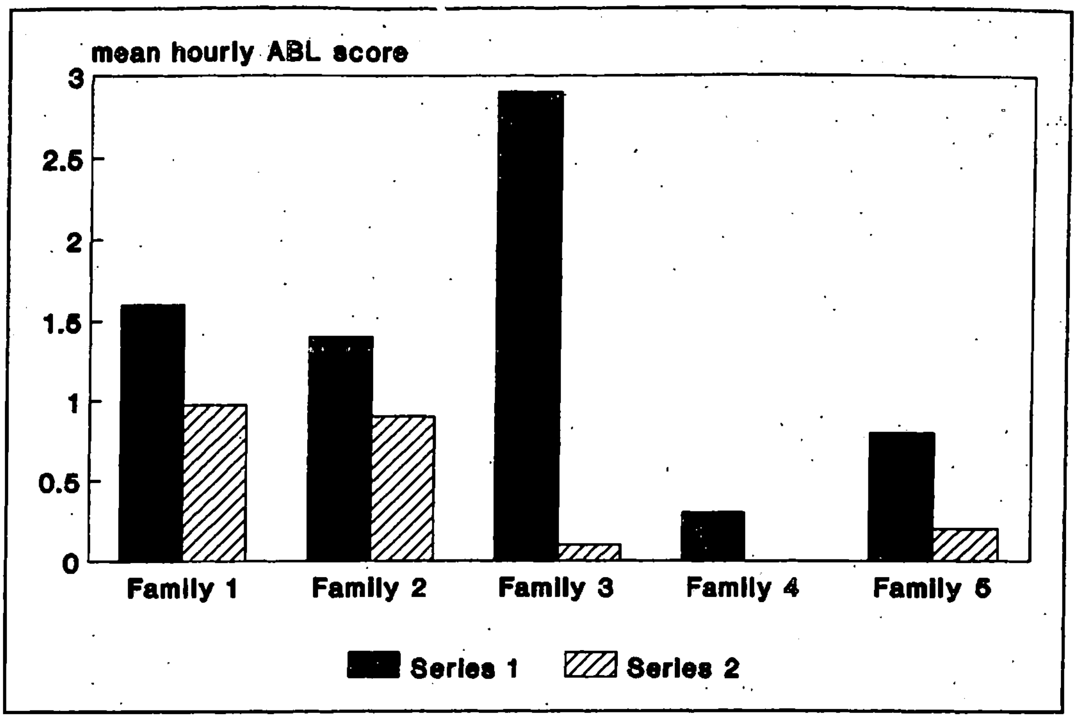


Fig 4.12 Mean number of times per hour that ABL was performed by the breeding male and female in the five study groups during the infant rearing study period.

Changes over time

To identify any significant changes in behaviour over time, the data were collapsed into six one-week blocks and the hourly mean per week per behaviour was calculated. Differences between the means were then tested using Friedman's two-way analysis of variance. Most behaviours did not change significantly over time. Three did however, *viz*: female leaving, Hinde index, and female tail anoint. The change in tail anointing was sufficiently strong to cause a significant change in female scent-mark totals as well.

Table 4.15 shows the overall mean hourly rate of female leaves per week over the six week period, while changes in the Hinde Index are shown in table 4.16.

Female approaches were highest in week 2 and Friedman's ANOVA is significant ($\chi^2 = 11.19, p<0.05$). No other behaviours were significantly elevated during week 2, although male approaches and male allogrooming were elevated at that time.

Changes in the Hinde Index with time were also significant (Friedman, $\chi^2 = 14.13, p<0.02$). While males were consistently responsible for maintaining contact throughout the study, they were most responsible for proximity maintenance in weeks 2, 3 and 6 and least responsible in weeks, 1, 4 and 5. In weeks 2 and 3, this is a reflection of the number of times females break contact combined with a high number of male approaches. In week 6 male approaches were considerably higher than those of females, while scores for leaves are more balanced, with female leaves being only slightly greater than those of males.

Table 4.17 shows fluctuation in hourly mean female tail anoint scores per week over the six weeks. Weeks 1 and 4 have elevated scores and the difference between the weekly scores is significant (Friedman $\chi^2 = 11.48, p=0.05$). A similar pattern is seen in total scent-marking scores (Friedman $\chi^2 = 11.15, p<0.05$). No other behaviours show this trend, with the possible exception of female leaving, which shows an inverse relationship to high tail anoint scores. Female leaving is lowest when tail anointing is highest.

4.3.4. Discussion

As in the newly formed pairs and established groups, males are responsible for making and maintaining contact and show higher ABL scores. Unlike the former two conditions, however, males allogroom the females more while females scent mark anogenitally more.

It is difficult to interpret the changes in Hinde index over the six weeks following the birth. In the study on new pairs, (study 4.1), it was found in several pairs that the female assumed responsibility for contact maintenance for short periods of a day or two. In one pair, this was demonstrated to coincide with a periovulatory period and may therefore be a reflection of oestrus. The changes in Hinde index shown in this study, however, are unlikely to be related to oestrus. Post-partum ovulation has been demonstrated to occur around 12 days after birth (Ziegler *et al.*, 1990b). It would therefore be predicted that the Hinde index would be low during the second week of the study, which was not the case. Perhaps instead it is a reflection of the male making contact with the infant rather than its mother, a hypothesis supported by the pattern of allogrooming. Although no data were taken on which part of the female was groomed, it was apparent that while the female was carrying the infant, the latter was a focus for male grooming. It was often difficult to know whether the infant or the female was actually the recipient of the male's grooming. It is interesting that male allogrooming was highest during week 2, just prior to the time when the male is expected to start carrying the infant, although there were no significant differences over time seen in male allogrooming. Occasionally, when it was obvious that the male was grooming the infant rather than the mother, he was also seen to investigate the infant manually and to sniff it. At times, there were apparent attempts to remove the infant from the mother, but none was successful in any group until week 4. Following successful infant transfers, grooming was usually discontinued. The relationship between allogrooming, infant carrying and infant transfer will be considered in detail in Chapter 6.

No explanation can be offered for the level of female anogenital scent marking being higher than that of the male, whereas no differences had been seen in other contexts. This appears to be due to the male anogenital scent-marking scores being reduced rather than those of the female being elevated. Scent marking in callitrichids is generally thought to be related to intra-group communication, although the function of the different scent-mark types is poorly understood (Epple 1970, 1972, 1986). It is unlikely that this relates to changes in the duration of the pair bond, as no significant difference in any scent-mark scores between males and females was seen in either new or long-established pairs. It is also unlikely to be due to changes in the female's reproductive status, as no cyclical change in anogenital scent marking was detected, nor was there a significant difference between male and female scores in newly-established pairs. It must be remembered, however, that it is unlikely that any female in the study of new pairs had more than one ovulation. As the duration of the ovulatory cycle is about 21 days (see Chapter 3), it is likely that the females in the groups with babies had two ovulatory periods during the study (unless they became pregnant on the first), as the study went on for six weeks. They would possibly have had a post-partum ovulation during week 2 and a second ovulation during week 5 or 6. This may have had the effect of highlighting differences between male and female anogenital marking scores if they are related to behaviour during the periovulatory period. Evidence presented in Chapter 3, however, suggests that scent mark frequencies do not change around ovulation.

Female tail anointing scores, on the other hand, did show cyclical changes. The 3 week interval in the score is compatible with the ovarian cycle length being about 21 days. However, it is unlikely to coincide with ovulation. Ziegler (1989) has shown that, in four *Callimico* females, post-partum ovulation occurred in the second week after birth when an infant was being reared. A single post partum ovulation was recorded at JWPT six days after birth occurred, but in this case the infant died. Thus, it is likely that the elevated tail anointing by the female is taking place during the follicular phase of the ovarian cycle. Cyclical changes in tail anointing were not detected in the newly established pairs, either due to the elevated socio-sexual behaviours masking these changes, or because of the fact that no monitoring of the female cycle phase was made when the male and female were introduced to each other. Therefore, the females were probably at different stages of the cycle during each week of that study.

Sexual behaviour and agonism were very infrequent, such that no analysis of changes over time could be carried out. Whether this is a reflection of the strength or weakness of the pair bond can only be speculated on. The high level of allogrooming by the male compared with the female, would indicate that the relationship between them is still close but, as mentioned earlier, it may well be related to the status of the female as an infant carrier rather than as a bonded partner. Only one breeding pair synchronised behaviour significantly. Lack of synchrony in the other breeding pairs may also be indicative of a weak relationship within them.

Study 4.4 Long-term changes in the pair relationship.

4.4.1 Aims

This study was designed to compare the behaviour of the adult male and female *Callimico* in newly-established pairs (condition 1), in established breeding groups (condition 2), and in groups rearing infants (condition 3).

4.4.2. Methods

Data from the three studies detailed in this chapter were compared using Kruskal-Wallis non parametric one-way analysis of variance to detect differences between the three conditions. This was carried out for each behavioural category performed by each sex. Where a significant result was indicated by the Kruskal-Wallis test, *post hoc* pairwise comparisons were made using the Wilcoxon test.

4.4.3. Results

Table 4.18 shows the behaviours in which significant differences were found between the three conditions. It also gives the relevant test statistic and probability level indicated by the test. No significant differences were found in any other behaviour categories using Kruskal Wallis one-way analysis of variance.

In all behaviour categories, whether significant differences were found between conditions or not, higher scores were found in condition 1 than in either condition 2 or 3 and often the condition 1 score was higher than both 2 and 3.

Table 4.18 Significant differences found in levels of behaviours across the three study conditions.

	MEDIAN SCORES				
Behaviour	Condition 1 New Pair	Condition 2 Established groups	Condition 3 Groups with babies	Kruskal Wallis Test	Pairwise Comparisons
Male activity	118.45	16.91	34.81	H=10.30 0.001<P<0.01	1v2 W=56.0 P<0.01 1v3 W=51.0 P<0.01
Female activity	116.2	16.94	36.61	H=11.01 0.001<P<0.01	1v2 W=57.0 P<0.01 1v3 W=51.0 P<0.01
Male approach	22.4	7.88	9.35	H=11.36 0.001<P<0.01	1v2 W=57.0 P<0.01 1v3 W=51.0 P<0.01
Female approach	9.925	4.875	2.0	H=11.63 0.001<P<0.01	1v2 W=56 P<0.01 1v3 W–51 P<0.01
Male leave	15.15	4.54	5.3	H=11.01 0.001<P<0.01	1v2 W=57 P<0.01 1v3 W=51 P<0.01
Female leave	11.97	6.01	6.15	H=11.01 0.001<P<0.01	1v2 W=57 P<0.01 1v3 W=51 P<0.01
Contact	49.9	14.5	47.3	H=6.48 0.02<P<0.05	1v2 W=53 P<0.05 2v3 W=25 P=0.055
Contact + proximity	82.1	29.2	64.2	H=7.23 0.02<P<0.05	1v2 W=53 P<0.05
Male scent mark	7.29	3.9	4.73	H=6.32 0.02<P<0.05	1v2 W=53 P<0.05 1v3 W=47 P=0.055
Female scent mark	5.48	3.3	3.29	H=6.38 0.02<P<0.05	1v2 W=52 P<0.05 1v3 W=49 P<0.05
Male allogroom	0.85	0.48	0.23	H=8.0 0.01<P<0.02	1v2 W=51.5 P=0.055 1v3 W=50.0 P<0.05
Male sprawl	2.53	0.45	0.46	H=11.23 0.001<P<0.01	1v2 W=57 P<0.01 1v3 W=51 P<0.01
Female sprawl	2.33	0.9	0.47	H=8.04 0.01<P<0.02	1v3 W=5 P<0.01
Female proceptive				H=11.01 0.001<P<0.01	
Mount				H=10.3 0.001<P<0.01	
Mount with thrust				H=11.01 0.001<P<0.01	

Spatial relationships

Levels of male and female locomotion were significantly higher in condition 1 than condition 2 by a factor of about seven and higher than in condition 3 by a factor of three, although there was no significant difference between conditions 2 and 3. The higher levels of locomotion in condition 1 were reflected in both approach and leave scores, while approach and leave scores for conditions 2 and 3 were not significantly different.

No significant difference was found in 'proximity' scores between the three conditions. 'Contact' scores did differ significantly ($0.02 < p < 0.05$), with higher levels of contact seen in both conditions 1 and 3 than in condition 2. The median scores for contact in conditions 1 and 3 are similar (49.9 and 47.3), but the difference between scores for conditions 1 and 2 are significant, while that between 2 and 3 is not, although it is close to the level of significance ($p = 0.055$). When proximity and contact scores are summed, the difference between conditions 1 and 2 are again significant while those for 2 and 3 are not.

Scent marking

Male and female scent-mark totals were significantly different across the three conditions, being significantly higher in condition 1 than in condition 2. In females, the difference between conditions 1 and 3 was also significant, while in males it was close to significance ($p = 0.055$).

The only individual scent mark type to show a significant difference was male anogenital scent marking, which was significantly higher in condition 1 than in condition 3 ($p = 0.014$). The difference between conditions 1 and 2 was close to significance ($p = 0.055$).

Affiliative Behaviours

Males solicited grooming by sprawling more frequently when newly paired than when in established pairs or in pairs with infants. Females, on the other hand, sprawled significantly more frequently only when newly paired. The level of female sprawling in established groups, however, was not significantly different from that of either newly paired animals or in groups with infants.

There was no significant difference in allogrooming scores between the three conditions, although allogrooming was considerably elevated during the early phase of the relationship. Fig 4.13 shows the levels of allogrooming in each pair during each phase of the study. Allogrooming scores of new pairs are around double those of breeding pairs, whether or not they have an infant.

Female proceptive behaviour differed across the three conditions, being significantly higher in new pairs than either in established groups or in groups with infants. There was no significant difference between the latter two conditions.

Male mounts and mounts with thrusting (copulation) followed the same pattern, but the low frequency of these behaviours did not allow pairwise comparisons to be made.

4.4.4. Discussion

These results show that, generally, where significant differences occurred in the behaviour of males and females across the three conditions, higher levels of those behaviours were found in newly-paired dyads than in established breeding pairs or in pairs with infants. Male and female locomotion, approach and leaves scores all showed this trend, while there was no significant change in Hinde Index values.

Scent-mark totals were also significantly elevated in both sexes in new pairs, although the only type of scent marking that showed a significant difference was male anogenital marking. Because the motivation and function of scent marking is poorly understood, it is difficult to interpret this finding. In *Callimico*, scent marking was thought by Lorenz (1972) to be particularly important in conveying information about the female's sexual status. This was not supported by this study of behaviour. Changes in scent-marking behaviour were not associated with stages of the ovulatory cycle.

Scent marks have also been shown recently to be important in maintaining reproductive suppression within groups of cotton-top tamarins, but this phenomenon has not been investigated quantitatively (Savage, 1988). Given that all females were pregnant in condition 2, it is not surprising that scent marking was lower than in condition 1, where females were cohabiting with a potential breeding partner for the first time and possibly undergoing ovulatory cycles for the first time. In condition 3, all the females would presumably have had a post-partum oestrus about 10-14 days following the birth of their infants, but may not have been sexually receptive at other times. This perhaps led to relatively low scent mark scores. Scent marks, however, undoubtably convey much more information than that needed to maintain reproductive suppression. Information on individual identity, age-sex class, dominance status and reproductive status may all be conveyed chemically (Epple 1986, Epple *et al.* 1987). The relatively higher scent-mark scores in the newly-paired animals probably reflect a stage of familiarisation. This probably reflects changes in the animals' own reproductive status as well (although not changes in the ovulatory cycle) and therefore whether this also reflects a developing pair bond must be a moot point.

Sexual behaviours were also significantly higher in condition 1 than in 2 and 3. This was true of female proceptive behaviours, male mounting and male copulation. These behaviours, together with elevated approaches and scent marks, show that courtship was indeed significantly higher in newly-paired animals than in established pairs and pairs with infants. Since there is no lactational anoestrus and ovulatory cycling has been shown to resume rapidly following a birth in *Callimico* (Carroll *et al.* 1990, Ziegler *et al.* 1989) the higher level of courtship in newly-paired animals is presumably due to pair-bonding effects rather than to the reproductive status of the females and therefore follows Parker's (1974) prediction that courtship should decline once a pair bond is formed.

The one behavioural parameter that differed from the general trend of scores for condition 1 being higher than those in condition 2 and 3 was the time spent in contact. Time spent in contact was significantly higher in new pairs than in established pairs without infants. Following the birth of the infant, however, contact between the male and female increased almost to the same level as in new pairs. On the face of it, this is contrary to Parker's prediction (1974) and in line with the prediction that behaviour in early bonding will reflect behaviour during infant rearing. This may be attributable to one of two causes. Firstly, the male may be mate-guarding (waiting until the female comes into oestrus so that he may mate her), as the females in conditions 1 and 3 were not pregnant. Secondly, in condition 3, he may be guarding the infant and this may reflect an indirect form of parental investment. As this increase in contact is not accompanied by a increase in courtship, it may be that this is indeed a form of parental investment. However, it is not accompanied by an increased tendency to perform ABL, the mobbing response to predators, and although no quantitive data on vigilance were taken, the males did not appear to be more vigilant. The male did, however, groom the female frequently. As mentioned above, the infant, rather than the female, may have been the focus of grooming, thus supporting the hypothesis that the increase in contact following the birth of the infant represents a paternal investment in guarding the infant.

General Discussion

In her review of monogamy in mammals, Kleiman (1977a) stated that there are several notable characteristics displayed in monogamous relationships. Overall, there should be a reduction of sexual dimorphism, both behaviourally and physiologically, the pair should spend long periods in close proximity and should exhibit synchronised behaviours. In a later paper, Kleiman (1981) also suggested that behaviour in a newly-bonded pair should reach equilibrium within a short time and they should display a high number of affiliative behaviours as compared to agonistic behaviours.

These points were discussed in Chapter 1 and refined to the following predictions.

(i) Behavioural sexual dimorphism during the early bonding period will follow the pattern exhibited during infant rearing

(ii) There should be no indication of dominance between the male and female

(iii) Outside ovulatory periods, the male should not be responsible for making or maintaining contact

(iv) Behaviour should be synchronised

(v) Allogrooming and time spent in proximity with the partner should be frequently seen and should increase with time

(vi) Sociosexual interactions should decrease with time

To what extent are these predictions supported by this study of *Callimico*?

Behavioural Sexual Dimorphism

Behavioural sexual dimorphism was apparent in several of the parameters measured. Most particularly, males made contact more frequently than females and were responsible for maintaining contact and proximity within the pair significantly more than the females. Males performed Arch Bristle Leaping (ABL), consistently more than the females, although in none of the study conditions was the difference between male and female scores quite significant.

When rearing infants, the difference in male and female anogenital scent marking scores was close to significance, but otherwise no significant differences in scent marking frequencies were detected between the sexes.

No significant differences were found in allogrooming or locomotion scores, although males did allogroom females more than *vice versa* in pairs rearing an infant.

Comparison of the behaviour of the adult pair in newly-established pairs, long-established pairs and long-established pairs rearing infants, showed that, with the exception of anogenital scent marking, behavioural sexual dimorphism had the same pattern throughout the study, with the male being responsible for making and maintaining contact and for initiating the ABL mobbing behaviour.

Dominance

There was no indication of dominance between the male and female at any time during any of the three studies. Agonism within the pair was all but absent. In this respect, the male and female were co-dominant.

Making and maintaining contact

Males are consistently responsible for making and maintaining contact except during ovulatory periods, when the female assumes that role for a day or two. Even when the females were pregnant, during the study of the long-established pairs (study 4.2), males were still responsible for making and maintaining contact within the pair.

The change during the ovulatory period is brought about by changes in female behaviour, suggesting that ovulation may be concealed from the male.

Synchrony

There was little indication of synchronisation of behaviour within the pair as indicated by the simultaneous performance of the same behaviour. Rather, bouts of similar behaviour overlapped. This may not be an indication of lack of synchrony or integration within the pair, however; there may be good reasons for not performing behaviours at the same time. In gibbons and siamangs, synchrony of behaviour is well documented (Chivers 1972, 1974) and interpreted as an indication of an integrated 'bonded' pair. Such large-bodied primates have little need for anti-predator vigilance and it is probably safe for all group members to forage at once. For smaller-bodied animals such as *Callimico*, there is a constant need for vigilance and it is unlikely that all group members can feed simultaneously. Such anti-predator vigilance has been reported in *S. oedipus geoffroyi* (Lindsay 1979), and *S. fuscicollis* (Terborgh 1983) and is suggested as a major selective force for mixed species associations among callitrichids in the wild (Terborgh 1983, Goldizen 1989).

Changes over time

Levels of allogrooming and time spent in proximity were both much lower in the established groups than in the new pairs. This may have been an effect of increased group size in studies of the established pairs and the rearing pairs, which were in groups of four or five animals, but in the study of the pairs rearing infants, time spent in proximity increased to the same level as seen in the new pairs. Clearly, this was a result of the infant birth rather than 'pair-bonding' effects. As such, it may be an infant guarding behaviour. It is also possible that this represents pair-bond reinforcement to ensure the presence of the male during infant rearing. If this were the case, however, it might be expected that the female would assume responsibility for making contact or for contact maintenance during this time. Instead, the male remains responsible both for making and maintaining contact. Lastly, the male may be mate guarding. In both the study of new pairs and the study of rearing pairs, the females were undergoing ovulatory cycles, while in the established pairs study they were pregnant. Maintaining contact may merely be a means of ensuring exclusive access to the sexually receptive female. In view of the attention paid to the infant by the male following the birth, however, it is most likely that infant guarding is the main function of the increased proximity of the male to the female during the infant rearing period.

Without testing the 'bond' by allowing an opportunity for an extra-pair breeding relationship to develop, it is impossible to say whether the reduction in time spent in proximity or the level of allogrooming with time is due to the existence of an established bond or to the lack of a bond. This will be discussed further below.

Sociosexual interactions also decreased with time, as predicted. Male mounts, mounts with thrusts and female proceptive behaviours were significantly elevated in the newly-paired animals.

Overall, what evidence is there for the existence of a strong pair bond in *Callimico*?

Firstly, there was a degree of affiliative behaviour between the male and female, particularly in the newly-cohabiting animals. This, however, decreased with time and, while time spent in contact increased later, it did so only following the birth of an infant. There was little evidence of synchronised behaviour among the breeding pairs and, among the established groups, the male and female interacted little. They did, however, feed together amicably, sleep together and undertook group protection together.

While this indicates that *Callimico* forms stable, long-lasting heterosexual relationships in captivity, there is little to suggest that any lasting bond exists between the partners. It may be that, having forged a breeding relationship, the male and female are not then bonded to each other but to the group. Group living conveys advantages for small primates, such as increased anti-predator vigilance, better defence of home range and increased foraging efficiency. It may be that maintaining the group is more important than maintaining the breeding relationship with any particular mate.

Considerably more research would be needed to test this. Realistic opportunities to desert would have to be given to the established pair to test the existence of the 'pair bond'. The effect of substituting a breeding animal for another of the same sex should be carried out. If a 'bond' needs to be forged with a particular animal, courtship and sexual behaviour should reflect that seen in the early phase of the relationship between a cohabiting pair.

The relationship within the breeding pair does not seem to be notably different from that of marmosets and tamarins studied to date. Behavioural sexual dimorphism has been reported in *Callithrix jacchus*, (Evans and Poole 1984), *Saguinus fuscicollis* (Epple 1977), *S. oedipus* (Price 1990) and *S. labiatus* (Buchanan-Smith 1989). In all these species, the males have been reported to be responsible for making and maintaining contact more than the females. In *C. jacchus* and *S. oedipus*, this has been shown not to be consistent across time. In the former, males do not approach females more than *vice versa* after the early phase of cohabitation is over (Evans and Poole 1984). In the latter, males approach the females more than *vice versa* when the female is not pregnant and just subsequent to a birth. During mid to late pregnancy, the female is responsible for contact regulation (Price 1990). In *Callimico* there is little variation seen. In only one pair, in which the female was pregnant, was the Hinde Index marginally in favour of female proximity maintenance.

It is perhaps most surprising that the *Callimico* pair spent so much time in proximity following the birth of an infant. As the female cares for the infant unaided for the first few weeks following the birth, one might predict that the male should only seek contact with the female when she is likely to conceive. It appears, however, that two factors are involved in this behaviour. One is the apparent concealment of ovulation. If a male is to be reasonably certain of siring the next infant, he must maintain close contact with the female. The other is that the male may be guarding the infant, thus increasing his parental investment prior to becoming involved in direct infant care. If this is the case, infant carrying and food sharing are not the only parameters to be considered when discussing *Callimico*'s reproductive strategy. Infant care will be discussed further in Chapter 6.

SUMMARY

1. Behavioural sexual dimorphism is apparent in *Callimico*. Males make and maintain contact, allogroom the females more than *vice versa*, and perform Arch Bristle Leaping more than the females.

2. The male and female are co-dominant throughout the relationship.

3. There is no evidence of synchronised behaviour as measured by simultaneous performance of behaviours.

4. All social and sexual behaviours measured were less frequent in the established than in the new pairs, significantly so for locomotion, time spent in proximity, scent marking, soliciting of grooming, proceptive behaviours and male sexual behaviour.

5. Following the birth of an infant, time spent in contact increased to the same level as seen in newly-cohabiting pairs. During this time, the infant rather than the female may be the object of the male's attention.

6. Ovulation appears to be hidden from the male. Changes in approach/leave behaviour resulted in occasional days when the female assumed responsibility for maintaining contact with her partner. For one female, this was shown to coincide with ovulatory periods as measured by hormonal assay, and with an associated rise in female proceptive behaviour. No other behavioural changes were found at these times.

CHAPTER 5 BONDING IN MULTIFEMALE SOCIAL GROUPS

5.1 Introduction

Among the marmosets and tamarins, both in the wild and captivity, social groups typically have only a single breeding female (*e.g.* Ferrari and Lopes Ferrari 1989, Goldizen 1990, Sussman and Garber 1987). As discussed in Chapter 1 (Section 1.4), it is generally thought that the evolution of the single-breeding-female group is related to the evolution of twinning and the consequent need of the female for assistance in rearing the two infants (Dunbar 1988, Goldizen 1990, Kleiman 1977, Sussman and Garber 1987). This complex evolutionary relationship hinges on the hypothesis that the callitrichid female is unable to rear her infants unaided. Evidence to support this comes from Dunbar's (1988) modelling of maternal time budgets indicating that in saddle-back tamarins (*Saguinus fuscicollis*), the female is unable to both carry and feed the entire litter to weaning. Goldizen (1987) has provided evidence that successful rearing of twins in wild groups of saddle-back tamarins is related to the number of helpers that are available in the group. It is, therefore, advantageous to the female to be the only one breeding in the group in order to ensure there is no competition for helpers within the group.

Captive studies have shown that mature daughters and unrelated females within callitrichid groups are prevented from breeding through physiological or behavioural mechanisms (*e.g.* Abbott 1986, Abbott *et al.* 1986, Brand 1981, Epple and Katz 1984). Reproductive suppression within callitrichid groups is a widely studied phenomenon in captivity, particularly in *C. jacchus* peer groups containing more than one female (*e.g.* Abbott and Hearn 1978, Abbott 1984). In this species, only the dominant female breeds within a group. This exclusive status is maintained by suppression of ovulatory cycles in subordinate females, apparently by a combination of behavioural and physiological mechanisms. Similar findings have been reported for *Saguinus fuscicollis* by Epple and Katz (1984) and for *S. oedipus* by French *et al.* (1984). In monogamous families as well, the mother maintains exclusive breeding status, but this is not simply a function of her dominance over her daughters. It has been shown in several species that, if a breeding female is removed from a group, a daughter may not attain breeding status spontaneously, even if sexually mature (Carroll 1986). Similarly, if a mature sibling heterosexual pair is removed from the group, the separated male and female will not breed with each other (Carroll, 1986). Heistermann *et al.* (1989) investigated families of cotton-top tamarins in which the mother had been removed. They found that the oldest daughter commenced ovulatory cycles in all cases, yet was not mated by her father. Clearly, while the presence of the mother prevents the daughter from cycling, some other mechanism prevents inbreeding within the group. Thus, different mechanisms maintain the mother's breeding exclusivity in the family as opposed to peer groups. These phenomena, however, are not without exception. Familial suppression of breeding of offspring within their natal group sometimes fails and rare occurences of incest have been reported in *C. jacchus* (Rothe and König 1991) and *S. oedipus* (Price and McGrew 1991). *Leontopithecus rosalia* appears to be the exception. In all-female peer groups of this species, subordinate females exhibit ovulatory cycles as well as the dominant female, and in families, daughters may cycle within their natal groups (French *et al.* 1989).

Callimico females have only a single infant. It may be predicted, therefore, that they have less need for help in rearing their infants and perhaps can even rear the infant unaided. If the need for help is reduced, the need for exclusive access to helpers should also be reduced. It may also be predicted, therefore, that reproductive suppression of subordinate peers of the same sex will not occur. Further, *Callimico* females should be more flexible in their social tolerance of other females, perhaps to the extent of forming stable polygynous breeding groups.

Evidence to support this comes from the few wild studies on *Callimico*, although this limited evidence should be regarded cautiously. Among wild *Callimico*, two breeding females have been reported in several of the groups studied. Two groups have been habituated to observers and both are reported to have possibly contained more than one breeding female (Pook and Pook 1979a, Masataka 1981a, 1981b). A third group with two breeding females has also been reported (Masataka 1981a).

Pook and Pook (1979a) speculated that their study group had more than one breeding female, based on the presence of two juveniles of similar age within the group. Juvenile and young adult marmosets and tamarins are, however, known to migrate between groups in the wild (Dawson 1977, Neyman 1977, Garber *et al.* 1984, Terborgh and Goldizen 1985, Stevenson and Rylands 1988). Nothing is known about the migration patterns of *Callimico*, but if juvenile migration is commonplace in this species, this may explain the observations of the Pooks.

Masataka (1981a) reported seeing two females, each carrying a young infant, within his study group. The infants were born 12 days apart during his study, which lasted from July to December 1979. This group was being attracted to a site artificially baited with food and therefore more than one social group may have been visiting the feeding station. Had the groups merged temporarily to take advantage of the food source, one would have expected evidence of competition between the groups at some time over the five months of the study. In fact, there was evidence that the group was composed of two sub-groups at both the beginning and end of the study and that each sub-group was based around a breeding female. There was, however, only one adult male in the group and he affiliated with both females. At the end of the study, it appeared that group fission may have been occurring, although the situation is complicated by the fact that three young males were introduced to the group by Masataka after they had been held in captivity by local villagers. The period of two months in the middle of his study during which greatest group cohesion was seen coincided with the period during which the infants were being reared by their mothers.

Unfortunately, neither the Pooks' nor Masataka's study group was trapped to establish beyond doubt its age-sex composition, and there are no weights for Masataka's captive animals. Masataka's estimations of age classes of his study animals are undoubtably inaccurate, as he refers to animals with estimated ages of two to four years as 'infants and juveniles' (Masataka 1981a, p. 24). *Callimico,* in fact reaches full adult size by two years old and females can breed at a little over a year (Beck *et al.* 1982, Carroll 1982). Indeed, recent evidence suggests that females removed from their natal group are capable of undergoing ovulatory cycles when less than a year old, so they can perhaps breed even earlier (C. Pryce pers. comm.).

Masataka (1981a) also visited the Pooks' study site in July and December 1979, one year after their study, and located their study groups on both occasions. On the second occasion, he found that two females in one group had produced young since his first visit and estimated that the young were about three months old.

While these studies indicate that wild groups of *Callimico* may contain more than one breeding female, no firm conclusions can yet be drawn about the composition of wild breeding groups. It has been pointed out that such large groups of *Callimico* as reported by the Pooks and Masataka (and more recently Buchanan-Smith 1991) are unlikely to be nuclear families, as it would take at least three to four years for a single breeding pair to produce seven infants (Pook and Pook 1981).

In captivity, marmosets, tamarins and *Callimico* are all typically kept in groups comprising a monogamous pair and their offspring. Departures from monogamy are rare because colony managers are aware of the reputed instability of non-monogamous groups, and normal management practices seek to avoid intragroup instability. Two recent surveys of *S. oedipus* and *C. jacchus* colonies have shown, however, that departures from monogamy do arise, although reports of polygyny are most infrequent (Rothe and König 1991, Price and McGrew 1991). In captive *Callimico* groups, departures from monogamy are also rare. Like the marmosets and tamarins, maturing offspring within *Callimico* groups are reproductively suppressed and the mother remains the only breeding female. There is only one report of a *Callimico* daughter becoming pregnant by her father while still cohabiting with her mother. This was at Edinburgh Zoo in October 1991. There had been no recent changes in group composition, the change in reproductive status of the daughter apparently being spontaneous. The infant was born live but died when three days old, having been taken by its grandmother, which was presumably unable to suckle it. There was no aggression within the group at this time (M. Stevenson pers. comm.).

If polygynous breeding groups of *Callimico* occur naturally and are stable, relationships within the group should be more typical of a polygynous group than of a monogamous group. This would be evident from weaker bonding between males and females than seen in the monogamous groups, characterised by reduced levels of allogrooming or resting in proximity or contact. Allogrooming relationships among polygynous primate species are reported to be characterised by females initiating grooming more frequently than males, females grooming males more frequently than the reverse and groomers tending to be of lower social rank than groomees. Kleiman (1977, 1981) states that most grooming in polygynous groups should be between females or between females and juveniles. Grooming patterns depend, however, on migration patterns within a species. If males migrate between groups, females within groups are often bonded through matrilines which are expressed in close grooming relationships [*e.g.* in macaques, savanna baboons, vervets, mangabeys and talapoins - reviewed by Melnick and Pearl 1987, most colobines (Robinson and Jansen 1987), and geladas (Dunbar 1988, Dunbar and Dunbar 1975)]. Where females or both sexes migrate, relationships between females are much less strong and allogrooming is rarely seen other than between males and females, or between mother and offspring (*e.g.* gorillas (Stewart and Harcourt 1987), chimpanzees (Goodall 1971, Kuroda 1980), red colobus (Struhsaker 1975). Thus, study of the social relationships within a group may give an indication of the underlying social structure of the species. Unfortunately, nothing is known of the migration patterns of *Callimico*. Other than the disappearance of a female out of Masataka's study group (Masataka 1981a, 1981b), and the disappearance of two unsexed animals from a second group (Masataka 1981a), no instances of possible migration have been recorded in the species. Further, little is known about the process of dispersal and migration among callitrichids. Both sexes migrate, and so far no field study has found a significant difference between the sexes in frequency of dispersal or the distance moved (Dawson 1977, Goldizen and Terborgh 1989, Neyman 1977).

In order to test the hypothesis that *Callimico* forms polygynous breeding groups, three trios, each consisting of a male and two females unrelated to each other or to the male, were established at JWPT. These trios were the focus of a study of their social relationships and, in order to monitor the reproductive state of the females, series of urine samples were taken from the females of two of the trios for radioimmunoassay of reproductive hormones (see Chapter 2).

More specifically, the study sought to answer the following questions:

1. Are captive groups with more than one potentially breeding female stable?
2. Does reproductive suppression occur in these groups?
3. Do the social relationships within the group during the first month of cohabitation reflect its stability?
4. Do the social relationships within the groups indicate that the females are competing for a limiting resource, *i.e.* the male as a potential caregiver for infants?

5.2 Methods

5.2.1. *Subjects*

Three trios were established, each of one male with two unrelated females. Table 5.1 shows the composition of each trio, the date it was formed and the age of each subject when the trio was established.

All the subjects were young, healthy, previously unmated adults that had recently been removed from their natal groups. The two females in each trio were known as ♀1 and ♀2. They were assigned 1 and 2 on the basis of age (the older female being ♀1).

5.2.2. *Housing and husbandry*

The first and third trios were housed in cages in JWPT's 'Behavioural Research Unit' (Oliver, 1983), while the second trio was housed in a similar unit within the zoo. These cages are described fully in Chapter 2.

The cages of the behavioural research unit are not on public display, whereas the outside area of the cage that housed Trio 2 is on public display. In all cases, the inside cages adjoin a large off-display area allowing viewing of the cage through a large window. In the behavioural research unit, this window is covered with a plastic film giving a smoked glass effect. This allows good viewing from the darker observation side into the light cage area, while reducing vision in the other direction. The zoo unit windows were originally covered with a plastic film, giving a mirrored 'one-way' glass effect. This film was, however, removed following the introduction of the male to the unit, as it was obvious that he was displaying to his own reflection. Following removal of the film, the subjects could clearly see the observer, even though the viewing area was kept darkened. They did, however, habituate quickly to the presence of the observer. No other callitrichid or *Callimico* groups were in visual, auditory or olfactory contact with any of the study groups.

5.2.3. *Establishment of the trios*

Captive callitrichid groups containing more than one unrelated female are notoriously unstable (Epple 1975, Kleiman 1979). Aggression between the females is commonplace, in some species resulting in severe injuries or even death, (Kleiman 1979). This aggression is more severe in the presence of a male. Single sex groups are more stable. It was therefore decided to mix the two females together for a period of time before introducing the male. The females in the first trio were together for 142 days before the introduction of the male, in the second trio for 32 days and in the third trio for 106 days. It was not possible to use a standard length time interval before introducing the male, for several reasons. Firstly, it was felt that not all females would be compatible and that some may take longer to establish a harmonious relationship than others. Secondly, management of the breeding colony took account of the necessity to allow all sub-adults to gain experience of rearing siblings within the natal group. This resulted in study animals not being available at the same time, resulting in a delay in establishing the study group.

The strategy of introducing the females to each other first and then introducing the male resulted in all three study trios being established without problems.

5.2.4. *Sampling procedure*

Each trio of *Callimico* was observed daily for the first five days following the introduction of the male and three or four times weekly thereafter, usually on alternate days, for the first four weeks of cohabitation. A total of 20 hours of observation was made on each group.

Behavioural categories sampled and the sampling methodology for the trio study are given in Chapter 2. By following a similar methodology to that used in the study of pair bonding (Chapter 4), direct comparisons can be made between that study and this.

Because only three trios were used, no statistical testing was carried out across the study groups. Differences within groups were tested using the Kruskal-Wallis one-way analysis of variance. Where a significant difference was found, *post-hoc* Wilcoxon's matched-pairs signed-rank test was used to detect differences between individuals. Unless otherwise stated, $p < 0.05$ was used as the level of significance.

5.3 Results

5.3.1 Stability of Trios

All three trios remained stable throughout the study period. Eventually, however, all of them had to be disbanded following extreme aggression between the two females. The aggression was so severe that at least one female in each trio required veterinary attention. Table 5.1 summarises the history of each trio.

Trio 1 remained stable for just over a year, during which time both females became pregnant and reared infants to independence. Neither study female conceived

Animal I.D.	Sex	Age at introduction to trio	Date ♀♀ introduced	Date ♂♂ introduced	Date trio disbanded	Comments
Trio 1						
M705	♂	3 years 11 months	16.04.84	05.09.84	22.07.85	Trio stable 320 days. Infants born 8.3.85 and 3.4.85. Both infants reared. ♀1 dominant following fight July 1985.
M786	♀1	2 years 4 months				
M817	♀2	1 years 11 months				
Trio 2						
M904	♂	2 years 1 month	15.05.85	16.06.85	12.05.86	Trio stable 326 days. Infants born 14.2.86 and 5.5.86. Both died 3 days old. ♀2 dominant following fight May 1986.
M866	♀1	2 years 2 months				
M872	♀2	2 years 1 month				
Trio 3						
M878	♂	2 years 7 months	20.07.85	03.11.85	19.12.85	Trio stable 46 days. Neither female pregnant. ♀2 dominant following fight December 1985
M922	♀1	1 year 9 months				
M947	♀2	1 year 8 months				

Table 5.1 Summary of the history of each of the three trios of Goeldi's monkey.

during the first four weeks of cohabitation during the behavioural study. Trio 2 was stable for a similar length of time, during which both females became pregnant. Both gave birth to live, full-term infants, but neither reared an infant beyond three days. Again, neither female conceived during the behavioural study. Trio 3 was stable for only 45 days. Neither female became pregnant.

All three trios were disbanded following severe fighting between the two females. The fighting occurred some time between 17.00 hrs and 08.00 hrs the following day. There had been no signs of tension or agonistic behaviour within the group immediately prior to the fight. The behavioural study had ended at the time of the fight in each case and hence the dominance relationship between the females prior to the fight is unknown. In all three cases, both females sustained injuries and one female emerged clearly dominant to the other. In trio 2, a two-day-old infant was killed during such fighting. In the other two trios, injuries were sustained only by the females.

In trio 1, the older female (♀1) emerged as dominant following the fight on 22.07.1985. The subordinate female sustained severe bites to the arms and legs, particularly the lower legs and ankles, while the dominant sustained multiple superficial bites. The subordinate female was found cowering on the cage floor at 08.00 hrs, while the dominant was sitting close to the male. Both females required veterinary treatment. The fighting between the females occurred after both had reared infants in the group that were three and four months old respectively (see Table 5.1).

In trio 2, the younger female (♀2) emerged as dominant. A similar pattern was seen in the injuries sustained. Both females were injured, although the dominant female was affected to a lesser degree. The two-day-old infant of the subordinant female was found dead, having sustained deep bite wounds to the right thigh. The subordinate female herself had bites to the face and head, the lower torso and the hind legs. The dominant female had also given birth three months before the fight on 14.02.1986, and her infant had died on the third day after birth, long before the outbreak of fighting between the females. In this case there was no suggestion that death had been caused by aggression. The only *post-mortem* finding was an infection of *E. coli* in several of the infant's organs.

As in trio 2, the younger female (♀2) in trio 3 was dominant over the other. Both females sustained multiple superficial bites. The injuries of the dominant female actually appeared more severe than those of the subordinate, but the latter was crouching immobile in a corner of the cage floor. Neither female was pregnant at the time of the fight. Radioimmunoassay of reproductive hormone metabolites present in the urine of the females revealed that the subordinate female had not been ovulating during the period of cohabitation with the male and the other female. Following the fight, the subordinate female was separated from the male and dominant female but remained in olfactory, auditory and visual contact with them. Hormone assay subsequently showed that, during this subsequent period of separation, her reproductive cycles rapidly assumed normal profiles (see Chapter 3).

In all trios, the severity of the injuries was such that survival of the animals would have been compromised without veterinary treatment. All the study females survived and later successfully reared infants either at JWPT or at other institutions.

5.3.2 *Behavioural Study*

Locomotion

Table 5.2 shows the mean hourly locomotion score for each individual within each trio. In trios 2 and 3, the male performed locomotion significantly more than either female, ($p<0.001$ Kruskal-Wallis test). In trio 1, the male's score for locomotion was considerably less than that of either female, but not significantly so.

Spatial relationships

Table 5.3 shows the length of time that members of each dyad within the trio were in proximity. These results are expressed graphically in Fig 5.1. In all three

Table 5.2 Mean hourly activity scores for each trio.

	TRIO 1	TRIO 2	TRIO 3
Male	38.1	118.7	110.2
Female 1	57.3	94.7	80.0
Female 2	52.8	51.0	67.1

Table 5.3 Mean hourly score for resting within 15 cm of another individual.

	Trio 1	Trio 2	Trio 3
Male/Female 1	59.6	27.2	17.0
Male/Female 2	83.6	50.0	43.6
Female 1/Female 2	48.4	21.6	8.4
All	27.6	53.9	7.6

Table 5.4 Hinde Index for each dyad within the three study trios.

DYAD	TRIO 1	TRIO 2	TRIO 3
♂ - ♀1	-19.4	21.3	-52.5
♂ - ♀2	19.8	15.0	-4.3
♀1 - ♀2	7.4	13.9	31.4

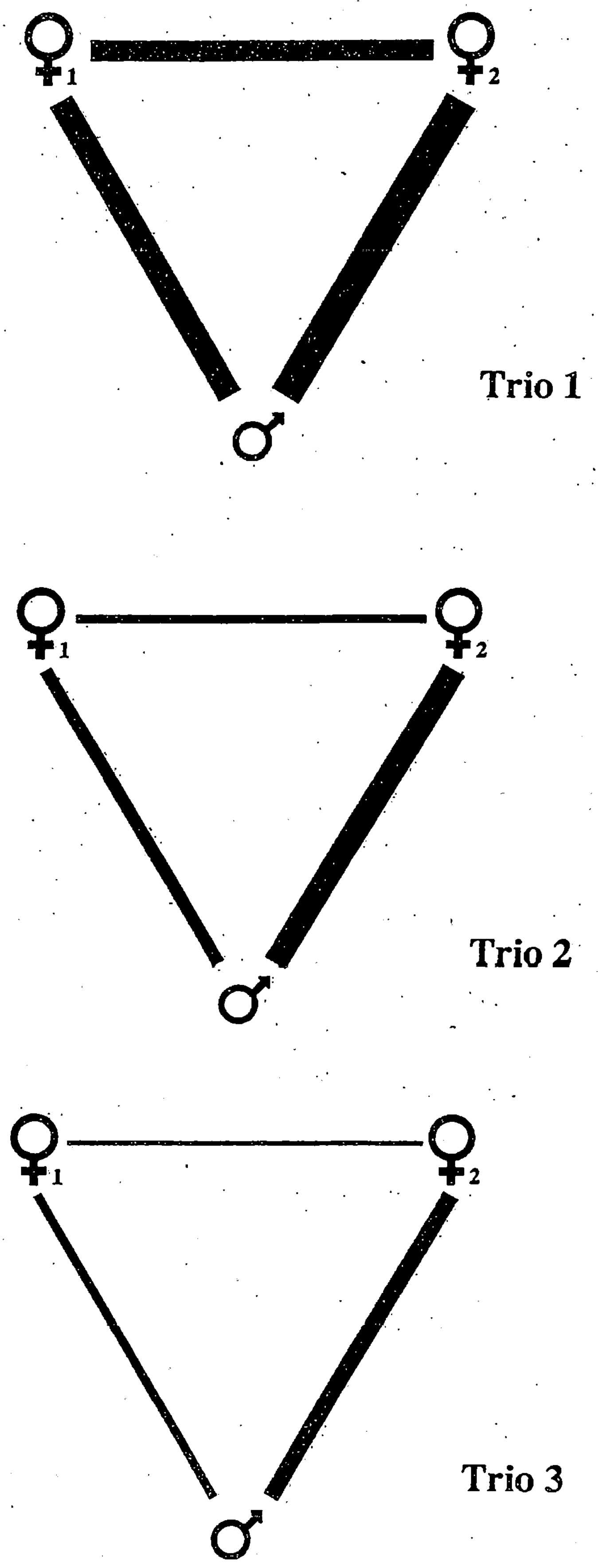


Fig. 5.1 Proximity sociogram of three male-female-female trios of Goeldi's monkeys. The time that the members of a dyad spent in proximity (<15cms) is proportional to the breadth of the connecting line.

trios, the females spent less time with each other than either did with the male. In trios 2 and 3 the male spent significantly more time in proximity of female 2 than with female 1 or than the females spent with each other (Kruskal-Wallis: $p<0.01$ for trio 2 and $p<0.001$ for trio 3).

Responsibility for initiating and maintaining proximity or contact, as measured using 'approaches' and the Hinde Index (I), is expressed in Fig 5.2 and Table 5.4, respectively. In the male/female dyads of trio 1, both females initiated contact more than the male. Female 1 approached the male more than *vice versa* on 17 of the 20 study days. The approach pattern in the male/female 2 dyad was much more equal, as the female approached the male more than *vice versa* on eight study days, while the reverse was true on four study days. On the other eight study days, approaches were equal in this dyad. The male approached female 2 significantly more than female 1 (Wilcoxon test $p<0.005$). Conversely, female 1 approached the male significantly more than did female 2 (Wilcoxon test $p=0.002$). The male tended to maintain contact with female 2 rather than with female 1 (i.e. over the study period, the Hinde Index was positive with female 2, negative with female 1). Thus, although the male approached both females more than vice-versa, he initiated and maintained contact with female 2 much more than with female 1. It is clear, therefore, that the male showed a preference for the younger of the two females. The older female both approached and was responsible for maintaining contact with the male, and in doing so was not peripheralised, spending 25% of the time resting in proximity to the male.

In trio 2, the male approached both females significantly more than they approached him (Wilcoxon test $p<0.01$). The male approached female 2 significantly more than he did female 1 (Wilcoxon test $p<0.01$), while female 1 approached him significantly more than female 2 did (Wilcoxon test $p<0.05$). Both females approached each other more than they approached the male, but not significantly so. The male was responsible for maintaining proximity with both females, the Hinde index being positive in both cases. There were only four study days when female 1 was responsible for maintaining contact with the male, and only three when female 2 was. Again, the male showed a preference for one female, while the female that was not preferred approached him more than the preferred female did.

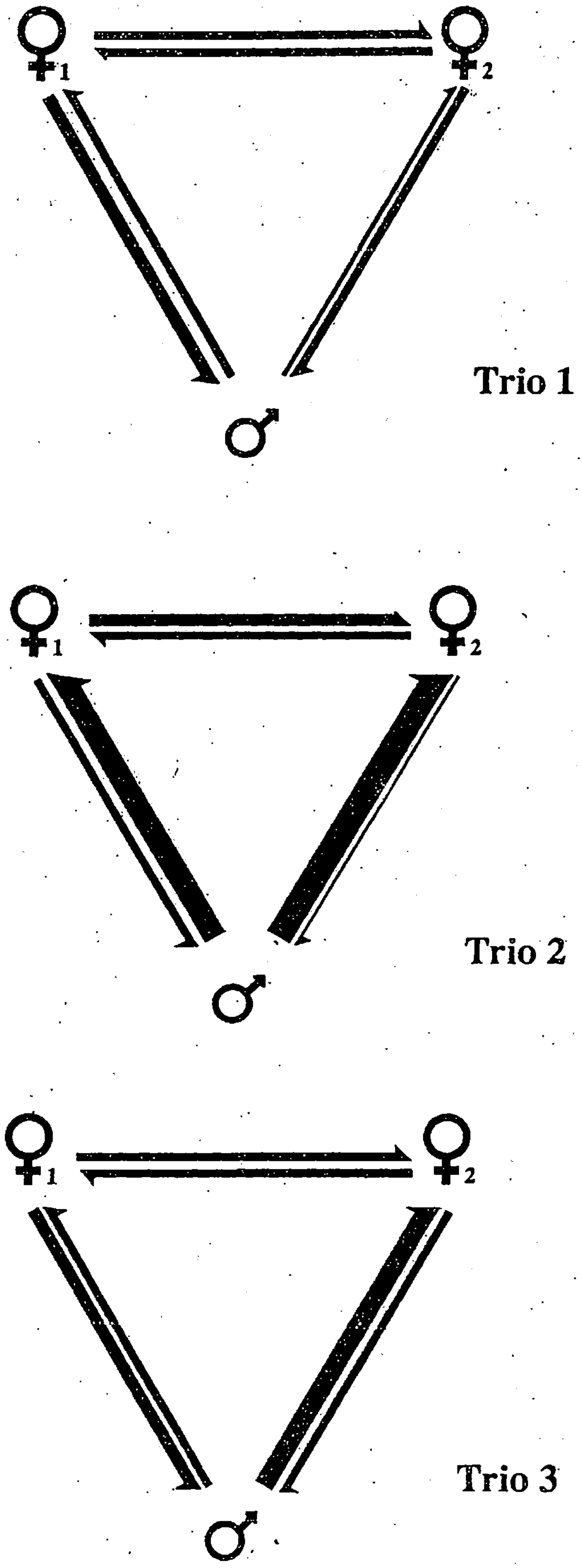


Fig. 5.2 Approach sociogram for three male-female-female trios of Goeldi's monkeys. The number of times one animal approached another is proportional to the breadth of the relevant connecting line.

In trio 3, the male initiated contact significantly more with female 2 than with female 1 (Wilcoxon test $p=0.001$). The male approached female 2 significantly more than vice versa (Wilcoxon test $p=0.02$), while female 1 approached the male significantly more than vice versa (Wilcoxon test $p=0.008$). Both females, however, were responsible for maintaining proximity with the male, i.e. the Hinde Index was negative for both. This indicates that, as well as initiating contact with female 2 by approaching, the male was also responsible for breaking contact with her by leaving. Over the 28 day study period, the Hinde Index for the male/female 1 dyad was negative on each study day. There were only two days during the study when the male approached female 1 more than *vice versa.* The Hinde Index for the male/female 2 dyad was positive on days 1 and 3 of the study, negative from day 4 to day 17, and positive from day 18 to the end of the study. The shift in Hinde Index around day 18 reflects a change in the approach pattern within the male/female 2 dyad. Up to day 18, the male approached female 2 more than vice versa on 6 of the 11 study days up to then. From day 18 onwards, the number of approaches made by female 2 to the male declined, while approaches made by the male to female 2 increased. Daily fluctuations in approaches and Hinde Index within the trio are shown in fig 5.3. Thus, in trio 3 - as in the other two trios - the male showed a clear preference for one of the females, while the less preferred female was consistently responsible for approaching and maintaining proximity with the male.

Thus, in each trio the male showed a clear preference for one of the females. In each case, the less preferred female approached and maintained proximity with the male significantly more than the preferred female did.

Allogrooming

Only two animals were seen allogrooming at any one time in a trio, never all three. Grooming relationships are expressed graphically in the sociograms in fig. 5.4. In trio 1, there was no significant difference in the time spent by the male grooming each of the females. The females, however, both spent significantly more time grooming the male than grooming each other (female 1, $p<0.05$, female 2, $p<0.005$ Wilcoxon test). Female 2 groomed the male significantly more than female 1 did ($p<0.01$ Wilcoxon test).

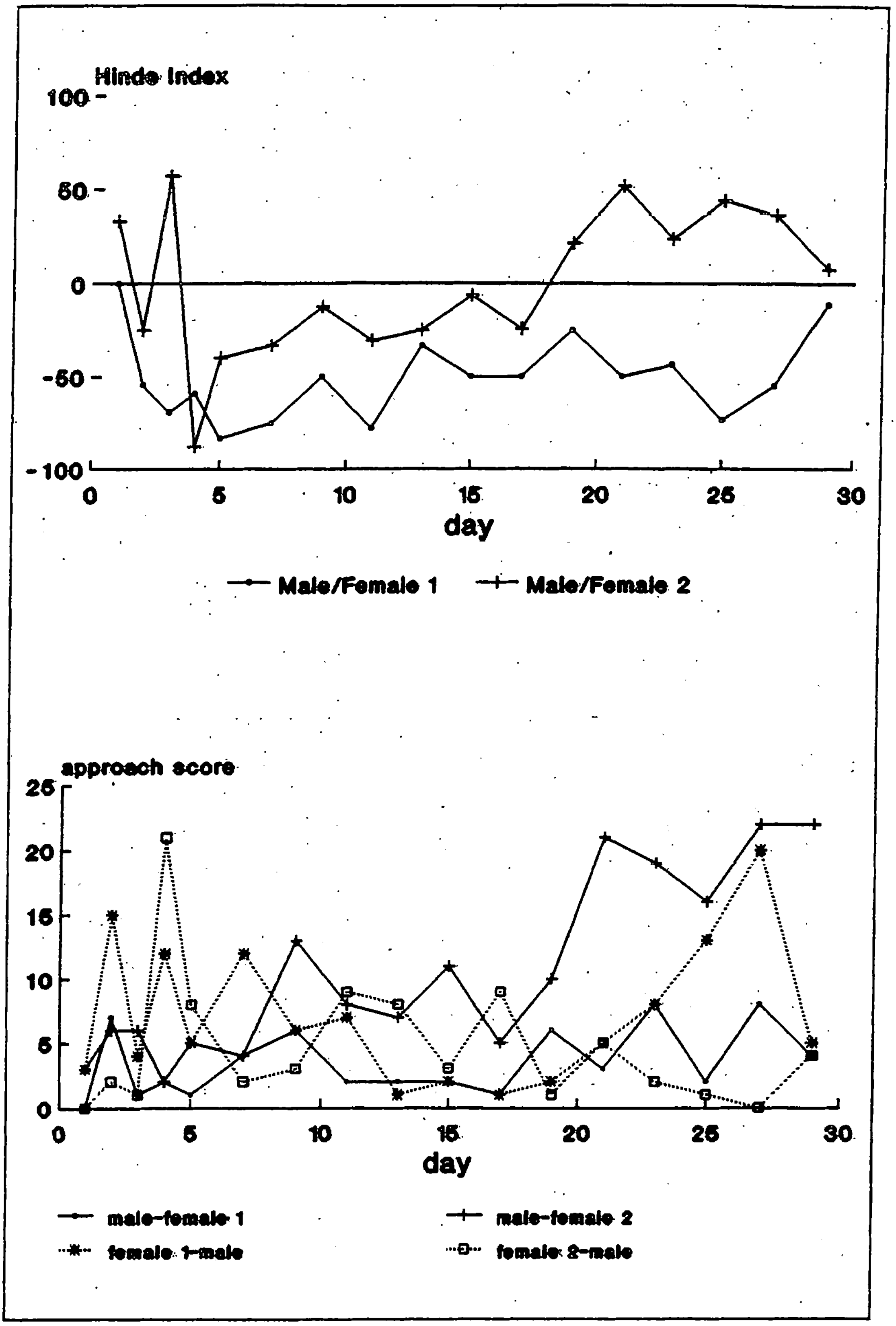


Fig 5.3 Male-female Hinde Index and approach scores for trio 3

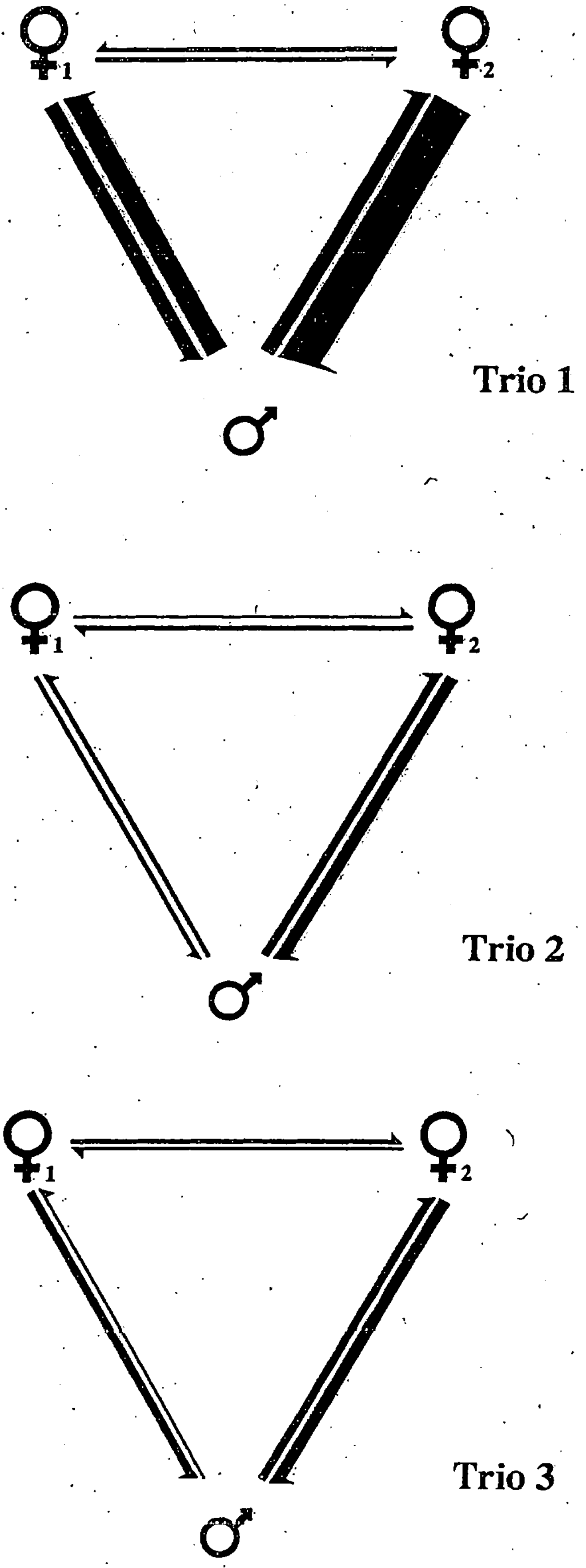


Fig. 5.4 Allogroom sociogram for three male-female-female trios of Goeldi's monkeys. The time spent allogrooming is proportional to the breadth of the relevant interconnecting line.

In trio 2, allogrooming was at much lower frequencies and, although female 2 groomed the male more than she did female 1, the difference was not statistically significant. There was no significant difference between the amount of time the male spent grooming either of the two females. Female 2 groomed the male significantly more than female 1 did ($p < 0.05$ Wilcoxon test).

In trio 3, the male groomed female 2 significantly more than he did female 1 ($p < 0.001$ Wilcoxon test). Further, female 2 groomed the male significantly more than she did female 1 ($p < 0.01$). Female 1 did not groom either the male or female 2 to any great extent, and was groomed by them even less so.

Scent Marking

The scent-mark scores for each individual are shown in Table 5.5. Tail anointing was the most frequently scored scent-mark type performed by all the study animals, accounting for 76.6% of all scent-mark scores.

Within trio 1, there were no significant differences in scent-marking frequency, either in total or in the individual scent-mark types. In trio 2, female 2 scent marked significantly more than female 1 (Wilcoxon test $p < 0.005$). This was reflected not only in the total scores, but also for scores for tail anoint and ventral rub. There was no significant difference in anogenital marking. In trio 3, female 1 scent marked significantly more than female 2 in total scent-mark scores and tail-anointing scores, but not in anogenital marking or ventral rubbing ($p < 0.05$ Wilcoxon test). Thus, in two of the three trios, one female scent marked significantly more than the other.

Sexual behaviour

Mean hourly scores for female presenting, male sniffing the female's genitalia, mounting and copulation (mounting accompanied by thrusting) are shown in Table 5.6 for each of the male/female dyads. Sexual behaviour between females was not seen. Heterosexual behaviour was seen throughout the study period in each trio. Spearman's rank correlation coefficient was used to test for correlations between the levels of present, sniff genitals, mount, and copulate. No significant correlations were

Table 5.5 Mean hourly scent mark scores for each of the study animals in the three study trios.

	TRIO 1			TRIO 2			TRIO 3		
	♂	♀1	♀2	♂	♀1	♀2	♂	♀1	♀2
TAIL ANOINT	1.5	5.2	3.9	4.5	2.2	5.1	6.4	2.5	5.0
NOSE RUB	0.5	0.5	0.1	0.6	0.4	1.6	0.9	1.0	1.2
VENTRAL RUB	0	0.1	0	0	0.2	0	0.1	0	0.1
ANOGENITAL	0.2	0.7	0.1	0.2	0.7	0.4	0.5	0.6	0.6
TOTAL	2.6	6.5	4.0	5.3	3.5	7.1	8.0	4.1	6.8

found. The levels of these categories of sexual behaviour also did not correlate with approach scores, leave scores, or Hinde Index.

In trio 1, female 2 presented to the male significantly more than did female 1 (Wilcoxon test $p<0.01$) and, although the male investigated her genitalia and copulated more frequently with her than he did with female 1, he mounted female 1 more. In trio 2, the male mounted female 1 more frequently than female 2, but he sniffed female 2 more. Female 1, on the other hand, presented to the male more than female 2 did. In trio 3, although female 2 presented significantly more than female 1, the male's attentions were divided between the females almost equally. A compared to the sexual behaviour seen in the newly established pairs in the pair bond study, (Chapter 4), there is little difference in the levels of male sexual behaviour, in spite of there being two females for him to interact with in the trios. In each trio, however, one female presented to the male more than did the other female. The scores of the females that presented more frequently in the trios are greater than any seen in the pair study, particularly the present scores of female 2 in both trios 1 and 3 (see tables 4.3 and 5.6).

Agonistic behaviour

Agonistic encounters between trio members were very rare during the study period. Such encounters were brief episodes of vocalisation and teeth-baring. Physical contact did not occur. Only five episodes were seen between the members of trio 1, three by the male directed at female 2 and two by female 1 directed at the male. In trio 2, the male was seen to be aggressive toward female 1 on four occasions and to female 2 only once. Both females were aggressive toward the male, female 1 on one occasion and female 2 on five occasions. In trio 3, only two agonistic encounters were seen, both directed by the male towards female 1.

Arch Bristle Leap (ABL).

Table 5.7 shows the mean hourly ABL scores for each individual and the scores for synchronised ABL, *i.e.* when performing the behaviour simultaneously with another individual. The sociogram in fig. 5.5 shows ABL scores where only two animals

Table 5.6 Mean hourly scores of various sexual behaviours within the study trios.

	TRIO 1		TRIO 2		TRIO 3	
	♂-♀1	♂-♀2	♂-♀1	♂-♀2	♂-♀1	♂-♀2
♀ present	1.3	5.4	1.7	0.9	1.6	4.1
♂ sniff genitals	0.5	0.8	0.1	0.9	0.2	0.3
♂ mount	2.7	1.5	1.2	0.5	0.7	0.6
♂ copulate	0.1	0.5	0.2	0	0	0.1

Table 5.7 Mean hourly score for Arch Bristle Leap (ABL) for each study animal.

	TRIO 1	TRIO 2	TRIO 3
MALE	2.0	6.2	8.6
FEMALE 1	5.1	2.3	5.9
FEMALE 2	4.9	4.6	7.4

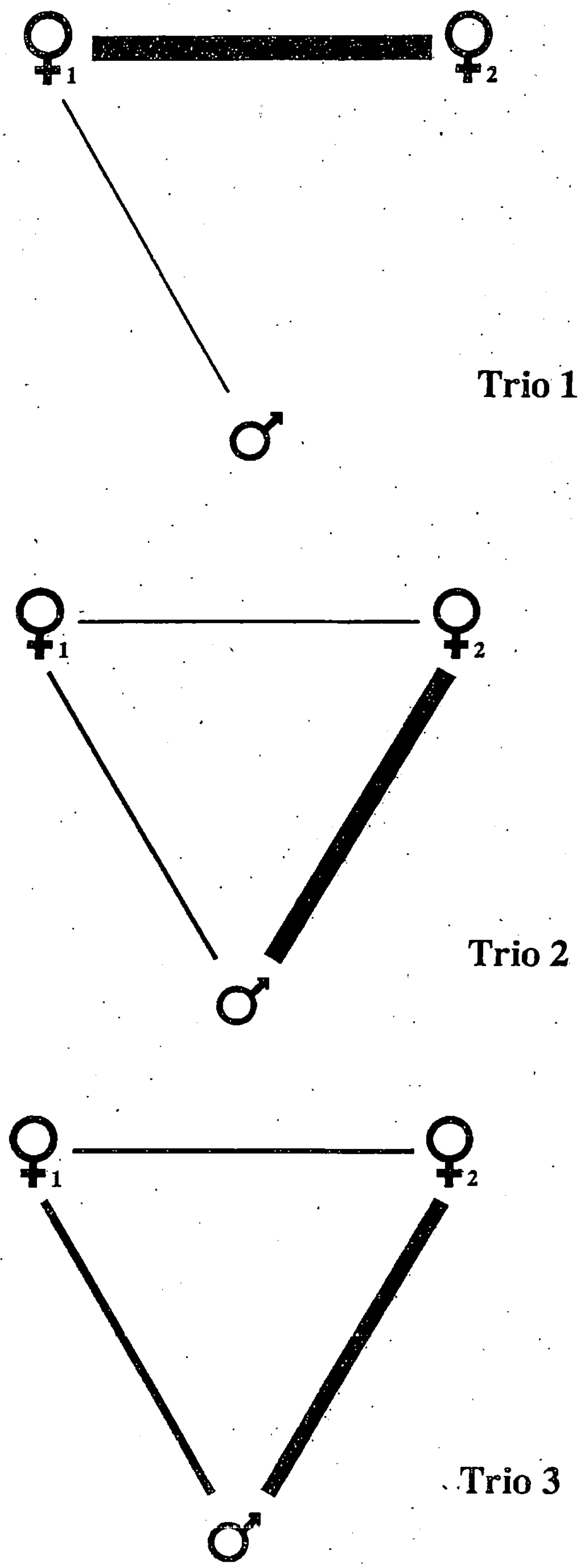


Fig. 5.5 Sociogram of simultaneously performed arch bristle leaping (ABL) in three trios of Goeldi's monkey. The breadth of the connecting line between two individuals is proportional to the number of scans in which the two were scored performing ABL simultaneously.

performed the behaviour.

In trio 1, most ABL was performed by the two females simultaneously. The male performed the display less than half as often as either female. In trio 2, the male performed ABL more frequently than either female. Mostly, this was done simultaneously with female 2. He synchronised this behaviour significantly more with female 2 than with female 1 (Wilcoxon test $p<0.05$). In trio 3, all three animals showed high levels of ABL, with the male performing most. The total ABL score for the trio was about double that of the other two trios. Both the male/female 1 and male/female 2 dyads in trio 3 perform more ABL than any other dyad.

Synchronised Behaviour

Fig 5.6 shows the level of synchronised behaviour within each trio. In all three, the male synchronised his behaviour more with one female than the other. In trios 1 and 3, the two females synchronised behaviour more with each other than with the male, while in trio 2 both females synchronised more with the male than with each other. The scores for all three members synchronising their behaviour was low in all the trios.

Thus, the results of this study of the behaviour of *Callimico* housed in groups each comprising one male and two females show that the relationships within each group were far from equal. In all three trios, the male had a stronger relationship with one female that the other.

To summarise each trio in turn:

In trio 1, the male rested in proximity more with female 2 than female 1, and he approached female 2 more than female 1. He sniffed the genitals of female 2 more than female 1 and copulated with her more. He synchronised his behaviour more with female 2. The male and female 2 allogroomed each other more than the male and female 1, although within the former dyad the female performed most grooming, while in the latter the male allogroomed more than the female did. Female 2 presented to the male significantly more than did female 1. During the

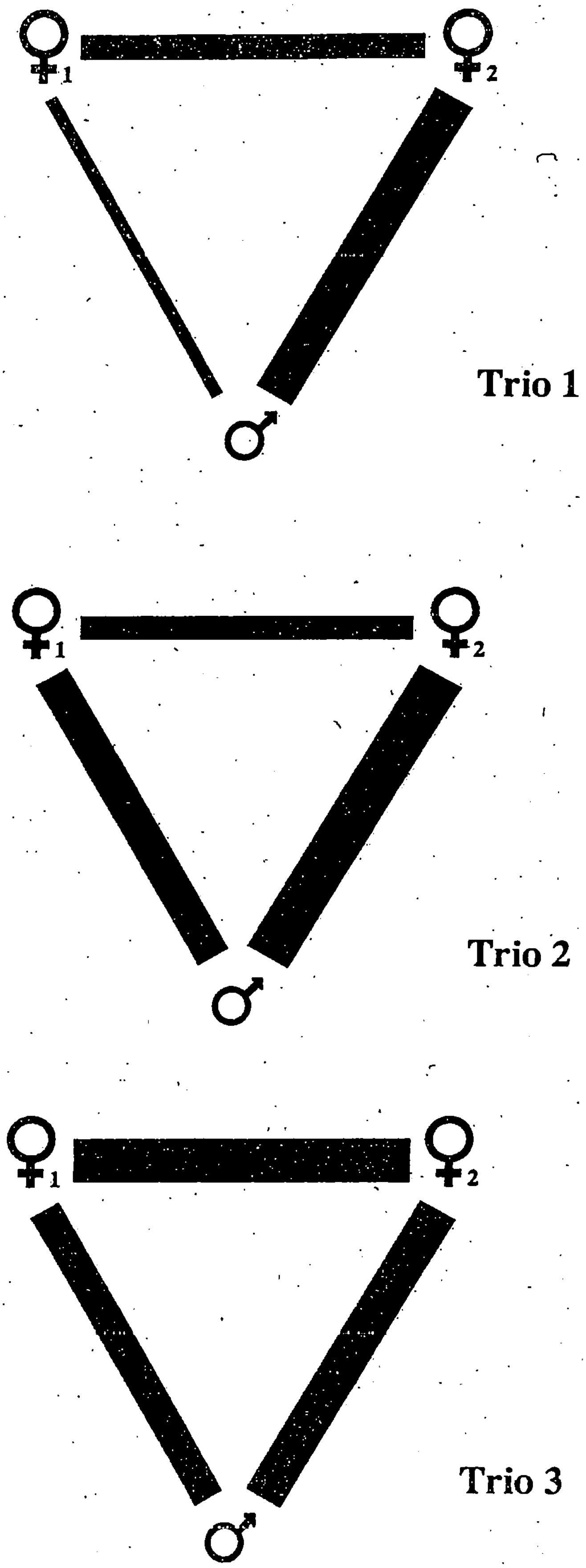


Fig 5.6 Synchrony sociogram for three trios of Goeldi's monkey. The breadth of the interconnecting line between any two individuals is proportional to the number of scans in which those individuals were scored performing the same behaviour.

study of the first four weeks of cohabitation, therefore, the male showed a preference for female 2, while Female 1 compensated for this by approaching and maintaining contact with the male. In spite of the preference shown by the male, Female 1 conceived before female 2 and was the 'winner' of the fight that resulted in the termination of trio 1.

In trio 2, the male rested in proximity with female 2 more than with female 1. The male-female 2 grooming relationship was stronger than male-female 1. More sexual behaviour, however, was seen between the male and female 1 than between the male and female 2. The male synchronised his behaviour more with female 2 than with female 1 and performed ABL with female 2 significantly more than with female 1. Female 2 became pregnant before female 1 and emerged from the eventual fight as the dominant female. Thus, apart from sexual behaviour, the male showed a clear preference for female 2. As in trio 1, the less preferred female was responsible for initiating contact with the male, while the male intiated contact with the preferred female. It is interesting that, in spite of his higher sexual behaviour with female 1 during the study period, female 2 conceived before female 1. Neither female conceived during the study period.

In trio 3, the proximity score for the male-female 2 dyad was significantly higher than for male-female 1 or female 1-female 2. Likewise, the male approached female 2 significantly more than female 1 and groomed her significantly more. Female 2 presented significantly more than female 1. The single copulation was with female 2. Female 2 emerged dominant from the eventual fight and was undergoing ovarian cyclicity at the time, whereas female 1's ovulatory cycles were suppressed at that time (see Chapter 3). Once again, the male showed a clear preference for one female and the less preferred female compensated for this by approaching him significantly more than *vice versa*.

The relationship between the females was generally less strong than that of the male with the females. In all three trios, for instance, the females spent less time in proximity with each other than either did with the male. In trios 2 and 3 the total approach score for the female-female dyad was less than that of the male and either female, although in trio 1 the total approach score of the female-female dyad was slightly more than that of male-female 2 and slightly less than that of male-female 1. A similar pattern was also seen with allogrooming relationships. In all three trios, total allogroom scores for the female 1-female 2 dyad were less than those of the male with either female, significantly so in trio 1.

However, not all behavioural categories reflected this trend. Arch Bristle Leaping (ABL) was performed significantly more in trio 1 by the two females than by the male. For the most part, the two females performed this simultaneously. Fig 5.4 shows that, where only two animals performed ABL, almost all was performed by the females, the male only participating alongside both females. This may account for the high female/female approach score of trio 1, as ABL inevitably involves the participants moving closer to each other in response to a perceived threat.

In trios 2 and 3, it was rare for the female/female dyads to perform ABL without the male, while in trio 1, they frequently did so. This low level of involvement by the male of trio 1 in ABL is reflected in the activity scores within the trio. The male from trio 1 seems to have been particularly inactive. Not only was he less active than either female in his trio, but he was less active than either of the males of trios 2 and 3 and by a factor of nearly 3. It may be that his relative immobility was the sole reason for the anomolous ABL scores and pattern in trio 1.

5.4 Discussion

This behavioural study clearly shows that in a trio the male has a stronger relationship with one female than with the other, and that the least strong relationship is that between the two females. As stated earlier, in most multifemale primate societies, female/female relationships are stronger than male/female relationships. This has been reported for most Old World primates, and is also true of some New World primates living in multifemale groups *e.g. Saimiri* spp (Vaitl *et al.* 1978, Baldwin and Baldwin 1981), and *Cebus* (Robinson and Janson, 1987). However, in other primates such as spider monkeys, *Ateles* spp, and guenons, *Cercopithecus* spp., female-infant relationships are stronger than either male-female or female-female (Cords 1984, Robinson and Janson 1987). Thus, it is apparent that *Callimico* does not exhibit social behaviour typical of polygynous social groups. Instead, the male forms a stronger bond with one female than the other and, eventually, the relationship between the females deteriorates into extreme aggression and a pair is left as a result. It should be noted, however, that grooming and proximity patterns seen within primates reflect the migration patterns of the species. Polygynous species in which females migrate between groups exhibit less strong relationships between females than do species in which females are kin-bonded. In the latter case, grooming and proximity patterns tend to follow matrilines within groups. Is the relatively low level of grooming and proximity a result of female migration within a polygynous social system, or is it the result of the species being monogamous? The eventual break-up of all three trios, leaving a monogamous pair, would suggest that the species is perhaps not as flexible in its reproductive strategy as the field data suggest and that perhaps the field data are either erroneous or anomalous.

In spite of this, the reactions of *Callimico* placed in a male-female-female trio differ strongly from those of a marmoset or tamarin, although socially there are also certain similarities. Epple (1972a, 1972b) reported that five out of six male-female-female trios of *Saguinus fuscicollis* were disbanded within 13 months due to aggression between the females. Unfortunately, no details are given on the length of time each group remained stable. However, unlike the *Callimico* groups in this study, aggression between the females was commonplace and a distinct dominance hierarchy was apparent. Similar findings have been reported for *Callithrix jacchus* trios, with aggression and a dominance hierarchy being apparent (Epple 1972b, Abbott 1984). Epple also reported (1977) that in male-female-female trios of both *C. jacchus* and *S. fuscicollis* the dominant female scent marked more frequently than the subordinate. This was also found in the *Callimico* groups in this study. In all three trios, the 'winner' of the final fight scent marked more than the loser, in trios 2 and 3 significantly so. In the *Callimico* groups, however, there was little overt aggression and no indication of a dominance hierarchy. The female-female relationship was characterised by a low level of interaction rather than by agonistic behaviour.

Undoubtedly, the most significant difference (both socially and in terms of evolution) between these *Callimico* trios and those *Callithrix* and *Saguinus* species studied to date is that in two out of the three *Callimico* trios there was no reproductive suppression of the subordinate females. In male-female-female trios of both *Callithrix jacchus* and *Saguinus fuscicollis*, the subordinate female fails to exhibit hormonal profiles indicative of ovulatory cycles (Abbott 1984, Epple and Katz 1984, Hearn 1977). In this respect, *Callimico* is more similar to *Leontopithecus,* in which subordinate females are not reproductively physiologically suppressed (French *et al.* 1989). Female-female relationships in *Leontopithecus* are also characterised by extreme aggression (Kleiman 1979). Reproductive suppression clearly did occur, however, in *Callimico* trio 3, which was particularly unstable, lasting only 48 days compared with about a year for trios 1 and 2. This is contrary to what might be expected from consideration of the Callitrichidae. Among the callitrichids, when physiological suppression of subordinate females occurs, groups remain stable. Where there is no physiological suppression, groups are unstable and characterised by aggression between the females. Even in *Callithrix* and *Saguinus*, if natural mother/daughter physiological suppression breaks down, either through experimental manipulation of groups (Hubrecht 1989) or through changes of group composition (Carroll 1986), the relationship between the females becomes agonistic. It is strange, therefore, that in this study of *Callimico*, the trio in which reproductive suppression did occur was the least stable of the three.

The male was sexually active to some extent with both females in all of the three *Callimico* trios, as measured by genital sniffs and mounts. Only in trio 1 was the male seen to copulate with both females during the behaviour study, but he certainly copulated with both females in trio 2 as well, as both females conceived. Their conception occurred outside the behaviour study period and, as a result, there are no data about the relationships within the group at that time. In trio 3, female 1 was not undergoing normal ovulatory cycles, which may account for her low level of sexual interactions.

While the level of sexual behaviour shown by the male within each trio was comparable with that of males in the study of newly-formed pairs, female presenting was seen to be elevated above the level seen in the pairs study. In trios 1 and 3, in particular, comparatively high levels of female presenting was seen. It is tempting to suggest that this is evidence of competition between the females for the male. The approach/leave patterns within the trios also suggests that there is competition between the females for the male. In every trio, the female preferred less by the male assumed greater responsibility for initiating proximity with the male, and in trio 1 particularly the less preferred female succeeded in achieving almost as much time in proximity with the male as the preferred female did. While competition between the females undoubtably did eventually express itself as conflict between them, the early period of cohabitation of the females with the male was mostly amicable. It is, however, difficult to explain the high level of female presenting if it is not an expression of competition for the male. Therefore it may be that, even though the females in the trios were not overtly aggressive to each other during the study, there was subtle competition occurring between them.

The results of the behavioural study clearly reflect the instability of trio 3. The females had almost no interaction with each other at all in any of the behavioural parameters measured. The male had a very strong bond with female 2, to the extent that female 1 was peripheral to the male/female 2 dyad. For the trio to be stable, therefore, it would seem that it is important for the females to have a relatively amicable relationship and for the male not to favour one female to the exclusion of the other. The trio in which the strongest relationship between the females was seen was trio 1, the trio that was reproductively most successful.

The strength of the relationships seen within the trios during the first month of cohabitation did not accurately reflect the eventual relationships within the group, *i.e.* it was not possible to predict which female would emerge as the 'winner' of the fight between them. If the strength of the bond between the male and female can be measured by allogrooming and time spent in proximity, the male in each of trios 2 and 3 had a stronger bond with the eventual female, while in trio 1 the male had a stronger bond with the eventual subordinate. It is quite likely, however, that relationships within trios 1 and 2 changed over the year that they were in existence. It is quite possible that a study of these two more stable groups a month prior to their break-up would have shown the same pattern of relationships seen in trio 3 a month prior to break-up.

If relatively equal relationships within the trio are important in maintaining stability, is it possible that the polygynous groups seen in the wild were made up of kin-bonded females that have a close relationship? The evidence from Masataka's studies (1981a, 1981b) suggests that this is not the case. Firstly, in his study group, the two breeding females appeared to be the central animals in two subgroups within the group. If the females had a close kin relationship, one would expect them to have close grooming and proximity relationships with each other. Outside the period when infants were reared, grooming between the male and each breeding female was greater than between the females themselves. Secondly, the only emigration from his group was that of a young adult female, while three young males introduced to the group remained with it. The relationship of the emigrating female with the other females was characterised by aggression, which led to her peripheralisation and eventual emigration. If female migration between groups does not occur, her relationship with at least one of the two breeding females would have been amicable.

Evidence from captivity also fails to support the hypothesis that related females would have a more stable relationship within multifemale groups. Multifemale groups comprising two sisters with an unrelated male, and a mother/daughter dyad with an unrelated male, have been no more stable over the long term than the trios in this study. The former group, at Cameron Wildlife Park, was stable for just over a year, during which time neither female reared an infant although both carried pregnancies to term (H. Dornbrack, pers. comm.). The second group, at Cologne Zoo, was stable for just over nine months after the unrelated male had been introduced. The mother reared an infant but attacked the daughter shortly after giving birth (U. Hick, pers. comm.).

It is unfortunate that no studies have followed a wild group over the longer term. Only such study of several groups will give a real indication of migration patterns within the species, and the long-term stability of polygynous groups in the wild. At the moment, it is impossible to comment on whether the instability of these captive trios is an artefact of being kept under confined conditions, where relatively close proximity is forced upon the group members.

SUMMARY

This study of the behaviour of *Callimico goeldii* in male-female-female trios has shown the following:

1. In two of the three trios, physiological reproductive suppression did not occur, while in a third, a subordinate female was suppressed in the presence of the dominant female.

2. Behavioural parameters did not indicate a typical polygynous social structure. They suggest that the male and one female have stronger relationship with each other than do either the male and the other female or the two females together.

3. In time, each group was reduced to a single pair through female-female aggression.

4. In the first month following the introduction of the male into each trio, the female/female relationship was the least strong, while the male showed a preference for one female over the other. In two trios, this preference was clearly for the female that eventually gained dominance and ejected the subordinate from the group. Dominance was established during a single aggressive encounter between the females that led to injuries of such severity that the subordinate had to be removed from the group.

5. Approach/leave patterns and levels of sexual behaviour suggest that there is some element of competition between the females for the male. Although the male's rate of sexual behaviour is similar to that of males in monogamous pairs, one of the females in each trio presented to the male much more than the other female, in two cases at considerably higher rates than seen in the monogamous pairs.

CHAPTER 6 INFANT CARE IN *CALLIMICO GOELDII*

6.1 Introduction

Infant rearing is a complex procedure involving many facets of infant care. Infant care can be divided into several categories of direct and indirect care. Direct care involves behaviours such as suckling the infant, infant carriage, grooming and food sharing, while indirect care includes vigilance against predators, group defence, and home-range defence. The typical mammalian pattern of infant rearing is that direct care is provided by the mother. In social species, indirect care may be provided by members of the group other than the mother. Among some social mammal species, however, direct care is also provided by individuals other than the mother. Suckling of infants is usually an exclusively maternal care pattern, but other conspecifics can transport the infant (*e.g.* among primates [Kleiman 1977a]) or provide the weanling with solid food (*e.g.* among several canid species [Kleiman 1977a]).

Why care?

Infant care involves a 'cost' to the carer either in direct energy expenditure, *e.g.* in lactation or infant carriage, or in the sharing of resources, *e.g.* through food sharing, sharing of sleeping sites, or in increased vulnerability to predation, as a result of group defence. Why then, should a non-parental carer care? The benefits to the mother may be to ensure that the maximum number of infants from a litter survive. It has been shown, for instance, that in black-backed jackals (*Canis mesomelas*), wolves (*Canis lupus*) and saddle-back tamarins (*Saguinus fuscicollis*), the number of surviving infants is directly related to the number of helpers available to the mother (Moehlman 1979, Harrington *et al.* 1983, Sussman and Garber 1987). Similarly, the benefit to the father is to maximise his reproductive success through increased survivorship of his offspring in either the current litter or in subsequent litters. Other related individuals also benefit through 'inclusive fitness' (Hamilton 1964). Such benefit decreases with decreasing relatedness to the infant; but full siblings to the infant accrue the same benefit in terms of fitness as does the father, as - like the parents - full sibs share 50%

of their genes with the infant. Theoretically, the degree of infant care shown should be related to the degree of relationship between the infant and the carer.

Caring may also benefit the carer in other ways. Firstly, infant care may lead to increased access to a mate. Price (1990), for instance, showed that male cotton-top tamarins were more likely to mate a female when carrying infants. Secondly, a juvenile or subadult may acquire important social or infant rearing skills through care of younger infants. Epple (1975) showed that captive juvenile saddle-back tamarins that have not had experience of caring for younger sibs were likely to show incompetent parental care with their own offspring. Similar effects have been described for golden lion tamarins (Hoage 1977) and cottontop tamarins (Tardiff *et al.* 1984). Lastly, it has been suggested that, if there are no vacant territories for a young adult to move into to breed, the latter may 'pay' for increased time in the natal group through infant care (McGrew and McLuckie 1986).

Theoretical predictions concerning extra-maternal care among New World primates

Lactation is the only aspect of maternal behaviour that is confined exclusively to the mother among primates. Among social species, infant carriage and provision of solid food can both be performed by other group members, as can group defence, *etc.*. Most studies of extra-maternal care among New World primates have focused on infant carriage. This is an energetically costly aspect of infant care and therefore has considerable consequences for the carer. Further, New World monkeys show considerable variety in patterns of infant carriage at the level of the genus.

The pattern of infant care within a species should reflect the selective pressures acting upon it. If, for instance, shared care evolved solely to allow the parents to maximise their reproductive output, then the non-parental carer has no direct benefit from caring. It would be predicted, therefore, that in this case time spent carrying should be related directly to the degree of relatedness of the carrier to the infant and that transfers to another individual should be initiated by the carrier when it becomes fatigued. If, on the other hand, care conveys direct benefits to the carer, it would be predicted that there should be competition to carry infants, with those individuals most likely to benefit competing most strongly to carry them.

Different predictions can be made about infant care patterns according to each of the possible benefits of care to the carer. These are listed below. It is unlikely, however, that these predictions can be regarded as mutually exclusive. It is probable that, in reality, caring conveys several benefits to the carer, and several classes of carer will benefit to some extent. Hence, it is to be expected that the behaviour of carers will to some extent reflect a compromise between the costs and benefits to all classes of carer in the group.

1. If caring occurs only to ensure that a litter is reared, it can be predicted that the parents would be the major caretakers.

2. If caring enhances a male's access to a female, it can be predicted that males would carry more during the female's oestrous or ovulatory period.

3. If caring allows subadults and juveniles to gain vital social experience, it can be predicted that there would be competition among them to carry the infants; but they would not necessarily be the major caretakers, as it is in the parent's interest not to risk the infant by allowing an inexperienced carer to care for it.

4. If caring allows young adults to remain in their natal group beyond sexual maturity, it can be predicted that non-breeding adults would be the major caretakers.

Care patterns among New World primates

Infant care patterns among the Platyrrhini range from the exclusively maternal, as in the larger cebid genera *Brachyteles, Lagothrix* and *Ateles* (Nishimura *et al.* 1988, Ramirez 1988, van Roosmalen and Klein 1988), to that shown by the callitrichids, where all group members may provide infant care, including immigrants to the group which may be only distantly related to the infant(s), if at all. Table 6.1 shows the patterns of infant care exhibited by various platyrrhine genera. The genus *Chiropotes* has been omitted, as there is no published account of infant rearing within a social group. The only account of infant rearing in this genus was provided by Hick (1968) for a captive pair from which the male had been removed shortly after the birth of

Genus	Care by mother	Care by father	Care by other adults	Care by subadults
Brachyteles	✓			
Lagothrix	✓			
Ateles	✓			
Alouatta	✓		♀♀ only	
Cacajao	✓	?* ‡	♂♂ only ‡	
Pithecia	✓	✓ ‡		
Cebus	✓	?* ‡	♂♂ only ‡	
Callicebus	✓	✓		✓
Aotus	✓	✓		✓
Saimiri	✓		♀♀ only	
Callimico	✓	✓	♂ & ♀	✓
Leontopithecus	✓	✓	♂ & ♀	✓
Saguinus	✓	✓	♂ & ♀	✓
Callithrix	✓	✓	♂ & ♀	✓
Cebuella	✓	✓	♂ & ♀	✓

Table 6.1 Infant carrying patterns among the Platyrrhini (excluding *Chiropotes*).
* indicates that carrying by adult males has been recorded, but that the genetic relationship with the infant is undetermined.

‡ indicates infant carrying <u>only</u> after the infant is capable of independent locomotion

the infant. The table is limited by the quality of information in the literature. Infant care among the callitrichid genera has been studied both in the wild and captivity, whereas there are accounts of infant rearing only in captivity for the genera *Lagothrix* and *Cacajao*, for instance.

The table shows that, in general, extra-maternal care is either absent or negligible among the larger-bodied forms, while it is consistently present among the smaller forms, albeit to varying degrees. As shared infant care among the Callitrichidae is often said to be linked to twinning, study of the infant care patterns of *Callimico* can help to separate the relative influences of twinning and body size.

The effects of body size on infant care in the Cebidae

Even if only the Cebidae are considered, there is an apparent relationship between body size and infant care pattern, with the smaller genera (*Aotus* and *Callicebus*) exhibiting more extra-maternal infant care than the larger genera. Why is such behaviour related to body size? Neonate weight scales in a negatively allometric fashion with maternal body weight, such that the weight of the neonate in proportion to that of the mother increases with decreasing maternal body weight. It may be predicted, therefore, that the smaller the mother's body size, the more energetically costly direct infant care such as carrying the infant becomes, and the more likely a female is to require help with infant rearing. This scenario is not entirely satisfactory, however, as in *Saimiri* (the smallest cebid with the largest infant relative to maternal weight) infant care by animals other than the mother is not a consistent feature of infant rearing. When it does occur in this species, it is in part dependent on the social status of the mother, is limited to other females, and occurs only after the infant has attained a certain degree of independence around the third or fourth week of its life. Females helped by carers are likely to be dominant animals, and helpers are likely to be female kin, usually older sisters of the infant (Baldwin and Baldwin 1981).

Body size, twinning and infant care in the Callitrichidae

While the precise nature of the relationship between body size and infant care patterns remains unclear, it has been suggested that body size has exerted a profound effect on another aspect of the reproductive biology of the New World monkeys. Leutenegger (1973) suggested that, following the general scaling relationships, dwarfism within the group led to neonate size being relatively large among the smaller forms. He considered that, as the mother's body size progressively decreased, the head of the neonate became progressively relatively larger, to the extent that the pelvis of the mother could no longer accommodate it safely during birth. He concluded that *Saimiri* (female weight 600g) was at the lower limit of size for producing a single infant and cited evidence from captivity of a high incidence of obstetric problems in the species, leading to infant mortality as high as 50%. Forms smaller than *Saimiri*, he hypothesised, need to reduce the size of the infant and do so by producing two smaller infants rather than one large one. This 'obstetric theory' for the origin of twinning has been widely accepted (see for instance Ford 1980, Sussman and Kinzey 1984, Sussman and Garber 1987), although Martin (1990, 1992) has recently pointed out that such a mechanism would be expected to lead only to a reduction in the size of the original single neonate and not necessarily to the production of twins.

Whatever the selective forces that led to twinning, it has generally been accepted that the high degree of extra-maternal infant care shown by the callitrichids is related to the twinning habit. It has been suggested that the high cost of pregnancy, lactation and carriage of twin infants results in the female being unable to rear both infants unaided (Clutton-Brock and Harvey 1977, Hershkovitz 1977, Kleiman 1977a). Dunbar (1988) provided evidence to support this hypothesis, using Altmann's (1980) model of maternal time budgets to predict that a female *S. fuscicollis* would be unable to rear both her infants without help.

While twinning may be related to infant care among the Callitrichidae, it is obviously not a factor in infant care among the Cebidae, none of which produces twins. Considerable infant care is shown by fathers in both *Callicebus* and *Aotus*, which have only single infants (Mason 1974, Kinzey 1981, Wright 1981, 1984, Dixson 1983). In both genera, infant carriage by the mother may represent as little as only

5% of total infant carriage time. Clearly, an explanation other than twinning must be found for the origin of extra-maternal care in the Ceboidea.

Infant care in *Callimico*

Callimico, the smallest New World primate having a single infant, provides a natural test of several hypotheses presented above. If Leutenegger's obstetric theory of the origin of twinning is correct, *Callimico* infants will be at least as large, relative to the mother, as those of the slightly heavier *Saimiri*. If this is the case, infant care patterns may either follow that of *Callicebus*, with considerable extramaternal care, or resemble that of *Saimiri*, with very little. If the infant is relatively small (of callitrichid size), however, and *Callimico* females are similar to the *S. fuscicollis* used by Dunbar (1988) in his modelling of maternal time budgets, then they should be able to rear their single infant unaided. Information available to date, in fact, shows that, after three weeks or so, *Callimico* group members other than the mother help with infant care (Heinemann 1970, Lorenz 1972, Beck *et al.* 1982, Carroll 1982). The only quantitative data previously published suggest that there is an abrupt change in infant care patterns around week 3, with the male becoming the primary carrier, as is seen from the first week in *Aotus* and *Callicebus* (Heltne *et al.* 1973). These data, however, refer to only two individual infants reared successfully by a single pair, and are complete (from birth through to weaning) for only the first offspring. As the latter was the pair's first infant, the father was the only extra-maternal caretaker available.

Further information on infant care in *Callimico* is clearly necessary to determine the caretaker pattern in family groups, which will in turn allow inferences to be made concerning the evolution and function of extra-maternal care among the New World primates.

This investigation of infant care in *Callimico* comprised three studies to achieve three goals.

1. Assessment of the effect of body size on reproduction in *Callimico*,

using allometric comparisons with the other ceboids to examine the relative size of the infant. This information can then be used for comparing infant care patterns among the New World monkeys.

2. Use of Altmann's (1980) model of maternal time budgets to predict whether *Callimico* females need extra-maternal help to rear their infant. The prediction can then be tested using data from this study.

3. To determine patterns of infant development and caretaking within family groups of *Callimico* and hence arrive at inferences regarding the motivations and benefits behind this behaviour.

6.2 STUDY 1 Allometry of neonate and litter size within the Platyrrhini

6.2.1 Aims

1. To assess the reproductive effort of *Callimico* using neonatal weight as a measure of this.

2. To test the obstetric hypothesis put forward by Leutenegger (1973) as an explanation for the evolution of twinning in the Callitrichidae.

6.2.2 Methods

The data on which this allometric comparison of litter and neonatal size within the platyrrhines is based are mainly from R. D. Martin and A. M. Maclarnon (pers. comm.) and are shown in Table 6.2. The adult body weights for two important species in this data set differ from those usually published, *viz*. those of *Leontopithecus rosalia* and *Cebuella pygmaea* being higher in both than values previously used in allometric comparisons. The weight of 626.3g (± se 11.9g) given for *Leontopithecus rosalia* in Table 6.2 is based on field data provided by Dr James Dietz (pers. comm.) for wild parous females. Parity was assessed using nipple length as an indicator. If

Species	♀ weight (g) F	Neonate weight (g) N	Litter size
Alouatta palliata	5824	480.0	1
Aotus trivirgatus	724	97.0	1
Ateles geoffroyi	7669	426.0	1
Ateles paniscus	8554	425.5	1
Callicebus moloch	1004	100	1
Cebus albifrons	2067	234.0	1
Cebus apella	2201	239.7	1
Cebus capuchinus	2578	230.0	1
Lagothrix lagotricha	5585	450.0	1
Pithecia monachus	2170	121.0	1
Pithecia pithecia	1604		1
Saimiri sciureus	699	95.2	1
Callimico goeldii	582	50.6	1
Callithrix argentata	353	35.1	2
Callithrix jacchus	287	27.0	2
Cebuella pygmaea	122	12.5	2
Leontopithecus rosalia	631	50.0	2
Saguinus fuscicollis	350	45.2	2
Saguinus labiatus	520	43.5	2
Saguinus midas	558	40.0	2
Saguinus nigricollis	350	49.3	2
Saguinus oedipus	425	44.0	2

Table 6.2 Maternal and litter weight data for a number of New World primates. (For marmosets and tamarins, litter weight (L) is assumed to be double the weight of an individual neonate, for the other species, litter weight is the weight of a single neonate)

Sources: R.D. Martin and A.M. Maclarnon (pers. comm.), Soini, 1988 [*Cebuella*], J. Dietz, pers. comm. [*Leontopithecus rosalia*].

the nipple was less than 3mm long, the female was regarded as nulliparous and its weight not used in the data set. The weight is a mean for 24 animals. Five females were captured and weighed twice, while one other female was captured and weighed on three occasions. Where multiple weights were available for a female, the mean for that female was calculated and used as a single value in calculating a mean adult female weight for the species. Unfortunately, it is not known whether the females were pregnant when weighed, as the weight of a full term litter in this species would be about 100g. This mean weight may, therefore, be inflated to some extent. It is, however, similar to the mean weight of non-pregnant adult female black lion tamarins (L. Cullen, pers. comm.). Unfortunately, Cullen's data are not available at this time. The weight of 122g for *Cebuella pygmaea* is from Soini (1988), who weighed 27 wild, non-pregnant adult breeding females. As these two species are the heaviest and lightest callitrichids, respectively, their weights exert a strong influence on any empirically determined allometric relationship for the group.

Two allometric comparisons were made. Firstly, in order to assess total reproductive output, using infant weight as an indicator, a comparison was made of <u>litter</u> weight against maternal weight. Secondly, to assess the effect of size of the neonate, a comparison was made of individual <u>neonate</u> weight against maternal weight.

Limiting the data used in the analyses to the Platyrrhini, rather than the whole order Primates, has both advantages and disadvantages. The main advantage is that it removes the possibility that differences between the suborders Platyrrhini and Catarrhini will mask differences between lower taxonomic groups. The main disadvantage is that the number of data points is reduced. Among other things, this increases the effects of measurement error, particularly for species at the extremes of the ranges under examination.

In common with most other studies on body weight effects, individual species are used here as the data points in the analysis. However, individual species within a genus share a recent common ancestry and may not, therefore, be independent, and a taxonomic bias enters the analysis when genera with differing numbers of species are considered. Choice of the taxonomic level for allometric analysis of primates has been specifically discussed by Harvey and Clutton-Brock (1985) and by Ross (1988). The former authors argue that the correct level of analysis should be the subfamily. This would, however, reduce the sample size to four if only the Platyrrhini are considered, effectively ruling out any analysis. Ross (1988), on the other hand, showed that a large amount of residual variation is found at the genus and species levels when the effect of body size is taken into account. When analysing at the genus and subfamily levels, up to 25% and 34%, respectively, of the variation is lost. She also found in her analyses that the results obtained at the species level were closely similar to those found in analyses at the higher taxonomic levels. Accordingly, in order to maximise the sample size, and maintain comparability with other studies, analysis was carried out at the species level in the present investigation.

Following standard methods for allometric analyses, the data were converted to logarithmic form to modify the curvilinear formula $Y = bX^a$ to the linear form, $\log y = a.\log X + \log b$. The best-fit line was determined using the formula for the slope of the reduced major axis provided by Sokal and Rohlf (1981) and given below.

$$a = s_y/s_x$$

where s is the unbiased standard deviation of the data set.

The standard regression formula using least-squares regression has been shown to be inappropriate for two biological variables, and consistently to underestimate the allometric exponent (*i.e.* the slope of the line - a) (Harvey and Mace 1982, Martin and Barbour 1989). The reduced major axis was chosen over the major axis because of the mathematical simplicity of the procedure used to determine the allometric exponent - a.

6.2.3 Results

Fig 6.1 shows the relationship between female body weight and total reproductive output at birth measured as litter weight. The empirical formulae for the relationship within the twinning forms (the Callitrichidae), the non-twinning forms

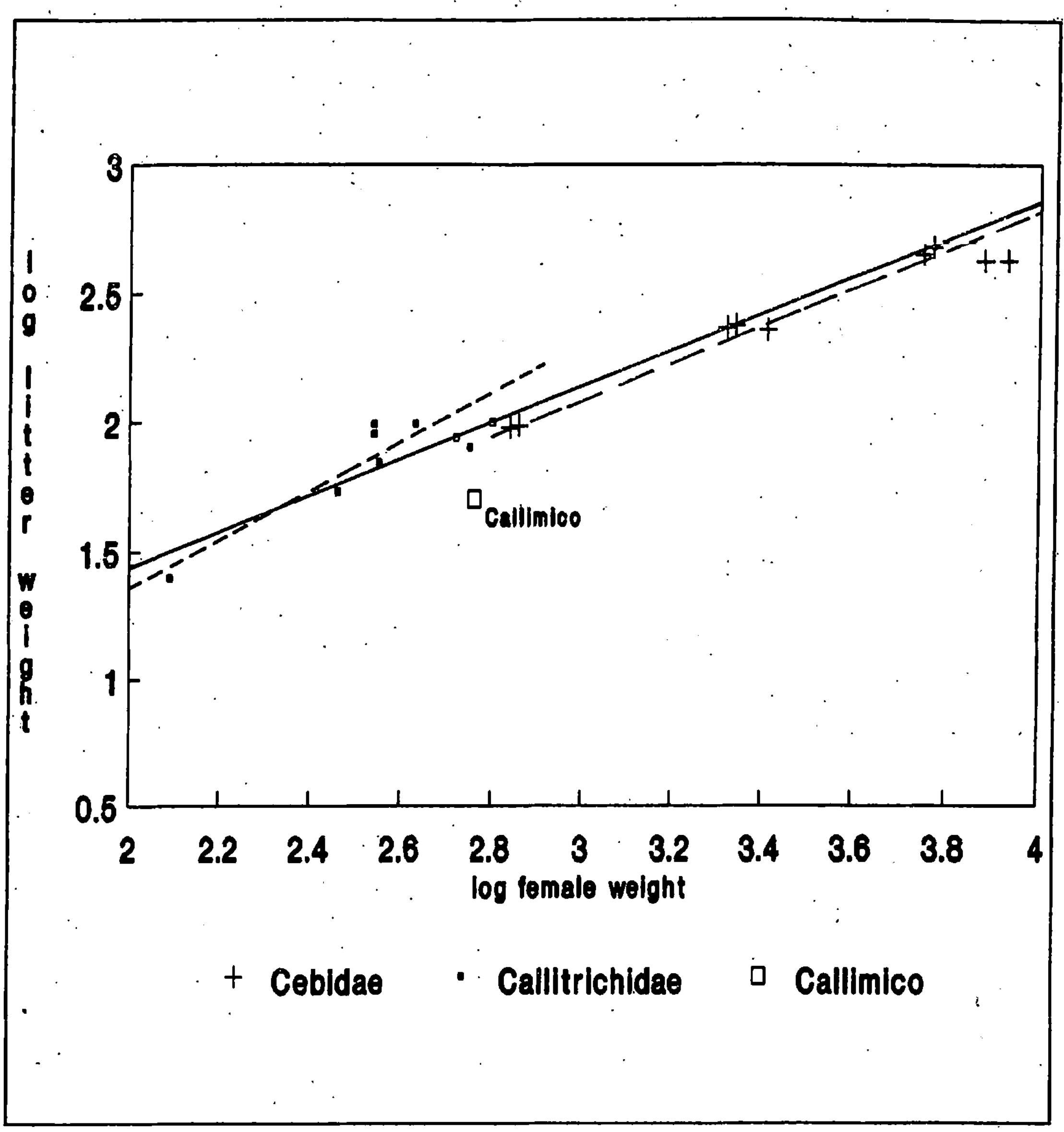


Fig 6.1 The allometric relationship between litter weight at birth and adult female weight.

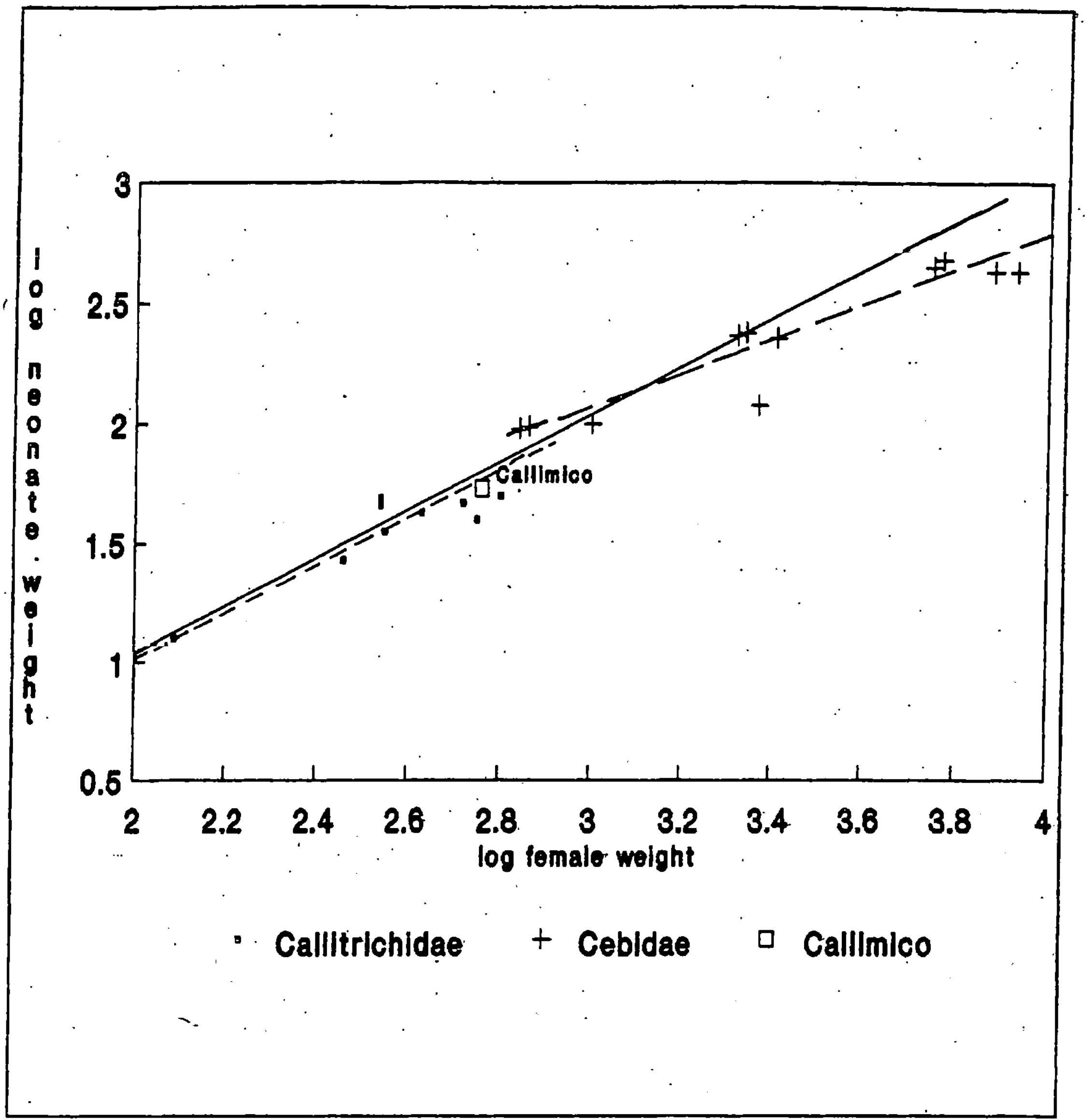


Fig 6.2 The allometric relationship between neonate weight and adult female weight in *Callimico*

(the Cebidae and *Callimico*), and the entire data set are given below:

Callitrichidae $Y = 0.906X - 0.46$
Cebidae and *Callimico* $Y = 0.633X + 0.116$
Platyrrhini $Y = 0.673X + 0.091$

It can be seen that all the species considered here except *Callimico* lie close to the line indicated for the entire Platyrrhini. *Callimico,* on the other hand, has a relatively reduced reproductive output in terms of neonate weight, as indicated by its position below that line. When the callitrichids are considered alone, the slope of the line is steeper than that of the complete data set, and the point for *Callimico* lies even further below this best fit line for callitrichids. The steepness of this line is due to the influence of the point for *Cebuella*. *Cebuella* may be a special case as it is the smallest callitrichid and is perhaps at the lower limit of dwarfing. If *Cebuella* is omitted from the data set, the slope of the line for the Callitrichidae is close to that of the cebid line.

Fig 6.2 shows the relationships between individual neonatal weight and maternal weight. The empirical formulae are as follows:

Callitrichidae $Y = 0.906X - 0.759$
Cebidae and *Callimico* $Y = 0.663X + 0.116$
Platyrrhini $Y = 0.906X - 0.753$

Examination of the data in a graphical plot shows a difference in individual neonate size between the twinning and non-twinning forms (fig. 6.2). An exception is, however, found with *Callimico*, which has an infant that is essentially the same size, relative to maternal weight, as those of the twinning callitrichids.

6.2.4 Discussion

The data presented here indicate that, when neonatal and litter sizes within the group are examined for the effects of maternal body weight, *Callimico* has a reduced reproductive output at birth compared to the other Platyrrhini. Goeldi's monkey produces a callitrichid-size infant, and yet does not twin, unlike the larger-bodied *Leontopithecus rosalia*, which does do so. This is contrary to the hypothesis put forward by Leutenegger (1973) that dwarfism, leading to small maternal size has in turn led to twinning. It supports Martin's argument (1990, 1992) that small maternal body size might lead to reduced infant size, but not necessarily to twinning.

Leutenegger's (1973) suggestion that there is a threshold of maternal body weight below which a single cebid-size infant is too large for the female to give birth to also conflicts with data for small-bodied *Tarsius* species. The ratio between neonatal weight and maternal weight for *Tarsius syrichta* and *T. bancanus* is far higher than for *Saimiri* or any of the clawed New World monkeys, yet these *Tarsius* species apparently give birth without any unusual problems (Martin 1992). Even if *Tarsius* is a special case, and a threshold in the neonatal weight/maternal weight ratio does exist among the platyrrhines, it would appear that this is not a clear threshold. The overall body weight range of female *Leontopithecus* (494g - 748g, J. Dietz, pers. comm.) is similar to that of female *Saimiri* (500g - 750g, Baldwin and Baldwin 1981). Captive *Callimico* females may also be heavier than some *Saimiri* females (at JWPT, a wild-caught *Callimico* female had a body weight of 650g); yet there is a clear difference in neonatal weight. Presumably, selection pressures operating on particular species lead to differing strategies with respect to reproductive output, which in turn affect neonatal body size.

Neonatal body size, and, through litter size, total litter weight have considerable effect on infant-rearing strategies. The effects of these factors are examined below.

6.3 STUDY 2 The effects of litter size on infant care in *Callimico*.

6.3.1 Introduction

Dunbar (1988) used Altmann's model of maternal time budgets to show that a female *Saguinus fuscicollis* would be unable to raise her twin infants unaided. The energetic demands of lactation and transporting the infants could not be supported within the time available for the female to expand her feeding and foraging behaviour. While she could rear one infant, she could not rear two. On the basis of infant weight alone, it can be predicted that a *Callimico* female should be able to rear her infant unaided. The capacity to do so, however, depends on the female's time budget as well as on the weight of her infant. If there is little resting time in the budget, she may be unable to expand her feeding time sufficiently to meet the energetic demands of infant rearing. In this case, the female may still require help with infant care. In their field study, Pook and Pook (1981) showed that *Callimico* was remarkably active, moving frequently and resting for only short periods. Do females have enough spare time to increase their feeding time in order to rear their infants unaided? This study uses Altmann's model of time budgeting, in the same way that Dunbar did, to predict whether *Callimico* females require help to raise their infants. These predictions are then tested using data from the behavioural study on infant rearing.

6.3.2 Methods

Prediction of infant rearing using maternal time budgets

Altmann's Model

Altmann (1980) proposed that the energy requirement to sustain lactation is directly related to the weight of the infant at any given time. By using a conversion factor to translate energy requirement into time spent feeding, and a 'coefficient of lactation' to predict the energy requirements of lactation, it is possible to predict the time that the female must spend feeding in order to meet the energy requirements of lactation by the following formula:

$$F_t = Am^{0.75} + A(i_0 + t\Delta i)^{0.75}/E$$

Where F_t = time feeding

A = constant converting energy requirement into time spent feeding

m = mother's body weight (kg)

i_0 = infant's weight at birth

Δi = increment in infant weight (kg/day)

t = infant age (days)

E = conversion coefficient of lactation ($0.6 < E < 0.8$)

The method used here differed slightly from that of Dunbar (1988) in that infant weight was estimated from an age/weight curve constructed from the weights of known-age infants in the captive colony at JWPT (see fig 6.3). It is likely that captive infants grow faster than their wild counterparts, as the captive mother has access to a good-quality diet that is presented in abundance. This method will, therefore, tend to overestimate infant weight and hence overestimate the time a female needs to feed while lactating. The absence of any data on infant weight gain in the wild precluded any alternative to this method.

The conversion coefficient for lactation (E) has been shown to lie between 0.6 and 0.8 for primates (Dunbar 1988). Accordingly, F_t was calculated using $E = 0.6$, 0.7, and 0.8 for the last day of each week of lactation up to week 8. The value of F_t was found to vary by only 2% overall depending on the value of E.

Taylor *et al.* (1980, in Dunbar 1988) demonstrated that total energy consumed by a weight-bearing animal is directly proportional to the ratio of the load being carried to the unloaded body weight. In order to calculate the time needed for feeding to compensate for extra energy expenditure due to carrying the infant, the following formula was used:

$$F_t = Am^{0.75} + Ai_t^{0.75}$$

where i_t = infant weight on day t.

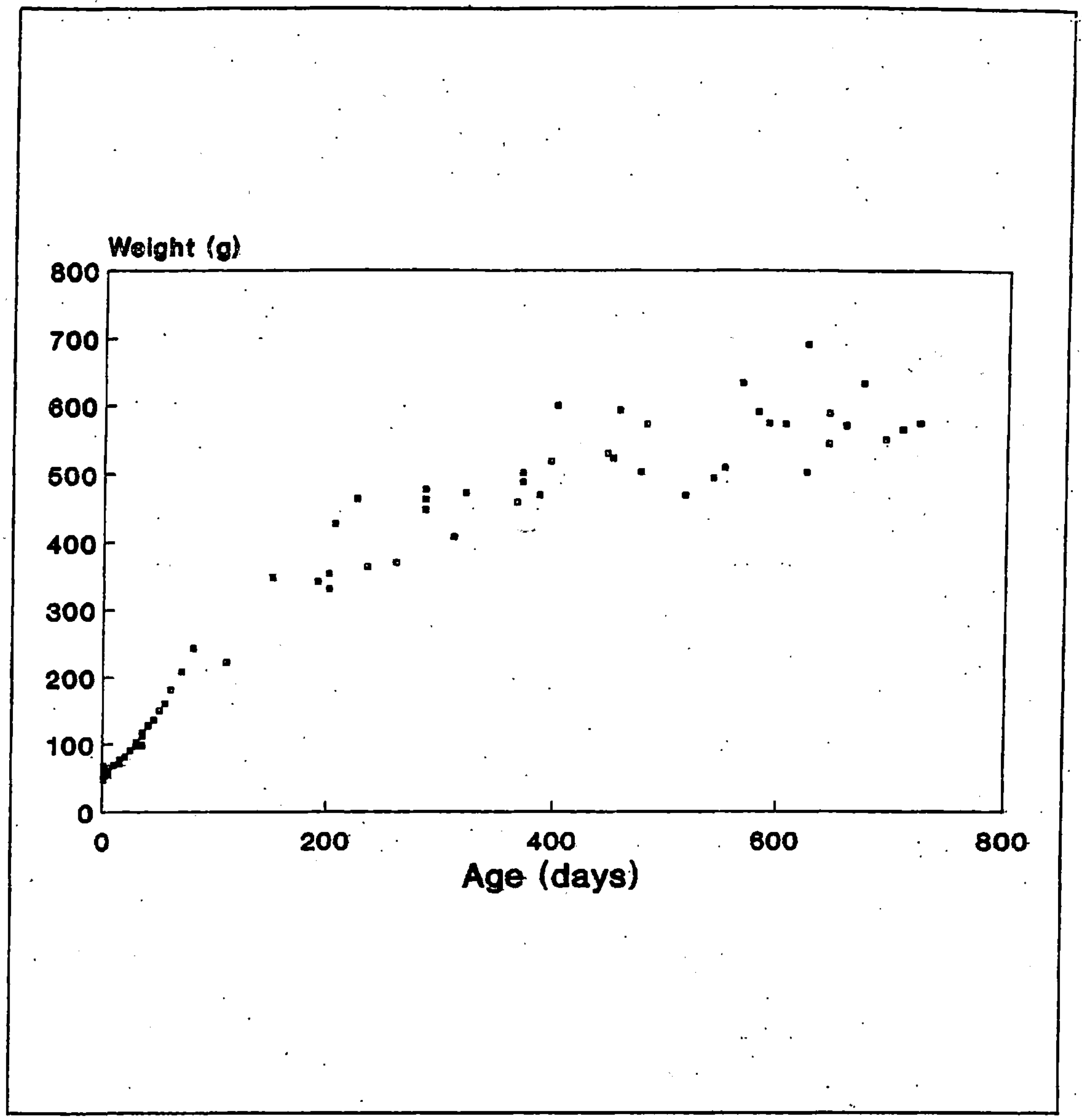


Fig 6.3 Weight/age curve for *Callimico* constructed using data from the captive colony at Jersey Wildlife Preservation Trust.

The constant for converting energy requirement into time spent feeding (A) is species-specific and was calculated using the time budget for wild animals provided by Pook and Pook (1981). They estimated that 23% of the time was spent feeding in the wild when no infants were being reared. This value is used in the equation

$$F_t = Am^{0.75}$$

to calculate the value of A.

It is difficult to assess the accuracy of the estimation of 23% as the time spent feeding, as Pook and Pook did not define their category of 'feeding'. Also, they did not present separate data on male and female feeding times. Presumably, 23% is an average for the entire group. It is known that the breeding female in their study group was in late pregnancy during their study, as the female gave birth two days before their study terminated. It is difficult, therefore, to compare this study directly with studies of other species, although the best information currently available is being used. Accordingly, these preliminary results should be interpreted cautiously.

Behaviour study

Following the methodology outlined in chapter 2, data were collected on infant carriage in five groups of *Callimico*. The identity of the carrier and the length of time it carried the infant were recorded on every other day. The sample period was 60 minutes on each observation day. Data were collected using point samples at 15-second intervals from the day of birth until the infant was recorded spending 50% of its time uncarried. This point was reached at different times in each group, varying from 6 to 8 weeks after birth among the five groups.

6.3.3 Results

Time budget modelling

Fig 6.4 shows the predicted increase in feeding time needed for a *Callimico* female to meet the energetic demands of lactation. Fig 6.4a is based on the value of

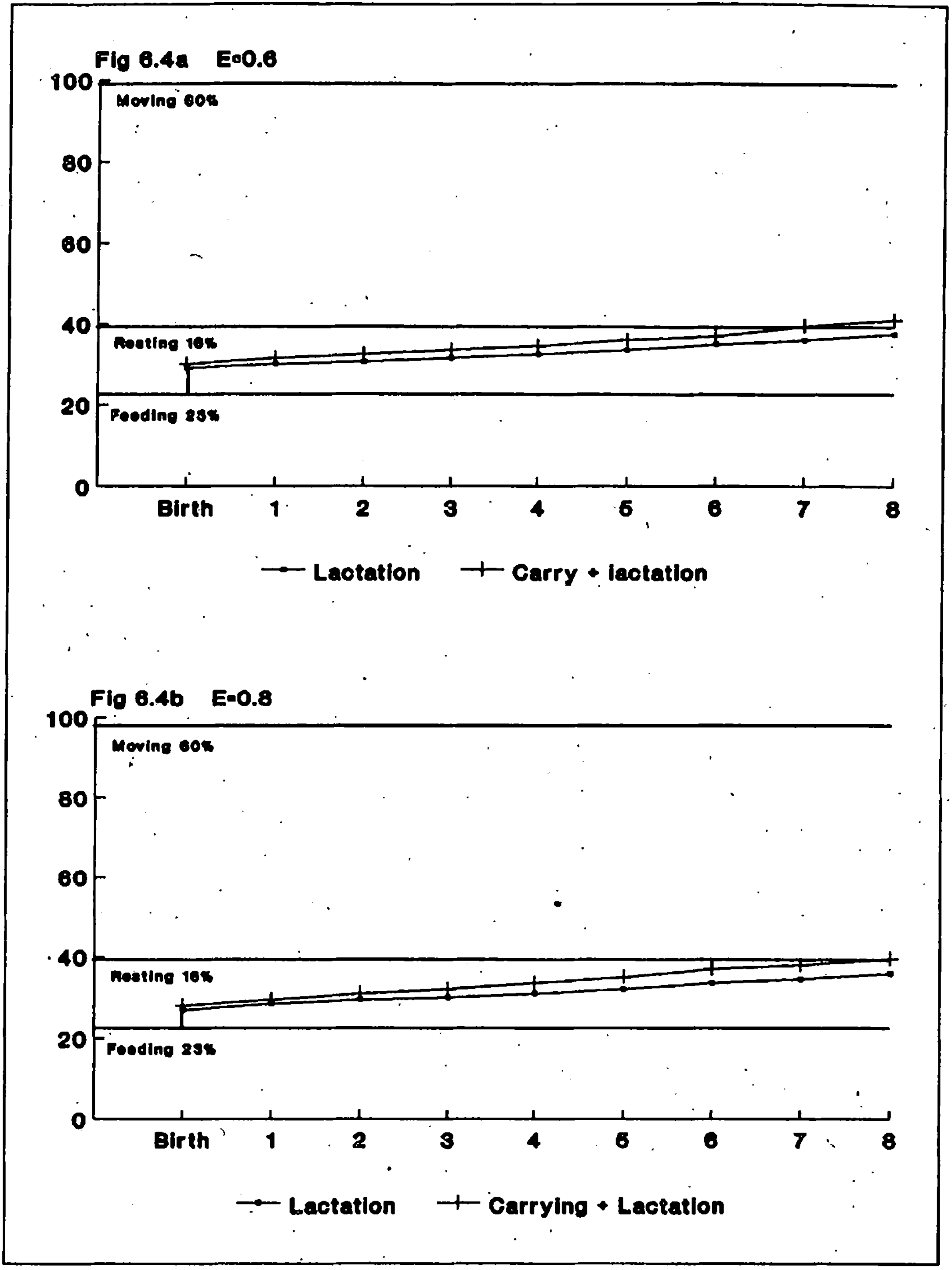


Fig 6.4 Predicted increase in feeding time necessary to sustain lactation and carrying of an infant through 8 weeks from birth using Altmann's Model of maternal time budgets. Fig 6.4a uses E=0.6 and Fig 6.4b uses E=0.8, where E is the conversion coefficient of lactation (see text). The calculations are based on field data for *Callimico* from Pook and Pook (1981).

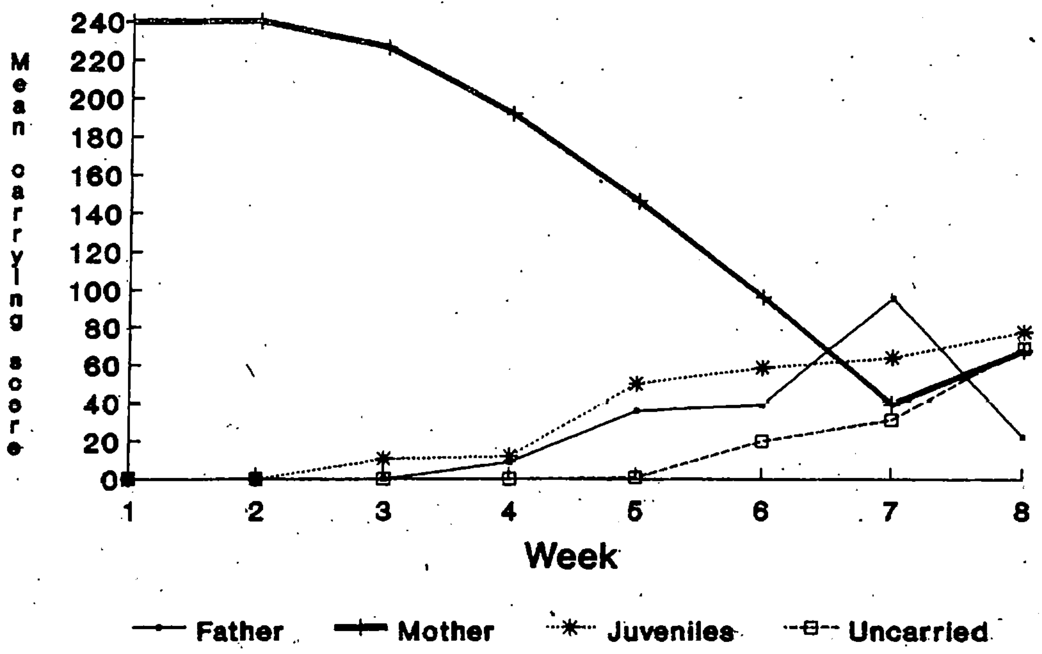


Fig 6.5 Changes in infant carriage pattern over the first eight weeks following birth.
Infant carriage is expressed as mean number of scans per hour in which carrying was scored for each class of animal.

E = 0.6, and fig 6.4b uses the value E = 0.8. Thus, the 'best case' and 'worst case' scenarios are presented. It can be seen that for E = 0.8 the female has enough feeding time to meet the demands of both lactation and infant carriage, while for E = 0.6, if the female has to carry as well as feed the infant, she will be unable to meet the extra demands of infant carriage at around week 7.

Behavioural study

Using data from the behavioural study of the five groups of captive *Callimico*, the mean weekly carrying time by each class of carrier was calculated up to week 8 following birth and presented in fig 6.5. This shows that, on average, maternal carrying time steadily declined from week 2, but it was not until about 5½ weeks after birth that it dropped below 50% of the time. Only between week 6 and week 7 did the mother carry the infant less than either the male or juveniles, and by that time the infant was spending about one eighth of its time uncarried. The time spent uncarried increased gradually from week 5 until, by the end of week 9, all study infants had reached the threshold of spending half their time uncarried.

6.3.4 Discussion

The time budget modelling predicts that the female *Callimico* should be able to rear her infant unaided, at least until around week 7. The behavioural data show that, in these captive study groups, the mother was receiving help from the third week in one group, and by the fifth week in four of the five groups. As predicted, she was receiving help in all the study groups by week 7. In general, however, by week 7 the infant was spending increasing amounts of time uncarried and both males and juveniles were carrying the infant more than was the female.

Overall, while there was considerable variation among the pairs as to the timing of changes in the infant care pattern, the general picture follows that predicted by the model of maternal time budgets. Previously published data, however, suggest that in this study the landmark changes in carer are, if anything, later than might be normal among *Callimico* groups (Beck *et al.* 1982, Carroll 1982). Furthermore, the model does not adequately explain the sudden change from exclusively maternal care to communal care. In Dunbar's (1988) use of this model, the *S. fuscicollis* mother can rear the twins unaided until they are about three weeks old. In *S. fuscicollis* and other callitrichids, however, communal infant care begins within days of birth rather than at the threshold of the mother's capacity for care. How can this difference be explained? Can the difference in care pattern seen among *Callimico* be the result of smaller litter size, or lower litter weight, or both? It seems unlikely to be related to litter size. Care patterns among the small platyrrhines that have single infants vary from almost exclusively male carrying in *Callicebus* to almost exclusively maternal carriage in *Saimiri*. This is contrary to what may be predicted on the basis of mother/infant body weight ratios, as *Saimiri* has a relatively larger infant, which is hence more 'costly' to carry. If a *Saimiri* mother can succeed alone, why not *Callicebus*, and more importantly, why not *Callimico*, which has a considerably smaller infant? Apart from the difference in infant care pattern between *Saimiri* and the other small New World monkeys, another obvious difference is in social group structure. While the marmosets and tamarins, *Aotus*, *Callicebus*, and *Pithecia* have groups with a single breeding female, *Saimiri* forms polygynous social groups. Thus, it would appear that a single breeding female has help to rear offspring, while if there are several breeding females in the same group they do not. *Saimiri* would appear, therefore, to be anomalous among the small New World monkeys. If the other forms are considered, the peculiar care pattern shown by *Callimico* would appear to be related to the small size of the infant. It may be significant that, at the time that the female *Callimico* receives help with infant carriage (*i.e.* when the infant is three to four weeks old) the infant has approximately doubled its body weight and weighs around 90g, a weight comparable to the litter weight at birth of a tamarin of similar body weight to *Callimico*. Lastly, the differences in infant-care pattern may be related to diet as suggested by Wright (1986). *Saimiri* are highly frugivorous and their high-energy diet may enable females to rear infants unaided. *Callicebus*, on the other hand, have a relatively low-energy diet - due to folivory - and females may, therefore, require help with infant rearing. The significant insect component in the diet of *Callimico* may reduce energy intake to the point that females may not be able to rear infants without help.

6.4 STUDY 3 The social dynamics of infant care in *Callimico*

6.4.1 Aims

This study was undertaken to examine the infant care pattern exhibited by *Callimico* and to use these data to test the predictions outlined in the introduction to this chapter regarding the evolution of extra-maternal infant care among the New World monkeys. These predictions are repeated here:

1. If caring occurs only to ensure that a litter is reared, it can be predicted that the parents would be the major caretakers.

2. If caring enhances a male's access to a female, it can be predicted that males would carry more during the female's oestrous or ovulatory period.

3. If caring allows subadults and juveniles to gain vital social experience, it can be predicted that there would be competition among them to carry the infants, but they would not necessarily be the major caretakers, as it is in the parent's interest not to risk the infant by allowing an inexperienced carer to care for it.

4. If caring allows young adults to remain in their natal group beyond sexual maturity, it can be predicted that non-breeding adults would be the major caretakers.

6.4.2 Methods

Infant carrying was studied in five groups of *Callimico* following the methodology given in Chapter 2. Group compositions are given in Table 2.3. The rearing of one infant was studied in each group from birth until the infant was recorded uncarried for 50% of an observation period.

The following parameters were recorded:

1. The time each group member spent carrying the infant.
2. The identity of the individual that initiated transfer of the infant to another carrier, *i.e.* the carrier, the recipient or the infant itself.
3. The identity of the two carriers involved in a transfer.

6.4.3 Results

1. Infant carrying time

The mean carrying time per hour of observation for each group is shown in table 6.3. The overall mean per week from the five groups is shown in fig 6.5. Table 6.3 shows that the mother was the predominant carrier of the infant in each group. In all groups except group 2, where the father did not carry the infant at all, the father carried the infant more than did either of the two juveniles. The Kruskal-Wallis non-parametric analysis of variance was used to test for any significant difference between the time spent carrying by the group members. Where a significant difference was found, *post-hoc* pair-wise comparisons were carried out using the Mann-Whitney 'U' test. It was found that, overall, a significant difference was found using the Kruskal-Wallis ANOVA (H = 13.62, significant at $p<0.05$). The pair-wise comparisons showed that the female carried significantly more than did the male or either of the two juveniles (in all three comparisons, $p=0.012$). Similar analyses were carried out using the data from the day at which extra-maternal care was first seen until data collection finished when the infant was independent 50% of its time, and also for the last four weeks of observation. In these two analyses, there was found to be no significant difference between the male and female in the amount of carrying performed, but the female carried significantly more than either of the two juveniles (♀ vs J1 $p= 0.04$ in both cases, ♀ vs J2 $p=0.02$ in both cases). Thus, once the other group members began to carry, the fathers carried slightly (but not significantly) less than the mothers, while the juveniles carried significantly less than the mothers. There was no significant difference between the fathers and juveniles in the amount of carrying performed.

Table 6.4 shows the mean weekly score for each class of carrier within each group. The figures indicate that there was considerable variation in the age of the

Table 6.3 Mean number of 15 second scans per hour in which each individual was scored carrying the infant in each group during the study.

	Group 1	Group 2	Group 3	Group 4	Group 5
Father	43.1	0	45.4	34.3	9.3
Mother	123.8	202.4	152.0	190.0	193.0
J1	35.8	18.6	19.7	3.1	10.4
J2	27.2	3.8	6.4	2.4	7.0
Uncarried	9.9	15.2	12.7	10.4	18.2

Table 6.4 Mean weekly carrying frequency for each class of individual in each study group. (The mean is expressed to the nearest whole number).

	WEEK								
	1	2	3	4	5	6	7	8	9
Male									
group 1	0	0	0	152	62	92	106	7	0
2	0	0	0	0	0	0	0	0	0
3	0	0	0	28	109	129	129		
4	0	0	0	0	22	225	225	69	
5	0	0	0	0	2	20	20	14	
female									
group 1	240	240	171	35	51	34	24	76	12
2	240	240	240	240	240	220	22	90	181
3	240	240	240	203	43	62	37		
4	240	240	240	240	208	69	13	96	
5	240	240	240	240	191	97	101	10	
Juv									
group 1	0	0	54	53	130	115	109	129	105
2	0	0	0	0	0	17	149	114	15
3	0	0	0	8	67	76	24		
4	0	0	0	0	9	40	0	6	
5	0	0	0	0	45	45	39	64	
off									
group 1	0	0	0	0	0	0	2	26	74
2	0	0	0	0	0	2	44	30	45
3	0	0	0	0	0	40	44		
4	0	0	0	0	2	16	2	69	
5	0	0	0	0	1	41	64	152	

infant at the point of the various landmark stages of development. For instance, the point at which extra-maternal care commenced varied from the third week to the sixth week. In groups 1 and 4, the father carried the infant from the fourth week, while in group 2 the father did not carry the infant at all. In group 1, juveniles were seen to carry the infant before the father did, but only on the day before. As this was on day 21, the juveniles are recorded as carrying the infant during the week before the father. In all other groups in which the father carried the infant, juveniles were seen carrying it either on the same day as the father or within two days of the onset of caretaking by the father.

Infant transfers.

Table 6.5 gives a synopsis of the transfer data. It shows the mean number of attempted transfers per hour, the percentage that were successful, and the percentage that each animal involved in the transfer initiated (*i.e.* the receiver, the carrier or the infant). It also shows the age of the infant when extra-maternal care first occurred, and the age at which it was first seen independent of carriers. Most transfer attempts were successful, indicating that there was little competition among carriers to either retain or take an infant. The table also indicates that most transfers are initiated by the infant (65%), while the receiver and carrier initiate only 19% and 13% of transfers, respectively.

Table 6.6 gives the percentage breakdown for responsibility for initiating transfers by weeks. It shows that, generally, the infant was increasingly responsible for transfers as it became older and more independent, while in the first weeks of transfers the receiver was responsible for more transfers in groups 1, 3, and 5. In group 2, transferring did not occur until later than in the other groups, by which time the infant was capable of independent locomotion and hence initiating transfers itself.

A total of 59 transfers of an infant from the mother to another carrier

Table 6.5 Several features of infant transfer showing, for each group, the number of attempted transfers, the percentage of attempts that were successful, the percentage that were initiated by the receiver (R), the carrier (C), or the infant (I), and the landmark ages at which the infant was first transferred to an extramaternal carrier and first seen uncarried.

	Mean No attempts per hour	% success	% initiated by			Age at 1st transfer	Age when 1st uncarried
			R	C	I		
Group 1	7.1	85.9	37.6	18.8	43.6	21 days	43 days
2	5.7	100	5.9	3.9	82.4	35 days	37 days
3	4.9	98.4	29.7	6.3	64.1	24 days	34 days
4	5.1	91.1	8.9	33.9	51.8	33 days	32 days
5	7.1	95.7	12.0	3.3	83.7	29 days	36 days
Mean	6.0	94.2	18.8	13.2	65.1	28.4 days	36.4 days

Table 6.6 The percentage of transfers per week (to the nearest percentage point) of observation that were initiated by the receiver (R), carrier (C), or infant (I) in each group.

WEEK	GROUP 1			GROUP 2			GROUP 3			GROUP 4			GROUP 5		
	R	C	I	R	C	I	R	C	I	R	C	I	R	C	I
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	100	0	0	0	0	0	60	40	0	0	0	0	100	0	0
5	75	16	9	0	0	0	86	7	7	17	50	23	33	0	60
6	50	32	18	38	0	63	6	6	88	12	27	62	7	7	86
7	11	50	39	0	17	83	10	0	90	0	40	60	0	0	100
8	5	24	68	0	0	100				0	33	67	0	7	93
9	0	13	87	0	29	71									

were recorded, 33 in group 1, none in group 2, 9 in group 3, 7 in group 4, and 10 in group 5. Of these transfers, only eight were initiated by the mother herself. The remainder were initiated either through the recipient approaching the mother and taking the infant, or through the infant spontaneously moving from the mother to another carrier. It is interesting that in group 2 no transfers took place from the mother to another individual. All transfers from the mother were accomplished by the infant moving onto the substrate and then onto another carrier, and none of these transfers was initiated by the mother.

6.4.4 Discussion

It is clear from the data presented above that the mother is the major caretaker of the *Callimico* infant, even though in three groups (1, 3 and 4) a clear shift in caretaking occurred when female carrying declined and male carrying increased. The timing of this shift in carrying was variable, occurring in weeks 4, 5, and 6 in groups 1, 3, and 4, respectively. In the other two groups, the female retained her role as major carrier until the last week of observation, *i.e.* when the infant was moving skilfully and spending a third or more of its time uncarried. Further, in both these groups the juveniles carried the infant more than the father. It would appear, therefore, that *Callimico* show considerably more flexibility in infant caretaking than previously thought.

The female is the major caretaker of the infant if the whole rearing period is considered, and in some groups she remains the major caretaker throughout the rearing period, with the male taking little or no part in direct infant care.

There appears to be little or no competition among carers to care in this species. Most transfers occur simply because the infant moves from one carer to another, and there were no overt signs of competition either to prevent the infant from moving to a particular individual, or for an individual to assume a position that might induce the infant to transfer to it. If the infant gave distress calls, either because the carrier was trying to rub the infant off, or if the infant was uncarried, it was often ignored for some time before another individual approached to pick it up. More transfers were initiated by the receiver than by the carrier, but no resistance was ever offered by the carrier to prevent the transfer taking place.

This infant-care pattern differs from the typical pattern seen among marmosets and tamarins, in which the male and other members of the group carry the infant from an early age. Even in *Leontopithecus*, a genus in which the female may care for the infants unaided for some time, it is reported that the father usually carries the infants by the end of the second week (Hoage 1977, 1982). Once infant care is shared within the group, female marmosets and tamarins generally assume a reduced role in infant care. This is also the case in *Callimico*, but not to the extent that the mother's contribution is less than that of any of the other group members. Furthermore, competition between carriers for the infant has been reported in at least two species of tamarin, *S. oedipus* (Price 1990) and *S. labiatus* (Pryce 1988). Such competition appears to be completely absent in *Callimico*.

It is rather more difficult to compare *Callimico* with the small cebids that show communal care of the infant. The studies on *Aotus* and *Callicebus* have concentrated on carrying duration rather than on the dynamics of transfers; but in both those genera the male is the major transporter of the infant from an early age (Mason 1974, Dixson 1982, Wright 1981, 1984). In *Callicebus*, at least, the female rarely carries the infant when she is not nursing it. It would appear, therefore, that the infant-care pattern of *Callimico* is unique.

According to the predictions stated in the introduction to this study, the following conclusions can be drawn about communal infant care in *Callimico*:

1. As the parents (and particularly the mother) are the major caretakers, it is likely that the function of communal care is to maximise the probability of the infant surviving.

2. The lack of any clear pattern of male involvement in infant carriage suggests that it is unlikely that the male has a reproductive advantage conferred by carrying an infant. Even if the male becomes involved in infant carriage at a relatively early stage, e.g. by the end of the third week, the female would almost certainly have already had a post-partum

ovulation, as this occurs about two weeks after birth (Ziegler *et al.* 1989, Carroll *et al.* 1990). The most frequent interbirth interval at JWPT is 168 days (Carroll, unpublished data), indicating that many females conceive at the post-partum ovulation prior to the male carrying the infant. Recent work with concurrent monitoring of behaviour and reproductive hormones at the Anthropological Institute of the University of Zürich has also shown that the post-partum ovulation in *Callimico* occurs while the female is caring for the infant exclusively (M. Jurke pers. comm.).

3. There is no evidence of competition among the juveniles and subadults to care for the infants. It is unlikely, therefore, that they are competing to learn infant-handling skills. This may be due to the limited occurrence of extra-maternal care (in comparison to marmosets and tamarins) and therefore a reduced need to learn both the skills of infant care and the social behaviours that accompany communal care.

4. As the subadults and juveniles never play a major role in caretaking, it is unlikely that they are 'paying' for remaining in the group beyond sexual maturity. The relatively low levels of extra-maternal care seen in this species would, in any case, reduce the value of such 'payment' compared with the marmosets and tamarins.

6.5 General Discussion

Goeldi's monkey has a unique pattern of infant care. While communal care is a common feature of infant rearing in the marmosets and tamarins, and paternal care is commonly seen in the monogamous *Callicebus* and *Aotus*, no other primate shows such a marked change in infant care after several weeks of exclusively maternal care, and yet before the infant is capable of independent locomotion. In *Saimiri*, the mother cares for the infant alone until it is able to move independently from one carrier to another, but extra-maternal care is not necessarily a significant part of infant rearing. Further, unlike the other small New World primates, fathers are not involved in infant care in *Saimiri* (Baldwin and Baldwin 1981). In *Leontopithecus*, the mother may care for the infant alone for up to two weeks before the typical callitrichid communal care pattern is adopted (Hoage 1977, Carroll 1982). Such lengthy periods of maternal care are most common among primiparous females; subsequent infants may be transferred to the males as early as when they are two days old (Carroll 1982).

The allometric analysis used in this chapter shows that *Callimico* neonates are small compared with the other platyrrhine species that produce only a single infant. In fact, the infant is about the size predicted for that of a callitrichid of similar body weight. All the other small cebids have comparatively large infants. Leutenegger (1973) hypothesised that, below a maternal body weight of 600g, the relatively large single infant produced by the cebids should be reduced by producing smaller twin infants. In fact, *Callimico*'s single infant shows that twinning is not a necessary consequence of dwarfism in the New World monkeys. Selection for a single small infant has apparently occurred in this species.

It is perhaps rather surprising that the *Callimico* infant is as small as it is. If, as Leutenegger suggests (1973), *Saimiri* is at the lower body weight threshold for a single large infant, why is the *Callimico* infant more than slightly reduced in size? The body weight range of female *Callimico* is only slightly less than that of female *Saimiri*, which produces an infant almost twice as large as that of Goeldi's monkey. Leutenegger (1973) cites the high incidence of perinatal death in captive *Saimiri* as evidence to support his hypothesis that there is a threshold maternal body weight below which the relative size of the neonate becomes too large to give birth to without problems. This argument is, however, flawed for two reasons. Firstly, perinatal death among captive squirrel monkeys may be high for a variety of reasons, of which obstetric difficulty is only one. No evidence has ever been presented indicating either that perinatal mortality is higher among squirrel monkeys in captivity than it is among callitrichids, or in the other small cebids (*Callicebus* and *Aotus*), or that the high incidence of failure of pregnancy is due to a high incidence of obstetric mishap. The figure of 50% cited by Leutenneger includes, for instance, spontaneous premature abortions. This is unlikely to be due to the size of the neonate's head. Secondly, if perinatal mortality for *Saimiri* were as high in the wild as the 50% cited by Leutenegger, there would clearly be considerable selection pressure acting on the species for the size of the infant to be reduced. An obstetric problem arising from an over-large infant is likely to compromise not only the survivorship of the infant but also that of the mother as well. It is, in fact, quite possible that high perinatal mortality among captive squirrel monkeys is an artefact of captivity, arising either through a good captive diet leading to a high incidence of large infants, or because of poor captive conditions leading to poor survivorship of the foetus pre- or postnatally. Clearly, it is important that an analysis of perinatal mortality in *Saimiri* be carried out in order to assess its causes, and hence any possible impact on the reproductive strategy of the species.

It nevertheless remains unclear why *Callimico* has such a small infant. If there is no strong selection pressure acting on *Saimiri* to reduce the size of the infant, why should such a pressure exist for *Callimico*? The small size of the *Callimico* infant suggests that the mother should be able to rear it alone. Application of Altmann's model of maternal time budgets (1983), based on Pook and Pook's (1981) field study, suggests that, by week 7, the female may be no longer able to support lactation to feed an infant of that size, and carry it as well. In fact, by week 7, the study infants were spending up to 50% of their time uncarried, and had already started to wean. In some groups, the mother remained the predominant infant carrier throughout the study, but overall the reduction in maternal contribution to carriage began earlier than would have been predicted on the basis of the maternal time budget. It is interesting, though, that infant weight is approximately double the birth weight when extra-maternal care becomes a feature of infant rearing. It is tempting to speculate that the commencement of extra-maternal care is in some way related to the attainment of the callitrichid litter weight. This is difficult to substantiate, however, as even a callitrichid female apparently does not need help at that stage of infant rearing.

The results of the behavioural study suggest that extra-maternal help has evolved simply to ensure the survival of the infant. If the mother does not necessarily need help to rear the infant, it seems that extra-maternal help is a device to reduce maternal energy expenditure without compromising the survivorship of the infant. Perhaps, by reducing maternal energy expenditure in one litter, it is possible that the female could have a second litter. Thus, *Callimico* would maintain a reproductive output similar to that of the sympatric tamarins that appear to be seasonal breeders, having only one litter per year (Pook and Pook 1981, Buchanan-Smith 1989). In captivity, *Callimico* can have two litters per year, and both Pook and Pook (1981) and Masataka (1981a, 1981b) have stated that their estimations of infant ages in wild groups also indicate that infants may be born at approximately six-monthly intervals.

Summary

1. An infant *Callimico* is about the size of a single callitrichid infant relative to maternal body size. This results in a lower reproductive output per litter for *Callimico* than for either callitrichids or cebids.

2. Use of Altmann's model of maternal time budgets indicates that *Callimico* females should be able to rear the infant unaided for at least the first seven weeks. Study of care-giving behaviour showed that extra-maternal care commenced between three and six weeks after the birth of the infant.

3. At the mean time that extra-maternal care begins, the infant is about double its birth weight, *i.e.* about the weight of a callitrichid litter at birth for a similar maternal weight.

4. The mother is the major caretaker when the entire study period is considered, and may maintain a role as major caretaker for as long as seven weeks.

5. There is no evidence of competition among carers to carry. Overall, transfers are most frequently infant-initiated. Prior to the infant being able to move independently, most transfers are receiver-initiated and are effected with no resistance from the carrier.

CHAPTER 7 GENERAL DISCUSSION

In this concluding chapter, the major findings of the thesis are reviewed and discussed with regard to reproduction in New World monkeys, the intermediate evolutionary position of *Callimico* and the current status of knowledge of the species in the wild. As a sequel to that, further areas of research are identified on the basis of predictions resulting from this and other studies.

Natural selection operates on individuals, leading to adaptation to the ecological niche of the species and to the evolution of strategies to maximise lifetime reproductive success. The adaptive radiation of the New World monkeys has been considerable, resulting not only in increases in body size from that of the ancestral form, but also in the evolution of dwarf forms. Life history strategies among the New World monkeys are also very varied. In particular, they exhibit a variety of social group sizes and structures. Polygyny, polyandry, polygynandry and monogamy are all seen as mating systems, and this is reflected in the age/sex structure of social groups. There is a complex relationship between maternal body size, ecological niche, litter size, neonate size, mating system and social group structure. The study reported in this thesis has examined certain aspects of that relationship among the small New World monkeys, with particular emphasis on litter size and neonate size, relationships between indiviuals within social groups and infant rearing. The starting point for this discussion chapter will be litter size and size of the infant among the New World monkeys. The relationship between litter size and weight, shared infant care, social group structure and social bonds will also be explored, with particular reference to *Callimico* and the specific results of this study.

7.1 Dwarfism, litter weight and neonate weight in the Platyrrhini

The analysis of neonate, litter and maternal weights among the New World monkeys reported in Chapter 6 demonstrated that litter weights scale to body size according to a well-defined allometric pattern irrespective of litter size. *Callimico*, however, is an exception to that pattern in having a lower litter weight than would be predicted according to maternal weight. Neonate size, on the other hand, scales allometrically only at the level of the family, with callitrichid neonates being smaller, relative to maternal size, than cebid neonates. *Callimico*, however, is unique among the non-twinning forms in having a callitrichid-size neonate.

It can be predicted that the production of a single small infant should have considerable consequences for the reproductive potential of *Callimico*, particularly in comparison with the callitrichids, which produce twice as many infants in each litter. This is particularly important if there is some niche overlap (and hence competition) between *Callimico* and the *Saguinus* species with which it is sympatric. In a recent analysis of life-history patterns among the Platyrrhini, Ross (1991) has demonstrated that the callitrichids and *Callimico* in fact maintain maximum reproductive capacities above those predicted for their body weights. In the marmosets and tamarins, this is achieved by having two litters of twins a year. *Callimico*, on the other hand, maintains its high reproductive potential by having a relatively early age of first reproduction as well as two litters a year, a point also made by Martin (1992).

Ross's (1991) data for age of first breeding and other reproductive parameters for the marmosets, tamarins and *Callimico* are based on captive colony records of unspecified origin. Unfortunately, there are no published data from the wild on age of first breeding for any callitrichid or *Callimico*, but data from captive colonies are open to bias from colony management practices. For instance, the largest captive colony of *Callimico* (Brookfield Zoo, Chicago), maintained a policy for at least six years of removing young from their natal groups at the earliest possible age in order to form new breeding pairs and hence maximise colony growth (B. Beck pers. comm.). Such practices will have an effect on the mean age of first breeding (the parameter used by Ross). It could be argued that the earliest recorded age of breeding for a species might be a better parameter to use, as this is less likely to be affected by colony management practices. According to this parameter, however, *Callimico* may not breed at an earlier age than the callitrichids. While *Callimico* may conceive as early as 11 months old, one study of captive *Saguinus fuscicollis* reported that two females conceived at the ages of seven and eight months respectively (Epple and Katz 1984). This conception age for *S. fuscicollis* resulted from an experimental pairing of an 'immature' female with an experienced breeding male. It is difficult to assess the relevance of this study as the early age of sexual maturation was undoubtably influenced by the experimental manipulation. Other studies have shown that social conditions affect sexual maturation in callitrichids. It has been shown in one study of cotton-top tamarins, for instance, that established ovarian cycling did not occur in young females until they were paired with adult males outside their natal groups, irrespective of their ages (Savage *et al.* 1988). If, however, the age of first conception has any relevance to breeding in these species under natural conditions, *Callimico* will have no advantage over the tamarins through early breeding. Firm evidence for early maturation in *Callimico* compared to the callitrichids comes from a recent study at the Anthropological Institute of the University of Zürich which compared female *Callimico* with common marmosets *Callithrix jacchus* under identical conditions. This study showed, through endocrine monitoring, that *Callimico* females are capable of ovulation at ten months old, considerably earlier than the common marmoset females that do not ovulate until 14 months old (C. Pryce pers. comm.).

The number of litters per year may also be affected by conditions in captive colonies. Most species of both marmosets and tamarins in captivity are capable of producing two litters a year. There is evidence that marmosets do so in the wild (Soini 1988, Stevenson and Rylands 1988, Ferrari and Lopes-Ferrari 1989), while tamarins, on the other hand, are usually seasonal breeders in the wild and hence have only one litter a year (Snowdon and Soini 1988, Kleiman *et al.* 1988, Ferrari and Lopes-Ferrari 1989). Circumstantial evidence from wild studies suggests that *Callimico* females breed twice a year as they do in captivity (Pook and Pook 1979a, Masataka 1981a). Thus, reproductive modelling based on captive colony records should be viewed cautiously and, until further study of these species in the wild is carried out, the question of reproductive rates among the the callitrichids and *Callimico* must remain open.

It was demonstrated in the analysis of the allometry of neonate size (Chapter 6) that Leutenegger's (1973) hypothesis of the evolution of twinning among the Callitrichidae cannot be sustained when one considers *Callimico*. The adult female *Callimico* has a lower body mass than *Leontopithecus*, yet does not twin. Clearly, selection for smaller infants is not necessarily accompanied by selection for twinning. The question arises, however, as to why *Callimico* has such a small infant. If Leutenegger (1973) was right in his inference that a reduction of neonate size was necessitated by reduction in size of the pelvic canal through dwarfing, why is the Goeldi's monkey neonate so much smaller than that of *Saimiri*? The implication of Leutenegger's hypothesis is that the single infant of these dwarf forms will be the maximum that the pelvic canal can accommodate. It may be that the size of Goeldi's monkey pelvic canal is half the diameter of that of the squirrel monkey, but no reviewer of the comparative morphology of the order Primates, or family Callitrichidae (*e.g.* Hershkovitz 1977, Martin 1990) has highlighted any marked differences in the anatomy of platyrrhine pelves. Clearly, some other explanation must be sought.

It is possible, for instance, that the extreme reduction of the neonate size is related to ecological conditions that do not allow *Callimico* to rear a neonate larger than about 50g, and that the single infant has been reduced in size accordingly. The cost of rearing the infant (in terms of lactation and infant carriage) is related to weaning size and postnatal growth rates. Lee *et al.* (1991) have shown that in primates weaning weight is approximately four times birth weight. Accordingly, rearing costs will be reduced by having a small infant that is weaned at a lower weight than a larger infant. Harvey *et al.* (1987) have also shown that weaning age is highly positively correlated with neonatal body weight and therefore postnatal growth rates are relatively faster among species with small neonates than those with larger neonates. On the other hand, a relatively small neonate may be related to gestational costs. Perhaps the female *Callimico* cannot carry a large foetus and therefore gives birth to a relatively small neonate, whereupon the costs may be shared with other group members. If this were the case, however, shared care would surely be seen early in infant development rather than occurring only when the infant has already doubled its birth weight.

There is some tentative evidence to support the hypothesis that the small neonate of *Callimico* is an adaptation to a poor-quality habitat. Pook and Pook's (1979a) field data showed that *Callimico* are remarkably active throughout the day, spending only around 26% of their time resting. It may be that they do not have enough extra time available to increase their feeding time sufficiently to rear a larger neonate. The species inhabits marginal habitat (Izawa 1979, Pook and Pook 1979a), which may limit the capacity of the female to invest resources in the infant. It seems a remarkable coincidence, however, that the size of the neonate of *Callimico* is reduced to that of a callitrichid neonate through this mechanism.

An alternative explanation, although also related to the ability to increase feeding time in order to increase reproductive potential, is that the ancestors of *Callimico* were twinning forms like the marmosets and tamarins and that reproductive output was reduced in Goeldi's monkey as a response to an energy-poor habitat. One way in which a twinning animal could do this is to produce a single infant. This interpretation is inherently unlikely, however, as it requires a non-twinning animal to make the evolutionary quantum leap to secondarily derived twinning, only to revert to a single infant thereafter. The considerable adaptive radiation shown by two genera of the twinning forms (particularly *Saguinus* and to a lesser extent *Callithrix*) suggests that twinning is part of a successful suite of characteristics and would be unlikely to be selected against.

Whatever the reason for the single small infant of *Callimico*, the allometric comparison made in Chapter 6 shows clearly that the species has a low reproductive output per litter (as measured by litter weight relative to maternal weight) compared with other platyrrhines, and has accordingly evolved a unique infant-rearing strategy.

7.2 *Infant size and infant rearing*

The evidence presented in the analysis of maternal/neonate weight ratios and of the maternal time budget (Chapter 6) indicates that *Callimico*'s relatively small, single infant does not create a burden that would be impossible for a female to cope with alone. By the time the infant is seven weeks old, however, it is becoming a substantial burden on the mother, and she would, therefore, benefit from having help with infant care.

It has been shown that, among the New World monkeys, extra-maternal care of infants is predominant among the smaller-bodied forms with the exception of *Saimiri* (Chapter 6). Below a maternal body mass of 1.5 kg, most species exhibit extra-maternal care within a few days of birth and the mother often ceases to be predominant in infant carriage. This occurs irrespective of the number of infants in the litter. The two exceptions to this are *Saimiri* and *Callimico*, which is particularly puzzling as *Saimiri* has the largest neonate relative to maternal size, whereas *Callimico* has the smallest among New World monkeys. In *Saimiri*, males do not care for infants, but extra-maternal care by females may sometimes occur when the infant is 3-4 weeks old (Baldwin and Baldwin 1981). In *Callimico*, extra-maternal care commences after the age of about three weeks and involves all other family members. Therefore, it would seem that, among the smaller New World monkeys, species that typically have social groups with a single breeding female exhibit extra-maternal care from an early age, while *Saimiri*, which has a polygynous breeding group, exhibits extra-maternal care only when the infant is capable of independently moving from one carrier to another. In the case of *Saimiri*, the infant-rearing pattern is probably related to its polygynous social group structure, which is unique among the smaller platyrrhines. In *Callimico*, on the other hand, the infant rearing pattern may be related to a tendency towards polygyny, or it may be related to the size of the infant.

It was demonstrated in Chapter 6 that the small infant can be reared by the mother unaided for up to seven weeks. Previously, the work of Heltne *et al.* (1973) and empirical observations of infant rearing in groups suggested that extra-maternal care typically occurred at about three to four weeks, but variation among rearing patterns shown by the groups in the present study led to some groups not exhibiting extra-maternal care for up seven weeks. At this time, the infant is active, moving independently of any carriers for some of the day, and feeding to some extent on solid food. Presumably, this variation represents individual fluctuations in the tolerence shown by mothers towards infants, as conditions of housing, husbandry and social group structure were similar in all the study groups. The upper extreme of seven weeks of exclusively maternal care coincides with that predicted by the maternal time-budget modelling. The variability in the timing of the switch from exclusively maternal care to shared care would allow adaptation to local conditions at the time of infant rearing. This study demonstrates only variability among females in infant care pattern; it is not known whether individual females show variability between litters.

On the basis of these data, it is tempting to assume that, if necessary, the mother could rear the infant to independence unaided. Indeed, the colony records at JWPT show that one female reared an infant to independence without helpers, following the death of the father prior to parturition. It must be remembered, however, that captive conditions are less demanding than natural conditions, and the infant-rearing pattern has of course evolved in response to natural conditions.

Masataka (1981a) found that the infant *Callimico* in the wild was transferred from the mother to another carrier at around two weeks old, much earlier than seen in this study, and earlier than has been reported elsewhere in captivity. Perhaps wild conditions do, indeed, induce early extra-maternal care. Energy spent foraging and travelling will be much greater in the wild than in captivity and the mother may be accordingly less tolerant of carrying the infant. On the other hand, *Callimico* neonates are extremely difficult to see even under captive conditions, when the observer may be no more than a metre from the mother and viewing her in good light. The black neonate is carried across the mother's shoulders and hidden in the long dorsal fur, particularly at the nape of the mother's neck, where the long hair at the base of the skull overlaps that of the upper back. It is possible, therefore, that the infants seen during Masataka's study were several days old when first seen, such that their subsequent ages were underestimated. Unfortunately, his study is the only record of infant rearing in the wild, and further study is needed to provide data on the variability in the age of the infant when extra-maternal care is first seen.

7.3 Litter size and the model of maternal time budgets

Dunbar (1988), using a model of maternal time budgets, has produced evidence that a female saddleback tamarin needs help to rear twins as the energetic burden of lactation and carriage cannot be met by the female alone. It therefore follows, as first suggested by Kleiman (1977), that the mother needs help to rear the infants and, accordingly, that selection has favoured the evolution of extra-maternal care. It should be remembered, however, that the model of maternal time budgets used by Dunbar, and the conclusions to be drawn from it, do not depend on the production of twins. From the mother's point of view, the most important factor is not the number of infants, but the weight of them. Whether the litter is one or two, if the litter weight is beyond the capability of the mother to both feed and carry it, she needs help to do so. The mother cannot receive help suckling the infants and help must therefore be in the form of carrying them. The production of twins does have the effect of making the burden more shareable, however. If one heavy infant is produced, the entire burden of carriage can only fall upon one individual at a time, whereas production of two smaller infants means that there is not only a reduced burden for the mother but also for her helpers. Thus, if a helper carries a large single infant, it is investing more energy per unit time than a helper carrying a single small infant, whether it is one of twins or the only infant in the litter. It seems reasonable that, following Trivers (1972), the greater the investment a helper makes in an infant, the more certain should be its genetic relationship with the infant. It may be predicted, therefore, that a helper to a large single infant may be a close relative (father or sibling), a situation that would favour small groups, and hence monogamy. Where the infant(s) is small, investment by a helper is comparatively lower, and the genetic relationship between infant and helper may not be so close. This is compatible with the observation that species with relatively large infants showing a strong element of extra-maternal care (*e.g. Aotus* and *Callicebus*) form monogamous breeding pairs which are the core of stable nuclear families. On the other hand, marmosets and tamarins, with relatively small infants, exhibit a range of social group structures and frequent immigrations and emigrations from groups (Ferrari and Lopes-Ferrari 1990).

7.4 Ecological factors

Ecological factors also affect the need for extramaternal care in the Altmann (1983) model, through the female's time budget. If the female has resting time available to permit expansion of feeding time, and can therefore increase her energy intake, she will be more able to meet the energetic demands of infant care. Thus, the ecological constraints affecting the species also influence its reproductive capacity. One of the problems with the model, however, is its assumption that feeding can be expanded into the time available, and that it will be as efficient as during 'feeding' bouts. This is unlikely to be the case, as:

a) food is not present in the environment in unlimited quantities;
b) the cost of the extra energy expenditure in feeding must also be recouped from a time when little energy is normally expended (resting);
c) resting time is not necessarily spent in a food-rich environment and the female may have to leave the group for a while in order to forage, while the remainder of the group rests.

The model would, therefore, tend to underestimate the energy requirement of the female.

Ecological factors also affect optimum group size and social organisation (Clutton-Brock and Harvey 1977). Examination of the group sizes of platyrrhines exhibiting regular shared care of offspring indicates that the truly monogamous species live in small groups that are almost certainly nuclear families, while the forms that exhibit a flexible mating system (including monogamy, polyandry or polygyny) live in larger groups. It is unclear whether the over-riding factor in determining group size is ecological or behavioural. Most likely it is a combination of the two. If the habitat limits the optimum group size of a species to fewer than six individuals, however, one might expect monogamy to be favoured, while polygyny or polyandry might be favoured by larger group sizes in species where extramaternal care occurs.

7.5 *Infant care and social organisation in Callimico*

If a female needs help with infant rearing, this has profound effects on the size and structure of the social group. It has been pointed out by several researchers that if a female needs help from other group members in rearing her infants, it is in her interests to be the only breeding female in that group and therefore to have the exclusive attention of her helpers (*e.g.* Kleiman 1977, Sussman and Garber 1987). If a female can accomplish this, it results in either a monogamous or a polyandrous mating system within a group, depending on the number of sexually active males. This argument is frequently used in discussion of the social organisation of the marmosets and tamarins. How does this argument apply to *Callimico*, which apparently has a reduced need for extra-maternal care? Due to the paucity of data on the dynamics of social organisation of the small cebids, the following discussion relates mainly to the marmosets and tamarins. The nature and consequences of reproductive suppression among female *Callimico* are discussed with regard to the mating systems that may be seen in the species.

The exclusive breeding status of females - physiological suppression versus conflict

In marmosets and tamarins, reproductive suppression of young adult females in their natal groups has been shown to occur either through physiological means, as in the genera *Callithrix* (*e.g.* Abbott 1984) and *Saguinus* (e.g. Epple and Katz 1984), or through behavioural means, as in *Leontopithecus* (French *et al.* 1989). Reproductive suppression of daughters also occurs in *Callimico* groups (Beck *et al.* 1988, Carroll 1988). Among the marmosets and tamarins, reproductive suppression occasionally fails and groups with more than one breeding female may occur either spontaneously, with a daughter conceiving in the presence of her mother (*e.g.* in a *Callithrix jacchus* group at Emmen Zoo, P. de Wit pers. comm.), or following a change in group composition. The most commonly reported change in group composition resulting in two females conceiving in captive callitrichid groups is the replacement of a breeding male with an unrelated male. If the group contains a mother and a sexually mature daughter, it is not uncommon for both females to conceive. This has been reported for several marmoset species, *e.g. C. jacchus* (Abbott 1984, Rothe and König 1991), *C. argentata* (A. Omedes pers. comm.), *Cebuella pygmaea* (T. Griede pers. comm.). A recent survey of colonies of cotton-top tamarins (*Saguinus oedipus*) revealed similar, although rare, occurrences of polygyny in that species (Price and McGrew 1991). Polygyny has not been reported among the lion tamarins (*Leontopithecus*) in captivity, although it has been reported for two groups in the wild (A. Baker pers. comm.). Typically, when polygyny does occur in captive groups of marmosets and tamarins, the groups are not stable over the long term. In several cases, the females became aggressive towards each other, leading to fighting and possibly serious injuries (Rothe and König 1987, A. Omedes pers. comm.). It is interesting that for *Leontopithecus*, in which no physiological suppression occurs and daughters may show ovarian cycles in their natal groups, conflict between mother and her mature daughters is well documented (Kleiman 1979). It must also be stated, however, that this so-called 'behavioural suppression' cannot be the only factor preventing incestuous mating within a group. French and Stribley (1987) demonstrated that daughters in *L. rosalia* groups may cycle within their natal group, yet did not link this either to signs of instability in the group or to signs that the mother prevented the daughter from gaining access to her father. The implication is that some passive mechanism was also preventing mating. Both Abbott (1984) and Carroll (1986) have suggested that some kind of incest-avoidance mechanism may operate within the nuclear family groups of several callitrichid species in captivity. This may also be the case in *Leontopithecus*. Whatever may be preventing mating in these *Leontopithecus* groups, it does seem that captive groups of callitrichids containing more than one breeding female are not stable over the long term, such that eventually (and typically suddenly) conflict between the females occurs, resulting in considerable injury to one or both combatants.

Polygyny in captive *Callimico*

Polygyny in *Callimico* has been known to occur in captivity, both following replacement of a breeding male in a group (Carroll 1986, T. Griede pers. comm.) and arising spontaneously (M. Stevenson pers. comm.). Again, however, polygyny has rarely been reported.

In the three experimentally established trios in this study, reproductive suppression of a subordinate female occurred in one, while both females conceived in the other two (Chapters 3 and 6). It may be significant that infants were reared to independence in only one trio, and that all three trios ultimately proved to be unstable as a result of female-female aggression. This occurred in Trio 3 of this study in spite of the subordinate female showing no signs of ovulatory cycles as measured by her hormonal profiles. It might have been expected that this trio, with one female having completely suppressed ovarian cycles, should have been rather more stable than the other two. It would appear that in spite of the suppression of the subordinate female, the social situation also affected the dominant female's ovulatory cycles, with erratic levels of oestrogens being excreted in the urine. Suppression of the subordinate female would also seem to have been rather tenuous, as she resumed normal hormonal profiles in spite of being housed in sight, sound and olfactory contact with the dominant female and the male, separated from them by only a mesh screen.

Overt aggression between the females was seen in all three trios of *Callimico* established in this study, in each of which the two females were unrelated to each other. Similar findings have been reported from other captive collections involving related females. At Cameron Wildlife Park, in a breeding group comprising two sisters with an unrelated male, both females became pregnant, but neither reared her offspring and overt hostility was seen between the females after a period of about a year (H. Dornbrack, pers. comm.). At Apenheul, in the Netherlands, a mother/daughter dyad was stable for over a year with an unrelated male before the females had to be separated (T. Griede, pers. comm.). The polygynous group at Edinburgh Zoo is still stable at the time of writing a year after the daughter conceived in the presence of her mother (M. Stevenson, pers. comm.). This group notwithstanding, it appears that - among both the callitrichids and *Callimico* - in groups where more than one female undergoes ovulatory cycles, hostility between the females eventually results.

There are no reports of polygyny among the monogamous cebid genera *Callicebus*, *Pithecia*, and *Aotus*, either in the wild or in captivity. The reproductive status of maturing daughters within their natal groups is unknown and there is no information on migration of juveniles or subadults in these species. In all these genera, it is unusual for groups to number more than four or five individuals (Wright 1981, Kinzey 1981) and it is accordingly assumed that offspring migrate from the group as they become physically mature. It is not known whether the departing subadults leave voluntarily or whether they are peripheralised by their parents and forced out of the group.

So far, the discussion has centred on prevention of pregnancy in other females. A further option is available to females, should their exclusive breeding status be threatened: infanticide. Price (1990) has pointed out that there are reports of infanticide among marmosets and tamarins where other means of suppression have failed to prevent pregnancy. Accordingly, she suggests that infanticide is an adaptive strategy among the callitrichids. In the present study, both females in Trio 2 became pregnant and neither infant survived beyond a week old, one having been severely bitten and dying from the injuries sustained. While it is impossible to tell whether this resulted from an attack on the infant or its mother, the ultimate effect of the attack was to kill the infant and force the mother's removal from the social group.

Polyandry in captive *Callimico*

Although they were once thought to be strictly monogamous in both mating system and social group structure (*e.g.* Kleiman 1977), the callitrichids are now more often thought of as displaying a flexibility not previously suspected. In particular, several studies have suggested that wild callitrichid groups may contain more than one breeding male (*e.g. S. mystax*, Garber *et al.* 1984; *S. fuscicollis*, Goldizen 1988; *C. humeralifer*, Rylands 1986). The present study did not examine polyandry in *Callimico*, and there is only one report of a multimale group in captivity. This was at JWPT and has been described by Carroll (1986). A female was introduced to a father/son dyad. After some aggression between the males, the son emerged the dominant and the father's testes atrophied. This dominance relationship remained stable over a two-year period and the father's testes remained atrophied. During this time, the son sired several offspring in the presence of his father and infant rearing within the group included caretaking by the older male. After a period of two years cohabitation with his son, the father was removed and paired with another female for three years up to his death. His testes remained atrophied and could not be located in either the scrotum or the abdomen on post-mortem examination. This rather extreme form of reproductive suppression among males has not been reported in captive callitrichid groups. As a single case, its significance cannot be assessed, but it may indicate that polyandry is not a reproductive strategy used by *Callimico*. Masataka's (1981a, 1981b) wild study group contained only a single adult male prior to the introduction of the three captive subadult males. He did not report any aggression between the resident male and those introduced. Pook and Pook's (1981) study group of eight individuals contained three males of adult size. Their social relationship was apparently amicable but their familial relationship was unknown. Another wild group containing nine individuals apparently did have more than one adult male, but their breeding status and social relationships were not determined (Buchanan-Smith 1991).

Monogamy in captive *Callimico*

This study has confirmed previous reports that captive groups of *Callimico*, comprising a monogamous pair and their offspring, are very stable over long periods. In the study of established pairs, the breeding male and female of Group 1 had been housed together for eight years and had reared ten infants during that time. The relationship between the male and female in each of the study groups was extremely amicable, with aggression between them being very rarely seen. An increase in group size, under captive conditions, occurs as a result of recruitment to the group through birth rather than through immigration. Those rare occasions in captivity when a male has 'migrated' into a group, such as described above, have resulted in profound changes in intra-group relationships and in particular have led eventually to the destabilisation of a previously amicable relationship between females. Thus, under captive conditions where immigration into groups does not occur, groups comprising a monogamous pair and their offspring are extremely stable. This does not, however, necessarily imply that this is a 'natural' social group structure. Although wild groups of *Callimico* have sometimes been reported as being effectively isolated from neighbouring groups (*e.g.* Pook and Pook 1979a, Izawa 1979), one study has reported groups in contiguous home ranges (Christen and Geissman in prep.). Even if there is some distance between neighbouring groups, it is unlikely that their isolation is complete. Social group structure under natural conditions is discussed later in this chapter in a section devoted to *Callimico* in the wild.

7.6 *Social bonds and social organisation*

An attempt to provide a satisfactory definition of a pair bond was made in Chapter 4, based on the dictionary definition of a bond as 'something which binds, fastens or holds together'. Thus, the term 'bond' implies that its existence reduces the likelihood of the bound parts becoming separated. In social behaviour, a bond is an attribute of a relationship, and care must be taken to avoid use of the term to describe a mating system. It was pointed out in Chapter 4 that a monogamous mating system does not require that the pair have any lasting social relationship. A bond may exist within any dyad, the term being most frequently used to describe either a mother/infant relationship, or the relationship between a mated pair - the pair bond. The definition of the pair bond made in this study was that it is a cohesion between a mated pair that encompasses and persists beyond the fertile period.

Where bonds exist within groups, they would help to stabilise the relationship between the bonded individuals which, in turn, would help maintain the stability of the social group. Social bonds, and particularly the pair bond, may be extremely important in species in which there is a component of cooperation in the social behaviour of the group. Cooperation may, for example, serve to maintain a territory, to rear an infant, or to exploit a food source. It may be predicted that the greater the degree of cooperation between individuals, the stronger the bond that would develop between them.

The existence of the pair bond has been commonly inferred either through observation of the social behaviour of the pair, or through testing the existence of the bond through intruder studies. Neither of these methods is satisfactory, although the former was used in this study. The use of observation of social behaviour alone in effectively identifying the presence of a bond is dependent on:

(i) the accuracy of the predictions made concerning the nature of the social interactions between a bonded pair and

(ii) some bonding behaviour being present and measurable while the bond exists, even if it is not always present to the same degree.

In this study the question arose "is the lack of interaction between the pair indicative of the absence of a bond or of the presence of a bond that is so well established that it needs little reinforcement?". It was argued that, if a bond exists, it cannot be maintained without reinforcement. On the other hand, unless the presence of a bond is tested in an effective way, the degree and nature of affiliative behaviour needed to maintain it cannot be assessed. In other words, unless a bond is demonstrated to exist, it is impossible to show an association between any behaviour pattern and bonding. Proximity, for instance, is typically used to characterise a bond, but an infant may huddle with its mother due to the mother/infant bond, while a female may huddle with a male either because she is cold or because there is a pair bond between them.

The device most frequently used to test the pair bond is that of the 'intruder paradigm'. The rationale behind this device is that, if a pair bond exists, the members of the pair will react in different ways to an intruder of the same sex than to an intruder of the opposite sex. Further, they will react differently depending on the presence or absence of their bonded mate. Anzenberger (1985) has provided a critique of the methodology used in previous studies with the intruder paradigm, emphasising the importance of attempting to control for the effects of territoriality, and of controlling conditions of the tests so that comparisons across studies can be made. While the use of the intruder tells something about the differential response of the male and female to an intruder, it is difficult to be sure *what* it is telling us. The reactions to an intruder are likely to be a combination of a territorial response as well as either mate guarding or exploiting the sudden availability of another potential mate. If the territory is a more valuable resource than the pair mate, the responses seen in the presence of the intruder are more likely to relate to territoriality than to mate guarding.

Most commonly, intruder paradigm studies have not allowed the intruder to come into contact with the study animals. This does not allow the possibility of desertion, which must be the ultimate test of the pair bond. If a pair bond is present in a relationship, it must reduce the likelihood both of desertion and of extra-pair matings. This cannot be effectively studied through short-term observations on the results of visual contact with an intruder for perhaps as little as ten minutes. There are only two intruder studies of New World monkeys that have allowed contact with the intruder, that of Buchanan-Smith (1989) on *S. labiatus* and that of Evans (1983) on *C. jacchus*. Only the former allowed a real opportunity for a partner to desert by allowing prolonged cohabitation of the pair with the intruder.

The use of trio studies does not test the pair bond, but rather examines social relationships under a different set of conditions. Few trio studies have been carried out on New World monkeys. Only Epple (1977, 1981) with *S. fuscicollis*, and Kleiman (1978) with *L. rosalia* established trios of either two males and one female, or one male and two females, and carried out concurrent studies on them. Price (1990) studied a polygynous group of cottontop tamarins at Stirling University. Her group arose spontaneously after a daughter became pregnant within her natal group.

The present study did not include testing of the pair bond in *Callimico*, and is therefore restricted in the limited interpretation that can be made of the results of the behavioural study.

The study of social bonding in heterosexual pairs of *Callimico* (Chapter 4) demonstrated that, in captivity, these pair-based groups are stable. There were few agonistic interactions within the groups, but there were in any case few interactions between members of long-established pairs that had reared infants. This pattern changed following a birth, when levels of proximity and contact both increased to levels similar to those seen in the early bonding phase. This presents the problem of interpretation mentioned earlier. Do these findings reflect the lack of a bond, or the presence of a bond that does not need reinforcement as it is so well established? It has generally been accepted that, once a bond has been established, the pair do not need to partake in courtship behaviour that may be costly in energetic terms (Parker 1974); but is it possible to determine whether the lack of social interaction is due to a bond having been established? Firstly, if Parker's hypothesis is correct for primates, one would expect mating to be seen only during ovulatory periods. In fact, although mating and other sexual interactions in *Callimico* do occur at only very low levels after the initial bonding period, they may be seen outside the ovulatory period of the ovarian cycle, or during pregnancy. Secondly, one would expect the bond to be maintained by low levels of positive social interaction. In this study, the levels of social interaction between the mated partners of the mated pair were not merely low, they were almost negligible. Furthermore, the behaviour of the male following the birth of the infant suggests that a re-establishment of the social bond is taking place. This is unlike pair-bonding in cebids such as *Aotus* (Wright 1981) or *Callicebus* (Mason 1971, Kinzey 1981). In these latter genera, levels of proximity, contact and grooming suggest that a strong pair bond is in place at all times, irrespective of the female's reproductive status.

It is, of course, in the interests of both sexes for there to be a strong social bond following the birth of the infant. For the female, it ensures the presence of a helper when she needs one. For the male, it ensures his close proximity to the female when she next ovulates, two weeks or so after birth. In *Callimico*, these events are unlikely to coincide as the switch to extramaternal care occurs one to four weeks after the likely time of a *post-partum* ovulation during the second week after a birth. Recent work examining infant rearing while carrying out concurrent hormonal monitoring has confirmed that post-partum ovulation in *Callimico* occurs before the male begins to participate in infant care (M. Jurke pers. comm.), which suggests that the timing of re-establishment of a close social relationship is due to factors other than allowing proximity to an ovulating female. It may be that the male performs an infant-guarding function prior to assisting directly with infant care. This would have a direct benefit in terms of fitness to both himself and the female. It would allow the female to assess the male's fitness, in his capacity as protector, and give the male access to the female when she ovulates.

If one of the functions of the pair bond is to ensure the presence of helpers for the female when rearing an infant, it would be expected that the female should invest more in the bond just prior to the time when that help is needed. In *Callimico*, this time falls between the birth of the infant and it reaching the age of three to seven weeks. In fact, the present study showed that the male was more responsible for bond-promoting behaviour than was the female during that time. There was no significant difference in levels of grooming between the male and female at this time, although overall the males did groom the females more than *vice versa*. Kleiman (1977) suggested that males in monogamous species should groom more than females, but - apart from one study of *C. jacchus* (Evans and

Poole 1984) and one of *L. rosalia* (Kleiman 1978) - there has been no evidence to support this either among the callitrichids or for *Callicebus* (Kinzey and Wright 1982).

When the male-female-female trios were studied, there was no evidence of strong female-female bonding as seen among the polygynandrous *Saimiri*. Indeed, the evidence suggested that there was some competition between the females for the male, competition that eventually resulted in the expulsion of one of the females from each trio. It may be that female-female bonding does occur along matrilines. If females do not migrate between groups, strong matrilineal bonding may occur between females. On the other hand, if females migrate between groups such bonding is not apparent (*e.g.* among gorillas, Harcourt 1979), even though the species may form polygynous groups.

In trio studies of callitrichids where the females were unrelated (as in this study on *Callimico*) fighting occurred between members of the same sex, resulting ultimately in the reduction of the trio to a heterosexual pair (Epple 1977, 1981, Kleiman 1978). In both cases, the investigators found that two male/one female trios were more stable than one male/two female trios. In both cases, they found that the multi-female trios were considerably more unstable than in this study, indicating a fundamental difference between *Callimico* and the Callitrichidae. *Callimico* appears to be considerably more tolerant of other females in the group than are the marmosets and tamarins studied to date, and there is no suppression of the ovulatory cycles of subordinate females in some polygynous *Callimico* groups.

7.7 *Reproductive physiology*

The interpretation of any study of reproductive behaviour will be limited by the degree of understanding of the underlying physiological processes. As well as being intrinsically important, a knowledge of such parameters as ovarian cycle length and gestation period allows better interpretation of changes in behaviour over time. Hormonal determination of the time of ovulation allows comparison with oestrous or other reproductive behaviour. An important component of this study of reproductive and social behaviour in Goeldi's monkey was the investigation into certain aspects of the reproductive cycle of the female. Prior to this study, the only available estimates of ovarian cycle length were based on behavioural changes (Lorenz 1972, Beck *et al.* 1982). Estimates of gestation periods were based either on interbirth intervals, or on inferred conception dates based on mating patterns (Lorenz 1972, Beck *et al.* 1982, Carroll 1982). The existence of a *post-partum* ovulation in the species was assumed, but had not been confirmed (Carroll 1982). This study showed that ovarian cycles could be monitored by measurement of oestrogen metabolites found in the urine, which allowed determination of basic reproductive parameters such as ovarian cycle length and gestation period, as well as allowing direct comparison of behavioural events with physiological events.

The major oestrogen metabolite was found to be oestrone-3-glucuronide, both during the ovarian cycle and during pregnancy. Ovarian cycle length determined through hormonal measurement (mean 24.1 days ± s.e. 0.9 days, n=9) compared well with the estimate based on behavioural changes (22-24 days, Lorenz 1972, Beck *et al.* 1982). The only other hormonal study of ovarian cycles in this species was of cycles in two females in which mean ovarian cycle length was 27.1 ± 3.1 days n = 9 (Christen *et al.* 1989). The gestation length of 145-155 days (n=3) determined hormonally in this study confirmed estimates based on behaviour (155-158 days, Lorenz 1972, Carroll 1982), and compared well with other hormonal studies (144-157 days, Ziegler *et al.* 1989). Furthermore, the occurrence of a *post-partum* ovulation followed by conception was demonstrated in one female, confirming that a female *Callimico* has the capacity to produce two infants a year. If this occurs regularly, the female may be almost continually pregnant.

Hormonal monitoring was essential in demonstrating that suppression of a subordinate female occurred in one of three polygynous groups established during the study. As a single occurrence, it is difficult to interpret its significance. It does, however, underline the statement made earlier that *Callimico* may be much more flexible in its reproductive behaviour than are the marmosets and tamarins.

Monitoring of ovarian cycles helped in interpretation of some aspects of the behavioural data. Reproductive behaviours such as genital sniffing, presenting and mating occurred at very low rates throughout the study, and it was not possible to identify an oestrous period. Hormonal monitoring of the ovarian cycle, with concurrent behavioural sampling, revealed that during the periovulatory period there was a significant increase in female proceptive behaviour. There was also some evidence that the female is responsible for maintenance of proximity with the male at this time, while the male is responsible for this at other times during the cycle.

There are few studies of marmosets and tamarins that compare reproductive behaviour with the stages of the ovarian cycle. Stribley *et al.* (1987) found no correlation in *Leontopithecus rosalia* between the stage of the cycle and behavioural events. They suggest that this indicates that females are continuously sexually receptive and that they have concealed ovulation. Similarly, French (1982, cited in Price 1990) found no correlation between behavioural changes and ovarian cycles in *Saguinus oedipus*. Brand (1984), on the other hand, reported that anogenital sniffing by male cotton-top tamarins varied significantly over the female cycle, and that female proceptive behaviour was highest during the non-fertile period of the cycle. This latter finding contrasts with this study of *Callimico*, in which female proceptivity was highest in the periovulatory period. This, together with the change in responsibility for maintaining proximity, the lack of any indication from the behaviour of the male that female attractiveness varies across the cycle and the observation that sexual behaviour may be seent during the other stages of the cycle, suggests that in *Callimico*, ovulation may be hidden from the male.

It was suggested by French *et al.* (1984) that concealed ovulation in cotton-top tamarins was related to a monogamous or polyandrous mating system and to the need of a female for helpers in infant rearing. Goldizen (1987b) suggested that saddleback tamarins may also conceal ovulation and that this is a necessary factor in maintaining polyandrous groups. If an ovulatory event were signalled to a male, selection would favour mechanisms that ensure certainty of paternity such as mate-guarding, which would not favour stable polyandrous groups. For polyandry to arise, males must have a roughly equal chance of siring offspring in the group, as males that are unlikely to have fathered offspring may benefit by deserting the female and searching for another potential mate (Goldizen 1987b).

While concealed ovulation in the marmosets and tamarins may help to maintain the presence of one or more males in a social group to assist with infant rearing, it is rather more difficult to explain in *Callimico*. The limited field studies on Goeldi's monkey have not reported the occurrence of polyandrous groups, and the species has clearly not developed the same degree of extra-maternal care as seen in the marmosets and tamarins. The question therefore arises as to why a system has evolved in *Callimico* that may ensure the sustained presence of one or more adult males in the social group. It is possible that the modelling of the maternal time budgets is faulty and that, in fact, the need for assistance with infant rearing is greater than is predicted by the modelling. Secondly, it is possible that in the wild extra-maternal care begins earlier than in captivity, as suggested by Masataka's (1981a) study, and that the presence of other adults in the group for infant rearing is more important than indicated by current knowledge. Thirdly, although the female may not need extra-maternal help to the same degree as do the marmosets and tamarins, the need may nevertheless be there and infant survival may be compromised by the absence of helpers. Maintaining the presence of a male through concealed ovulation and either continuous or sporadic sexual receptivity is one way that the female may ensure the presence of at least one helper.

7.8 Callimico in the wild

One of the problems of a study on social behaviour under captive conditions is that those conditions, by their nature, limit the behaviour of the study subjects. There are no opportunities for immigration and emigration from groups. There is no opportunity for an animal to 'choose' its pair mate. In the colony at JWPT, there are no disputes at 'territorial boundaries', as conspecifics are never housed in adjacent cages. Accordingly, care is needed in extrapolating the findings of a study like this to the natural situation. However, while some findings may be artefacts of the captive environment, many will be extremely valuable in understanding the social behaviour of the species in the wild. The final part of this discussion chapter attempts to link the findings of the study to current knowledge of the natural behaviour of *Callimico* in the wild.

Isolation of groups

Most of the researchers who have studied *Callimico* in the field agree that it is found at low densities, *e.g.* Pook and Pook (1979) estimated a population of only 1 - 2.5 animals per km^2. As they reported a home range of 35-60 ha, they therefore estimated that groups may be isolated from each other by several kilometers (Pook and Pook 1979a, 1979b). These findings concur with those of Izawa (1979), although Cameron *et al.* (1989) estimated their population density to be 9.6 animals per km^2, rather higher than the level estimated by previous authors. Pook and Pook (1979a) suggested that multi-female breeding groups of *Callimico* were an adaptation to low population density and the low probability of encountering a potential mate from another group. These observations of isolated groups with little chance of immigration and emigration suggest that captive conditions for *Callimico* are, in fact, quite similar to those in the wild. Most recently, however, Christen and Geissman (in prep.) reported on a polyspecific group of 15-17 animals containing 5-6 *Saguinus labiatus*, 7-8 *S. fuscicollis* and 3 adult *Callimico*. This group had a home range of 80 ha, larger than any previously recorded for any of the three species it contained, and the home range was adjacent to the home ranges of two other *Callimico* groups. It would appear, therefore, that groups of *Callimico* in some areas may be isolated from each other, while in other areas they are not.

It is difficult to assess the accuracy and reliability of any of these field data. Only Pook and Pook's study (1979a, 1979b) and Christen and Geissman's study (in prep.) examined home range size. In both cases, study of their main groups was limited - five weeks (Pook and Pook 1979a) and six weeks (Christen and Geissman, in prep.). Pook and Pook concentrated their observations on their focal study group while Christen and Geissman surveyed the area around the home range of the focal group, thus gaining information on surrounding groups as well. These studies were conducted at different times of the year; Pook and Pook's took place in September/October during the early part of the wet season, while Christen and Geissman's was conducted in June/July at the height of the dry season. It might be predicted that daily travel distances and hence home range size would be different in the two seasons. If, for instance, food is scarcer in the dry season, the animals lay respond in one of two ways. They may reduce activity and energy expenditure, to a minimum, travelling and feeding less than when food is abundant. Alternatively, travel distance (and home range size) may be increased in order to find food. Thus, if the latter strategy is followed, groups that are isolated in the wet season may be in adjacent or even overlapping home ranges in the dry season. Clearly, further study is needed to provide additional information on seasonal effects on home range size; but at the moment it is impossible to say whether the different results of the two studies are due to seasonal effects or to study methodology.

If the Pooks' assessment of population density and inter-group distance is accurate, the result would be large groups of Goeldi's monkey with subordinates in the group having little chance of emigration. The group would become increasingly inbred with time, perhaps to the point where deleterious effects might be seen. Among captive primates, even low levels of inbreeding have been shown to have a detrimental effect on mortality rates (Ralls and Ballou 1982). Data from the British Isles regional studbook for *Callimico* (Carroll and Vaartjes 1989) show that infant mortality is higher among inbred infants than among non-inbred infants (Carroll, unpublished data).

Many years of data from the records of colonies of captive *Callimico* have shown that reproductive suppression of daughters occurs in families, and may continue even after the death of the mother (Carroll 1986). Is such reproductive suppression an artefact of the confined conditions of captivity? It is possible that the greater dispersal of individuals in the wild leads to a greater likelihood of failure of fertility suppression, thereby allowing a daughter or son to breed within their natal group. There is recent evidence, however, that reproductive suppression in *Saguinus oedipus* is maintained through scent marks (Savage *et al.* 1988). Similar findings have been made with common marmosets (D. Abbott pers. comm.). If this is the case among *Callimico*, the distance that individuals disperse during the day may be unimportant if all the individuals in the group sleep together at a single site in contact with each other.

Dispersal strategies

The isolation of groups has the effect of reducing the likelihood of emigration and immigration. Among marmosets and tamarins, encounters at territorial boundaries represent at least one situation in which possible transfers between groups may occur, and they also provide opportunities for meeting potential mates. Hubrecht (1984) saw mating between members of different groups of *Callithrix jacchus* during an intergroup encounter. Similar observations were made by Goldizen (1988) on *S. fuscicollis*. No encounters at territorial boundaries have ever been described in *Callimico*, and if groups are, indeed, isolated, emigrants must travel outside their home range before they encounter their nearest neighbouring group.

Pook and Pook (1979a) suggested that isolation of *Callimico* groups was due to their specialised habitat requirement of dense understorey. If this is so, emigrating *Callimico* must travel not only long distances but also through unsuitable habitat in order to encounter other conspecifics. This scenario of separate groups isolated in islands of suitable habitat seems rather improbable for several reasons:

1. If reproductive suppression occurs in the same way as in the captive groups, the death of one of the breeding pair would result in the cessation of breeding in the group until an immigration into the group occurs.
2. Limitation of immigration and emigration would restrict opportunities for non-breeding group members to attain breeding status.
3. Izawa's (1979) description of habitat types inhabited by *Callimico* suggests that, rather than being a habitat specialist, it is very generalised in its habitat requirements, as long as there is a well-developed scrub layer present. Most recently, a field study has found *Callimico* in forest without a dense scrub understorey (A. Christen pers. comm.), thus indicating that perhaps the species is even more flexible in its requirements than previously thought.

A further aspect of breeding that is affected by dispersal strategies is that of the age of first breeding in females. Data from captive colonies suggests that this is important in enabling *Callimico* to maintain a high R_{max} (Martin 1990, 1992, Ross, 1991). If, however, reproductive suppression operates in wild groups as it does in captive groups, daughters would be unable to breed early unless suppression is removed. Information from captive *Callimico* suggests that young females may start breeding in several ways:

(1) The father may leave the group and be replaced by an immigrant male that mates with all the females in the group;
(2) The daughter may leave the group and pair with an unmated male;
(3) The daughter may leave the group and enter another group, breeding with one of the males in that group.

The evidence from the present study suggests that a group with two unrelated breeding females would be unstable and possibly hazardous for the females in that group. The stability of groups that contain related females that breed while cohabiting remains to be tested. Unfortunately, the paucity of data from wild *Callimico* does not allow an assessment of the likelihood of a daughter leaving her natal group and finding a mate. The low population density and high intergroup distance seen in this species would suggest that such encounters are unlikely. Until further information on the migration pattern of *Callimico* is available, the question of how, and at what age, a female may meet a breeding partner must remain open.

Fidelity to a female, or to a home range?

One aspect of the social behaviour in which the isolation of groups has a considerable impact is that of intragroup social relationships and pair bonding between the breeding animals. There is evidence from this study that the pair bond between the breeding pair is not particularly strong (Chapter 4). Is it possible, therefore, that a male is 'bonded' to the home range (site fidelity) rather than the female with which he cohabits in that home range? If Pook and Pook's hypothesis about *Callimico*'s habitat requirements are correct, it would suggest that a home range encompassing suitable habitat is a much scarcer commodity than a female, and would therefore be a limiting factor for a male. A male would, therefore, be active in defending the home range, or perhaps a core territory within the home range. There is some evidence to support this in the study, as the males were found to perform ABL consistently more than other group members. It is possible that this behaviour was a response to a perceived threat to a female rather than a territorial threat, but the performance of ABL by the male induced the performance of the display by all group members, thus perhaps maintaining the territory and maintaining group cohesion at the same time.

Group size

Group size of *Callimico goeldii* in the wild has been reported to range from two to eight or nine individuals (Moynihan 1976, Izawa 1979, Pook and Pook 1979a, Masataka 1981a,1981b, Cameron 1987, Buchanan-Smith 1991, Christen and Geissman in prep). The larger groups have either been assumed to contain more than one breeding female (Pook and Pook 1979a) or have been known to do so (Masataka 1981a). Buchanan-Smith (1991) did not speculate on the composition of her group of nine individuals, but made the point - as had Izawa earlier (1979) - that a group of this size could have arisen within three years from a single pair if females gave birth about every six months, as they do in captivity. If there is little opportunity for emigration from the group, the group would merely increase in size. Contrary to the opinion of Lyon *et al.* (1987) that five may be the limit of a captive group of *Callimico*, groups of up to ten have formed in captivity, from a single breeding pair, with no apparent instability (pers. obs.).

The alternatives to such groups arising from a single pair are:

1. That immigration into a group has occurred, resulting in the presence of unrelated non-breeding individuals in the group.
2. That immigration has resulted in the presence of other adults that may breed in the group. This may result in polyandry, polygyny or polygynandry.
3. That two small groups have temporarily merged to form a larger social unit.

There is little evidence for or against any of these alternatives. The Pooks' study group remained stable in its composition throughout the study period of 11 weeks (Pook and Pook 1979a). Masataka (1981a, 1981b) did not find any immigration into his group, although there was evidence that it was unstable and fragmenting toward the end of his study period. Unfortunately, Masataka's group was not a natural group (three captive individuals having been introduced into it), and may have been artificially maintained in the study area through the use of the baiting platform. No other groups were studied long enough to be sure of their size.

Group composition

Two of the three reports of large wild groups of *Callimico* have reported the assumed or demonstrated presence of more than one breeding female. The composition of smaller groups has not been commented on, but they have been assumed to be monogamous (Heltne *et al.* 1981). What predictions can be made about the mating strategies that may be found in wild groups in the light of the research carried out here?

1. Polyandry

Polyandry is a rare mating strategy that will only evolve under special conditions (Trivers 1972, Emlen and Oring 1977, Emlen, 1984). The occurrence of polyandry in marmosets and tamarins is closely linked to the twinning habit and the female's need for help with infant care from the time of birth of the infants (*e.g.* Dunbar 1988, Goldizen 1987a, 1987b). In order to ensure that helpers are present to care for infants, it has been suggested that females conceal ovulation, and that the consequent lack of paternal certainty induces males to stay to help with rearing the infants (Stribley *et al.* 1987). Further, Price (1990) has demonstrated that infant carrying in cottontop tamarins increases the likelihood that a male will mate with the female. It may be found that there are other devices that induce males to stay with the group to assist with infant rearing.

The lack of paternal care in *Callimico* demonstrated in the study of infant rearing (Chapter 6) would suggest that there has been no selection pressure for polyandry to evolve. Indeed, there is no evidence from field studies that this mating system occurs naturally, although this may merely reflect the limited scope of the field studies to date. There was some evidence presented in this study to suggest that ovulation may be concealed in *Callimico*, *viz.* matings are not confined to ovulatory periods and, while female proceptivity was higher during the periovulatory period, female attractiveness was not found to vary across the cycle. While these traits may help support a polyandrous mating system, as pointed out above, they may also help promote other mating systems as well.

2. Polygyny

It has been pointed out earlier that the evidence for polygyny occurring in *Callimico* in the wild is preliminary, although there are strong indications that it does occur. The lack of reproductive suppression of the subordinate female in a majority of the multi-female study groups provides a framework within which polygyny can occur. The ultimate instability of the multi-female groups, however, suggests that such a mating strategy may not be stable in the long term. Evidence from Masataka's (1981a) study supports this.

Polygyny that is based on a familial relationship, through which matrilines can develop within groups, was not explored in this study. Evidence presented from other cases in captivity, however, tentatively suggests that such groups may be no more stable than those based on unrelated females.

3. Polygynandry

Polygynandry was not studied in this project. There is no evidence to indicate whether it occurs in the wild, although it is possible that Masataka's study group was polygynandrous by the end of his study period (Masataka 1981a, 1981b). Although his second male was not seen mating in the group, he was associating closely with one of the breeding females, while the breeding male was associating more with the other breeding female.

4. Monogamy

Evidence from the captive colonies of *Callimico* has clearly shown that social groups based on monogamy are stable in the long term (Beck *et al.* 1982, Carroll 1982). The results of the present study support this, although there is little evidence of a lasting pair bond within the breeding pair. It is highly likely, therefore, that social groups based on monogamy are stable in the wild as well. This does not, of course, mean that monogamy is necessarily the most frequently encountered mating strategy, but it is likely that, when it arises, it may continue for a long period of time.

The stability and longevity of monogamous groups is likely to depend on the level of immigration into a group. Again, evidence from captive groups suggests that, if a sexually mature male enters a group, daughters as well as the mother would be available as mates (Carroll 1986). If the group remains stable, it may thus become polygynous (if the new male mates with mother and daughters), polyandrous (if both males mate with the mother) or polygynandrous (if both males mate with mother and daughters). Similarly, if a female enters a group, it will be a potential mate for the resident male or for any sexually mature sons within the group, again leading to polygyny or polygynandry. The apparent instability of polygynous groups would suggest that eventually such groups would fragment, perhaps resulting in monogamy once again.

7.9 A comment on the evolution of some reproductive traits in the Callitrichidae and *<u>Callimico</u>*

The marmosets and tamarins and Goeldi's monkeys possess reproductive characteristics that result in their having a relatively high r_{max} for their body weight (a 'fast' life history pattern, Ross 1991). These characteristics include a high birth rate and high growth rate (both gestationally and *post partum)*, and all have the capacity to breed at a relatively early age in comparison to the small cebids. *Callimico* differs from the marmosets and tamarins in having a single infant and perhaps an even earlier age of sexual maturation, but shares other characteristics with them such as shared infant care, relatively small neonates and the reproductive suppression of daughters within natal groups (although not necessarily in peer groups). Ross (1991) argued that the common ancestor of *Callimico* and the marmosets and tamarins had a single infant, that the neonate was small, relative to mother's body size, and that paternal care was already a feature of infant rearing prior to the evolution of twinning. Indeed, since twins are unlikely to survive without extra-maternal care, these features are perhaps <u>necessary</u> precedents to the evolution of twinning in the Callitrichidae.

Ross (1991) also suggested that reproductive suppression of subordinate females would lead to selection for a high birth rate (*i.e.* twins in the Callitrichidae) so that a previously suppressed female can 'make up for lost time' once she starts to breed. In *Callimico*, early reproduction is likely to be important in maintaining a high r_{max} and, hence, there would be less selection pressure for a high birth rate in this species. As stated earlier, however, the removal of reproductive suppression is necessary before a daughter may breed and this is dependent on the migration pattern of *Callimico* in the wild.

7.10 FUTURE STUDY

7.10.1 Future study in the wild

There is no substitute for in-depth, sustained study of social behaviour and social dynamics under natural conditions. That is not to say that study of the species in captivity is not valuable, but rather that a sound knowledge of the natural behaviour of the species is necessary in order to provide a framework for scientific investigation in captivity by testing hypotheses through controlled manipulation of the subject. Interpretation of the present study is hampered by the lack of information from the wild and I would suggest that the following areas of study should be examined as a first step towards addressing this situation:

1. <u>Composition of wild groups</u> - Knowledge of the composition of wild groups is essential in understanding the dynamics of immigration and emigration, and how these affect social behaviour such as infant rearing. While it may be possible to determine the sex ratio of a group through passive observation, it is impossible to

determine the age classes of the group members without close inspection of the genitalia, scent-gland fields, and nipples. It is, therefore, vital that groups be trapped to assess their age-sex composition. Valuable morphometric data could also be taken during such an excercise, and the animals could be permanently marked by tattooing or through the use of subcutaneous microchip transponders. Radio transmitters for telemetry studies could also be fitted at this time if such a study were planned. These devices allow groups to be located rapidly, and hence facilitate habituation of groups to observers. These techniques are being used in the field study of lion tamarins in Brazil and have proved to be invaluable (Kleiman *et al.* 1986).

2. Relatedness within social groups - In order to understand social dynamics of these wild groups, an assessment of relatedness of the group members should be carried out. This could be achieved through DNA studies of blood and tissue samples taken when groups are trapped for marking and age-sex assessment. DNA studies may also allow the level of relatedness between individuals in different groups to be assessed.

3. Stability of wild groups - The long-term stability of wild groups is an important element in comprehending their social and reproductive strategy. While certain information on this can be determined through direct observation of groups, regular trapping of groups (perhaps annually), to determine changes in composition would yield better information over the long term. If the composition of several neighbouring groups has been determined, and the group members marked, the dynamics of immigration and emigration would be better understood, as would the possibilities of group fission as recently observed in *Callithrix flaviceps* (Ferrari 1987).

4. Reproductive suppression in wild groups - Long-term monitoring of known-age individuals will allow an assessment of reproductive suppression within wild groups. It is unlikely, however, that hormonal monitoring of wild females could be carried out, as lengthy series of samples of either blood or urine are needed to assess ovarian cyclicity. If techniques for monitoring hormone levels in faeces were to prove useful in monitoring ovarian cycles in *Callimico*, this technique could

possibly be used in the field. Monitoring of reproductive activity in young females would also provide valuable information on age of first breeding in the wild.

5. Spatial arrangement of social groups and interactions with neighbours - Interaction with neighbouring groups plays an important role in intergroup migration. It is, therefore, important to know the distances between groups, the frequency of interactions between groups and the nature of such interactions. This information could only be obtained through observation of habituated groups.

6. Socioecology of wild groups - Observation of habituated groups is the only way to obtain information on the ecology and social behaviour of the species in the wild. Such observation would give data on the ecological niche of *Callimico*, and niche separation from sympatric primate species, intragroup social dynamics, sexual dimorphism of behaviour, and infant-rearing strategies.

7.10.2 Future study in captivity

There are several areas in which further study of the species in captivity would be valuable. Wild groups cannot easily be examined to determine the reproductive status of females through hormone assay of blood or urine. It is also difficult to manipulate wild groups in order to test hypotheses regarding, for instance, pair bonding, the effect of different social group structures on infant rearing, *etc*. Further captive study would, therefore, be useful in the following areas:

1. Reproductive suppression - The nature of reproductive suppression has not been fully explored in *Callimico*. Considerable scope remains for research into the nature of familial reproductive suppression. Do daughters cycle in their natal groups? Do they cycle if their mother is removed from the group? Do they cycle if an unfamiliar male is housed in proximity to them?

Similarly, further research into reproductive suppression of subordinate females in groups of unrelated animals is necessary to determine whether predictions can be made about the circumstances under which suppression of the subordinate occurs. For instance, relative age of the females may be one such factor, breeding status and length of time cohabiting prior to the introduction of the male may be another.

Lastly, the factors governing the permanence of reproductive suppression should be studied. If a female is removed from her natal group (simulating an emigration) and later meets a brother or her father (simulating a return to her natal group), is that female now a potential breeding partner?

2. Study of ovarian cycles through faecal hormone monitoring - The measurement of levels of steroid hormones in faeces has been found to be useful in indicating ovarian function in some ungulates and studies of faecal hormone levels in at least one primate species are under way (K. Hodges pers. comm.). This technique should be assessed in Goeldi's monkey and the marmosets and tamarins, as it would allow ovarian cycles to be monitored more easily in wild groups.

3. Social bonding in captive groups - The apparent lack of a pair bond between the breeding pair in this captive study was rather surprising. Future research could be designed to test the hypothesis that the pair are faithful to the territory rather than to each other. This could be achieved through intruder studies carried out both in the home cage of the pair, and in an unfamiliar cage. Subjects in an unfamiliar cage can be given a choice between the opportunity of an extra-pair mating and returning to the home cage.

4. The stability of polyandrous social groups - Multi-male social groups of tamarins have been found to be more stable than multi-female groups. Multi-male groups have not been studied in *Callimico*. Are they long-term stable social units? What social relationships are formed in such groups, and do both or all the males mate with the female? If so, do all the males mate during an ovulatory period, and hence have a chance of siring an offspring, and, if so, is it possible to determine the identity of the sire through DNA studies and to relate him to social relationships?

5. The stability of multi-male and multi-female groups based on a kin relationship - This study did not explore polygamy based on kin relationships.

Although anecdotal information suggests that multi-female groups based on kin are no more stable than those with unrelated females, this subject is worthy of further study, particularly in the light of the failure of reproductive suppression when an unfamiliar male is introduced to a sister-sister or mother-daughter dyad. Social relationships within these groups should be studied as well as their duration and long-term stability.

Callimico goeldii is undoubtedly a most important research primate at this time. Continued study of the species will enable further testing of hypotheses relating to infant care and twinning in the small New World monkeys. An understanding of its evolutionary relationship with other platyrrhines will help to elucidate the evolution of parental care patterns and the selective forces behind communal rearing of young. A sound understanding of its socioecology will help to explain its fragmented distribution and low population density. Is this due solely to human-influenced habitat changes, or is the species disadvantaged for other reasons? Is the species in competition, through niche overlap, with sympatric tamarins? The upper Amazon basin is undergoing rapid colonisation by impoverished humans and hence, is facing rapidly changing land use. Past experience has shown that this will lead to a depauperate wildlife community. The *Leontopithecus rosalia* project in south-eastern Brazil has shown that focused attention on a single species may help in the conservation of entire habitats. Similarly, attention focused on Goeldi's monkey will aid its conservation in the wild, the conservation of its natural habitat and, hence, the conservation of the other inhabitants of that habitat.

REFERENCES

ABBOTT, D.H. (1978): The physical, hormonal and behavioural development of the common marmoset *Callithrix jacchus jacchus*. In: Biology and Behaviour of Marmosets, ed. by H. Rothe, H-J Wolters and J.P. Hearn, Eigenverlag Rothe, Göttingen, pp. 99-109.

ABBOTT, D.H. (1984): Behavioural and physiological suppression of fertility in subordinate marmoset monkeys. Amer. J. Primatol. 6: 169-186.

ABBOTT, D.H. (1986): Social suppression of reproduction in subordinate marmoset monkeys (*Callithrix jacchus jacchus*). In: A Primatologia No Brasil Vol 2, ed by M T de Mello, Brasilia, Sociedade Brasiliera de Primatologia, pp. 1-16.

ABBOTT, D.H. (1988): Natural suppression of fertility. Symp. Zool. Soc. Lond. 60:7-28.

ABBOTT, D.H. and HEARN, J.P. (1978): Physical hormonal and behavioural aspects of sexual development in the marmoset monkey, *Callithrix jacchus*. J. Reprod. Fert. 53:155-166.

ABBOTT, D.H., McNEILLY, A.S., LUNN, S.F., HULME, M.J. and BURDEN, F.J. (1981): Inhibition of ovarian function in subordinate female marmoset monkeys (*Callithrix jacchus jacchus*). J. Reprod. Fert. 63:335-345.

ABBOTT, D.H., KEVERNE, E.B., MOORE, G.F. and YODYINGYUAD, U. (1986): Social suppression of reproduction in subordinate talapoin monkeys, *Miopithecus talapoin*. In: Primate Ontogeny, Cognition and Social Behaviour, ed. by J.G. Else and P.C. Lee, Cambridge University Press, Cambridge, pp. 329-341.

ABBOTT, D.H., HODGES, J.K. and GEORGE, L.M. (1988): Social status controls LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). J. Endocr. 117:329-339.

ALLCHURCH, A.F. (1985): Nutritional Handbook: A Collection of all the diets in current use at the Jersey Wildlife Preservation Trust. Jersey Wildlife Preservation Trust, Jersey.

ALTMANN, J. (1974): Observational study of behaviour: sampling methods. Behaviour 49:227-267

ALTMANN, J. (1980): Baboon Mothers and Infants. Harvard University Press, Cambridge, Mass.

ALTMANN, J. (1983): Costs of reproduction in baboons (*Papio cynocephalus*). In: The Cost of Survival in Vertebrates, ed. by W.P. Aspey and S.I. Lustick, Ohio State University Press, Columbus, pp. 67-88.

ALTMANN, J., WARNEKE, M. and RAMER, J., (1988): Twinning among *Callimico goeldii*. Int. J. Primatol. 9:165-168.

ANDO, A., NIGI, H., TANAKA, T. and OHSAWA, N. (1976): Routine measurement of urinary total estrogens of the female Japanese monkey as an index for estimating the time of ovulation. Primates 17:89-94.

ANDREWS, J. (1986): The present status and future management of the Goeldi's monkey (*Callimico goeldii*) in captivity in the British Isles. Discussion papers in conservation 46. University College, London.

ANZENBERGER, G. (1985): How stranger encounters of common marmosets (*Callithrix jacchus jacchus*) are influenced by family members: the quality of behavior. Folia Primatol. 45:204-224.

ANZENBERGER, G. (1988): The pairbond in the titi monkey (*Callicebus moloch*): Intrinsic versus extrinsic contributions of the pairmates. Folia Primatol. 50:188-203.

ANZENBERGER, G., MENDOZA, S.P. and MASON, W.A. (1986): Comparative studies of social behavior in *Callicebus* and *Saimiri*: Behavioral and physiological responses of established pairs to unfamiliar pairs. Amer. J. Primatol. 11:37-51.

BALDWIN, J.D. and BALDWIN, J.I. (1981): The squirrel monkeys, Genus *Saimiri*. In: Ecology and Behaviour of Neotropical Primates Vol. 1, ed by A.F. Coimbra-Filho and R.A. Mittermeier, Academia Brasileira de Ciências, Rio de Janeiro, pp. 277-331.

BECK, B.B., ANDERSON, D., OGDEN, J., RETTBERG, B., BREJLA, C., SCOLA, R., and WARNEKE, M., (1982): Breeding the Goeldi's monkey *Callimico goeldii* at Brookfield Zoo, Chicago. Int. Zoo Yb. 22:106-114.

BONNEY, R.C., DIXSON, A.F., and FLEMING, D. (1979): Cyclic changes in the circulating and urinary levels of ovarian steroids in the adult female owl monkey (*Aotus trivirgatus*). J. Reprod. Fert. 56:271-280

BOX, H.O. (1975): Quantitative studies of behaviour within captive groups of marmoset monkeys (*Callithrix jacchus*). Primates 16:155-174.

BRAND, H.M. (1981): Urinary oestrogen excretion in the female cotton-topped tamarin *Saguinus oedipus oedipus*. J. Reprod. Fert. 62:467-473.

BRAND, H.M. (1984): Reproductive Behaviour and Endocrinology of the Cotton-topped Tamarin *Saguinus oedipus oedipus* (Callitrichidae, Primates). PhD Thesis, University of London.

BRIDGEWATER, D.D. (1972): Saving the Lion Marmoset. The Wild Animal Propagation Trust, Wheeling, West Virginia.

BROWN, J.L. (1987): Helping and Communal Breeding in Birds. Princeton University Press, Princeton, New Jersey.

BUCHANAN-SMITH, H.M. (1989): The Social Organisation and Mating Systems of the Red Bellied Tamarin (*Saguinus labiatus labiatus*): Behavioural Observations in Captivity and in the Field. Ph.D. thesis, University of Reading.

BUCHANAN-SMITH, H.M. (1991): Field observations of Goeldi's monkey, *Callimico goeldii*, in northern Bolivia. Folia Primatol. 57:102-105.

BYRD, K.E. (1981): Sequences of dental ontogeny and callitrichid taxonomy. Primates 22:103-118.

CAMERON, R., WILTSHIRE, C., FOLEY, C., DOUGHERTY, N., ARAMAYO, X. and REA, L. (1987): Bolivia '87 An Oxford University Conservation Project. Final report. Unpubl.

CARROLL, J.B. (1982): Maintenance of the Goeldi's monkey *Callimico goeldii* at Jersey Wildlife Preservation Trust. Int. Zoo Yb. 22:101-105.

CARROLL, J.B. (1985): Pair bonding in Goeldi's monkey *Callimico goeldii* (Thomas, 1904). Dodo, J. Jersey Wildl. Preserv. Trust 22:57-71.

CARROLL, J.B. (1986): Social correlates of reproductive suppression in captive callitrichid family groups. Dodo, J. Jersey Wildl. Preserv. Trust 23:80-85.

CARROLL, J.B. (1988): The stability of multi-female breeding groups of Goeldi's monkey, *Callimico goeldii*, at Jersey Wildlife Preservation Trust. Dodo, J. Jersey Wildl. Preserv. Trust 25:37-43.

CARROLL, J.B. (in press): The captive breeding of the genus *Callithrix* at the Jersey Wildlife Preservation Trust. In: A Primatologia no Brasil Vol. 3.

CARROLL, J.B. and VAARTJES, S. (1989): The British Isles Regional Studbook for Goeldi's monkey *Callimico goeldii* 1989. Jersey Wildlife Preservation Trust, Jersey.

CARROLL, J.B., ABBOTT, D.H., GEORGE, L.M. and MARTIN, R.D. (1989): Aspects of urinary oestrogen excretion during the ovarian cycle and pregnancy in Goeldi's monkey *Callimico goeldii*. Folia Primatol. 52:201-205.

CARROLL, J.B., ABBOTT, D.H., GEORGE, L.M., HINDLE, J.E. and MARTIN, R.D. (1990): Urinary endocrine monitoring of the ovarian cycle and pregnancy in Goeldi's monkey (*Callimico goeldii*). J. Reprod. Fert. 89:149-161.

CHIVERS, D.J. (1972): The siamang and the gibbon in the Malay Peninsula. Gibbon and Siamang 1:103-135.

CHIVERS, D.J. (1974): The siamang in Malaya. Karger, Basel .

CHRISTEN, A., DOBELI, M., KEMPKEN, B., ZACHMANN, M. and MARTIN, R.D. (1989): Urinary excretion of oestradiol-17B in the female cycle of Goeldi's monkey (*Callimico goeldii*). Folia Primatol. 52:191-200.

CHRISTEN, A. and GEISSMAN, T. (1992): Primate survey in northern Bolivia with special reference to Goeldi's monkey, *Callimico goeldii*. In Prep.

CLEVELAND, I and SNOWDON, C.T. (1984): Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus o. oedipus*). Anim. Behav. 32:432-444.

CLUTTON-BROCK T.H. and HARVEY P.H. (1977): Primate ecology and social organisation. J. Zool., Lond., 183:1-39.

COATES A. and POOLE, T.B. (1983): The behaviour of the callitrichid monkey *Saguinus labiatus* in the laboratory. Int. J. Primatol. 4:339-371.

COIMBRA-FILHO, A.F. (1990): Sistemática, distribuição geográfica e situação atual dos símios Brasileiros (Platyrrhini-Primates). Rev. Brasil. Biol., 50(4):1063-1079.

COIMBRA-FILHO, A.F. and MITTERMEIER R.A. (1973): Distribution and ecology of the genus *Leontopithecus* Lesson, 1840 in Brazil. Primates 14:47-66.

CORDS, M. (1984): Mating patterns and social structure in red-tail monkeys (*Cercopithecus ascanius*). Z. Tierpsychol. 64:313-329.

CRONIN, J.E. and SARICH, V.M. (1978): Marmoset evolution: the molecular evidence. Primates Med. 10:12-19.

CRUZ LIMA, E. da (1945): Mammals of Amazonia. Vol. 1, General Introduction and Primates. Belem do Pará, Rio de Janeiro.

CZEKELA, N.M., REICHARD, T. and LASLEY, B.L. (1991): Urinary hormone analysis as a diagnostic tool to evaluate the ovarian function of female gorillas (*Gorilla gorilla*). J. Reprod. Fert. 82:255-261.

DAWSON, G.A. (1977): The composition and stability of social groups of the tamarin, *Saguinus oedipus geoffroyi*, in Panama. In: The Biology and Conservation of the Callitrichidae, ed. by D.G. Kleiman, Smithsonian Institute Press, pp 23-39.

DIXSON, A,F. (1982): Some observations on the reproductive physiology and behaviour of the owl monkey *Aotus trivirgatus* in captivity. Int. Zoo Ybk. 22:115-119.

DIXSON, A.F. (1983): The owl monkey (*Aotus trivirgatus*). In: Reproduction in New World Primates, ed. by J. P. Hearn, Lancaster, International Medical Publishers, pp. 181-215.

DIXSON, A.F., ANZENBERGER, G., MONTEIRO DA CRUZ, M.A.O., PATEL, I. and JEFFREYS, A.J. (1992): DNA fingerprinting of free-ranging groups of common marmosets (*Callithrix jacchus jacchus*) in NE Brazil. In: Paternity in Primates: Genatic Tests and Theories, ed. by R.D. Martin, A.F. Dixson and E.J. Wickings, Karger, Basel, pp. 192-202.

DOLLMAN, G. (1937): Exhibition and remarks upon a series of skins of marmosets and tamarins. Proc. Zool. Soc. Lond. Ser. C, 107:64-65.

DUNBAR, R.I.M. (1988): Primate Social Systems. Croon Helm, London.

DUNBAR, R.I.M. and DUNBAR, P. (1975): Social Dynamics of Gelada Baboons. Karger, Basel.

DUNBAR, R.I.M. and DUNBAR, P. (1980): The pairbond in klipspringer. Anim. Behav. 28:219-229.

DUTRILLAUX, B., LOMBARD, M., CARROLL, J.B. and MARTIN, R.D. (1988): Chromosomal affinities of *Callimico goeldii* (Platyrrhini) and characterization of a Y-autosome translocation in the male. Folia Primatol. 50:230-236.

EASTMAN, S.A.K., MAKAWITI, D.W., COLLINS, W.P. and HODGES, J.K. (1984): Pattern of excretion of urinary steroid metabolites during the ovarian cycle and pregnancy in the marmoset monkey. J. Endocr. 102:19-26.

EGOZCUE, J., PERKINS, E.M. and HAGEMENAS, F. (1968): Chromosomal evolution in marmosets, tamarins and pinchés. Folia Primatol. 9:81-94.

EMLEN, S.T. (1984): Cooperative breeding in birds and mammals. In: Behavioural Ecology: an Evolutionary Approach, 2nd Edition, ed. by J.R. Krebs and N.B. Davies, Blackwell Scientific Publications, Oxford, pp. 305-339.

EMLEN, S.T. and ORING, L.W. (1977): Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

EPPLE, G. (1970): Maintenance, breeding and development of marmoset monkeys, Callithricidae, in captivity. Folia Primatol. 12:56-76.

EPPLE, G. (1972a): Social communication by olfactory signal in marmosets. Int. Zoo Yb. 12:36-42.

EPPLE, G. (1972b): Social behaviour of laboratory groups of *Saguinus fuscicollis*. In: Saving the Lion Marmoset, ed. by D.D. Bridgewater, Wild Animal Propagation Trust, Wheeling, Minnesota, pp. 50-58.

EPPLE, G. (1975): The behaviour of marmoset monkeys (Callitrichidae). Primate Behaviour 4:195-239.

EPPLE, G. (1977): Notes on the establishment and maintenance of the pair bond in *Saguinus fuscicollis*. In: The Biology and Conservation of the Callitrichidae, ed. by D.G. Kleiman, Smithsonian Institute Press, pp. 231-237.

EPPLE, G. (1978): Overt aggression and scentmarking behaviour in *Saguinus fuscicollis*: the effects of castration in adulthood. A brief report. In: Biology and Behaviour of Marmosets, ed. by H. Rothe, H-J. Wolters and J.P. Hearn, Eigenverlag Rothe, Gottingen, pp. 191-197.

EPPLE, G. (1981): Effect of Pair-bonding with adults on the ontogenetic manifestation of aggressive behavior in a primate *Saguinus fuscicollis*. Behav. Ecol. Sociobiol. 8:117-123.

EPPLE, G. (1986): Comunication by chemical signals. In: Comparative Primate Biology, Conservation and Ecology Vol. 2, ed. by G. Mitchell and J. Erwin, Alan Liss Inc. New York, pp. 531-580.

EPPLE, G. and LORENZ, R. (1967): Vorkommen, Morphologie und Function der Sternaldrüse bei den Platyrrhini. Folia Primatol. 7:98-126.

EPPLE, G. and KATZ, Y. (1984): Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus fuscicollis*). Amer. J. Primatol. 23:87-98.

EPPLE, G., BELCHER, A.M., GREENFIELD, K.L., SCOLNICK, L., SMITH, A.B., KUDERLING, I. and ZELLER, U. (1987): Making sense out of scents: species differences in scent glands, scent marking behavior and scent mark composition in the Callitrichidae. Int. J. Primatol. 8:434 (Abstract only).

EVANS, S. (1981).Monogamy in the Common Marmoset. PhD Thesis, University of Wales.

EVANS, S. (1983): The pair bond of the common marmoset, *Callithrix jacchus jacchus*: An experimental investigation. Anim. Behav. 31:651-658.

EVANS, S. and POOLE, T.B. (1983): Pair bond formation and breeding success in the common marmoset *Callithrix jacchus jacchus*. Int. J. Primatol. 4:83-97.

EVANS, S. and POOLE, T.B. (1984): Longterm changes and maintenance of the pair bond in common marmosets *Callithrix jacchus jacchus*. Folia Primatol. 42:33-41.

FAIRBANKS, L.A. (1990): Reciprocal benefits of allomothering for female vervet monkeys. Anim. Behav. 40:553-562.

FEISTNER, A.T.C. and PRICE, E.C. (1990): Food-sharing in cotton-top tamarins *(Saguinus oedipus)*. Folia Primatol. 54:34-45.

FEISTNER, A.T.C. and PRICE, E.C. (1991): Food offering in New World primates: Two species added. Folia Primatol. 57:165-168.

FERRARI, S.F. (1987): Social organisation and behaviour of the marmoset *Callithrix flaviceps*. Int. J. Primatol. 8(5):492 (Abstract only).

FERRARI, S.F. and LOPES FERRARI, M.A. (1989): A re-evaluation of the social organisation of the Callitrichidae, with reference to the ecological differences between genera. Folia Primatol. 52:132-147.

FORD, S.M. (1980): Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. Primates 21(1):31-43.

FORD, S.M. (1986): Comment on the evolution of claw-like nails in callitrichids (marmosets/tamarins). Amer. J. Phys. Anthrop. 70:25-26

FRAGASZY, D.M., SCHWARZ, S. and SHIMOSAKA, D. (1982): Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). Amer. J. Primatol. 2:191-200.

FRENCH, J.A. and CLEVELAND, J. (1984): Scent marking in the tamarin, *Saguinus oedipus*: Sex differences and ontogeny. Anim. Behav. 32:615-623.

FRENCH, J.A. and SNOWDON, C.T. (1981): Sexual dimorphism in responses to unfamiliar intruders in the tamarin *Saguinus oedipus*. Anim. Behav. 29:822-829.

FRENCH, J.A. and STRIBLEY, J.A. (1985): Patterns of urinary oestrogen excretion in female golden lion tamarins (*Leontopithecus rosalia*). J. Reprod. Fert. 75:537-546.

FRENCH, J.A. and STRIBLEY, J.A. (1987): Synchronisation of ovarian cycles within and between social groups in golden lion tamarins (*Leontopithecus rosalia*). Amer. J. Primatol. 12:469-478.

FRENCH, J.A. and STRIBLEY, J.A. (in press). The reproductive endocrinology and behaviour of the golden lion tamarin. In: A Case Study in Conservation: The Golden Lion Tamarin Ed. by D.G. Kleiman. Smithsonian Institution Press, Washington D.C.

FRENCH, J.A., ABBOTT, D.H., SCHEFFLER, G, ROBINSON, J.A. and GOY, R.W. (1983): Cyclic excretion of urinary oestrogens in female tamarins (*Saguinus oedipus*) J. Reprod. Fert. 67:177-184.

FRENCH, J.A., ABBOTT, D.H. and SNOWDON, C.S., (1984): The effect of social environment on oestrogen excretion, scent marking and sociosexual behaviour in tamarins (*Saguinus oedipus*). Amer. J. Primatol. 6:155-167.

FRENCH, J.A., INGLETT, B.J. and DETHLEFS, T.M. (1989): The reproductive status of non-breeding group members in captive golden lion tamarin social groups. Amer. J. Primatol. 18:73-86.

GARBER, P.A., MOYA, L. and MALAGA, C. (1984): A preliminary field study of the moustached tamarin *Saguinus mystax* in north-eastern Peru. Folia Primatol. 42:17-32.

GOELDI, E.A. and HAGMANN, G. (1904): Prodromo de um catalogo da colleccao de mammiferos no museu do Para (1894-1903). Bol. Mus. Goeldi Hist. Nat. Ethn. 4(1):35-106.

GOLDIZEN, A.W. (1987a): Facultative polyandry and the role of infant carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). Behav. Ecol. Sociobiol. 20:99-109.

GOLDIZEN, A.W. (1987b): Tamarins and marmosets: Communal care of offspring. In: Primate Societies, ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, T.T. Struhsaker, University of Chicago Press, Chicago, pp. 34-43.

GOLDIZEN, A.W. (1988): Tamarin and marmoset mating systems: Unusual flexibility. Trends Ecol. Evol. 3:36-40.

GOLDIZEN, A.W. (1989): Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). Behav. Ecol. Sociobiol. 24:79-89.

GOLDIZEN, A.W. (1990): A comparative perspective on the evolution of tamarin and marmoset social systems. Int. J. Primatol. 11(1):63-83.

GOLDIZEN, A.W. and TERBORGH, J. (1986): Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). In: Primate Ecology and Conservation, ed. by J. Else and P. Lee, Cambridge University Press, London, pp. 191-198.

GOLDIZEN, A.W. and TERBORGH, J. (1989): Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. Amer. Nat. 134:208-224.

GOODALL, J. (1971): In the Shadow of Man. Collins, London.

HAMILTON, W.D. (1964): The genetical evolution of social behaviour. J. Theor. Biol. 7:1-52.

HARCOURT, A.H. (1979): Social relationships among female mountain gorillas. Anim. Behav. 27:251-274

HARLOW, C.R., HULME, M.J., LUNN, S.F., HENDERSON, C. and AITKEN, J. (1983): The relationship between plasma progesterone and the timing of ovulation and early embryonic development in the marmoset monkey. J. Zool. (London) 201:273-282.

HARRINGTON, F.H., MECH, L.D. and FRITTES, S.H. (1983): Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav. Ecol. Sociobiol. 13:19-26.

HARVEY, P.H. and MACE, G.M. (1984): Comparisons between taxa and adaptive trends: a problem of methodology. In: Current Trends in Sociobiology, ed. by Kings College Sociobiology Group, Cambridge University Press, Cambridge, UK, pp. 343-361.

HARVEY, P.H. and CLUTTON-BROCK, T.H. (1985): Life-history variation in primates. Evolution, Lawrence, Kans. 39:559-581.

HARVEY, P.H., MARTIN, R.D. and CLUTTON-BROCK, T.H. (1987): Life histories in comparative perspective. In: Primate Societies. ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, The University of Chicago Press, Chicago and London, pp. 181-197.

HAWKINS, R.A. and OAKEY, R.E. (1974): Estimation of oestrone sulphate, oestradiol-17β and oestrone in peripheral plasma: concentrations during the menstrual cycle and in men. J. Endocr. 60:3-17.

HEARN, J.P. (1978): Fertility and infertility in the marmoset monkey *Callithrix jacchus*. In: Biology and Behaviour of Marmosets. ed. by H. Rothe, H-J. Wolters and J.P. Hearn, Eigenverlag Rothe, Gottingen, pp. 59-67.

HEARN, J.P. and LUNN, S.F. (1975): The reproductive biology of the marmoset monkey, *Callithrix jacchus*. In Breeding Simians for Developmental Biology. Laboratory Animal Handbooks 6. Ed by F.T. Perkins and P.N. O'Donoghue, pp.191-203.

HEINEMANN, H. (1970): The breeding and maintenance of captive Goeldi's monkeys *Callimico goeldii*. Int. Zoo Yb. 10:72-78.

HEISTERMANN, M., PRÖVE, E., WOLTERS, H-J. and MIKA, G. (1987): Urinary oestrogen and progesterone excretion before and during pregnancy in a pied bare-face tamarin (*Saguinus bicolor bicolor*). J. Reprod Fert. 80:635-640.

HEISTERMANN, M., KLEIS, E., PRÖVE, E. and WOLTERS, H-J. (1989): Fertility status, dominance, and scent marking behavior of family-housed cotton-top tamarins (*Saguinus oedipus*) in absence of their mothers. Amer. J. Primatol. 18:177-189.

HELTNE, P.G., TURNER, D.C. and WOLHANDLER, J. (1973): Maternal and paternal periods in the development of infant *Callimico goeldii*. Amer. J. Phys. Anthrop. 38:555-560.

HELTNE, P.G., WOJCIK, J.F. and POOK, A.G. (1981): Goeldi's monkey, Genus *Callimico*. In: Ecology and Behaviour of Neotropical Primates Vol. 1, 169-209, ed. by A.F.Coimbra-Filho and R.A. Mittermeier, Academia Brasileira de Ciencias, Rio de Janeiro.

HERNANDEZ-CAMACHO, J. and COOPER, R.W. (1976): The non-human primates of Colombia. In: Neotropical Primates, 35-69, ed. by R.W. Thorington jr. and P.G. Heltne, National Academy of Sciences, Washington D.C..

HERSHKOVITZ, P. (1977): Living New World Monkeys (Platyrrhini) Vol 1, University of Chicago Press.

HEYMANN, E.W., ZELLER, U. and SCHWIBBE, M.H. (1989): Muzzle rubbing in the moustached tamarin *Saguinus mystax* (Primates:Callitrichidae) - behavioural and histological aspects. Z. Saugetierkunde 54:265-275.

HICK, U. (1968): Erstmalig gelungene Zucht eines Bartsakis Vater:Rotrückensaki, *Chiropotes chiropotes* (Humboldt, 1811), Mutter: Weissnasensaki, *Chiropotes albinasus*(Geoffroy et Deville 1848) im Kölner Zoo. Freunde des Kölner Zoo, 11(2):35-41.

HIDDLESTON, W.A. (1977): The production of the common marmoset *Callithrix jacchus* as a laboratory animal. Unpublished.

HILL, W.C.O. (1959: The anatomy of *Callimico goeldii* (Thomas), a primitive American primate. Trans. Amer. Philos. Soc. 49:1-116.

HILL, W.C.O. (1966): On the neonatus of *Callimico goeldii* (Thomas). Proc. Roy. Soc. Edinburgh, ser. B, 69:321-33.

HINDE, R.A. (1982): Ethology: Its Nature and Relations with other Sciences. Fontana Paperbacks, William Collins, Glasgow.

HINDE, R.A. and SPENCER-BOOTH, Y. (1967): The behaviour of socially living rhesus monkeys in their first two and a half years. Anim. Behav. 15:169-196.

HINDE, R.A. and ATKINSON, S. (1970): Assessing the roles of social partners in maintaining mutual proximity as exemplified by mother-infant relations in rhesus monkeys. Anim. Behav. 18:169-176.

HOAGE, R.J. (1977): Parental care in *Leontopithecus rosalia rosalia*: Sex and age differences in carrying behavior and the role of prior experience. In: The Biology and Conservation of the Callitrichidae, ed. by D.G. Kleiman, Smithsonian Institution Press, Washington D.C., pp. 293-306.

HOAGE, R.J. (1982): Social and physical maturation in captive lion tamarins, *Leontopithecus rosalia rosalia* (Primates: Callitrichidae). Smithson. Contrib. Zool. 354:1-56.

HODGES, J.K., and EASTMAN, S.A.K. (1984): Monitoring ovarian function in marmosets and tamarins by the measurement of urinary estrogen metabolites. Amer. J. Primatol. 6:187-197.

HODGES, J.K., CZEKELA, N.M., and LASLEY, B.L. (1979): Estrogen and luteinising hormone secretion in diverse primate species from simplified urinary analysis. J. Med. Primatol. 8:349-364.

HODGES, J.K., GULICK, B.A., CZEKELA, N.M. and LASLEY, B.L. (1981): Comparison of urinary oestrogen excretion in South American primates. J. Reprod. Fert. 61:83-90.

HODGES, J.K., BRAND, H.M., HENDERSON, C., and KELLEY, R.W. (1983): The levels of circulating and urinary oestrogens during pregnancy in the marmoset monkey (*Callithrix jacchus*). J. Reprod. Fert. 67:73-82.

HODGES, J.K., BEVAN, D.J., CELMA, M. HEARN, J.P., JONES, D.M., KLEIMAN, D.G. KNIGHT, J.A., and MOORE, H.D.M. (1984): Aspects of the reproductive endocrinology of the female giant panda (*Ailuropoda melanoleuca*) in captivity with special reference to the detection of ovulation and pregnancy. J. Zool. Lond. 203:253-267.

HUBRECHT, R.C. (1984): Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*) at Tapacura, Brazil. Primates 25:13-21.

HUBRECHT, R.A. (1985): Home range size, use and territorial behaviour in the common marmoset *Callithrix jacchus jacchus* at the Tapacura field station, Recife, Brazil. Int. J. Primatol. 6:533-549.

HUBRECHT, R.C. (1989): The fertility of daughters in common marmoset (*Callithrix jacchus jacchus*) family groups. Primates 30:423-432.

IMMELMANN, K. (1980): Introduction to Ethology. Plenum Press, New York.

INGRAM, J.I. (1977): Interactions between parents and infants, and the development of independence in the common marmoset (*Callithrix jacchus*). Anim. Behav. 25:811-824.

IUCN (1990): IUCN Red List of Threatened Animals. IUCN, Gland, Switzerland and Cambridge, UK.

IZAWA, K. (1979): Studies on peculiar distribution pattern of *Callimico*. Kyoto Univ. Overseas Res. Rep. New World Monkeys, 1979:1-19.

KINGSLEY, S. (1980): Reproductive Physiology and Behaviour of captive Orangutans (*Pongo pygmaeus*). PhD Dissertation, University of London.

KINGSTON, W.R (1969): Marmosets and tamarins. Lab. Anim. Handb., 4:243-250.

KINGSTON, W.R. (1975): The breeding of endangered species of marmosets and tamarins. In: Breeding Endangered Species in Captivity, ed. by R.D. Martin, Academic Press, London, pp. 213-222.

KINZEY, W.G. (1981): The titi monkeys, Genus *Callicebus*. In: Ecology and Behaviour of Neotropical Primates Vol. 1, ed. by A.F. Coimbra-Filho and R.A. Mittermeier, Academia Brasiliera de Ciencias, Rio de Janeiro, pp. 241-177.

KINZEY, W.G. and WRIGHT, P.C. (1982): Grooming behaviour in the titi monkey (*Callicebus torquatus*). Amer. J. Primatol. 3:267-275.

KIRKWOOD, J.K. and UNDERWOOD, S.J. (1984): Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). Folia Primatol. 42:180-187.

KLEIMAN, D.G. (1977): Monogamy in mammals. Quart. Rev. Biol. 52:39-69.

KLEIMAN, D.G. (1978): The development of pair preferences in the lion tamarin (*Leontopithecus rosalia*): male competition or female choice? In: Biology and Behaviour of Marmosets, ed. by H. Rothe, H.J. Wolters and J.P. Hearn. Eigenverlag Rothe, Göttingen, W. Germany, pp. 203-208.

KLEIMAN, D.G. (1979): Parent-offspring conflict and sibling competition in a monogamous primate. Amer. Nat. 114:753-760.

KLEIMAN, D.G. (1981): Correlations among life history characteristics of mammalian species exhibitting two extreme forms of monogamy. In: Natural Selection and Social Behavior, ed. by R.D. Alexander and D.W. Tinkle, Chiron Press, New York, pp. 332-344.

KLEIMAN D.G. and MACK, D.S. (1977): A peak in sexual activity during mid pregnancy in the golden lion tamarin, *Leontopithecus rosalia* (Primates: Callitrichidae). J. Mamm. 58(4):657-660.

KLEIMAN, D.G., HOAGE, R.J. and GREEN, K.M. (1988): The lion tamarins, genus *Leontopithecus*. In: Ecology and Behavior of Neotropical Primates Vol. 2, ed. by R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho and G.A.B. Fonseca, World Wildlife Fund, Washington D.C., pp.299-347.

KLEIMAN, D.G., BECK, B.B., DIETZ, J.M., DIETZ, L.A., BALLOU, J.D. and COMBRA-FILHO, A.F. (1986): Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies and reintroduction. In: Primates The Road To Self-Sustaining Populations, ed. by K. Benirschke, Springer-Verlag, New York, pp. 959-979.

KUMMER, H. (1978): On the value of social relationships to non-human primates: A hueristic scheme. Soc. Sci. Info. 17(4/5):687-705.

KURODA, S. (1980): Social behaviour of the pygmy chimpanzees. Primates 21:181-197.

LACK, D. (1968): Ecological Adaptations for Breeding in Birds. Methuen & Co., London.

LASLEY, B.L., MONFORT, S.L., HODGES, J.K., CZEKELA, N.M. (1981): Comparison of urinary estrogens during pregnancy in diverse (primate) species. In: Fetal Endocrinology, Proceedings 1st Oregon Regional Primate Center Symposium on Reproductive Biology. Academic Press, New York, pp. 111-126.

LEE, P.C. (1989): Family structure, communal care and female reproductive effort. In: Comparative Socioecology, ed. by V. Standen and R.A. Foley, Blackwell Scientific, Oxford, pp. 323-340.

LEE, P.C., MAJLUF, P. and GORDON, I.J. (1991): Growth, weaning and maternal investment from a comparative perspective. J. Zool., Lond 225:99-114.

LEUTENEGGER, W. (1973): Maternal-fetal weight relationships in primates. Folia Primatol. 20:280-293.

LEUTENEGGER, W. (1980): Monogamy in callitrichids: A consequence of phyletic dwarfism? Int. J. Primatol. 1(1): 95-98.

LINDSAY, N.B.D. (1979): A report on the field study of Geoffroy's tamarin, *Saguinus oedipus geoffroyi*. Dodo, J. Jersey Wildl. Preserv. Trust 16:27-52.

LORENZ, K. (1970): Studies in Animal Behaviour, Vol. 1.

LORENZ, R. (1969): Notes on the care, diet and feeding habits of Goeldi's monkey. Int. Zoo. Yb. 9:150-155.

LORENZ, R. (1970): Second generation bred in Goeldi's monkey, *Callimico goeldii*, Callimiconidae, Primates. Int. Zoo News 17:79-80.

LORENZ, R. (1971): Goeldi's monkey *Callimico goeldii* Thomas 1904 preying on snakes. Folia Primatol. 15:133-142.

LORENZ, R. (1972): Management and reproduction of the Goeldi's monkey *Callimico goeldii* (Thomas 1904), Callimiconidae, Primates. In: Saving the Lion Marmoset, ed. by D.D. Bridgewater, Wild Animal Propagation Trust, Wheeling, W. Virginia, pp. 92-109.

LUCKETT, W.P. (1974): The comparative development and evolution of the placenta in primates. Contrib. Primatol. 3:142-234.

LUNN, S.F. (1978): Urinary oestrogen excretion in the common marmoset, *Callithrix jacchus*. In: Biology and Behaviour of Marmosets, ed. by H. Rothe, H-J. Wolters and J.P. Hearn, Eigenverlag Rothe, Gottingen, pp. 67-93.

LYON, M., GOLDMAN, L. and HOAGE, R. (1985): Parent-offspring conflict following a birth in the primate *Callimico goeldii*. Anim. Behav. 33:1364-1365.

MALLINSON, J.J.C. (1975a): Breeding marmosets in captivity. In: Breeding Endangered Species in Captivity, ed. by R.D. Martin, Academic Press, London, pp. 203-212.

MALLINSON, J.J.C. (1975b): The design of two marmoset complexes at the Jersey Zoological Park. JWPT Twelfth Annual Report 12:21-26.

MARTIN, R.D. (1990): Primate Origins and Evolution, A phylogenetic reconstruction. Chapman and Hall, London.

MARTIN, R.D. (1992): Goeldi and the dwarfs: the evolutionary biology of the small New World monkeys. J. Human Evol. 22:367-393.

MARTIN, R.D. (1992a): Female cycles in relation to paternity in primate societies. In: Paternity in Primates: Genetic Tests and Theories, ed. by R.D. Martin, A.F. Dixson and E.J. Wickings, Karger, Basel, pp. 238-274.

MARTIN, R.D. and BARBOUR, A.D. (1989): Aspects of line fitting in bivariate analyses. Folia Primatol. 53:65-81.

MARTIN, R.D., SEATON, B. and LUSTY, J.A. (1975): Application of urinary hormone determinations in the management of gorillas. Jersey Wildl. Pres. Trust, Ann. Rep. 12:61-70.

MASATAKA, N. (1981a): A field study of the social behaviour of Goeldi's monkeys (*Callimico goeldii*) in north Bolivia. I. Group composition, breeding cycle and infant development. Kyoto Univ. Overseas Res. Rep. New World Monkeys II:23-32

MASATAKA, N. (1981b): A field study of the social behaviour of Goeldi's monkeys (*Callimico goeldii*) in north Bolivia. II. Grouping pattern and intragroup relationship. Kyoto Univ. Overseas Res. Rep. New World Monkeys II:33-41.

MASATAKA, N. (1982): A field study on the vocalisations of Goeldi's monkey *Callimico goeldii*. Primates 23(2):206-219.

MASATAKA, N. (1983): Categorical responses to natural and synthesised alarm call in Goeldi's monkeys (*Callimico goeldii*). Primates 24:40-51.

MASON, W.A. (1971): Field and laboratory studies of social organisation in *Saimiri* and *Callicebus*. Prim. Behav. 2:107-138.

MASON, W.A. (1974): Comparative studies of social behavior in *Callicebus* and *Saimiri*: Behavior of male-female pairs. Folia Primatol. 22:1-8.

MASON, W.A. (1975): Comparative studies of social behavior in *Callicebus* and *Saimiri*: strength and specificity of social attraction between male-female cagemates. Folia Primatol. 23:113-123.

MASTERS, A.M. and MARKHAM, R.J. (1991): Assessing reproductive status in orang-utans by using urinary estrone. Zoo Biol. 10:197-207.

McGREW, W.C. and McLUCKIE, E.C. (1986): Philopatry and dispersion in the cotton-top tamarins *Saguinus (o.) oedipus*: an attempted laboratory simulation. Int. J. Primatol. 7:399-420.

MELNICK, D.J. and PEARL, M.C. (1987): Cercopithecines in multimale groups: genetic diversity and population structure. In: Primate Societies, ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, University of Chicago Press, Chicago and London, pp. 121-135.

MENDOZA, S.P. and MASON, W.A. (1986): Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). Anim. Behav. 34:1336-1347.

MIRANDA RIBEIRO, A. de, (1912): Zwei neue Affen unsere Fauna. Brasilianische Rundschau 2(1):21-23.

MIRANDA RIBEIRO, A. de, (1941): Commentaries on South American Primates. Mem. Inst. Oswaldo Cruz 35(4):779-851.

MITTERMEIER, R.A., RYLANDS, A.B. and COIMBRA-FILHO, A.F. (1988): Systematics: species and subspecies - an update. In: Ecology and Behavior of Neotropical Primates, Volume 2. Ed. by R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho and G.A.B. Fonseca. World Wildlife Fund, Washington D.C., pp 13-75.

MOEHLMAN P.D. (1979): Jackel helpers and pup survival. Nature 227:382-383.

MOYNIHAN, M. (1976): The New World Primates. Princeton University Press, Princeton, New Jersey.

NAGLE, C.A., DENARI, J.H., QUIROGA, S., RIARTE, A., MERLO, A., GERMINO, N.I., GOMEZ-ARGANA, F. and ROSNER, J.M. (1979): The plasma pattern of ovarian steroids during the menstrual cycle in capuchin monkeys (*Cebus apella*). Biol. Reprod. 21:979-983.

NAPIER, J.R. and NAPIER, P.H. (1967): A Handbook of Living Primates. Academic Press, London.

NEVILLE, M., CASTRO, N., MARMOL, A. and REVILLA, J. (1976): Censusing primate populations in the reserved area of the Pacaya and Samiria rivers, Department Loreto, Peru. Primates 17:151-181.

NEYMAN, P. (1977): Aspects of the ecology and social organisation of free ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Biology and Conservation of the Callitrichidae, ed. by D.G. Kleiman. Smithsonian Institute Press, Washington D.C., pp. 39-73.

NISHIMURA, A., FONSECA, G.A.B., MITTERMEIER, R.A., YOUNG, A.L., STRIER, K.B. and VALLE, C.M.C. (1988): The muriqui, Genus *Brachyteles*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. Fonseca, World Wildlife Fund, Washington D. C., pp. 577-610.

OLIVER, W.L.R. (1983): A behavioural research unit; the concept and design of a new observational research facility at the Jersey Wildlife Preservation Trust. Dodo, J. Jersey Wildl. Preserv. Trust 20:79-90.

OMEDES, A. and CARROLL, J.B. (1980): A comparative study of pair behaviour of four callitrichid species and the Goeldi's monkey *Callimico goeldii* at Jersey Wildlife Preservation Trust. Dodo J. Jersey Wildl. Preserv. Trust 17:51-62.

ORIANS, G.H. (1969): On the evolution of mating systems in birds and mammals. The American Naturalist. 103:589-603.

PARKER, G.A. (1974): Courtship persistence and female-guarding as male time investment strategies. Behaviour 48:157-84.

POCOCK, R.I. (1917): The genera of Hapalidae (Marmosets). Ann. Mag. Nat. Hist., ser.8, 20:247-258.

POCOCK, R.I. (1920): On the external characters of the South American monkeys. Proc. Zool. Soc. Lond. 1920:91-113.

POCOCK, R.I. (1925): Additional notes on the external characters of some platyrrhine monkeys. Proc. Zool. Soc. Lond. 1925:27-47.

POOK, A.G. (1975): Breeding Goeldi's monkey (*Callimico goeldii*) at the Jersey Zoological Park. JWPT Twelth Ann. Rep. 12:17-20.

POOK, A.G. (1978): A comparison between the reproduction and parental behaviour of the Goeldi's monkey (*Callimico goeldii*) and of the true marmosets (Callitrichidae). In: Biology and Behaviour of Marmosets ed. by H. Rothe, H-J Wolters and J.P. Hearn, Göttingen, W. Germany, pp. 1-14.

POOK, A.G. and POOK, G. (1979a): A field study on the status and socioecology of the Goeldi's monkey (*Callimico goeldii*) and other primates in northern Bolivia. Unpublished report to the New York Zoological Society.

POOK, A.G. and POOK, G. (1979b): The conservation status of the Goeldi's monkey *Callimico goeldii* in Bolivia. Dodo. J. Jersey Wildl. Preserv. Trust 16:40-45.

POOK, A.G. and POOK, G. (1981): A field study of the socio-ecology of the Goeldi's monkey (*Callimico goeldii*) in northern Bolivia. Folia Primatol. 35:288-312.

POOLE, T.B. (1978): A behavioural investigation of 'pair bond' maintenance in *Callithrix jacchus jacchus*. In: Biology and Behaviour of Marmosets ed. by H. Rothe, H-J Wolters and J.P. Hearn, Göttingen, W. Germany, pp. 209-216.

POOLE, T.B. (1985): Social Behaviour in Mammals. Blackie, Glasgow and London, UK.

PRICE, E.C. (1990): Reproductive strategies of cotton-top tamarins. Unpublished Ph.D. Thesis, University of Sterling.

PRICE, E.C. and McGREW W.C. (1991): Departures from monogamy in colonies of captive cotton-top tamarins. Folia primatol 57:16-27.

PRYCE, C.R. (1988): Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. Anim. Behav. 36:1455-1464.

PRYCE, C.R., ABBOTT, D.H., HODGES, J.K. and MARTIN, R.D. (1988): Maternal behaviour is related to prepartum urinary oestradiol levels in red-bellied tamarin monkeys. Physiol. Behav. 44:717-726.

RALLS, K. and BALLOU, J. (1982): Effects of inbreeding on infant mortality in captive primates. Int. J. Primatol. 3:491-505.

RAMIREZ, M. (1988): The woolly monkeys, Genus *Lagothrix*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho and G.A.B. Fonseca, World Wildlife Fund, Washington D. C., pp. 539-575.

REMANE, A. (1956): Paläontologie und Evolution der Primaten. In: Primatologie, ed. by H. Hofer, A.H. Shultz and D. Starck. Karger, Basel, pp. 267-378.

RETTBERG, B. (1986): *Callimico goeldii*: 1983 International Studbook. Chicago Zoological Society, Chicago.

ROBINSON, J.G. and JANSON, C.H. (1987): Capuchins, squirrel monkeys and atelines: Socioecological convergence with Old World Primates. In: Primate Societies, ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, University of Chicago Press, Chicago and London, pp. 69-83.

ROOSMALEN, M.G.M. van and KLEIN, L.L. (1988): The spider monkeys, Genus *Ateles*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R. A. Mittermeier, A.B. Rylands, A. F. Coimbra-Filho and G. A. B. Fonseca, World Wildlife Fund, Washington D. C., pp. 455-537.

ROSENBERGER, A.L. (1977): *Xenothrix* and ceboid phylogeny. J. Human Evol. 6:461-481.

ROSS, C. (1988): The intrinsic rate of natural increase and reproductive effort in primates. J. Zool., Lond. 214:199-219.

ROSS, C. (1991): Life history patterns of New World monkeys. Int. J. Primatol. 12:481-502.

ROTHE, H. and KÖNIG, A. (1987): Polygynes verhaltenin einer Weissbüschelaffengruppe (*Callithrix jacchus*). Zoologischer Garten 57:368-369.

ROTHE, H. and KÖNIG, A. (1991): Variability of social organisation in captive common marmosets (*Callthrix jacchus*). Folia Primatol. 57:28-33.

RYLANDS, A.B. (1981): Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Arapuana, Mato Grosso. Primates 22:46-59.

RYLANDS, A.B. (1986): Infant carrying in a wild marmoset group *Callithrix humeralifer*: Evidence for a polyandrous mating system. In: A Primatologia no Brasil 2, ed. by M. T. de Mello, Sociadade Brasileira de Primatologia, Brasilia, pp. 131-145.

SAVAGE, A., ZIEGLER, T.E. and SNOWDON, C.T. (1988): Sociosexual development, pair bond formation, and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus oedipus*). Amer. J. Primatol. 14:345-359.

SCANLON, C.E., CHALMERS, N.R. and da CRUZ, M.A.O.M. (1988): Changes in the size, composition, and reproductive condition of wild marmoset groups (*Callithrix jacchus jacchus*) in North East Brazil. Primates 29:295-305.

SCHEFFRAHN, W. and GLASER, D. (1977): Polymorphism and formal genetics of transferrins in *Saguinus midas tamarin*, Link, 1795. J. Human Evol. 6:605-608.

SEUÁNEZ, H.N., FORMAN, L., MATAYOSHI, T., and FANNING, T.G. (1989): The *Callimico goeldii* (Primates, Platyrrhini) genome: Karyology and middle DNA repetitive (LINE-1) DNA sequences. Chromosoma 98:389-395.

SIEGAL, S. (1956): Non parametric statistics for the behavioural sciences. McGraw-Hill, London.

SIMPSON, G.G. (1945): The principles of classification and a classification of mammals. Bull. Am. Mus. nat. Hist. 85:1-350.

SNOWDON, C.T. and SOINI, P. (1988): The tamarins, Genus *Saguinus*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R. A. Mittermeier, A.B. Rylands, A. F. Coimbra-Filho and G. A. B. Fonseca, World Wildlife Fund, Washington D. C., pp. 223-298.

SOINI, P. (1988): The pygmy marmoset, Genus *Cebuella*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R. A. Mittermeier, A.B. Rylands, A. F. Coimbra-Filho and G. A. B. Fonseca, World Wildlife Fund, Washington D. C., pp. 79-129.

SOINI, P. and SOINI, M. (1982): Distribución geográfica y ecología poblacional de *Saguinus mystax* (Primates, Callitrichidae). Informe de Pacaya No 6 Ordeloreto, DRA/DFF, Iquitos, Peru.

SOKAL, R.R. and ROHLF, F.J. (1981): Biometry, 2nd Edition. W.H. Freeman & Co, San Francisco.

STEARNS, S.C. (1976): Life history tactics: a review of the ideas. Q. Rev. Biol. 51:3-47.

STEVENSON, M.F. and POOLE, T.B. (1976): An ethogram of the common marmoset (*Callithrix jacchus jacchus*): general behavioural repertoire. Anim. Behav. 24:228-235.

STEVENSON, M.F. and RYLANDS A.B. (1988): The marmosets, genus *Callithrix*. In: Ecology and Behaviour of Neotropical Primates Vol.2, ed. by R. A. Mittermeier, A.B. Rylands, A. F. Coimbra-Filho and G. A. B. Fonseca, World Wildlife Fund, Washington D. C., pp. 131-222.

STEWART, K.J. and HARCOURT, A.H. (1987): Gorillas: variation in female relationships. In: Primate Societies, ed. by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, University of Chicago Press, Chicago and London, pp. 155-165.

STRIBLEY, J.A., FRENCH, J.A. and INGLETT, B.J. (1987): Mating patterns in the golden lion tamarin (*Leontopithecus rosalia*): Continuous receptivity and concealed oestrus. Folia Primatol. 49:137-150.

STRUHSAKER, T.T. (1975): The Red Colobus Monkey. University of Chicago Press, Chicago.

SUSSMAN, R.W. and GARBER, P.A. (1987): A new interpretation of the social organisation and mating system of the Callitrichidae. Int. J. Primatol. 8(1):73-92.

SUSSMAN, R.W. and KINZEY, W.G. (1984): The ecological role of the Callitrichidae: A review. Amer. J. Phys. Anthrop. 64:419-449.

SUTCLIFFE, A.G. and POOLE, T.B. (1978): Scent marking and associated behaviour in captive common marmosets (*Callithrix jacchus jacchus*) with a descripition of the histology of scent glands. J. Zool. Lond. 185:41-56.

SZALAY, F.S. and DELSON, E. (1979): Evolutionary History of the Primates. Academic Press, New York.

TARDIFF, S.D., RICHTER, C.B. and CARSON, R.L. (1984): Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. Amer. J. Primatol. 6:377-380.

TAYLOR, C.R., HEGLUND, N.C., McMAHON, T.A. and LOONEY, T.R. (1980): Energetic cost of generating muscular force during running: a comparison of large and small animals. J. Exp. Biol. 86:9-18.

TERBORGH, J. (1983): Five New World Primates. A Study In Comparative Ecology. Princeton University Press, Princeton, New Jersey.

TERBORGH, J. and GOLDIZEN, A.W. (1985): On the mating system of the cooperatively breeding saddleback tamarin (*Saguinus fuscicollis*). Behav. Ecol. Sociobiol. 16:293-299.

THOMAS, O. (1904): New *Callithrix*, *Midas*, *Felis*, *Rhipodomys*, and *Proechimys* from Brazil and Ecuador. Ann. Mag. Nat. Hist. ser. 7 12:455-464.

THOMAS, O. (1913): On some rare Amazonian mammals from the collection of the Para Museum. Ann. Mag. Nat. Hist. ser. 8 11:130-136.

THORNDIKE, E.E. (1968): A microscopic study of the marmoset claw and nail. Amer. J. phys. Anthrop. 28:247-262

THORNBACK, J. and JENKINS, M. (1982): The IUCN Mammal Red Data Book. Part 1 The Americas and Austalasia. IUCN, Gland.

TOWNSLEY, J.D. (1974): Estrogen excretion of the pregnant baboon (*Papio papio*). Endocrinology 95:1759-1762.

TRIVERS, R.L. (1972): Parental investment and sexual selection. In: Sexual Selection And The Descent Of Man, ed. by B. Campbell, Aldine Publ. Co., Chicago, pp. 136-179.

VAITL, E.A., MASON, W.A., TAUB, D.M. and ANDERSON, C.O. (1978): Contrasting effects of living in heterosexual pairs and mixed groups on the structure of social attractions in squirrel monkeys (*Saimiri*). Anim. Behav. 26:358-367.

WARNEKE, M. (1988): 1988 International Studbook *Callimico goeldii*. Chicago Zoological Society, Chicago.

WICKLER, W. and SIEBT, U. (1983): Monogamy: an ambiguous concept. In: Mate Choice., ed. by P. Bateson, Cambridge University Press, Cambridge, U.K., pp.33-50.

WILSON, E.O. (1975): Sociobiology. The New Synthesis. Harvard University Press, Cambridge, MA.

WITTENBERGER, J.F. and TILSON, R.L. (1980): The evolution of monogamy: Hypotheses and evidence. Ann. Rev. Ecol. Syst. 11:197-232.

WOLFE, L.G., OGDEN, J.D., DEINHARDT, J.B., FISHER, L. and DEINHARDT, F. (1972): Breeding and hand rearing marmosets for viral oncogenesis studies. In: Breeding Primates, ed. by W.B. Beveridge, Karger, Basel, pp.145-147.

WOLFENDEN, G.E. (1981): Selfish behaviour by Florida scrub jay helpers. In: Natural Selecion and Social Behaviour., ed. by R.D. Alexander and D.W. Tinkle, Chiron Press, New York, pp. 257-260.

WOLFHEIM, J.H. (1983): Primates of the World. Distribution, Abundance, and Conservation. University of Washington Press, Seattle and London.

WRIGHT, P.C. (1981): The night monkeys, Genus *Aotus*. In: Ecology and Behaviour of Neotropical Primates. ed. by A.F. Coimbra-Filho and R.A. Mittermeier, Academia Brasileira de Ciências, Rio de Janeiro, pp. 211-241.

WRIGHT, P.C. (1984): Biparental care in *Aotus trivirgatus* and *Callicebus molloch*. In: Female Primates: Studies by Women Primatologists, ed. by M.F. Small, Alan R. Liss, Inc., New York, pp. 59-75.

WRIGHT, P.C. (1986): Ecological correlates of monogamy in *Aotus* and *Callicebus*. In: Primate Ecology and Conservation., ed. by J.G. Else and P.C. Lee, Cambridge University Press, Cambridge, UK, pp. 159-167.

ZIEGLER, T.E., SAVAGE, A., SCHEFFLER, G. and SNOWDON, C.T. (1987a): The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus oedipus*) under varying social conditions. Biol. Reprod. 37:618-627.

ZIEGLER, T.E., BRIDSON, W.E., SNOWDON, C.T., and EMAN S. (1987b): Urinary gonadotropin and oestrogen excretion during the postpartum estrus, conception and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). Amer. J. Primatol. 12:127-140.

ZIEGLER, T.E., SNOWDON, C.T. and WARNEKE, M. (1989): Postpartum ovulation and conception in Goeldi's monkey *Callimico goeldii*. Folia Primatol. 52:206-210.

ZIEGLER, T.E., SNOWDON, C.T. and BRIDSON, W.E. (1990a): Reproductive performance and excretion of urinary estrogens and gonadotrophins in the female pygmy marmoset (*Cebuella pygmaea*). Amer. J. Primatol. 22:191-203.

ZIEGLER, T.E., SNOWDON, C.T., WARNEKE, M. and BRIDSON, W.E. (1990b): The endocrinology of pregnancy in the Goeldi's monkey, *Callimico goeldii*. J. Reprod. Fert. 89:163-168.