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Behaviour of the black flying fox *Pteropus alecto*: 2. Territoriality and courtship

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Flying foxes are commonly thought of as highly social mammals, yet little is known about the dynamics of their social interactions at a day roost. The aim of the present study was to examine the nature of the seasonal activities of territoriality and courtship amongst wild flying foxes in Australia. Focal observations were conducted at two permanent roosts of black flying foxes *Pteropus alecto* during periods of peak social interaction in the summers of 1999 and 2000 in urban Brisbane, Queensland. Observations of male territoriality were conducted at dawn and began eight weeks prior to the commencement of mating. The majority of defense bouts (87%) consisted of ritualised pursuit, while 13% of bouts involved physical contact expressed as either wrestling or hooking. One male with an unusually large territory took significantly longer to defend it than other males with less territory to defend. Observations of courtship revealed repetitive courtship sequences, including pre-copulatory approaches by the males, copulation attempts and grooming/resting periods. Thirty-four complete courtship sequences incorporating 135 copulation attempts were recorded over two seasons. Females actively resisted courtship approaches by males, forcing males to display a continuous determination to mate over time where determination can be considered an indicator of 'fitness'. The courtship bout length of females with suckling young was significantly longer ($\bar{x}$ ± SE; 230.9 ± 22.16 s) than that of females unencumbered by large pups (158.5 ± 9.69 s), although the length of copulations within those courtships was not (45.6 ± 5.19 versus 36.2 ± 3.43 s).

Key words: *Pteropus alecto*, Australia, territorial defense, courtship, mating

INTRODUCTION

Australian mainland flying foxes have a predominantly coastal distribution and in some areas the ranges of two or three species overlap. Along the east coast between Bundaberg in Queensland and Bowraville in northern New South Wales (Hall and Richards, 2000), populations of *Pteropus poliocephalus* and *P. alecto* exist sympatrically throughout the year and may be joined by large numbers of the nomadic *P. scapulatus* during the summer months (Birt and Markus, 1999). The region of geographic overlap between these three species represents an area of high human population density and corresponding loss of forest habitat to agriculture and urban expansion, resulting in the increased concentration of populations into small forest remnants. Pressure on flying fox populations has further been exacerbated by increased sympatry through the southern extension of the distribution of *P. alecto* into the range of *P. poliocephalus* (Hall and Richards, 1991).

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In South East Queensland, the site of the current study, the steady loss of native forest since European settlement (Catterall and Kingston, 1993) continues to drastically reduce natural roosting and foraging habitat. Many flying fox camp sites are now located in small patches of remnant or regrowth forest in increasingly urbanised areas (Birt *et al*., 1998) and available roosting space is limited. However, despite the dense settlement of some camps, many flying foxes prefer to occupy a personal roosting space (Bradbury, 1977; Markus and Blackshaw, 2002) and try to maintain some distance from their nearest neighbours. In addition, each species of flying fox in a shared camp has a particular roosting location relative to the other species present (Birt and Markus, 1999). To date, broad scale observations on 'territorial' behaviour of this nature comprise the majority of published research on flying fox behaviour, and little information about the dynamics of social behaviour amongst flying foxes living in close proximity to each other is currently available.

Past studies have shown that much social interaction among flying foxes occurs seasonally. Early observations by Ratcliffe (1932) and Nelson (1965) and further described in Markus and Blackshaw (2002) showed that most social behaviour at a camp occurs within four general contexts: mother-infant interaction, juvenile play, territorial defense and courtship/mating. All of these contexts arise during the six-month period that begins with the bats' aggregation at maternity camps for the birthing season and culminates in the following mating season. For species resident in South East Queensland, this period coincides with the summer months of October to March. After a six-month gestation, the birthing season of October/November initiates a period of intense, affiliative interaction between females and their pups that largely excludes adult males (Markus and Blackshaw, 2002). During the later stages of this rearing period, the establishment and defense of male courtship territories marks the onset of adult social interaction that occurs within the two-month courtship/mating season in March/April. At the conclusion of mating, social interaction declines sharply as individuals disperse into smaller camps throughout their range for the winter. Social interaction during the remainder of the year is limited to occasional bouts of juvenile play and brief agonistic interactions during the defense of personal roosting or foraging space (Markus and Blackshaw, 2002).

Territoriality and courtship amongst flying foxes occur in sequence within the same season. Records of social interactions within a wild flying fox colony during the courtship/mating season are limited and have been based predominantly on two studies in the 1960s by Nelson (1965) and Neuweiler (1969). In Australia, detailed observations have focused exclusively on *P. poliocephalus* (Nelson, 1965). Nelson (1965) noted that sexual segregation occurred during the birthing season from September to December, and that males subsequently initiated contact with females in December/January. This observation suggests that males moved into the regular roosting spaces of the females, which accords with observations made by Neuweiler (1969) that male *P. giganteus* established and defended their territories around the roosting spaces of females. Female *P. giganteus* were frequently observed to 'escape' from a male and to land near another male, who would promptly proceed to court, and during the peak season mate with, the female (Neuweiler, 1969). While this aspect of female mate selection (or rejection) was not recorded in *P. poliocephalus* (Nelson, 1965), female *P. poliocephalus* were occasionally observed to initiate precopulatory behaviour with a male, an action which was never observed

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in *P. giganteus* (Neuweiler, 1969). Both researchers noted that the females' responses towards male mating overtures changed from active and vocal resistance initially to reduced resistance and greater willingness to mate during the peak mating season (Nelson, 1965; Neuweiler, 1969). The two studies indicate that there are subtle, but possibly important, differences in the interactions between males and females of different flying fox species during mating.

The present study focuses on the behaviour of *P. alecto*, one of many species whose social behaviour has not previously been examined in any detail. In addition to filling a substantial gap in knowledge about flying foxes in general and this species in particular, this information is fundamental as a baseline for the assessment of potential behavioral changes with changing resource availability in the future. Future research will reveal whether the on-going loss of roosting habitat leads to increased competition for roosting and courting space and therefore to increased aggression between con-specific flying foxes. The study examines the social interactions of adult *P. alecto* at a roost during the courtship/mating season, which represents the period of peak camp occupancy. Within the context of territoriality, specific aspects observed include the vigour of defense and aggression, and the study specifically tests the hypothesis that agonistic interaction during territorial defense is often ritualised and thus conserves energy and prevents injury to conspecifics. Within the context of courtship, particular emphasis is placed on aspects of monogamy versus polygyny, the reproductive history of courting females, and on the physical structure and duration of courtship sequences. In addition to the main foci, preliminary observations of interactions between sympatric populations of *P. alecto* and *P. poliocephalus* were conducted to gain an initial indication of competition for roost space between these two species.

Materials and Methods

Observations of territorial and courtship/mating behaviour were conducted in Brisbane, Australia, over two years and focused on the local courtship/mating period of February to late April of 1999 and 2000. Focal observations were made with the aid of binoculars at two colonies, Indooroopilly Island (27°31'S, 153°03'E) and Norman Creek (27°29'S, 152°60'E). At the more isolated Indooroopilly Island site, a two-week period of habituation preceded the commencement of data collection. The bats were judged to have been habituated and thus to behave normally when they no longer responded visibly to the observer's presence.

Observations of Territoriality

A territory was defined as a space that was defended by a male against male competitors and could be shared with one or more females or with several other un-paired males (i.e., a bachelor tree). Data collection of territorial behaviour commenced during first light, i.e., as soon as individual *P. alecto* became visible. The sky near the study section of the colony was visually scanned for individuals approaching in flight, and their landings at the camp were closely observed. Once a bat had landed in a tree, timing with a stopwatch commenced and the behaviour of neighbouring animals was observed. If the newly arrived bat was tolerated without vocalisation or pursuit, no recording of its landing was made and it was considered to be a resident (RM). If the incoming bat was physically pursued and/or took flight, it was considered to be an 'intruder' (IM) and the timing of the interval between its initial landing and its subsequent departure was recorded, along with the action of the defending bat (e.g., chase, hook, vocalise). Intrusion bouts were defined as the period from the arrival/landing of the intruding male to his departure. The observed size of a male flying fox's territory was measured in feet of branch length (vertical, horizontal and diagonal) and varied from approximately 5 to 22 'branch-feet' (bf), i.e., ~150–660 cm. This unit of measurement was considered most practical as it allowed the length of the flying fox (ca. 30–35 cm, i.e., one foot) to be used as a visual measure of branch length. This facilitated the approximation of territorial size from the distance of approximately 20 m from which it was made. The size of a territory was indicated by the proximity of the nearest male neighbour

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and was delineated at a point between the two males. It was not possible to determine any overlap of territories in the space between two males as territorial bouts generally involved a resident defending branch space against a foreign male, i.e., not a neighbor, who subsequently flew away. The duration of territorial defense bouts were not normally distributed and were thus analysed using a Mann-Whitney *U*-test.

Observations of Courtship and Copulatory (Mating) Behaviour

Observation on the pre-copulatory and copulatory behaviour of *P. alecto* also commenced post-dawn. The colony was visually scanned for any one of the following signs of courtship or mating: male approach of female, followed by sniffing and/or licking of her uro-genital area ('approach/sniff', 'u-g lick'); male direction of a continuous braying, donkey-like vocalisation at a female ('approach/scream'); female vocalisation at male and pushing him away with her wing ('push away'); or copulation as indicated by the copulatory dorso-ventral position of male. On observing any of the above indicators, timing commenced immediately and ceased only when one or both courting flying foxes adopted a resting position and ceased interaction with each other for more than a few minutes. A 'courtship sequence' comprised all interactive behaviours between a male and a female during courtship/mating up to the cessation of any interactions, and included grooming, vocalising, active rejections and copulation bouts. Sequences generally consisted of several 'courtship bouts', i.e., interactive behaviours between a male and a female up to, and including, a copulation/intromission attempt. Within a courtship sequence, the duration of each copulation bout was also recorded. Courtship sequence data were analysed using a Student's *t*-test. All calculations were performed with Statistica for Windows (StatSoft, 1995). In addition to detailed observations of courtship and mating, some notes were also made on the distribution of individuals in observed sections of the colony over time.

Results

Territorial Behaviour

Active territorial defense had commenced when preliminary observations began in late January, eight weeks prior to the onset of the mating season in late March. Both males and females were present at the camp and male *P. alecto* scent-marked their territorial branch space by rubbing their necks and shoulders along branches and tree trunks within this space. Scent-marking occurred throughout the day and particularly prior to the evening fly-out. In densely occupied trees, territories were small (i.e., 2–3bf), while in sparsely populated trees, territories were often larger (11bf+). Territories comprising several parallel branches measured many more branch-feet in size than a territory comprising only a single branch. Territorial defenses were only observed in response to encroachment along defended branches. Branches of separate territories were often widely spaced and not within reach of other branches above or below as is the growth pattern of many eucalypt trees in which flying foxes roost. The linear nature of territorial defense bouts may therefore have been a reflection of tree shape rather than of the linearity of territories *per se*.

A total of 62 territorial defense bouts in which a male landed in another male's territory were observed and recorded over two seasons. In 61 instances, the intruding male eventually flew off, while in one instance, the resident male appeared to depart. Territorial defense bouts were divisible into two categories: (i.) defense bouts involving physical contact between the resident and the intruder (13%; $n = 8$) and (ii.) defense bouts involving no physical contact between the two (87%; $n = 53$). Contact bouts involved the resident male hooking at, wrestling with or wing slapping the intruding male until the latter flew off. On one occasion, a violent wrestling bout resulted in the intruding male being pushed off the branch until he lost his footing and was forced to fly off. Defense bouts without physical contact involved the intruding male departing of his own accord without any prompting (4.8% of total bouts observed), after being approached or chased

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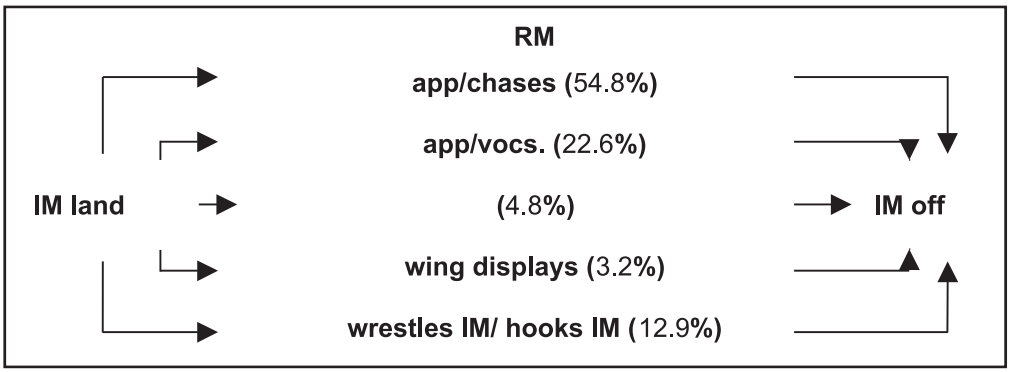


FIG. 1. Sequences of defense bouts (n = 62) during a male *P. alecto*'s defense of his territory during the mating seasons of 1999 and 2000. Abbreviations: IM — intruding male, RM — resident male, app — approach, voc — vocalising, wing disp — threatening wing display, hook — hooking opponent with thumb claws

by the resident male (54.8%) or after being threatened with a wing-display by the resident male (3.2%) (Fig. 1). Some defense bouts (22.6%) were accompanied by loud vocalisations of the resident male.

The analysis of territorial defense bouts was complicated by the fact that observations over time included multiple observations of at least two males and this increased the risk of a skewed outcome through non-independent observations. Known multiple observations of individuals were therefore analysed separately. The median (± quartile range) duration of the intrusion bout, i.e., the period between the landing of the intruding male and his departure, was 3 ± 4.5 s (range: 1–52; n = 46) when no contact occurred and 9 ± 2.0 s (range: 2.5–11; n = 5) when physical contact did occur. The duration of intrusion bouts appeared to be related to the size of the resident male's territory. Eight observations of territorial defense were made of a male defending an unusually large territory of several long branches (22bf) which appeared to increase the time it took for him to reach a male intruding at the edge of this territory. Indeed, comparisons of the duration of defense bouts of this male (16.5 ± 6.3 s; n = 8) with all other independent observations (i.e., by eliminating other multiples) (9 ± 8.7 s; n = 51) were highly significant (Mann-Whitney U-test, U = 56, Z adjusted = 3.30, $P < 0.001$).

Preliminary observations of sympatric populations of *P. alecto* and *P. poliocephalus* at the Indooroopilly Island camp yielded no evidence of aggression between the species, although individuals were regularly seen to share particular roost trees in areas of overlap within the camp. On one occasion, a male *P. poliocephalus* was observed to land in an all-male tree occupied only by *P. alecto* males. After being approached and sniffed by the closest *P. alecto* male, he was tolerated in the tree and continued to roost there for several days. In all other instances of roosting sympatry, individuals of both species occupied the same branches without any observed agonistic behaviours (author's unpubl. data).

Courtship/Mating Behaviours

The courtship/mating period of *P. alecto* extended over a period of approximately seven weeks in 1999 and nine weeks in 2000. Observations focused on the peak courtship period of March/April in both years. Courtship and mating comprised a large component of the diurnal activity patterns of the bats during this time. While the majority of visible males courted only

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a single female, several polygynous groups consisting of a male and up to four females were also observed. The presence of dependent offspring did not influence the nature of the females' relationships either towards monogamy of polygyny. Both lactating (i.e., females with current season's young; $n = 16$) and non-lactating females ($n = 21$) were observed in single pairs and polygynous groupings. Courting and mating consisted of a repetitive sequence of behaviours leading up to, and including, one or more copulation attempts. A total of 69 male courtship approaches were recorded over two seasons (Fig. 2). Of those, 32 consisted of approaches early in the season that did not lead to attempted copulation, and 37 comprised copulatory sequences, incorporating 135 copulation attempts, that were timed and analysed.

A mean (± SE) number of 3.8 ± 0.37 courtship bouts and copulation attempts were recorded per courtship sequence ($n = 34$). Courtship bouts lasted an average of 188.8 ± 11.36 s ($n = 123$) and copulation attempts within these bouts had a duration of 40.5 ± 3.03 s ($n = 135$). Of the couples observed courting, 16 females had juvenile young from the current birthing season (i.e., were lactating) while 21 had no current young (i.e., non-lactating). Comparisons of the courtship bout lengths of these two population sub-sets showed that the courtship bouts of lactating females were significantly longer with an average duration of 230.9 ± 22.16 s ($n = 53$) than those of the currently non-lactating females with an average of 158.5 ± 9.69 s ($n = 65$ — Student's *t*-test, $t = 3.18$, $d.f. = 116$, $P < 0.05$). Nevertheless, measurable differences were not detected in the number of bouts per courtship sequence (4.0 ± 2.00, $n = 15$ versus 3.8 ± 0.37, $n = 34$; $t = 0.33$, $d.f. = 47$, $P >> 0.05$) nor in the duration of copulations (45.6 ± 5.19, $n = 62$ versus 36.2 ± 3.43, $n = 73$; $t = 1.54$, $d.f. = 133$, $P > 0.05$). Males surrounded by multi-female groups were not observed to mate with more than one female during any observation session, leaving the dynamic of apparently polygynous groups unexplored.

Courtship sequences

All 69 courtship bouts were initiated by a male by approaching the female roosting closest to him with his head angled forward towards her uro-genital region ('approach/sniff'). No female approaches were observed. This initiation of pre-copulatory behaviour was met with either of two kinds of responses by the females — if tolerated, the female remained in the standard roosting position and the male proceeded to lick the female's vaginal opening. If not tolerated, the female responded by turning away from the male, beating at him with her wings, wrestling with him, mouthing/biting at him, pushing him away using her wrists or feet or by inverting to make her uro-genital area inaccessible to him.

Males persisted with attempts to access the females' uro-genital opening, licking it intensively for a period ranging from several seconds up to a minute (Fig. 3a) presumably to stimulate her to submit to copulation. Licking was then followed by attempts to turn the female or to move behind her to achieve a dorso-ventral alignment (i.e., the female's back towards the male's chest) for copulation. Females avoided male copulation attempts by persistently facing the male and making intromission impossible or by fending him off in a wrestling bout. Continued attempts to turn or move behind the female often resulted in mutual circling by both bats, one in pursuit and the other in avoidance.

Once alignment was achieved, the male restrained the female by biting into the fur on her scruff and by restraining her wings with his own. In the majority of instances observed, females struggled either

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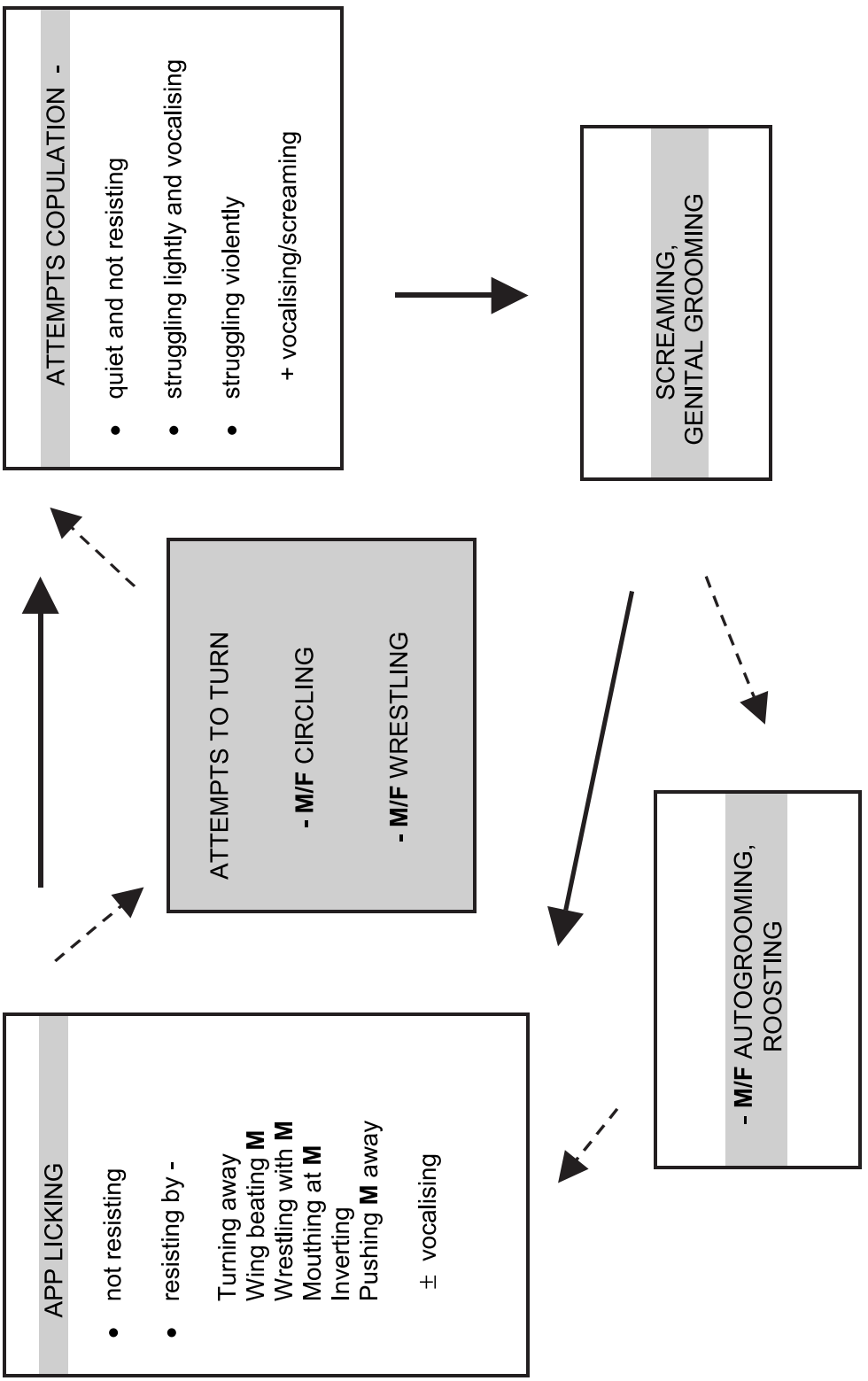


FIG. 2. Courtship sequence of *P. alecto*. Abbreviations: F — female, M — male, UG — urogenital. Arrows indicate sequential actions; stippled arrows indicate optional actions. Gray bars indicate male actions, dot points indicate female responses

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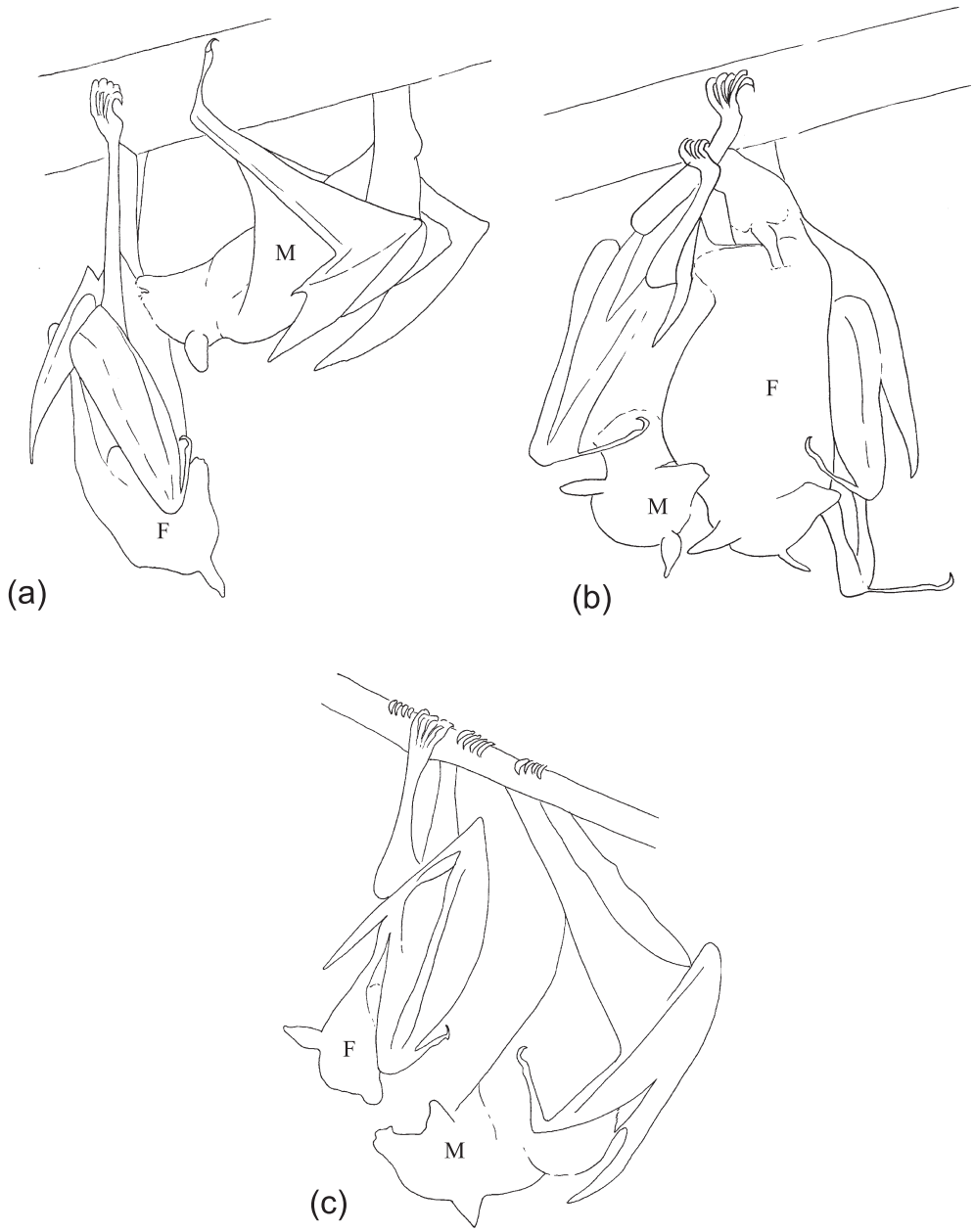


FIG. 3. Copulatory behaviour of *P. alecto*: (a) pre-copulatory licking ('approach/lick'); (b) copulation (intromission), (c) post-copulatory screaming of the male ('donkey call'). F — female, M — male

intermittently or continuously during attempts at intromission before releasing their foothold of the branch on which they had been roosting and grasping the males' legs for support instead. A male thus supported the weight of the female as well as his own during copulation (Fig. 3b). The female's reaction to being restrained varied from

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quiet submission to the more common response of struggling. Many females were heard to produce 'whooping' vocalisations during copulation. Occasionally, continued struggling during attempted intromission was so vigorous that the female slipped (presumably after releasing her foot-hold) and almost dropped to the ground.

Copulation attempts ranged in duration from a few seconds to a maximum of over three minutes and concluded with the sudden release of the female by the male. Males vocalised loudly (the 'donkey call') immediately upon release of the female (Fig. 3c) and then proceeded to groom/lick the penis. The female usually resumed roosting immediately but occasionally also groomed her genital region. Autogrooming or inactivity of one or both individuals signaled the end of a copulation bout and ultimately the end of the courtship sequence.

Up to 12 copulation bouts were observed per courtship sequence. Subsequent intromission attempts within a courtship sequence often decreased in duration, probably indicating the male's increasing fatigue. Courtship was further hampered in couples where the female had large offspring by her side. Juveniles of courted females were often observed to actively interfere in the mating process by pushing underneath the females' wing to suckle, and thereby loosening the hold of the male. In all observed instances, the female tended to the juvenile's demands, which undoubtedly contributed to the longer duration of courtship bouts of lactating females when compared to females without young. Many sequences were only observed partially because observations commenced at an indeterminate time into the sequence. The longest sequence observed lasted 37 min. and included six copulations lasting a total of 266 s. Intervals between copulation bouts within a sequence generally lasted 10–60 s before the male resumed the vaginal licking of the female and thereby initiated the next bout of courtship.

Discussion

Territoriality

Ritualised agonistic behaviour

The dispersal of intruders from a territory most often took the form of implied aggression rather than actual physical contact. No obvious injuries were inflicted on either defending or intruding males during observed territorial disputes. The male flying foxes' defense of a territory focused only on other males, and, as in other mammals such as elephant shrews, coyotes and gibbons (Poole, 1985), members of the opposite sex were tolerated and regarded as potential mating partners (Neuweiler, 1969). As in many primate species (Jolly, 1985), territoriality in *P. alecto* was mainly expressed as a stereotyped display of prowess. On recognising the resident male's intent to defend his branch space as indicated by his inclination towards, vocalisation at, or brief pursuit of the intruder, many intruders flew off immediately and did not wait for the resident to take up pursuit in earnest. This ritual reduced the energy expenditure of both males and minimised the injury of males in the colony.

Competition and mating aggregations

The maintenance of territories in any animal species indicates competition for a limited resource (Poole, 1985). While the determination of sex ratios is difficult in a large flying fox colony and no data exist, the few observed incidents of aggressive physical competition for females observed suggest either a fairly even distribution of sexes or a preponderance of sexually mature females compared to males. Both cases would provide an adequate resource of

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mating partners for the males. Female flying foxes reach sexual maturity in their second or third year (McIlwee and Martin, In press) and only semi-dependent young are exempt from the pool of potential mating partners. In the two colonies studied, the majority of flying foxes had partners, and aggregations of single males in bachelor trees gradually disappeared as the males presumably either left the colony or recruited a female mating partner by establishing a territory around her roosting space. The observation of a number of polygynous groupings also suggested that even sex-ratios may not result in all individuals finding a partner. The large number of less aggressive territorial invasions may serve as practice competition for younger or less successful males, who eventually leave the colony once all available females have been partnered. The low incidence of physical contact during male territorial defense in *P. alecto* confirmed the expectation of ritualised behaviour in this highly colonial species. Agonistic behaviour primarily took the form of non-contact pursuit and aggressive vocalisations.

The displacement of a 'resident' male *P. alecto* by a subsequently arriving 'intruding' male proved to be exceptional in that it only occurred once. The almost immediate departure of the resident on the arrival of the second male without any physical challenge by either individual suggested that the 'resident' male may in fact have been an intruder who had arrived at the territory prior to the actual resident. A mechanism by which a flying fox may identify a resident is by smell. An alternative explanation for the departure of the initial male is his displacement by a higher ranking male. In the absence of solid data about the structural hierarchy of *P. alecto* in a colony, both options remain hypotheses to be examined during future studies.

Definition of territory

Males used strategic scent-marking of branches and trunks to delineate a territory and to indicate their claim to any females within this space. Scent marking is commonly used to denote individual spacing in other mammals, for example amongst primates such as Hanuman langurs (Jolly, 1985). Previous studies of olfaction in mammals have suggested that scent-marking may enable an intruding animal to match the scent of a marked territory with the territorial owner (Gosling, 1983). In flying foxes, the use of territorial scent-marking had previously been observed in *P. poliocephalus, P. gouldi* (=*alecto*) and *P. scapulatus* (Nelson, 1965), and the secretion of musk also in the Indian *P. giganteus* (Neuweiler, 1969). However, in the latter species the function of this secretion was considered uncertain. Although Neuweiler (1969) noted that the secretion was strongest in males during the mating season, he did not observe the marking of territories and noted that 'neither within nor outside of the mating season did the secretion appear to attract or repel conspecifics' (Neuweiler, 1969: 175). As he saw the self-dousing of both males and females with secretion in the wild outside of the mating season, it is conceivable that in some instances Neuweiler observed the urine-bathing (e.g., Courts, 1996) of individuals as opposed to the sex-specific distribution of musk among males during the mating season. Urine spraying at the limits of a territory and over objects and vegetation has also been observed in red deer (Carranza *et al*., 1990), where its suggested function in scent-marking is yet to be tested through further research.

Courtship/Mating

The commencement of the mating period several weeks after the initial establishment of territories in late January was

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previously reported in *P. poliocephalus* by Nelson (1965). Copulation attempts amongst *P. alecto* commenced in mid-to-late March. After approximately 6–8 weeks of outright rejection of the males' advances, the females gradually reduced their resistance by occasionally tolerating pre-copulatory sniffing, licking of the genital region and mounting attempts. Resistance to copulation has also been observed in *Rousettus aegyptiacus* (Kulzer, 1972) and in *P. giganteus* (Neuweiler, 1969). Neuweiler (1969: 186) further noted that "not once did I observe that a female showed an interest in a male or initiated copulation". In contrast to mutual grooming observed in *P. poliocephalus* (Nelson, 1965), pre-copulatory grooming and genital licking were entirely unidirectional in *P. alecto*. Female *P. alecto* were not observed to groom males other than their own infants during or outside the courtship period.

The continued resistance of the females to mating prolonged the courtship and required the male to be highly motivated in addition to requiring physical stamina. Willingness to mate appears to be independent of the timing of ovulation, as *P. poliocephalus* are known to mate throughout March but females do not conceive until late April (Towers and Martin, 1985). The deliberate prolonging of courtship by female animals with high parental investment has been discussed by McFarland (1993) and has been interpreted as the female's strategy for testing a male's fitness. In the current study of *P. alecto*, active struggling of the female, pushing away of the male, loud vocalisations, and evasive body positioning to prevent intromission were routinely observed during courtship; in *P. giganteus,* continued resistance to copulation was observed for the duration of the mating season (Neuweiler, 1969). Thus, although female *P. alecto* were not observed to actively select a mate, the endurance and determination of the courting male was tested through the prolonged courtship ritual. Further studies of courtship would be useful to assess whether active mate-selection perhaps takes place during earlier stages of courtship not monitored during the present study.

In addition to assessing a male *P. alecto*'s fitness and determination to mate, the courtship process continued to challenge his physical strength and endurance throughout the mating period. This was particularly apparent during copulation. Male tried to control the female by biting deeply into the scruff of her neck, restraining her wings with their own to prevent flapping and eventually forcing her to release her foothold on the branch and to hold onto his legs for support. Scruff biting has also been observed in *R. aegyptiacus* (Kulzer, 1972), and the copulation of *P. alecto* accorded precisely with the reported manner of mating of *P. giganteus* (Neuweiler, 1969). Males were clearly advantaged when females were encumbered by suckling pups, as reflected by longer courtship and copulation bouts when compared to females without pups.

The courtship of *P. alecto* was very vocal and characterised by the females' 'whooping' vocalisation during copulation, and the persistent, loud male vocalisations (reminiscent of donkey braying) during courtship approaches and the end of each copulation bout. Loud female vocalisations during mating are also heard in species such as elephant seals (Cox and Le Boeuf, 1977), where the purpose is to intensify competition between males and to invite interference from stronger males during copulation. However, active interruption of intromission by other males in response to female 'whooping' has not been reported in flying foxes, and the function of this vocalisation during copulation remains unclear. Male 'braying' vocalisations, by comparison,

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almost always precede courtship approaches and appear to alert the female to the male's willingness to mate. During the peak mating period, even the slightest movement of a resting female elicited loud 'braying' directed towards her, leaving no doubt about the male's intentions.

A number of cues signal the completion of a successful copulation (as defined by male ejaculation) in other animals. Visual indicators may include the deposit of mating plugs, instant loss of erection on withdrawal by the male, and the cessation of further copulation attempts at least in the short term. Observations of *P. giganteus* showed that successful copulation is clearly indicated by a number of characteristics, including the male's release of the female without loud vocalisations, the instantaneous loss of penile erection and the visibility of seminal fluid on the female's vulva (Neuweiler, 1969). However, although extensive courtship and more than 134 copulations were observed over many weeks in the present study, no evidence of successful copulation was apparent at any time. Intromission inevitably concluded with the withdrawal of the erect penis and was accompanied by loud screams of the male. The cessation of courtship attempts generally appeared to be due to fatigue and was followed by a resting period. Neuweiler's (1969) observations of *P. giganteus* showed that successful copulations began to occur several weeks after the commencement of courtship and continued for four to six weeks before decreasing in frequency and success. The absence of these observations in the present study may reflect some aspect of the timing of the observation periods, which may inadvertently have preceded the period associated with successful copulations. *Pteropus alecto* dispersed from the colony within eight weeks of the commencement of mating; observations were conducted while mating dominated the activity patterns of the colony, and had ceased several days prior to the bats' departure. The early departure of the bats may suggest that the mating period of *P. alecto* is shorter than that of *P. giganteus* (Neuweiler, 1969), although this would not explain the apparently incomplete courtship process. However, observations of *P. poliocephalus* have shown that mating colonies may disperse spontaneously in response to flowering resource flushes elsewhere (P. Eby, pers. com.). As inter-colony movements of *P. alecto* within suburban Brisbane commonly follow local flowering patterns (own unpubl. data), this may explain the sudden departure of courting adults in the present study and suggest that successful mating occurred in another camp.

Observations of the *P. alecto* colony throughout the mating season revealed a consistent roosting pattern in the observed section of the camp. Couples and polygynous groups were distributed identically over many weeks, and this, in conjunction with the known territoriality of the bats, strongly suggested that specific animals showed site fidelity over time within the roost. Although visually unmarked, the many apparent 'pairs' of flying foxes suggested monogamy in a large section of the population. However, Neuweiler (1969) noted that the impression of monogamous pairings in *P. giganteus* was an artifact of constant roosting patterns, and that apparently 'monogamous' males mated with any female that entered their territory. Further observations of individually identifiable *P. alecto* are required to assess the sexual relationship between mating aggregations of that species.

The findings of the present study have shed some light on the social dynamics within a flying fox colony through a focus on territoriality and courtship. Male territories were shown to be established via scent-marking, and territorial defense against other males is largely ritualised and does not

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result in obvious injury. The relatively low levels of aggression suggested an adequate supply of mating partners, due either to relatively even sex ratios within the colonies, or to a preponderance of mature females in relation to males. Courtship was observed as a long and vigorous process and the male's advances were met with active female resistance over many weeks. This resistance appeared to reflect a sexual selection process by forcing males to display physical strength and an enduring determination to mate. The issue of partner choice and sexual selection remains somewhat unresolved, however, as males never appeared to fail the selection test and active female choice was not observed. A further finding of unresolved importance was the lack of evidence of successful copulations, despite many observations of courtship sequences and copulations. The results highlight the need for further field observations beyond the predicted courtship season and location, which are likely (based on observations of other flying foxes) to reveal both active partner choice and visual evidence of copulations. The absence of conflict between sympatric species indicated a general tolerance amongst flying foxes that facilitates the use of limited roosting space at a camp. As natural roosting habitat continues to decline and populations of flying foxes increase in rural and urban areas, the resulting pressure on resources may be expressed in a reduced tolerance of individuals in the future.

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