

CHAPTER 5.BEHAVIOUR.Introduction.

Several aspects of behaviour have been covered in some detail in other Chapters. Feeding behaviour, the co-ordination of night flights, and return in the morning have previously been discussed. Thermoregulatory behaviour is considered in detail in the following chapter while many aspects of mating and reproduction are dealt with separately in Chapter 7. It remains, in this chapter then, to deal almost exclusively with the behavioural side of mating and reproduction in the areas of territorial behaviour, copulation, the mother-young relationship and juvenile behaviour. Finally some brief notes on interspecific interactions with the Little Red Fox, P. scapulatus and several bird species are made.

A very important aspect of the life history of flying foxes which was not studied in any detail in this work is the area of vocalisation. Flying foxes have been demonstrated to have a very rich 'vocabulary' - equalled among mammals only by primates, with at least 22 separate calls used to "convey information regarding the psycho-physiological state of one animal to another" (Nelson, 1964). Vocalisations are employed in the areas of mother-young communication, agonistic behaviour, reproduction and warning and alarm. Different Pteropus species show minor differences in their calls but the general patterns are similar (Nelson, 1964).

Territorial Behaviour.

Individuals within a species occupy the same niche and must compete for the same food and living space. Intraspecific fighting acts to space out individuals or groups in the occupied areas. It secures for each the territory necessary for survival, preventing overcrowding and promoting the species' distribution. Fighting also arises from competition for mates

resulting in the selection of stronger and 'fitter' individuals for reproduction. Such fighting rarely results in serious injury or death, but usually ends when the loser leaves or adopts a submissive posture which effectively inhibits the winners aggression (Eibl-Eibesfeldt, 1961).

In all respects the above is true of flying foxes. Within their daytime camp, Grey Headed Flying Foxes P. poliocephalus typically establish and maintain breeding territories for 3 to 5 months between December and April. Temporary night-time feeding territories are also established and defended for some time within the period from September to April (Nelson, 1965b).

The daytime territory consists of a relatively small section of a tree from which 'intruders' are excluded. The size of the territory depends to a considerable extent on the reproductive strategy of the resident male - as both monogamous and polygamous males exist. The territories of monogamous males seen in the study were smaller than those of polygamous males. Consequently polygamous males were more mobile and had more roosting sites than did monogamous males.

Defence

Territories are defended mostly by males, although occasionally females are involved in defence. When a bat lands within a territory the resident male immediately climbs rapidly towards it. At this stage one of several things may result. Firstly if the intruder is a juvenile it utters a high pitched repetitive squeak which has the effect of making the male lose its aggression (This call is not described by Nelson, 1964). The male in these cases usually sniffed the juvenile and retreated - allowing it to remain. If the "intruder" is a resident of the territory i.e. an adult female or its young, the male again very briefly sniffs the animal then retreats. If the intruder is not a resident, two results are possible.

The intruder may stay and fight, or leave the territory by flying or climbing away from the approaching male. Climbing in this manner usually carries it into another territory where it is again chased by the resident male. This may be repeated several times until the intruder flies off or occasionally is chased into a 'neutral' undefended area where it will remain alert for some time before settling down or leaving.

The other alternative is for intruders to stand their ground. Fighting ensues immediately with no preliminary behaviour such as sniffing or wariness (raising the question of how the resident male instantaneously identifies the animal as an intruder - probably either by sight or behaviour). Fighting, as seen in plate 2k, is performed by very rapidly 'stabbing' at the opponent with the thumb claws and sometimes by biting the animals face, body or wings. Loud vocalisations are made throughout the fight. In all fights seen involving known animals, the territorial male was the victor. The only two exceptions to this are discussed below. On some occasions the males performed a 'victory wing flap', flapping the folded wings rapidly against the sides of the body several times.

Fights are brief, lasting only several seconds, usually with little or no damage done. However, on occasions the animals became very aggressive and in several instances both animals fell from the tree while engaged in close fighting. An alternative method of territory defence seen at both feeding sites and in the camp involved the defending animal flying at, and landing on an intruder, causing it to fall, while the resident animal remained on the perch.

During the February-March period an unusual unreported behaviour was observed. Many flying foxes were seen returning to the roost during

the night from approximately 9 p.m. onwards. The territorial males being watched at this time were in their usual position but were intermittently mobbed by 10-20 flying bats. The residents would ^{hand} with wings extended and call very loudly as the bats flew nearby, sometimes landing. The territorial males would rapidly approach the intruders who sometimes flew off but often stayed and fought with the male. A polygamous male was seen to repel 5 or 6 bats within 30 seconds in this manner. These raids were seen only once in the daytime but on several occasions at night. They often lasted for an hour or more and the target trees being mobbed changed several times. The sex and age of the raiders is unknown but they appeared to be adults, and presumed to be males.

The only two conditions under which a territorial male was seen to 'lose' a fight were in conflicts with a resident female and her young, both together and separately. The outcome of male-female fights depends on the conditions under which they occur. After territories have been established, but prior to the mating season, the males are very attentive to the females and frequently attempt to sniff and lick the female's genital areas. The females, often aided by the young, vigorously repel the male, not allowing him at this time to enter her part of the territory. Only wing claws were used in these encounters and the male gave only a token defence. Presumably these incidents indicate the female's are sexually unready, therefore reluctant to participate in any sexual activities. These early encounters, when the young are only 3-4 months old, obviously provide fighting experience for the young.

After the mating season has begun the situation changes considerably. When the male approaches the female he may be repelled or allowed to lick the female prior to copulation. If the female objects, the male at this stage will briefly 'box' the female until she assumes the submissive

position with her wings folded at her sides, the thumb claws folded beside her chin, the legs bent to draw the body up towards the branch and her chin held against her chest. The whites of her eyes are also visible. (The only other occasion when the whites of eyes are visible is during mating when the male tightly holds the skin of the female's neck in his mouth - making the female's eyes appear to bulge out. The fact that the whites are displayed when the animal is submissive may be akin to demonstrating sexual subordination, similar to that found in anal presentation of some primates). Immediately after copulating the female again repels the male successfully.

These facts apparently indicate that the female is dominant, or allowed by the male to be dominant, except when she is sexually receptive. Furthermore the young appear to acquire their mother's status. This is illustrated by the repulsion of an adult male by his absent female's 5 month old young. On one of these occasions the male baby attempted to climb past the territorial male which was roosting on the female's perch. The male partly opened his wings and performed an open-mouthed 'grin' (usually seen only after mating) to the young, and then attempted to attack the baby and bite it. The much smaller young fought back with teeth and wing claws causing the adult male to retreat to a different perch. This scene was repeated several times but after the female had been absent for a considerable period during the day the male was not repelled by the young.

When the male attacked the baby in the mother's presence, she quickly went to its aid and repelled him. Perhaps the male is initially repelled by the baby alone because he has been conditioned to anticipate the female's attack. Nelson (1965b) provides no clue to this behaviour, stating that males never openly attack the young.

When the female was absent from her perch, the male would regularly

occupy her position, rapidly vacating it on her return. The reason for this is unclear but may be to 'protect' his investment with a minimum energy expenditure. The majority of would-be intruders would not land merely as a result of the males presence. Thus with little effort he saves his females perch for her return, and retains his chance of reproductive success.

Injuries resulting from fighting and mating usually consisted of small holes and tears in the wing membranes, often occurring near the 2nd joint of the 1st finger, and erroneously referred to as 'bullet holes' by both Ratcliffe (1931) and Nelson (1965b). These wounds heal very rapidly. Within a week or so the hole contracts and forms a scab. This falls off to leave a small pale scar with no perforation (George - pers. comm.).

Scent Marking.

Both male and female flying foxes possess scent glands which cover the scapular area. These glands are bigger in males and largest in both sexes during February to April when territories are maintained and mating occurs (Nelson, 1965a). The flying foxes probably mark to identify a territory that will be defended against other flying foxes. Ralls (1971) states that animals usually mark where they are likely to attack another member of the same species and are likely to win if they do attack. This situation would apply to both territorial and non-territorial encounters.

Flying foxes were seen to mark most frequently prior to their departure, and on their return from feeding flights. They also often marked after expelling intruders from their territories. Marking was first noticed on 4th February, 1981 and last seen on 31st August, 1981, long after it should have ceased. Females were never noticed scent marking, but possess scapular glands, and may mark on some occasions.

Sexual Behaviour.

Once the territories are established there is a brief period before the female is sexually receptive. At this time many males were noticed hanging slightly higher than the females - bringing their nose into close association with the females genitals. As already stated the males were excluded from the females' portion of their territory at this time. However, as the mating period approached the male was allowed to get progressively closer. A relatively common behaviour was for the male to hang above the female and rest his wing claw on the females perch, sometimes between the mother and her baby. At this time males may also be seen stretching their wings in the direction of females. These actions appear to be aimed at passively asserting the males' position within the group.

Copulation.

See plates 2L and 3.

A typical copulation is initiated by the cautious, almost stealthy approach of the male towards the female. He hangs near her, usually with an erection and persistently licks the females vaginal area. Often at this time the female will turn her back to the male so that he cannot lick her. The male may use his wing claws to turn her around or more often simply move so that he again has access. The licking continues for some minutes, the male occasionally stops to lick his penis, probably to maintain his erection. The female may at times lick her own vaginal area and occasionally invert to urinate. By this time the baby, if present has usually climbed off the mother to roost nearby. The female may restrict the males' actions by placing her foot on his head, using her wing claws to pull or push his head away or at times place her foot on his penis. The male soon tires of this and attacks the female, who then assumes the submissive posture as outlined earlier. The male continues licking and attempts to climb behind the female. At this time the female may rotate to face the male and thwart

his efforts. Almost always however he succeeds in grasping the female by the skin at the back of her neck with his mouth, effectively stopping her from biting. Simultaneously, he uses his thumb claws to hold the struggling females' folded, rapidly beating wings. The males erect penis is large (8 cm) and mobile. Once the female is held the male lifts his penis between her legs and feels for the vaginal opening with its tip - probably aided by the wet fur flattened around it in an inverted cone shape as a result of licking. (The fact that the female can safely present her back to him prior to licking may mean this function is more important to the male than the female.) Once the pair are coupled the female continues vigorously flapping her wings - occasionally losing her grip on the branch. At these times she is totally supported by the male.

The animals remain coupled from several seconds to over a minute during which time they are extremely vocal. The male sometimes thrusts but most often does not. At the end of this period the females neck is either released by the male or she breaks the males grip. She then rapidly swings upward or may attempt to bite the males wrist, leg or penis. The female then almost invariably licks her vaginal area while the male licks his flaccid penis. The male then may leave voluntarily, or be repelled by the female, or resume licking to repeat the performance once or twice more. One pair of recognisable animals were seen to mate in three separate bouts between 6.30 and 11.30 a.m. - with a total of five successive penetrations. This frequency was not unusual. Initially mating occurs throughout the day but towards the end of the season is more common in the morning (significant at .05 level for data between 21/4 and 16/9. Males approached females most often in the morning with a significance of .005 for the same data).

Males approaching females were successful in copulating with them in just under 20% of recorded cases (13 out of 66). On occasions a polygamous

male was seen to move around his territory and court up to four females in succession, without copulating.

An interesting phenomenon was often observed which is unreported in the literature. Typically a foreign female would land within an occupied territory. Instead of attacking, the resident male would approach her, vaginally lick and then attempt to copulate. At this point most females flew off, but others remained and mated with the resident male. After mating the female was allowed to stay within the territory. This was definitely observed with a known 'monogamous' male and almost certainly with a known polygamous male.

Masturbation.

Males were occasionally seen licking their penis and masturbating by rubbing their chin vigorously sideways across the ventral surface of the erect penis. This activity was relatively brief, 10-30 seconds, and almost invariably concluded with the male enclosing himself inside his unfolded wings, apparently losing co-ordination.

Homosexual Behaviour.

Nelson (1965b) states that homosexual behaviour occurs between adult males and females. It was never seen in this study except between juveniles, but could well have existed between adults in the unobserved period from October to December and thus escaped attention.

Juvenile homosexual behaviour was restricted to wrestling and sniffing the genitals of other juveniles - the strict individual spacing maintained by adult P. poliocephalus being absent at this time.

Mother-Young Behaviour.

The length of the mother-young association can be maintained anytime

from 4 to 9 months, varying widely between individuals. For the first 3 or 4 weeks the baby clings almost constantly to the female and is carried to and from the feeding sites on the mothers chest. The young clings to her fur and large fleshy nipple with its unusually hooked claws and curved teeth. The female regularly licks the young at this age - paying particular attention to the anus and genitals. The young are able to invert and defecate normally at age 6 weeks. The babies are well co-ordinated at 3-4 weeks of age and can scratch, clean, and threaten with outstretched wings. At this age they are also left behind at the roost in creches at night. To leave the young, the mother licks the baby until it climbs onto the perch. After a short time she then flies off to feed. In the morning the mother returns to the creche, flying overhead and calling. The young reply and the female eventually lands, sniffs the young and either exposes her chest or pushes the young away if it is not hers. (The majority of the information in this section is taken from Nelson, 1965b).

In November and December infant mortality is high. Young were found dead daily at Gordon towards the end of December. (Young, 1972, reports that mortality of young Microchiropterans within roosts may act as a means of regulating colony size, and experimentally supported this theory). When the young are older they engage in static flight by flapping the wings without releasing their hold of the branch, as the adults fly out to feed. Gradually small flights were made from the creche and by the 9th February, 1981 the young were not taken to the creche but simply left in the adults territory. The few young in each tree climbed together, usually congregating near the top and later dispersed by flying. Presumably they flew out of the colony for a short distance as a search of the colony at this time revealed few juveniles.

For as long as mother and young are associated, the female plays a protective role. She defends the baby from aggressive males and even at the

age of around 8 months a young was observed to climb to its mother in reaction to a nearby disturbance.

Mothers were often seen wrestling playfully with their young. The young used their mouths and wing claws to 'attack'; the females retaliate using their mouths only. As the young grew older the females showed obvious signs of wanting to get away from the young, either by climbing away, or stopping the young from getting too close by gently biting their wrists. Several times when this was happening the territorial male approached and appeared about to attack the young. The female in all cases immediately attacked and repelled the male, taking the young under her wing.

On the 2nd March, 1981 the first juvenile groups were seen and became increasingly common after that time. The last female with young was seen on the 28th July, 1981, long after the majority of mother-young pairs had separated.

Juvenile Behaviour.

Juvenile groups were often quite large and usually not homogenous, with at least some adults present. These groups were not especially sedentary either, being present in areas on some days and absent on others. This is probably related to the fact that the juveniles are easily disturbed and at Gordon were sometimes displaced by people and machinery noises. Mutual grooming among juveniles was seen only once when an individual licked another's head. Wrestling was occasionally observed and had homosexual overtones, as previously discussed. Little information was obtained on juveniles in this study, as juvenile groups were only rarely within distance of the observation site.

Interspecific Interactions.

Little Red Fox, P. scapulatus - these bats were present at the colony from approximately the 27th December, 1980 to 6th February, 1981. By day the bats roosted together, often in clumps on the edge of the colony near the Grey Headed Flying Fox, P. poliocephalus creches. The Little Red Fox, P. scapulatus formed a discreet group but usually there were some trees occupied by both Little Reds, P. scapulatus and Grey Headed Flying Foxes, P. poliocephalus - generally females with young. No aggression was seen between either species but they were separated to some extent by the habit of Little Reds, P. scapulatus invariably roosting lower in the trees than the Grey Headed Flying Foxes, P. poliocephalus.

At dusk the Grey Headed Flying Foxes, P. poliocephalus were nearly always airborne before the Little Reds, P. scapulatus. By the time the Grey Headed Flying Foxes, P. poliocephalus began to stream out to the East and West the Little Reds, P. scapulatus had begun circling prior to leaving and eventually joined the columns of Grey Headed Flying Foxes, P. poliocephalus.

Birds.

The flying foxes' wing-spread alarm reaction to birds has already been discussed as has the feeding and possible predation on young by Kookaburras, Dacelo gigas and Ravens, Corvus coronoides. A final point which hasn't been discussed is the general mixing of bats and birds. Of the many species seen in the colony, only Ravens, Kookaburras and Rainbow Lorikeets, Trichoglossus haematodus were seen actually on perches inhabited by bats. Other species either flew overhead, roosted in trees or parts of trees not occupied by bats, visited the 'occupied' sections at night when the bats were absent or inhabited the understorey. Presumably the camp as a whole represents a significant 'block' of occupied space on which the majority of less aggressive bird species are reluctant to intrude.