CHAPTER 7. REPRODUCTION AND SOCIAL ORGANISATION

Numbers, Temporal Occupancy, Categories and Associations.

The number of P. poliocephalus at Gordon fluctuated considerably, with total counts varying between 5,990 and 12,980. Almost certainly the larger figure is exceeded in some seasons, while at other times the colony is deserted. Some 1,2000 P. scapulatus were also present in the colony at the onset of observations but later left en masse.

According to local residents, prior to 1981 the colony was deserted each Winter. Nelson (1965a) reports that some individuals, mostly juveniles, do form Winter camps, but, as Dwyer (1966) found for Miniopterus schreibersii, there is an "unaccounted absence of most of the population during the Winter". Ratcliffe (1931) believed P. poliocephalus migrated north at this time, while Nelson (1965a) believed they merely dispersed to live singly or in small groups.

The late Summer (February-March) population of P. poliocephalus at Gordon may be divided on the basis of age, sex and reproductive status to give the following categories:-

(i) current young born in October,

(ii) yearlings- born the previous October, not yet reproductive,

(iii) adults - territorial males - monogamous
- polygamous
non-territorial males,

(iv) females .

These categories were associated as follows; the females mostly bore their young in October. Some mothers wean their young in February and March but others retained them as late as the 28th July, 1981;

Yearlings - tended to congregate together in large numbers with a few adults, presumeably surplus males.

Territorial males - Monogamous males - by definition were associated with only one female, usually accompanied by her young.

- Polygamous males - were associated with two or more females which initially had young but appeared to wean them earlier than females in monogamous association.

Non-territorial males - were difficult to recognise but appeared to congregate together, or be associated with yearlings and newly weaned young.

Distribution of Flying Foxes within the Colony.

Individual Spacing - unlike P. scapulatus, P. poliocephalus at all times maintained strict individual spacing of approximately 30-50 cm. The only exception to this is found in juveniles, mother young pairs and copulating adults. Reference to Figure 8 demonstrates this point well. The method by which individuals 'space out' appears to be through wing extention as discussed earlier. The distance maintained is presumeably enough to allow the performance of most activities unhindered by nearby individuals. It is also usually adequate to allow each animal to be maximally exposed to direct sunlight.

Territories - territories provide a rigid structure to the day roosting community. The size of territories of flying foxes is difficult to accurately assess, probably being best measured as length of perch patrolled or volume of space occupied. The relationship of these two vary depending on the vegetation structure.

Comparison of a polygamous and monogamous male roosting in the same tree showed that while the polygamous male patrolled a vertical distance of 3-4.5 m the monogamous male patrolled only 1.5 m. Furthermore the polygamous male in this case had 6 specific sites which he regularly occupied. The monogamous male had three. The polygamous male initially

had four females which later increased to 8 by the end of the breeding season.

Nelson (1965b) states that polygamous groups occur in the centre of the colony, and that 'subordinate animals' - presumeably monogamous males, non-territorial males and juveniles, form a protective buffer zone against predation, around the colony.

Observations at Gordon support Nelson's scheme to a limited extent, except that monogamous and polygamous territories were found within the same tree, and juvenile groups, rather than forming a protective ring, tended to congregate on the northern boundary of the colony.

In November and December the creches in which the young were left at night were also found on the northern boundary of the colony, as was the population of P. scapulatus which visited briefly in the summer of 1980/81. The significance of the topography of this section and its use in this manner is not understood.

During the period in which territories were maintained the zonation of density was quite pronounced. The majority of the area covered by the camp, consisted of area controlled by territorial animals. At the northern boundary near the creche there was a considerable concentration of juvenile animals which were in greater density than territorial animals. Around the perimeter of the camp, with the exclusion of the northern side, there was usually a zone where trees were inhabited by only a few animals - these were apparently adult males which Nelson (1965b) refers to as guard animals. Their occupation of these trees was irregular, but simply by being on the perimeter they inadvertently fill the role of guard.

Due to seasonal movements, the weaning of young, and the largely

transitory nature of territorial behaviour, there is immense temporal variation in social organisation, with reported seperation and recombination of the sexes. (Nelson, 1965a). Fragmentary evidence from this study however, suggests that in some years at least, some male and female pairs or groups may recombine.

According to Nelson (1965a, 1965b) the majority of animals within the summer camp will initially be pregnant females and females with young. General observations made at Gordon on the 25th October, 1981 appeared to corroborate this finding. The only female which could readily be distinguished under any circumstances due to her highly abnormal colouring returned to within 2 m of her old 1980/81 roost after a winter absence of 2-3½ months, suggesting that females at least demonstrate some site attachment from year to year. During the observation period from 31st January, 1981 to 15th July, 1981 this female was always present at the same site. In this period she was also seen to mate with three different males sequentially. Her initial mate was monogamous. The status of the later males is uncertain but they appeared to be polygamous. In another observed group the resident polygamous male was displaced by another polygamous male. This appears to indicate that females are sedentary whereas males are sedentary for only as long as they can successfully defend their territory.

If the males were to successfully defend the same territory from one year to the next then presumeably they would be reunited with the female(s) from the previous year(s). Supporting evidence for this is relatively scant again, due to difficulties in individual recognition. However, one polygamous male that was distinguishable occupied the same territory throughout the winter, being continually present from 20th May, 1981 until last seen on 16th September, 1981 - the last day of structured observations.

From the preceding discussion it is suggested that females are site specific and that only males are involved in the selection of a territory which includes one or more females. This is contrary to Nelson's (1965b) unsupported belief that mates are selected prior to territory establishment. As stated earlier territory defence is performed largely by the male although the female may help. The majority of fighting performed by females however, is against the territorial male for the purpose of rejecting his sexual advances and excluding him from her small portion of territory such that the female effectively has a territory within the male's territory. Bradbury and Emmons (1974) describe a system of sexual organisation for Emballonurids (Microchiroptera) which shows some basic similarities to the system proposed here, in that major temporal variation in social organisation includes change in the identities of territorial males. Future work with tagged individuals could readily substantiate the theory forwarded here.

During winter, territory defence was greatly reduced in intensity. The area defended was also greatly reduced, being little larger than was normal for maintenance of individual spacing. The method of defence at this time was by passive threat rather than active pursuance and/or fighting. By mid-winter the animals within the observation trees were almost exclusively males. Active defence of the territory by the territorial male under these conditions would be both expensive (in terms of energy expenditure) and pointless, so it is understandably reduced.Scent marking at this time was also almost totally absent - being seen once on the 31st August, 1981 and not for some weeks prior to then.

At this time also, the formerly stable boundaries of the colony were far less stable.. The perimeter moved considerably from day to day as the increasingly non-territorial population moved irregularly within and around the colony.

Mating.

Copulation of both P. poliocephalus and P. scapulatus was observed at Gordon.

P. scapulatus - were observed mating and scent marking at Gordon between 23-31st January, 1981. They had vacated the camp by 6th February, 1981. Nelson (1965a) states that mating in this species occurs "probably in late November and early December", while Hall and Richards (1979) give no date for mating or conception of this species except to state that young are born in April-May but are sometimes seen in January-February. No young were seen at Gordon, or at temporary P. scapulatus camps at Kootingal and Tamworth at this time. The method of mating of P. scapulatus was slightly at variance to that of P. poliocephalus. In P. poliocephalus the male hangs behind the female and uses his wing claws to restrain the females wings as previously described in Chapter 5. In P. scapulatus the males wing claws are held tightly across the females abdomen. In each of the several P. scapulatus matings seen the male involved was always one of the larger, darker coloured individuals mentioned in Chapter 1. These males however, only constitute a small proportion of the observed male population. Whether this implies that they are older than the remaining males or whether in some way their dominance is manifested phenotypically is unclear. This apparent dimorphism of the male population is a phenomenon not noted in the literature. Captive specimens of both types held by the author have remained largely unchanged (except for colour variation) since their capture in January. Furthermore, of some 120 P. scapulatus obtained after a 'shoot' at Moore Creek, Tamworth, only two of these were 'dominant males'.

P. poliocephalus - as stated in an earlier Chapter P. poliocephalus were seen to mate from 22nd February, 1981 to 19th August, 1981 with peak activity from March to May. This is far longer than stated by Nelson (1965a) and probably was a result of the abnormal continued Autumn-Winter occupation of

the colony.

Factors Effecting Reproduction.

Reproduction in P. poliocephalus does not appear to be related to rainfall, as several other workers have reported for various Megachiropteran species overseas. (Mutere, 1967; Fayenuwo and Halstead, 1974; Okia, 1974). This is to be expected as rainfall in the major part of P. poliocephalus' range is relatively even throughout the year (Leeper, 1970). The highly synchronous pattern of predominantly October births appear to be more related to food availability, such that the young are being fed, and learn independence, when food is abundant (Nelson, 1965a).

According to Nelson (1965a) sexual maturity is reached in both sexes at an age of around 18 months. This figure implies then, that a female born in October, 1981 may have her first offspring in October, 1983. Young males would presumeably be unable to successfully obtain and defend a territory at this age and therefore probably reproduce at a later age than females. Nelson (1965a) found a reproductive success of 65% in first year adult females and 100% for later age classes. This indicates that for second year and later age classes of adult females, potential and realised reproductive capacity are probably one and the same. The 100% figure further implies no diminution of reproductive success for older females. This raises the questions of the length of their natural lifespan and the length of their reproductive life, and whether the two can be meaningfully distinguished. Keen and Hitchcock (1980) working with the Microchiropteran, Myotis lucifugus, on a long term banding scheme found two individuals aged 29 and 30 years which showed no outward signs of senescence, such as wear of canines. For P. poliocephalus however, considerable tooth wear is sometimes evident in individuals shot in fruit orchards. This undoubtedly reflects on diet as well as age. No figures could be found for longevity in this species but it is possible that similar ages may be attained by Megachiropterans.

Mother-Young Association.

From the literature the length of pregnancy for P. poliocephalus is 6 to 6½ months (Ratcliffe, 1932; Nelson, 1965a). (This is longer than the figure quoted by Baker (1939) of approximately 5 months for other, usually smaller, Pteropus species.)

A six month pregnancy is within the limits of the observations of this study as mating peaked in April and parturition was almost complete by the end of October. If conception occurred in mid April the length of pregnancy derived from these results is approximately 6 months. Mating far beyond this April date indicates that females do not cease copulation after conception occurs. In one case at least, mating definitely occurred 2½ to 3 months after conception occurred, as evidenced by dates of mating and parturition for one individual. This is contrary to Nelson's (1965a) findings which indicate that mating ceases after conception.

The young at birth are well developed and weigh in the vicinity of 75 gm., (Bartholomew, et.al., 1964). The females pelvis is C-shaped in cross section to allow passage of the large headed, well-developed young. The brain of Pteropids is the largest in relation to other body parameters of all Chiropterans (Findley, 1969; Pirlot, 1970) . As seen in Figure 34, the newborn young already has the typical adult colouring, but is incompletely furred.

As stated previously the young are typically carried to the feeding area for the first 3-4 weeks and later are left behind in creches at the camp. At this time, considerable mortality was evident. This heavy mortality is almost certainly as a result of:

(i) mothers being shot feeding in orchards with subsequent starvation of young,

(ii) falls of the young from the nursery trees,

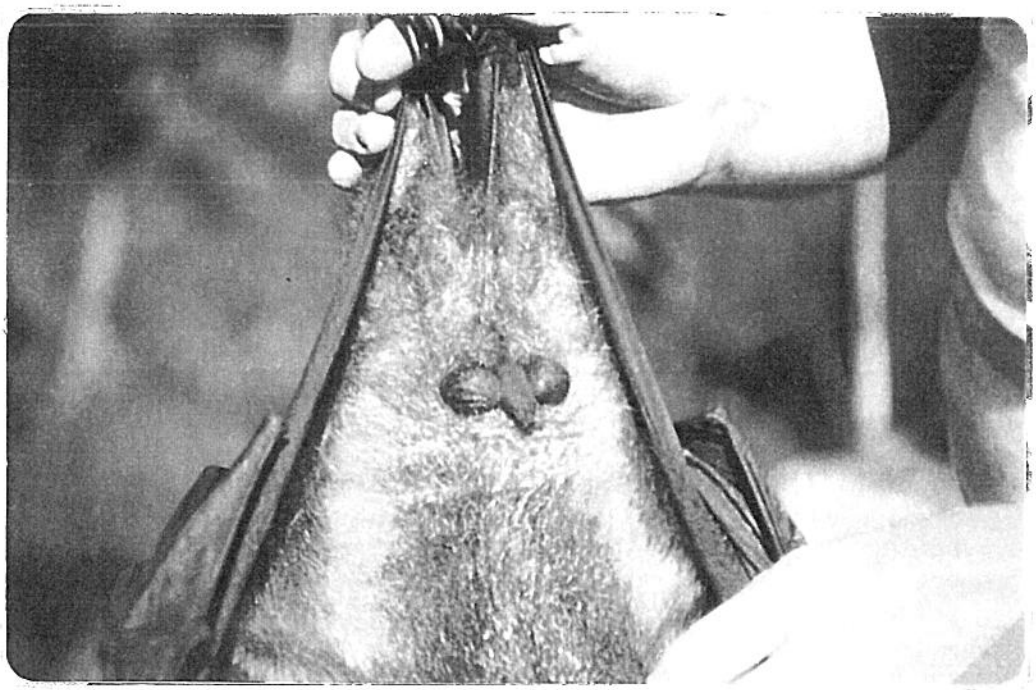

Fig. 33. Exposed testes of male P. poliocephalus.

Again, knowledge of the recent thermoregulatory experience of the male, accurate measurement of temperatures within the animal's immediate vicinity, and the extent of its exposure to direct sunlight is crucial for better interpretation of these observations. A second recording of scrotal testes at 14°C. was observed in a male immediately after mating. They were withdrawn several minutes later.

Clustering. There are numerous reports of clustering in Pteropids in the literature (McNab,1969, Jones, 1972, Noll, 1979a). This behaviour was observed regularly by the comparatively small Pteropus scapulatus at the Gordon colony and in captive scapulatus, but was not exhibited by P. poliocephalus. The only instance where anything like clustering was observed with P. poliocephalus was at an ambient temperature of 3.4°C. when an adult bat climbed down to another adult bat and hung beside it so that they were touching. They hung together for approximately 90 minutes until

the extension of the bond "beyond lactation has not been recognised in any other species of bat". Observations in this study strongly suggest that P. poliocephalus provides a second example of this phenomenon. The result, if not the cause of this phenomenon, in the species' southern limit, is that the cost of maintenance of homeothermic body temperature for both mother and young is significantly reduced.

Social pressure in some cases appears to outweigh the benefits of the above-mentioned system. Young P. poliocephalus at Gordon were observed to be retained for extended periods (i.e. beyond March-April)in monogamous associations. Young of females in polygamous association were weaned considerably earlier. The male plays no part in raising the offspring except indirectly by defending his territory against intruders. Conversely, the males aggression toward the young may speed its departure.

Case History

As a means of demonstrating some of the points made in this and other chapters it is useful to briefly note the major events in the life of one female and her young. The female in question, and her young, were unmistakeable due to body colouring and are pictured on Plate 2c.

3.1.81 Female first seen flying out to the West to feed. No young seen attached.

31.1.81 Found perched in tree with young.

4.2.8. Baby and mother both repelled resident male using wing claws.

18.2.81 Female and baby both return from feeding - 33 minutes difference in return.

22.2.81 Female defending baby against resident male.

12.3.81 First signs of aggression by female to keep young away.

26.3.81 Baby sexed positively as a male.

27.3.81 Female first observed mating - continually associated with monogamous male. Baby and mother hanging 1 m apart as a result of earlier mating.

30.3.81 Mother absent all day - baby repels male off mothers perch.

2.4.81 Mother still absent - Male has displaced young off mothers perch

7.4.81 Mother returned - resumed perch. Baby again wrapped within wings of mother. Resumes mating with male - presumeably same male.

21.4.81 Male losing sex drive. Twice held female without completing sex act.

2.6.81 Baby attempting to suckle. Mother grooming baby. Baby strongly attacked male.

9.6.81 Disturbance in colony - female climbed to perch 1 m higher-the first time seen away from her perch.

23.6.81 Mating with new male, probably polygamous.

8.7.81 Female mated with another new, much larger male, possibly polygamous. Baby present for last time.

14.7.81 Female displaced by other bat - roosting 0.5 metre higher.

15.7.81 Female roosting 2 m higher. Present for last time.

16.7.81 Female and baby both absent.

25.10.81 Female returned, roosting 2 m lower than original perch. Has normal coloured off-spring - sex unknown.

Discussion and Conclusion.

In summary, the social system of P. poliocephalus is found to have several major components, including the elaboration of the pair bond to give male territoriality and harem formation, extension of the mother-young bond beyond lactation,and the development of group foraging - as covered in Chapter 3.

The majority of new information contained in this work concerns behavioural thermoregulation and some aspects of social organisation. In some areas the information obtained agrees with that contained in the literature. In many cases, however, there was considerable disagreement. This indicates that despite the value of early works by Ratcliffe(1931,1932) and Nelson (1964, 1965a, 1965b) it is now demonstrated that there are large components

of this species' behaviour and social organisation that are in need of revision. This study partially fulfills this requirement and provides the basis for future work.

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