Behaviour of the Black Flying Fox Pteropus alecto: 1. An Ethogram of Behaviour, and Preliminary Characterisation of Mother-Infant Interactions

Authors: Markus, Nicola, and Blackshaw, Judith K.

Source: Acta Chiropterologica, 4(2) : 137-152

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/001.004.0203

Acta Chiropterologica, 4(2): 137–152, 2002
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Behaviour of the black flying fox *Pteropus alecto*: 1. An ethogram of behaviour, and preliminary characterisation of mother-infant interactions

NICOLA MARKUS[1] and JUDITH K. BLACKSHAW[2]

[1]*Veterinary Pathology and Anatomy, University of Queensland, St. Lucia, QLD 4072, Australia*
E-mail: nmarkus30@hotmail.com
[2]*School of Veterinary Science and Animal Production, The University of Queensland, St. Lucia, QLD 4072, Australia*

The black flying fox *Pteropus alecto* is one of four species of flying fox found on the Australian mainland. Little information exists about the specific behaviour of this species, and no framework for the study of its behaviour has yet been constructed. In the study reported here, two *P. alecto* colonies were observed at two day roosts in South East Queensland, Australia, between 1998–2000. Observations focused on solitary and social actions in general and on mother-infant interactions in some detail and led to the construction of an ethogram that defines each action structurally and functionally, describing accompanying vocalisations where appropriate. Diurnal activity patterns of *P. alecto* throughout the year consisted predominantly of roosting, grooming and sleeping, and involved little social activity. Social interactions were largely restricted to the seasonal contexts of the birthing/rearing period of October to March and the subsequent courtship/mating season of February to April. In all, 74 behavioural units were defined with the aim of facilitating further research and the implementation of effective conservation strategies for the species.

Key words: *Pteropus alecto*, Australia, behaviour, ethogram, birth, maternal interactions

INTRODUCTION

Flying foxes (Megachiroptera: Pteropodidae) are gregarious mammals that live in large colonies of hundreds, to several hundred thousand, of individuals on islands of the Indian Ocean, India, Pakistan, Nepal, Burma, South East Asia, Philippines, Indonesia, New Guinea, Australia and the western Pacific Ocean (Hall and Richards, 2000). Australia is home to seven species of *Pteropus*, four of which can be found on the mainland. Traditionally, flying foxes form large, diurnal aggregations (roosts/camps) amongst the foliage and the branches of trees (Ratcliffe, 1932; Kunz, 1982; Pierson and Rainey, 1990) in forests or forest remnants (Nelson, 1963). In recent decades, however, diminishing forests have led to the urbanisation of many roost sites by encroaching development (Birt *et al*., 1998). The resulting proximity of flying foxes to humans in residential, industrial and rural areas has led to increasing conflict. Issues arising from noise, odour, fecal pollution and perceived disease-threat associated with large, urban camps, and the bats' utilisation of cultivated fruit, continue to require

careful management. However, as yet, a lack of detailed information about the behaviour of flying foxes, and the absence of a methodological framework in which to study them, complicate both the management and conservation of this group of ecologically important wildlife.

Unlike Microchiroptera, flying foxes in general do not echolocate; excellent vision and acute hearing and olfaction facilitate the expression of a wide range of behavioural responses to sensory perceptions. Sight is the primary means of their navigation (Moehres and Kulzer, 1956), and the similarity of the visual cortex of flying foxes to that of lemurs suggests either a common ancestry between Megachiroptera and Primates (Pettigrew, 1986) or the convergent evolution of the two (e.g., Lapointe *et al*., 1999; Van Den Bussche *et al*., 2002). While the optimum auditory sensitivity of *P. scapulatus* has been shown to range from 2–11 kHz (Calford and McNally, 1987), Nelson (1963) found that the majority of flying fox communication takes place at between 4–6 kHz at which sound carries well and is not deflected by small obstacles (Calford and McNally, 1987). The acute auditory awareness of flying foxes can be observed by their constantly moving pinnae and by their fast responses to foreign sounds such as rustling, cracking or grating (Moehres and Kulzer, 1956). Excellent hearing is also vital to the intraspecific communication between individuals. A study of the vocal repertoire of flying foxes showed that their diversity of more than 25 individual is equaled only by primates (Nelson, 1964), and a recent study identified five distinct call types in *P. poliocephalus* (Christesen and Nelson, 2000). Reactions to optical, auditory as well as to physical and chemical stimuli lead to a wide range of physical responses that are classifiable into behavioural units.

The behaviour of flying foxes is commonly described as a function of the specific ecological context in which it occurs. Within the genus *Pteropus*, social and physical aspects of reproductive behaviour (e.g., courtship, mating and parturition) have been outlined for the Australian *P. poliocephalus* (Ratcliffe, 1932; Nelson, 1963, 1965; Martin *et al*., 1987; Puddicombe, 1990; Martin, 1998), *P. scapulatus* (Ratcliffe, 1932) and *P. alecto* (Nelson, 1963; Vardon and Tidemann, 1998), and internationally for *P. rodricensis* (Kunz *et al*., 1994), *P. livingstonii* (Courts, 1996) and *P. giganteus* (Bhatt, 1942; Neuweiler, 1969). Maternal care has been described in *P. poliocephalus* (Nelson, 1963, 1965), *P. giganteus* (Neuweiler, 1969), *P. rodricensis* (West and Redshaw, 1987) and *P. livingstonii* (Courts, 1996), while aggressive defense of roosting and/or foraging sites has been observed in *P. poliocephalus* (Nelson, 1965; Puddicombe, 1990), *P. rodricensis* (Young and Carroll, 1989), *P. livingstonii* (Courts, 1996) and *P. giganteus* (Neuweiler, 1969).

Apart from large-scale ecological studies, most behavioural observations to date have been conducted in captive settings. Very few detailed accounts exist of the behaviour of flying foxes in the wild. The most comprehensive studies of this nature have focused on *P. giganteus* in India (Neuweiler, 1969) and on *P. poliocephalus* in Australia (Nelson, 1965). The only published ethogram of flying fox behaviour to date was based on the observations of captive *P. livingstonii* at Jersey Wildlife Preservation Trust (Courts, 1996). No comparable frame-work for the observation of flying foxes in their natural environment has yet been published. The aim of this study was to describe in detail all behavioural 'units' observed at two camps of black flying foxes (*P. alecto*) in suburban Brisbane, Australia, as a basis for further detailed study of the behavioural patterns of flying foxes.

Material and Methods

Observations of bats took place at two Brisbane colonies, Indooroopilly Island (27°31'S, 53°03'E) and Norman Creek (27°29'S, 152°60'E), throughout 1998–2000. Around 150 bats were observed at the former site and 120 at the latter for a total of over 65 hours. To determine the optimal daily time period(s) for behavioural observations (i.e., peak solitary/social activity periods), preliminary observations were conducted over a number of weeks and a diurnal activity profile was established by observing the camp at Indooroopilly Island for one entire day from fly-in at first light until fly-out at dusk. Once dawn was established to be the peak predictable activity period at the roosts, observations focused primarily on this period. However, observations were also made at other times of day, and additional nocturnal observations were made of juveniles that remained in camp once adults flew out dusk, and of adults foraging away from the camp sites.

Detailed accounts of social behaviour were obtained during the birthing (November) and mating (January-April) seasons of the bats in the summer months of 1998/99 and 99/00. Observations were abandoned during periods of heavy rain, during which all activity ceased. Behaviours were classified either as solitary or social postures or actions. Solitary behaviour is definedas that which is performed by a single bat without apparent interaction with, or effect on other individuals. Behaviour is considered social if it involves two or more animals and is directed away from the active individual, even if no physical contact is involved. The construction of the ethogram follows Lehner (1979) and Jensen *et al*. (1986). Units of behaviour are ordered contextually – solitary units are separated into roosting, stationary actions, locomotion, auto grooming and feeding, and social units are divided into four categories – territoriality, courtship/mating, birthing/maternal interactions and play behaviour. In addition, the observed behaviours of *Pteropus alecto* could be divided into individual behavioural units (postures and actions), physical aspects of these units and the context(s) in which these behaviours took place (see Table 1). In situations where behaviours were commonly accompanied by vocalisations, a description of the vocalisation is included. As the contexts of territoriality and courtship are described in detail elsewhere (Markus, 2002), the current results focus on solitary activities and social behaviour in the contexts of birthing and mother-infant interactions.

Results

Solitary (Non-Social) Behaviour

Roosting

The diurnal activity patterns of *P. alecto* consisted predominantly of the solitary activities of roosting, sleeping and grooming. Although the bats were awake for extensive periods of the day (as indicated by their open eyes), most roosted inactively and reacted only to an occasional disturbance by sharply turning towards it. Much activity was governed by subtle variations in weather. During cooler parts of the day such as early in the morning and during cloudy periods, sudden exposure to direct sunlight resulted in the opening and stretching of wings. During hotter periods and in the middle of the day, wing-fanning decreased when a breeze picked up and increased when it dropped. Reactions of individuals varied with the level of their exposure to the elements within the roost. Flying foxes in the tops of trees were at once more likely to be exposed to sun during cooler periods and to breezes during hotter periods than individuals that roosted amongst denser vegetation and lower amongst branches and foliage. Heavy rain resulted in the cessation of all activity and the bats roosted with wings folded across their bodies.

Grooming

Individuals were observed to groom thoroughly following their return to camp in the morning and repeatedly throughout the day. Morning grooming activity was often triggered by the first rays of sun reaching bats in the tops of trees and comprised of extensive and thorough cleansing of all body surfaces. These activities required considerable dexterity. Rapid motions of the tongue and foot claws were used to lick, scratch and comb larger surfaces such as

the front of the body ('general groom') and the face, and the tongue was also used to clean crevices between toes and wrist bones. Particular care was taken during the cleaning of the wings ('wing groom'), which involved vigorous licking and the pulling of the extended wing over the head and scapular region. Slower and more deliberate movements of the claws were used to clean ear canals ('ear groom') and teeth ('tooth groom'). In males, prolonged genital grooming frequently resulted in an erection of the penis.

Once settled in position (e.g., 'hang relaxed'), *P. alecto* rarely moved about during the day unless disturbed by noise, sudden activity near the camp or perceived 'predators' such as large crows or humans. Most disturbances elicited responses from only a few individuals as reflected by an adjustment in roosting position ('hang tense'), a visual assessment of the threat ('sway alert') and a continued fixed gaze in the direction of the threat. Assessments of the perceived threat resulted variously in the resumption of relaxed roosting or in the elicitation of a shrill alarm call from one or more individuals roosting at the periphery of the colony. The latter reaction often resulted in a general scrambling (e.g., using 'climb') of individuals away from the direction of the threat and sometimes in 'take-off' and 'flight'. Individuals returned to their roosting positions and resumed roosting after periods of 10–20 minutes once the disturbance/threat had ceased. Other diurnal short distance movements ('shuffle') increased during the mating season, while brief, circular flights within the camp were often observed on very hot days. On several occasions, bats were observed to fly low and open-mouthed across the water surface of the river adjoining the camp at fly-out, resulting in the scooping up and drinking of water.

Distribution and individual spacing within the roost

Although specific rank-indicative behaviours and their possible relationship to roost site location were not identified in the present study, the camps observed had highly similar distributions of *P. alecto* throughout both seasons. Individuals roosted 30 cm apart on average, and stronger tree branches housed up to a dozen bats. Most remained in the same locations for the entire summer observation periods. Specific areas within the roost consistently contained particular social groupings such as an all-male tree, a sub-adult section, and sections accommodating mostly females with young and small polygamous (harem) groups. Similarly, specific sites along individual branches were continuously occupied by animals of the same sex and body size which were therefore assumed to be the same individuals. In the smaller camp at Norman Creek, several branches accommodated only single, male individuals. This was particularly evident prior to the onset of the mating season. Densely populated sections of the Indooroopilly Island camp showed similarly consistent groupings that contained larger numbers of animals. Distributions of flying foxes remained comparable over time even when other potential roosting sites were unoccupied.

Social Behaviour

The social behaviour occurred in two distinct seasonal contexts: birthing/rearing (November–February) and courtship/mating (March–April), with some overlap between these seasons around February/March. The period following the formation of maternity or summer camps for the birthing of young focused almost exclusively on the interactions between females and their infants. The mating season, by contrast, simultaneously marked the period of

peak agonistic interaction between males and peak interaction between the sexes at the camp.

General territoriality and recognition of individuals

Agonistic behaviour characterised the defense of courtship territories by adult males during the mating season. At other times of year, territorial behaviour was limited to short interactions during the dawn fly-in period. While some individuals landed immediately at their chosen roosting location, many were forced to traverse the roost spaces of neighbouring bats to reach their own. This usually resulted in aggressive vocalisations and occasional 'hooking' from bats defending their section against the intruder. Once at the correct location, neighbouring animals were observed to sharply face and bend in the direction of ('lean towards') the new arrival, apparently for the purpose of olfactory recognition. Other social interactions at the roosts were generally limited to short, vocal outbursts if the wing-stretching of one individual resulted in accidental contact with a roosting neighbour.

Mother-infant interactions

Parturition.—Births occurred from late October to late December and increasing numbers of females were seen with small pups underwing. Few parturitions were clearly observable. One parturition at the roost was observed almost in its entirety in the morning between 8.30–9.00 am but others may also have occurred at other times of the day. During labour, the female remained in the standard, vertical roosting position and only occasionally bent forward to vigorously lick her uro-genital region ('vaginal licking'). No obvious contractions were visible to the observer. The birth occurred in three distinguishable phases, the first delivering the head, the second the remaining body and the third the placenta. A quadrupedal 'cradling' position was adopted just prior to each delivery phase and again prior to the expulsion of the placenta. Delivery was accompanied by a smooth transition from the quadrupedal position to the normal, head down roosting position ('hang relaxed') which allowed the female to support the neonate with her wings and move it towards one of her two teats. Once attached to a teat, the female immediately proceeded to vigorously lick the infant ('infant groom') to remove birthing fluids and presumably to stimulate it.

Early infancy.—Associations between females and their offspring were the most affiliative interactions within the camps. Physical contact between mother and infant remained uninterrupted for the first three to four weeks after birth. During the first four weeks of life, infants remained covered by the wings of the mothers for much of the day. Female *P. alecto* were observed to thoroughly lick the bodies, heads and wings ('infant groom') of their young several times a day. As early as during the first two weeks of life, pups were physically active and were often observed attempting to flap their wings beneath those of their mothers. Females accommodated energetic infant behaviour and either opened and relaxed their wings to facilitate the infant's movement or firmly refolded them to subdue the infant. During the first four weeks, pups continued to cling to the females even in flight and were carried to the adult's nocturnal foraging sites.

Late infancy.—From approximately four weeks of age, infants were left roosting in the camp at night while adults foraged throughout the urban landscape. Adult bats, presumed to be females by their subsequent actions in seeking out pups, returned to the roost intermittently throughout the night. After spending most of the night roosting in silence, infants could be heard uttering shrill 'chirrup' calls whenever an adult

returned to camp during the night and in the morning. On landing near a young, the female and the infant immediately moved towards each other and the female proceeded to sniff the young before embracing it with her wings. No males were ever observed interacting with young in this way. During the following weeks, young, non-flying individuals were seen to move about the camp at night and occasionally aggregated in small clusters in the absence of the adult bats. Individuals were seen moving along branches by 'shuffling' and 'climbing', and later in the season by covering short distances in flight. Due to the difficulty of observing behaviour in densely foliated roosts at night, regular observations of young ceased at this point of their development. However, incidental observations of young *P. alecto* on several occasions revealed actions interpretable as play behaviour. Pairs of young males were occasionally observed to wrestle silently ('mock wrestling') by mouthing ('mock-biting') at each others faces and wings while pushing or pulling each other with folded wings. This action differed from observed territorial disputes by the absence of accompanying vocalisations, and by its prolonged and repeated occurrence that did not culminate in the departure of either individual. Individuals remained at close proximity to each other and often wrestled with their chests pressed against each other for several minutes.

Discussion

Solitary Behaviour

Distribution and individual spacing within the roost

The majority of solitary actions and postures observed in *P. alecto* appeared to be similar to those observed in other species. The consistent distribution of *P. alecto* within the camp suggested that individuals were loyal to established roost sites over time. Although individual flying foxes were not marked for visual identification, observations concurred with those of other species with particular natural markings (*P. giganteus, P. poliocephalus*) that have previously been observed roosting in the same positions at a roost over long periods of time (Neuweiler, 1969; P. Eby, personal communication). Neuweiler (1969) noted that, in the absence of disturbance, individual *P. giganteus* returned to the same roosting position over many weeks. Roosting positions of this species within a colony were thought to reflect a vertical rank-order, with the most dominant animals occupying the safer, upper branches, and weaker and younger males (recognisable by markings specific to younger individuals) the lower parts of the trees (Neuweiler, 1969). The maintenance of a personal roosting space appears to be typical for most species of *Pteropus* and many other bats (Bradbury, 1977). Based on observations to date, the marking of individuals for observation purposes remains at once a challenging aspect of flying fox research and one that promises to reveal some pivotal aspects of the social order of *Pteropus*.

Grooming

The remarkable dexterity displayed by flying foxes while grooming, and the regular bouts of grooming activity observed throughout the day, served a number of functional outcomes. In addition to the removal of food remnants accumulated during nocturnal foraging bouts, wing grooming releases sebum from glands at the base of the vibrissae and distributes lipid droplets produced by the epidermis across the wing membrane (Crowley and Hall, 1994). This action conditions the membrane and simultaneously helps to prevent the build-up of bacteria and fungal spores on sections of membrane that are subject to

limited air-flow during roosting (Crowley and Hall, 1994). The slow and deliberate movements of the foot claws used by *P. alecto* to clean ear canals and teeth are considered to be particular to flying fox grooming (Neuweiler, 1969). The observation of prolonged penile grooming concurred with similar observations on *P. giganteus* by Neuweiler (1969) and *P. poliocephalus* by Nelson (1965) and Puddicombe (1990). In *P. alecto*, grooming of the penis was a particular feature of the courtship/mating cycle (Markus, 2002) and occurred at the conclusion of each copulation bout. Nelson (1965) considered penile grooming in general to have a masturbatory function, but genital grooming in the present study never led to ejaculation.

Social Behaviour

General territoriality and recogition of individuals

Outside of the contexts of birthing, maternal behaviour (rearing) and courtship, social interactions within the flying fox colony were largely non-tactile and served mainly to distinguish individuals within the colony. The action of briefly leaning towards a new arrival at a roost, for example, was also observed in *P. poliocephalus* (Nelson, 1965) and *P. giganteus* (Neuweiler, 1969) and effects the olfactory identification of the individual. This action was also observed between female and infant *P. alecto* when females returned to the roost at dawn. Once all individuals had returned to their respective roosting positions, general activity ceased unless disturbances occurred to the colony as a whole or to the roosting space of individual *P. alecto*.

Mother-infant interactions

The formation of maternity or summer camps for the birthing of young has been well documented in the past (Ratcliffe, 1932; Nelson, 1965; Parry-Jones and Augee, 1992). Following the aggregation of females in early October, births of *P. alecto* in Brisbane occur from late October to late December, slightly later and more prolonged than the late September to late October period observed by previous authors (e.g., Ratcliffe, 1932; Nelson, 1965).

Parturition.—The initial onset of labour in *Pteropus* involves few signs of uterine contractions (West and Redshaw, 1987) and was not detectable in the current study. Once observable, the parturition postures adopted by female *P. alecto* were typical for the birthing process of *Pteropus*. The quadrupedal (sometimes tripedal) 'cradling' position adopted by *P. alecto* just prior to delivery and again prior to the expulsion of the placenta has also been observed in *P. rodricensis* (West and Redshaw, 1987; Kunz *et al*., 1994), *P. poliocephalus* (Nelson, 1965) and *P. scapulatus* (G. M. O'Brien, pers. comm.). A horizontal delivery position, differentiated only by the female's widely-spread legs, has also been described for *Cynopterus sphinx* (Ramakrishna, 1950, cited in Martin, 1998) and *P. poliocephalus* (Martin, 1998).

During delivery, pauses of various lengths have been observed in a number of species. Between ten minutes (Nelson, 1965) and several hours (average: 50 minutes) may elapse between the delivery of the head and the body of *P. poliocephalus* (Martin *et al*., 1987; Martin, 1998), and an interval of at least forty-five minute was previously observed in *P. alecto* (M. Graydon, unpubl. data). A much longer interval of over sixteen hours was observed in a captive *P. scapulatus* between the first stage of parturition mid-afternoon and the delivery of the infant the following morning (N. Markus, personal observation). Martin *et al*. (1995) refer to the delivery of pups in two stages as 'punctuated parturition'; M. Graydon (unpublished data), however,

describes parturition in three phases, including the onset phase (*in-utero* alignment of the foetal head and its emergence at the vaginal opening), the quiescent phase (emergence of the head, pause, and the next major contraction) and the expulsion phase that culminates in the delivery of the foetus.

Post-partum expulsion and consumption of the placenta in *P. alecto* accorded with observations of captive *P. rodricensis* (West and Redshaw, 1987), *P. giganteus* (Neuweiler, 1969) and *P. poliocephalus* (Martin *et al*., 1987). In the latter species, the placenta was often shared with other adults (Martin *et al*., 1987). Records of unassisted placental delivery in the above-mentioned species differed from observations by Kolb (1972) on *M. myotis*. In that species, placental delivery was actively aided by the newborn which hung independently shortly after delivery and moved away from its mother while still attached to the umbilical cord, thus placing tension on the cord and encouraging the expulsion of the placenta. The exceedingly slow mastication of the placenta by female *P. alecto* accorded with West's and Redshaw's (1987) observations that *P. rodricensis* appeared to find the placenta 'a difficult item to eat'. A delay of 75 minutes between a birth and the delivery of the placenta in the present study compared with a range of five minutes to nearly two hours recorded for *P. rodricensis* (West and Redshaw, 1987). The function of this prolonged connection of the infant to its mother via the umbilical cord has been proposed to be that of a safety rope, preventing the newborn from falling irretrievably immediately after birth (Kolb, 1972; M. Graydon, unpublished data). The mechanism of the infant flying foxes' suckling is likely to contribute to the expulsion of the placenta as it does in other mammals (West and Redshaw, 1987).

Early infancy.—The uninterrupted physical contact between *P. alecto* mothers and infants during the first three to four weeks after birth appears typical for megachiropterans (Nelson, 1965; Neuweiler, 1969; Kulzer, 1972; Puddicombe, 1990). Unlike young *M. myotis* which are left at the roost immediately after birth (Kolb, 1972), new-born *Pteropus* remain attached to the females in flight and accompany them on their nocturnal foraging forays. At the dusk fly-out, female *P. alecto* were observed to carry their pups tucked tightly to their ventral surface. During this early period, females maintain scrupulous hygiene and dispose of the excreta of their infants by ingestion (Neuweiler, 1969). Meticulous care of young is also the norm in many microchiropterans, including *Myotis lucifugus*, *Antrozous pallidus* and *Phyllostomus hastatus* (Bradbury, 1977). Early activity such as wing-flapping in *P. alecto* pups was also seen in *P. giganteus* from about two weeks of age (Neuweiler, 1969) and initiates the development of flight muscles.

Late infancy.—From approximately four weeks, infant flying foxes (*P. alecto*, *P. poliocephalus* and *P. giganteus*) are left alone in the camp at night after the adults fly out at dusk to forage (Nelson, 1964, 1965; Neuweiler, 1969). Observations of *P. alecto* infants left scattered throughout the camp contrasted with Nelson's (1965) observations of infant *P. poliocephalus* that were left collectively in one 'nursery' area of the camp. An aggregation of young *P. alecto* was observed once older pups became increasingly mobile and moved around the camp by climbing and short flights between branches. As in *P. poliocephalus*, the return of the female *P. alecto* triggered high-pitched, trilling 'location calls' (Nelson, 1964) from the infants that alerted the females to their whereabouts. According to Kulzer (1972), location calls of young *Rousettus aegyptiacus* were not sufficiently distinctive to allow each mother

to recognise her own offspring and highlighted the importance of the olfactory identification (i.e., 'lean towards') also seen in the present study. Neuweiler (1969) similarly observed female *P. giganteus* to push away and reject calling young other than their own after briefly sniffing their neck region. Olfaction continued to play a vital role in the identification of individuals in the adulthood of *P. alecto* and featured prominently in the territorial defense and courtship contexts (Markus, 2002).

The very limited observations of play in young *P. alecto* were likely to be reflective of the young age of the pups observed rather than of the rarity of this behaviour. Formal observations concluded towards the end of the mating season of both years, and incidental observations of young males mock-wrestling were made later in the year in July. Play behaviour in flying foxes has been described by Neuweiler (1969) as the practicing of aggressive and sexual behavioural patterns characterised by an absence of vocalisations. Neuweiler (1969) interpreted this behaviour in *P. giganteus* to contribute to the establishment of rank amongst juvenile animals as he observed only young males performing this type of play. No female play behaviour was observed in the current study. Future detailed studies of the play behaviour of young *P. alecto* are needed to fully explore the role of these behaviours in their social development.

The ethogram presented here represents the first detailed description of the behaviour of *P. alecto* recorded during intensive observation periods over two years. Rather than as a finite catalogue of behaviour (Appendix), it should be used as a base index to be expanded and amended by future research. Many aspects of behaviour, such as foraging and social interactions at foraging sites warrant further extensive investigation and will be vital to increasing our understanding of flying fox behaviour and facilitate their conservation in the future.

Acknowledgements

We are deeply grateful to Dr. Les Hall for his moral and technical support throughout this study, and to Gary Godbold and Rod Williams for their assistance with constructing a viewing platform at Indooroopilly Island. We also thank two anonymous reviewers for comments on the manuscript. This research was supported by a University of Queensland Graduate Award and the Australian Geographic Society.

Literature Cited

Bhatt, J. R. 1942. On the mating of flying-foxes (*Pteropus giganteus*). Journal of the Bombay Natural History Society, 43: 514–516.

Birt, P., N. Markus, L. Collins, and L. Hall. 1998. Urban flying-foxes. Australia Nature, 26(2): 55–59.

Bradbury, J. W. 1977. Social organization and communication. Pp. 1–72, *in* Biology of bats, Vol. 2 (W. A. Wimsatt, ed.). Academic Press, New York, 651 pp.

Calford, M. B., and K. I. McNally. 1987. Hearing in flying-foxes (Chiroptera: Pteropodidae). Australian Mammalogy, 10(2): 97–100.

Christesen, L. S., and J. Nelson. 2000. Vocal communication in the grey-headed flying fox *Pteropus poliocephalus*. Australian Zoologist, 31: 447–457.

Courts, S. E. 1996. An ethogram of captive Livingstone's fruit bats *Pteropus livingstonii* in a new enclosure at Jersey Wildlife Preservation Trust. Dodo, Journal of the Wildlife Preservation Trust, 32: 15–37.

Crowley, G. V., and L. S. Hall. 1994. Histological observations on the wing of the grey-headed flying fox (*Pteropus poliocephalus*) (Chiroptera: Pteropodidae). Australian Journal of Zoology, 42: 215–231.

Hall, L. S., and G. C. Richards. 2000. Flying foxes: fruit and blossom bats. University of New South Wales Press, Sydney, 135 pp.

Jensen, P., B. Algers, and I. Ekesbo. 1986. Methods of sampling and analysis of data in farm animal ethology. Birkhaeuser Verlag, Basel, 86 pp.

Kolb, A. 1972. Birth of a bat. Image Roche Medical Photo Reports, 49: 5–13.

Kulzer, E. 1972. African fruit-eating cave bats: Part 1. African Wild Life, 23(1): 38–46.

KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55, *in* Ecology of bats (T. H. KUNZ, ed.). Plenum, New York, 425 pp.

KUNZ, T. H., A. L. ALLGAIER, J. SEYJAGAT, and R. CALIGUIRI. 1994. Allomaternal care: helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera: Pteropodidae). Journal of the Zoological Society of London, 232: 691–700.

LAPOINTE, F. J., G. BARON, and P. LEGENDRE. 1999. Encephalization, adaptation and evolution of Chiroptera: a statistical analysis with further evidence for bat monophyly. Brain, Behavior and Evolution, 54: 119–126.

LEHNER, P. N. 1979. Handbook of ethological methods. Garland STPM Press, New York, 403 pp.

MARKUS, N. 2002. Behaviour of the black flying fox *Pteropus alecto*: 2. Territoriality and courtship. Acta Chiropterologica, 4: 153–166.

MARTIN, L. 1998. Posture and pauses during parturition in flying-foxes (Genus *Pteropus,* suborder Megachiroptera). Australian Zoologist, 30: 437–442.

MARTIN, L., P. A. TOWERS, M. A. MCGUCKIN, L. LITTLE, H. LUCKHOFF, and A. W. BLACKSHAW. 1987. Reproductive biology of flying-foxes (Chiroptera: Pteropodidae). Australian Mammalogy, 10(2): 115–118.

MOEHRES, F. P., and E. KULZER. 1956. The orientation of flying foxes (Chiroptera-Pteropodidae). Zeitschrift für vergleichende Physiologie, 38: 1–29.

NELSON, J. E. W. 1963. The biology of the flying-fox (Genus *Pteropus*) in south-eastern Queensland. Ph.D. Thesis, University of Queensland, Brisbane.

NELSON, J. E. 1964. Vocal communication in Australian flying-foxes (Pteropodidae; Megachiroptera). Zeitschrift für Tierpsychologie, 21: 857–870.

NELSON, J. E. 1965. Behaviour of Australian Pteropodidae (Megachiroptera). Animal Behaviour, 13: 544–557.

NEUWEILER, G. 1969. Verhaltensbeobachtungen an einer indischen Flughundkolonie (*Pteropus g. giganteus*, Bruenn.). Zeitschrift für Tierpsychologie, 26: 166–199.

PARRY-JONES, K. A., and M. L. AUGEE. 1992. Movements of grey-headed flying-foxes (*Pteropus poliocephalus*) to and from a colony site on the central coast of New South Wales. Wildlife Research, 19: 331–340.

PETTIGREW, J. D. 1986. Flying primates? Megabats have the advanced pathway from eye to midbrain. Science, 231: 1304–1306.

PIERSON, E. D., and W. E. RAINEY. 1990. The biology of flying foxes of the genus *Pteropus*: a review. Biological Report, 90(23): 1–14.

PUDDICOMBE, R. 1990. Social structure and behaviour of the grey-headed flying fox. Pp. 42–46, *in* Flying Fox Workshop Proceedings (J. M. SLACK, ed.). Wollongbar Agricultural Institute, Wollongbar.

RATCLIFFE, F. N. 1932. Notes on the fruit bats (*Pteropus* spp.) of Australia. Journal of Animal Ecology, 1: 32–57.

VAN DEN BUSSCHE, R. A., S. R. HOOFER, and E. W. HANSEN. 2002. Characterization and phylogenetic utility of the mammalian protamine P1 gene. Molecular Phylogenetics and Evolution, 22: 333–341.

VARDON, M. J., and C. R. TIDEMANN. 1998. Reproduction, growth and maturity in the black flying-fox, *Pteropus alecto* (Megachiroptera: Pteropodidae). Australian Journal of Zoology, 46: 329–344.

WEST, C. C., and M. E. REDSHAW. 1987. Maternal behaviour in the Rodrigues fruit bat *Pteropus rodricensis*. Dodo, Journal of the Jersey Wildlife Preservation Society, 24: 68–81.

YOUNG, J. A., and J. B. CARROLL. 1989. Male-female associations in (the) captive Rodrigues fruit bat *Pteropus rodricensis*. Dodo, Journal of the Jersey Wildlife Preservation Trust, 26: 48–60.

Received 30 January 2002, accepted 07 October 2002

APPENDIX. An ethogram of the behaviour of *Pteropus alecto* at a day roost

Behavioural Unit	Description	Context	Vocalisations
	Roosting		
1. Hang relaxed	Bat hanging bipedally or monopedally with wings folded across body or loosely by sides of body	Standard roosting position	
2. Hang alert	Attentive roosting position — body relaxed, eyes open and ears directed towards a source of interest	E.g., approaching observer, predator	
3. Hang tense	Knees are angled giving an inverted 'hunched' appearance; wings folded by sides of body and slightly pulled back; head and ears inclined toward direction of perceived threat; often leads to 7. Note: Gradients of stress may be reflected by the angle of the knee and the degree of contraction of the leg muscles. Extreme fear and avoidance was observed in captive *P. alecto* to result in a hunching of the entire body upwards and towards the ceiling of the cage	Stress or alarm, e.g., approaching observer, predator	
4. Wing droop	Roosting while drooping one wing downward and grasping branch with other thumb for extra support	Thermoregulation	
5. Lean away	As in 3., but with torso leaning away from direction of perceived threat	Avoidance	
6. Lean towards	Wings folded by sides or across body; body actively inclined forward, apparently to identify olfactory signals	E.g., identification of another bat	
7. Sway alert	Knees angled and body hunched as in 3.; head and body moving from side to side; wings relaxed, folded across body or extended forward; ears and eyes directed toward source of interest	Perceived threat, e.g., approach of large bird or ground predator	
8. Swivel	Rotation of body up to 180° while roosting relaxed (1.) and monopedally	Rejection of another bat; maximizing exposure to sun in winter	
9. Turn	Rotation of body while roosting alert (2.) and bipedally with wings folded loosely by sides		
10. Sleep	Roosting position as in 1.; wings folded across body, head tucked in with nose underneath wings.		
	Stationary Actions		
11. Stretch	Full extension of wing(s) from shoulder(s) and of fingers from wrist; wing(s) tensed and extended sideways or forward of body for a few seconds before relaxing		
12. Reach	Extension of thumb-claw towards an object in an attempt to pull it close; usually followed by sniffing	Examination of object such as a branch or food item	
13. Sniff	Forward tilt of head towards of object or other bat as in 6. to inhale and assess scent	Identify neighbours; assess reproductive status	

APPENDIX. Continued

Behavioural Unit	Description	Context	Vocalisations
14. Grasp	Manipulation of object with wrist or with foot	E.g., holding a large food item while feeding	
15. Invert	Suspension of body by thumbs and release of feet to achieve a hanging, 'upright' position	Defecation; bearing down by female during labour (see Parturition)	
16. Wing fan	Wings extended loosely in front of body; rhythmic extension and contraction of one or both open wings effecting the movement of air towards the body and across the wing membrane	Cooling action in hot conditions or sign of agitation such as after rejected courtship attempts	
17. Pant	In-and-exhalation through wide open mouth with tongue sometimes loosely protruding	Cooling action during very hot conditions	
18. Yawn	Slow wide opening of the mouth with tongue slightly protruding and often 'snapping' toward lower jaw before closing of mouth		
19. Wing flick	Sudden extension of wings often causing a snapping sound before retraction and relaxation of wings	E.g., at conclusion of an autogrooming session	
	Locomotion		
	Bipedal (BP) — alternate placement of feet one in front of the other to move forward; wings folded loosely by sides	Short distance movement along branch	
	Quadrupedal (QP) — movement along a branch by simultaneous grasping with alternate thumb and foot, i.e., left thumb/right foot → right foot/left thumb …	Usually used for faster movement through larger area of tree	
20. Shuffle – BP	Short distance BP back-and-forth movement along branch		
21. Climb – QP	Use of thumb hooks and feet with body up-right for upward movement along a trunk; thumbs and feet may be used alternately as in 18. or hooks may be used simultaneously to pull the body up, with feet then following and grasping the trunk to push		
22. Ground flap – QP	Flapping of both wings simultaneously as in flight accompanied by a pushing motion of the feet while horizontally on the ground to achieve forward movement	Accidental dropping to the ground and attempt to reach a nearby object (tree) to climb to canopy or take off in flight	
23. Swimming	As in 22., but along water surface and towards edge of water body	Usually accidental immersion while skimming water to drink in flight	
24. Crawl – QP	See *Quadrupedal* description above		
25. Take off – BP	Standard bipedal roosting position with head tilted towards ground and back slightly arched; this is followed by one or two beats of the extended wings to		

APPENDIX. Continued

Behavioural Unit	Description	Context	Vocalisations
	raise body from vertical position, release of the branch and a slight drop in altitude until wing motion sustains body in flight		
26. Flight	Simultaneous up and down motion of wings to sustain body in a horizontal position (head facing forward) and propel it forward. A flight speed of 20–25 km/h may be reached (L. Hall, pers. com.)	Relocation to foraging range, movements within a camp etc.	Occasional single brief 'chirrup' to prevent collision with another bat
27. Glide	Smooth forward flight motion with decreasing altitude, involving outstretched wings but no flapping	Approach of landing site, leading up to 28.	
28. Land	Transition from flight to suspension from an object or branch; may be preceded by a brief, vigorous hover of 3–4 wing beats before connection is made. Destination is approached in gliding flight (see 27.) from above or behind and grasped with feet in passing. Having passed over the top of the branch and feet connected with it, wings are folded and body swings into a vertical roosting position		
Fly-out/Fly-in		Departure from/arrival at roost at dusk and dawn, respectively	
	Autogrooming		
29. General groom	Cleaning of the front of the body (chest, stomach, genitalia), wing-bones, membranes and legs using a quick, vigorous licking motion. Also used on feet and in crevices such as between wrist-bones, toes etc.	Hygiene function, performed several times per day	
30. Wing groom	Apart from licking as described in 29., this involves the rubbing of loosely extended wings over and around the head, particularly around the muzzle area, and across the scapular glands in the neck. During this action, eyes are often closed and the tongue protruding	Release of sebum from glands at base of vibrissae; rupturing of lipid droplets in epidermis and distribution of lipids across wings (Crowley and Hall, 1994)	
31. Genital groom (M)	Licking of body and head of erect penis without urinating or ejaculating		
32. Comb	Grooming of back, face, head and shoulders with leg angled at the knee and bent to reach areas inaccessible by tongue		
33. Tooth groom	Raking motion, inserting hind-foot claws into gaps between teeth which are bared with lips retracted		
34. Ear groom	Several hind-foot claws are inserted into the ear canal and moved slowly and deliberately inside the ear		
35. Scratch	Vigorous back and forth motion of foot claws across area of body; generally distinguished from 32. by speed and sudden onset of motion	Grooming and response to acute irritant	

APPENDIX. Continued

Behavioural Unit	Description	Context	Vocalisations
36. Scent bath	Vigorous side-to-side rubbing of the neck across the erect penis while wings relaxed and open or wrapped loosely around head; results in dousing of body with odorous secretion (urine?) which is then distributed over body and wings by dragging open wings across the head as in 28.	Performed only by males	
	Feeding		
37. Chew	Mastication of food items (fruit, flowers) resulting in the extraction of juices and non-fibrous material.		
38. Lick	Extraction of nectar and pollen from flowers using the tongue; may include sucking action		
39. Spit	Ejection of fibrous material from corner of mouth on completion of chewing; head is tilted to side and ejecta are dropped from corner of mouth		
40. Drink	Open-mouthed flight across surface of river or lake, usually at fly-out. Bat flies close to water surface, briefly lowering the head and scooping water into mouth during flight. May be repeated several times.		
	Parturition		
41. Vaginal licking	Intensive prolonged licking of the vaginal opening without grooming of other body parts	Labour — preparation for birthing	
42. Labour Invert	Suspension of body from branch by thumbs and release of feet for several seconds as in 15., but without defecating	Labour — bearing down in preparation for parturition	
43. Birth — Phase 1. (Head)	While inverted or hanging quadrupedally, the female first expels only the head of the pup	Parturition	
44. Birth — Phase 2.	Stage 1. is followed by a pause lasting from several minutes to several hours while the female rests bipedally and grooms the prenate.	Parturition	
45. Birth — Phase 3. (Body)	Either in a quadrupedal or roosting position (see text), the female rapidly ejects the body of the neonate with a single push, supporting the pup with her foot. Infant attaches to females' nipple almost immediately, while the latter proceeds to lick, alternating between grooming the infant and her own vaginal opening	Parturition	
46. Placental expulsion	Delivery of afterbirth about one hour or so following delivery of infant; female inverts and/or hangs quadrupedally before ejecting the placenta. This is followed by chewing of the umbilical cord and the consumption of all or part of the placenta.	Parturition	
	Territoriality		
	Behaviours performed by males during the mating season		
47. Wing flex	Sudden audible opening and flexing of wings forward with body and head angled forward; may be accompanied by loud vocalisations and movement towards perceived source of threat	Threat behaviour towards adversary encountered at close quarters, eg: large bird	Loud, rasping scream, only heard occasionally

APPENDIX. Continued

Behavioural Unit	Description	Context	Vocalisations
48. Scent-mark	Vigorous rubbing of scapular glands (neck) along branch or leaves at edges of territory surrounding defended females; most often observed prior to fly-out at dusk	Olfactory signaling of territorial boundaries	
49. Chase	Bipedal or quadrupedal active pursuit of intruder through branches of tree in defense of territory; may involve loud vocalisation and hooking but often does not involve any physical contact	Defense of roosting or feeding site against 'intruder', e.g., bat or bird	
50. Hook	Rapid swiping of thumb claw in direction of aggressor with apparent intent to threaten or scratch	Attack or defense; combat	
51. Wrestle	Use of folded wings and wrists in combat to fend off another bat; usually restricted to brief bouts of several seconds in length	Used amongst males in territory disputes or by females rejecting attempts to mate	
52. Bite	Used in combat; usually directed at head of opponent	Aggressive defense of territory	
	Courtship/Mating		
53. Approach/Screams	Approach towards female with head angled forward and while emitting loud, harsh, continuous vocalisations towards her ears. Vocalisations may last up to several minutes.	Initiation of courtship; possibly intended to effect submission of female or to signal willingness to mate	Continuous, harsh screeches directed towards a female; reminiscent of a braying donkey
54. Uro-genital sniff	Action as in 13., directed by male toward genital opening of female	Assessment of reproductive status?	
55. Uro-genital lick	Intensive licking of female genital opening by courting male, ostensibly to arouse and subdue female for copulation; may occur in several bouts prior to attempted copulation	Precedes copulation attempts by male	
56. Grasp-restraint	Extension of wrists with wings relaxed or loosely folded to forcibly hold another bat, eg: the female for copulation	Dorso-ventral restraint of female by male attempting copulation	
57. Scruff bite	Male biting scruff of female to subdue her during copulation; behaviour used in conjunction with the grasp-restraint	Restraint of female during copulation	
58. Copulation	Using 56. & 57., male attempts intromission while vocalising loudly and restraining the struggling female. Copulation process may be repeated many times before fertilisation is achieved as evidenced by seminal fluid oozing from the female genital opening		Female: usually softer, whooping call
59. Intromission	Successful copulation attempt with male penis inserted into female vaginal opening		
60. Break	Cessation of (unsuccessful?) copulation bout, indicated by the release of the female by the male		Male: continuous hoarse screaming

APPENDIX. Continued

Behavioural Unit	Description	Context	Vocalisations
61. Turn attempt	Courting male's attempt to manipulate female into a dorsoventral position for mating; action often resisted by females, hence classed as attempt only	Positioning for intromission	
62. Cop-interfere	Physical interruption of copulation by another bat by pushing face or wings between mating couple or by biting at male	Juvenile interfering with copulation of mother	
63. Swivel-reject	See 8.; often followed by short distance movement away from rejected bat	Rejection of courtship	
64. Face-reject	Opposite action of swivel-reject; deliberate facing of courting male by female to prevent copulation; may be countered by turn-attempt (see above)	Rejection of copulation attempt	
65. Push away	Physical distancing of proximate male by female using her wrists	Rejection of courtship or copulatory behaviour	
66. Wing flap	Folded wings are slightly extended, then suddenly contracted to sides of body, sometimes repeatedly.	Highly agitated action of female rejecting copulation attempts or of male being rejected	Loud, chittering sound
	Mother-Infant Interactions		
67. Infant groom	Extensive and thorough licking of an infant by its mother	Hygiene; Bonding? Removal of urine and faeces	
68. Suckle	Extraction of milk from mammary glands in the females' wing-pit. This may continue for three to four months or longer.	Feeding of infant	
69. Play-wrestle	Action as in 51., but without vocalisation and usually of a longer duration than during combat. Performed amongst juvenile bats (usually males) or by a mother with her young.	Social activity usually observed during peak diurnal activity periods, ie. following fly-in at dawn and prior to fly-out at dusk	
70. Food share	Infant licks at mouth of mother while the latter is feeding on fruit or nectar	Adult foraging; introduction of infant to appropriate adult foods	
	Infant Behaviour		
71. Static flight	Energetic flapping of wings, sometimes raising body to a horizontal position, while maintaining pedal contact with branch	Strengthening of wing and chest muscles in preparation for flight	
72. Greeting	Infant in standard roosting position or leaning towards mother, facing in general direction of approaching mother	Return of mother to infant	High pitched trilling sound, usually emitted at the return of the mother at dawn
	Play Behaviour		
73. Mock biting	Action as in 53., but implemented in an affiliative context	Play between mother and infant or two (usually male) juveniles or sub-adults	This behaviour is characterized by an absence of vocalization
74. Mock wrestling	As in 51., but in a non-aggressive context		