

Spatio-temporal vigilance architecture of an Australian flying-fox colony

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Abstract The social structure of animal aggregations may vary considerably in both space and time, yet little is known about how this affects vigilance. Here, we investigate the vigilance architecture of a colony of wild-living grey-headed flying-foxes (*Pteropus poliocephalus*) in Australia and examine how spatial as well as temporal variation in social organization influences social and environmental vigilance. We sampled color-marked individuals at different stages of the reproductive cycle and the year and at different locations in the colony to examine the effects of temporal and spatial factors on social and environmental vigilance. We found that vigilance architecture reflected the social structure of the colony, with the highest environmental vigilance being displayed by bats at the periphery of the colony, and the highest social vigilance by bats that roosted at intermediate distances from the colony's edge. Furthermore, we found that vigilance levels

reflected changes in reproductive state, with social vigilance increasing toward the mating season, particularly in males. Our findings show that spatial and temporal variation in social structure can have differential effects on social and environmental vigilance. This highlights the necessity to differentiate between functions of vigilance to understand fully vigilance architecture in aggregations of social animals.

Keywords Cooperation · Risk dilution · Antipredatory strategies · Behavioral monitoring · Chiroptera

Introduction

Individuals that occupy central positions in colonially breeding vertebrates frequently have higher fitness than peripheral conspecifics (reviewed by Krause and Ruxton 2002). This pattern is commonly explained as an outcome of the allocation of limited resources to fitness-relevant traits such as reproduction and survival, reflected in life history trade-offs (Stearns 1992). In stationary groups, centrally located animals often experience increased reproductive success, higher collective defense benefits, lower rates of offspring loss, and lower exposure to adverse environmental conditions compared to peripheral ones (Hamilton 1971; Krause 1994; Rattenborg et al. 1999; Krause and Ruxton 2002; Caro 2005). On leks, position sometimes even functions as an indicator of quality, and females commonly prefer socially dominant central males (Balmford 1991; Hovi et al. 1994). Accordingly, in many colonial species, competition among individuals for centrally located breeding territories is intense (Price 1984; Balmford et al. 1992; Roithmair 1994; Bart and Earnst 1999), which sets the stage for trade-offs between fitness-

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relevant characters potentially involving safety. A way to demonstrate these trade-offs is to look at relevant behavior of animals in different positions.

Vigilance behavior, the scanning by an individual of its surroundings, is commonly used in behavioral ecology as a measure of an individual's perceived risk of predation (Martin and Bateson 1996). However, there are multiple functions of vigilance (e.g., Hirsch 2002; Cameron and Du Toit 2005) that can potentially be told apart (Jones 1998). This has rarely been achieved (but see Rose 1998). Tests for trade-offs between different functions of vigilance are also mostly lacking. In species forming stable colonies, temporal and spatial variation in the allocation of vigilance to social (targeted at conspecifics) and environmental (antipredatory) functions may be expected, since in the context of group living, both types of vigilance represent time-consuming behaviors that relate to different fitness-determining variables, in particular survival and reproductive success, respectively. Periods of social instability, such as times of reproduction, may highlight the relative importance of social versus environmental vigilance. Thus, they may potentially also more clearly show conflicts between the two types of vigilance. This can be considered to be of particular interest to the study of safety architecture in groups.

Flying-foxes (*Pteropus* spp.) provide ideal models for studying the effects of spatial and temporal variation in safety in groups. *Sensu* Nelson, the idea behind the “guard hypothesis” (Nelson 1965) is that peripheral individuals have an important role in maintaining the safety of the colony since they are presumably the first to spot predators. *Pteropus poliocephalus*, the grey-headed flying-fox, has been described to use true acoustic “alarm calls”, specific high-pitched calls that may alert others when a potential threat is detected (Wilkinson 1995). Foraging-related causes of vigilance, usually important confounding variables (Hirsch 2007), do not apply to flying-foxes since food resources are absent in forest patches occupied by flying-fox colonies. Furthermore, flying-foxes offer an opportunity to test multiple predictions made in the context of vigilance theory. The “edge effect” (Hamilton 1971; Colagross and Cockburn 1993; Bumann et al. 1997) predicts individuals at the periphery of groups to be more vigilant than more centrally located animals. According to the “group size effect”, individual vigilance is also expected to decline as group size increases (Elgar 1989; Roberts 1996; Blumstein et al. 2001; for exceptions in primates see Treves 2000). Substantial support has been found for both effects (see reviews by Elgar 1989; Krause and Ruxton 2002; Caro 2005).

Here, we investigate the vigilance architecture of a colony of grey-headed flying-foxes. In particular, we examine how spatial and temporal variations in social

organization concurrently influence social and environmental vigilance. We test the following predictions. First, the spatial position of an individual should significantly affect vigilance behavior (“edge effect”). In particular, environmental vigilance should be greater on the periphery because of increased risks of predation there, but social vigilance might be greater in more central positions due to increased competition for territories and mates or simply for social monitoring reasons. Second, vigilance behavior should vary over time, as has been predicted by Kunz et al. (1998), since the reproductive status of the individuals and consequently composition of the colonies changes over time. Females first nurse, then wean their young and finally select males to mate with, and males progressively establish and defend their territories as the mating period approaches. Third, flying-foxes should exhibit comparatively low overall vigilance in their diurnal colonies because of the enormous size of flying-fox colonies (“group size effect”) and the necessity for animals to sleep during the day.

Materials and methods

Study area and animals

P. poliocephalus is a large species of fruit bat endemic to Australia. Animals migrate seasonally along the subtropical to temperate eastern coastline of the continent. During the mating season, they form reproductive colonies of many thousand animals at predictable locations (Hall and Richards 2000). Rapid decline has reduced populations from many millions in the 1930s (Ratcliffe 1932) to about 400,000 animals. This drastic reduction in population size makes this highly social species vulnerable to extinction as it relies on a complex network of colony sites (Eby and Lunney 2002). Site fidelity of individuals is high both within and between years (Welbergen 2005). When individuals return to their breeding colonies from their annual migration, females raise their young, and males establish mating territories preferably in the centers of the colonies. Competition among reproducing males is fierce, with frequent injuries and concomitant declines in body condition (Welbergen 2005).

Our study was conducted at Dallis Park, Murwillumbah, northern New South Wales (153°23'06" E, 28°21'24" S). The landscape was composed of pastures, orchards, sugar cane fields, and remnants of subtropical rainforest with gallery forest along rivers. The study colony consisted of between 27,000 (2003) and 17,000 (2006) flying foxes; the reduction in population size was due to illegal habitat clearing at the diurnal roost site. It was located in a swampy bushland area dominated by paperbark (*Melaleuca* spp.) and eucalyptus (*Eucalyptus* spp.) and was subject to extensive research efforts since the early 2000s (Welbergen

2005; Welbergen 2006; Welbergen 2008; Welbergen et al. 2008). It was the most important maternal flying-fox colony in the region. The colony formed annually in October and dispersed with the onset of migration in May. The animals frequently foraged in the surrounding reserves belonging to the UNESCO-listed “Gondwana Rainforests of Australia” World Heritage.

Seven species of potential predators (Hall and Richards 2000) were regularly present at Dallis Park, including two canid species, the red fox (*Vulpes vulpes*) and dog (*Canis familiaris*), three species of raptors, the white-bellied sea eagle (*Haliaeetus leucogaster*), wedge-tailed eagle (*Aquila audax*) and Brahminy kite (*Haliastur indus*), and two species of reptiles, the Australian lace monitor (*Varanus varius*) and carpet python (*Morelia spilota*). All of these species are active diurnally. Birds mostly perch hunted from trees at the edge of the colony or in the vicinity. Reptiles used a similar strategy but climbed up in the vegetation using foliage as camouflage where possible. The site was also within the distribution range of the powerful owl (*Ninox strenua*), a nocturnal hunter which preys on *P. poliocephalus* and has been shown to feed preferentially on flying-foxes around Brisbane ± 150 km away (Pavey et al. 1994). There is clear evidence that predators affected the flying-foxes in the colony. We found fresh, partly devoured carcasses on the ground and frequently observed eagles and pythons hunting from perches on trees in the colony during the day. Eagles also caught bats in the air (personal observation; Welbergen 2006). Predators often caused disturbances in the colony, such that several hundred flying-foxes left their perches. Furthermore, it has been shown that the presence of an eagle near the colony delayed the evening emergence of bats (Welbergen 2006).

The choice of study colony was influenced by several key criteria relevant to vigilance studies (see Krause and Ruxton 2002). It was semioval, with a distinct forest edge along open grasslands with few bushes and solitary trees, occupying an area of ~ 1.5 ha with estimated maximum lengths and widths of 160 and 92 m, respectively. The trees used by the flying foxes were very evenly spread throughout the colony, characterized by relative structural homogeneity with a continuous stratum of branches of few dominant species. Density assessments in different colony areas (Welbergen 2005) showed that there was no substantial spatial variation in animal density that could have influenced the results of this study. Foliage was sparse, allowing for very good observation conditions throughout the canopy from a distance, facilitated by grassy slopes around the colony. Also, the colony was easily accessible on foot, with the soft ground cover of ferns and herbs making it possible for the observer to walk quietly. The animals had been habituated to the regular presence of a “man with hat” since the onset of ecological studies in

2001 to minimize observer bias, a habituation that is easily accomplished in flying-foxes (Brooke et al. 2000; Welbergen 2006). These ideal observation conditions make us confident that the observed differences in behavior were representative and not primarily due to the shape or density of the colony or differential visibility of animals. We established a trail system in the colony using GPS reference points, tree tags, animal position color flags and reflective tape to support our own navigation within the colony.

Observation protocol

To test our predictions, we recorded vigilance behavior in adult flying foxes in 2002, 2005, and 2006. The majority ($\sim 69\%$) of animals present during those years were *P. poliocephalus*; a smaller number of the more tropical and invading black flying-fox *P. alecto* roosted mainly in the periphery. Data were collected only on adult bats.

Spatial variation in vigilance was studied by collection of independent samples throughout the colony from mid-January to mid-February in 2002 and 2006, when most females had weaned their young but well before the peak period of territoriality in males and mating (for general life history, see timeline of events included in Fig. 4). At this time, females tended to roost quietly with weaned young, while territorial disputes in males were intensifying. To address temporal variation in vigilance, individual flying foxes were identified by thumb bands or unique features, their exact locations were recorded, and animals were consecutively repeatedly sampled once between the 10th and the 19th of every calendar month from November 2005 to April 2006. For this part of the work, we used only animals in central or intermediate colony positions. Included were females with dependent young and males. Attempts to find and resample a focal animal were made up to three times, on different days. When a bat was not encountered after three attempts, it was excluded from further analyses. All sampling was conducted only between 8:00 AM and noon.

Vigilance observations

We defined vigilance in this study in a narrow sense as “eyes open and looking beyond the immediate substrate or the animal’s own body” (modified from Hirsch 2002) and differentiated between “social” and “environmental” vigilance events to account for functional differences relating to the target of vigilance. An event was termed “social” if the individual was looking directly at another close-by individual (e.g., approaching, fighting, staring; typically individuals targeted were awake; mother–young interactions were not recorded) and “environmental” if the individual’s gaze was directed elsewhere (e.g., into foliage or distant

vegetation, at the ground or into empty space). This conservative approach to the definition of environmental vigilance was chosen to ensure that all vigilance that could potentially directly yield information about predators was covered. While we cannot exclude the possibility that social vigilance events also yield antipredatory information (e.g., a flying fox spots a predator not noticed by the observer from the corner of the eye while fighting with another bat), this was highly unlikely to be the primary purpose of looking directly at a conspecific. Vigilance data were collected from opportunistically chosen observation points on the ground using 300 s continuous focal animal samples (Martin and Bateson 1996). For each sample, the frequencies, durations, and types of vigilance events were recorded continuously.

Observations were made using a 22-60x Optolyth TBG 80 spotting scope, 10×42 WB Swarovski binoculars, a hand-held office tape recorder and a stopwatch. Continuous behavioral data were recorded in writing and a Sony HandyCam was used to record, review and verify data. Individuals show very high fidelity to their exact location in the colony (Welbergen 2005) and this allowed us to repeatedly sample individuals that could reliably be identified by powder-coated and numbered stainless steel color bands or unique individual markings such as missing nails or limbs, membrane scar patterns, light or dark fur spots and portions, extent and tone of collar, or any combination of these. Only samples taken between 1 h after flying foxes had arrived in the colony at dawn and 1 h before bats emerged from the colony at dusk were included in the spatial analyses.

Along with vigilance, we recorded date, time of day (hh:mm), sex/age (male, female with or without young), and within-colony position (central, intermediate, peripheral; adapted from Di Blanco and Hirsch 2006). Each bat was assigned a colony position by drawing a straight line from the center point of the colony, determined by GPS on a field map, through the position of the individual to the edge. This distance was then divided by three, and the individual was, by means of its exact position, assigned to a category accordingly. Bumann et al. (1997; in an extension of Hamilton 1971) predicted an elevated predation risk only for individuals on the very edge of a group, so because our study colony covered a large area, we adjusted the classic categories of positions (peripheral vs. central only) by inserting an intermediate category, and we assigned all individuals in the inner half of the peripheral category to the intermediate category to highlight a potential edge effect. We also recorded the height above ground at which individuals hung in the vegetation (in 4 m increment categories, 0–4, 5–8 m etc.) since individuals close to the ground or open air space might be at a higher risk of predation in this three-dimensional colony setting. We

tested for and found no effect of time of day in our data. All positioning was done using a Garmin GPS 12 or Etrex Vista.

We recorded frequency of vigilance as the number of vigilance events in any 300 s sample; we recorded the frequencies of social or environmental vigilance events separately and also combined them as total vigilance. Average duration of vigilance events in a sample was calculated as cumulative duration of all events divided by the number of events. Proportion of time spent vigilant was the cumulative duration of all bouts divided by the duration of the sampling interval (300 s). If a vigilance event extended beyond the 300-s sampling period, only the part within the period was recorded. Sampling was terminated if it coincided with any disturbance that caused more than 20 individuals to leave their perches within a 50-m radius of a focal individual. The sample affected was discarded. Sampling resumed no earlier than 20 min after the disturbance. If an individual moved or turned out of sight during sampling, the sample was discarded.

Statistical analysis

We used general linear model (GLM) procedures to analyze our data. A multiple analysis of variance (MANOVA) was employed initially, and significant results were followed by univariate ANOVAs for each response variable with Tukey HSD post hoc comparisons. Bonferroni correction was applied if necessary. Simple and double multivariate repeated measures general linear modeling (RM-GLM) was used for comparison of vigilance frequencies of animals from different age/sex classes within the colony over time (within-subject factor: time, between-subject factor: sex/age, independents: vigilance variables). Height was entered as a categorical variable. Since there were no significant differences in vigilance between years, we pooled all data across years. Values are given as mean ± standard error, and data were checked for normality and homogeneity of variance. Statistical tests were carried out using SPSS version 15.0. All tests were two-tailed, and the significance level α was set at $P < 0.05$.

Results

Frequencies of vigilance significantly correlated with proportions of time spent vigilant as well as with average durations of vigilance events ($r_p = 0.414$, $P < 0.001$, $n = 800$ and $r_p = 0.401$, $P < 0.001$, $n = 800$, respectively). Overall patterns of vigilance were the same for all three measures of vigilance, and thus, henceforth, we will only consider the effects of spatial and temporal factors on frequencies of vigilance. For comparison with other taxa, the mean

proportion of time spent vigilant was 0.058 ± 0.004 , and vigilance bouts lasted on average 8.24 ± 0.61 s. Differences in bout length depending on type of vigilance were not found. The majority of animals observed during our study were nonvigilant throughout the entire 300 s sampling period and had their eyes closed (see Fig. 1).

Spatial variation

Vigilance frequency differed significantly between positions within the colony (Table 1, Fig. 2). The frequency of social vigilance was higher for animals occupying intermediate positions than for those in central or peripheral locations (Fig. 2a). The frequency of environmental vigilance also differed significantly between positions. However, it was higher in peripheral than in intermediate and central positions (Fig. 2b). The total frequency of vigilance did not differ significantly between the positions of animals in the colony (Fig. 2c) although flying-foxes in the periphery were, on average, more frequently vigilant. Frequency of vigilance was, however, not significantly affected by roosting height of the flying foxes in the vegetation (Table 1). The frequency of vigilance within these data also differed significantly with age/sex (Table 1, Fig. 3). We found that males and single females were more frequently socially vigilant than were females with young (Fig. 3a). There were no significant differences among the age/sex classes in the frequency of environmental vigilance (Fig. 3b). Males exhibited more frequent total vigilance compared to females with young (Fig. 3c).

Temporal variation

The frequency of vigilance changed over time (Fig. 4). In males (Fig. 4a; 15 of 20 bats were still present after

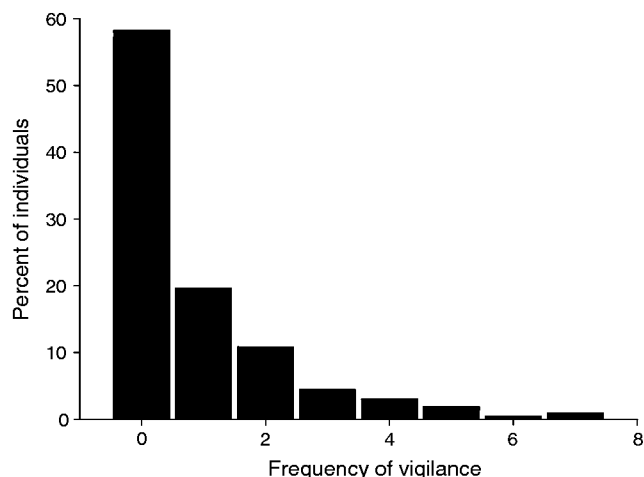


Fig. 1 Distribution of frequencies of vigilance per 300 s, in flying-foxes of both sexes roosting in trees during daytime ($n=800$)

6 months), the frequency of social vigilance was lower at the beginning of the breeding period and increased significantly toward mating ($F_{5,15}=5.66$, $P<0.001$), while environmental vigilance did not vary significantly ($F_{5,15}=0.41$, $P=0.838$). The total frequency of vigilance increased significantly around the mating season ($F_{5,15}=2.65$, $P=0.030$). We also found that the frequencies of social and environmental vigilance differed significantly ($F_{5,15}=2.45$, $P=0.037$), with social vigilance levels initially lower and later higher than environmental vigilance and that there was a significant interaction between vigilance type and month ($F_{5,15}=3.27$, $P=0.008$). This effect was most pronounced in March, when social vigilance was on average three times as high as environmental vigilance. In females (Fig. 4b; 8 of 15 bats were still present after 6 months), there were no significant differences over time in the frequencies of vigilance (Social: $F_{5,8}=1.04$, $P=0.412$; Environmental: $F_{5,8}=1.31$, $P=0.283$; Total: $F_{5,8}=1.72$, $P=0.155$). Moreover, the frequencies of social and environmental vigilance did not differ significantly for females ($F_{5,8}=1.73$, $P=0.140$). Sex did not affect the frequency of environmental vigilance over time ($F_{1,23}=0.58$, $P=0.717$), but females were significantly less frequently socially vigilant than males ($F_{1,23}=11.53$, $P=0.003$). Finally, total frequency of vigilance over time was significantly lower in females than in males (see Fig. 4; $F_{1,23}=4.09$, $P=0.009$).

Discussion

Our results show that individuals in colonies of Australian flying-foxes adjust their vigilance in response to spatial as well as temporal factors. By differentiating social and environmental vigilance, we were able to highlight differences and changes over the course of the reproductive cycle, and witnessed sexes display diverging vigilance dynamics when functions of vigilance were considered separately. Previously, safety benefits in colonies of flying-foxes have been only anecdotally described (Hall and Richards 2000), and predictions about vigilance have remained untested (Kunz et al. 1998). Here, we provide detailed evidence that vigilance in flying-foxes fits central elements of vigilance theory. While patterns of vigilance have been previously described in a wide range of other vertebrates (Elgar 1989; Krause and Ruxton 2002; Hirsch 2007), our study is the first to address vigilance organization in bats and one of the very few to separate functions of vigilance.

Analysis of spatial variation in vigilance revealed an edge effect as predicated by “marginal” predation, a central concept of Hamilton’s selfish herd theory (1971). This is interesting because our model system was a stationary and continuous, three-dimensional mammalian aggregation

Table 1 Interactions among the positions of individual flying-foxes within the colony, sex/age of bats and hanging height in relation to the frequency of vigilance

	Total		<i>E</i>		<i>S</i>		<i>df</i>
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Position	2.709	0.201	5.860	0.009	4.877	0.024	2
Age/sex	4.447	0.036	4.997	0.021	4.149	0.048	2
Height class (hc)	2.958	0.056	2.627	0.099	2.520	0.120	4
Position × age/sex	0.985	1.000	1.125	1.000	0.493	1.000	4
Age/sex × hc	2.396	0.081	2.274	0.105	2.921	0.029	6
Position × hc	1.290	0.816	2.727	0.084	1.003	1.000	4
Position × hc × age/sex	0.728	1.000	1.233	0.801	0.109	1.000	1

The table shows the GLM results for the total frequency of vigilance (total), environmental vigilance (*E*) and social (*S*) vigilance as well as interaction effects

comprised of many thousands of fruit bats in which the considerable risk dilution might have been expected to cause individuals to reduce vigilance to extremely low levels even at the edge. Data on environmental (presumably primarily antipredator) vigilance confirms an edge effect; the bats occupying the outermost trees in a colony reflected an elevated risk of predation in their vigilance behavior. The result that social vigilance was elevated in intermediate compared to both peripheral and central positions may be explained by the male/female ratio in this area with relatively more single females in the intermediate colony areas at the time of sampling, potentially leading to more interactions. Previous studies in birds have found such sex ratio effects (*Serinus serinus*; Domenech and Senar 1999). Central positions are presumably safer than any other, and since mother–young interactions were not included in social vigilance by definition, this may have led to low social vigilance results in this category. Total vigilance was lowest in the colony center, slightly higher in intermediate areas, and highest in the periphery, which may reflect the existence of a risk gradient as suggested by Bumann et al. (1997). In contrast, hanging height in the vegetation did not affect vigilance, possibly because animals stayed clear of branches that were close to the ground and neither ground nor aerial predators would have found much cover within the colony. Approaching predators coming from outside the colony would have been detected by edge individuals, as suggested by Nelson (1965). Hirsch (2002) points out that a primarily social monitoring function would also be consistent with the lack of an effect of height on vigilance.

Temporal variation in our data confirmed that times of social instability such as the mating period had an influence on vigilance, with overall levels of vigilance increasing toward the mating season. In males, social vigilance increased markedly as the mating season approached, a pattern confirming predictions made by Kunz et al. (1998) in a study in the greater spear-nosed bat (*Phyllostomus*

hastatus). Similar results were found in roe deer (*Capreolus capreolus*; San Jose et al. 1996). Presumably, our data are mostly explained by territorial aggressive behavior such as fights and the constant displays done by males, reflecting their need to remain alert to intruders and monitor mates (San Jose et al. 1996; Kunz et al. 1998). As the mating season approached, females no longer devoted the majority of their time to interaction with their offspring, as was the case during the earlier part of the study period, but on average became more alert to the events in their vicinity. Females, however, generally spent considerably less time on social vigilance than males, as described for white-faced capuchins (*Cebus capucinus*) in Costa Rica (Rose and Fedigan 1995). In previous studies that did not distinguish between functions of vigilance, males have been found to be more vigilant than or equally vigilant to females in a range of mammals such as primates (Cheney and Seyfarth 1981; Boinski 1988; van Schaik and van Noordwijk 1989; Koenig 1998; Steenbeek et al. 1999) and ungulates (Prins and Iason 1989; Burger and Gochfeld 1994) as well as birds (Waite 1987; Domenech and Senar 1999); however, some studies differed (Burger and Gochfeld 1994; Ebensperger et al. 2006). Seasonal changes in vigilance have also been observed (Ginnett and Demment 1997). This study highlights the importance of both considering vigilance in the context of the reproductive cycle and distinguishing functions of vigilance. Considering levels of environmental vigilance alone in the two sexes did not yield differences over time, yet monitoring social vigilance did.

A relatively low yet constant level of environmental vigilance was detected even in the putatively safer central and intermediate colony areas, a pattern also shown in groups of coatis (*Nasua nasua*; Di Blanco and Hirsch 2006). Since flying foxes sleep during the day, any vigilance they exhibit is traded off against sleep, suggesting that there must be clear benefits to environmental vigilance, despite the fact that the “dilution hypothesis” suggests that

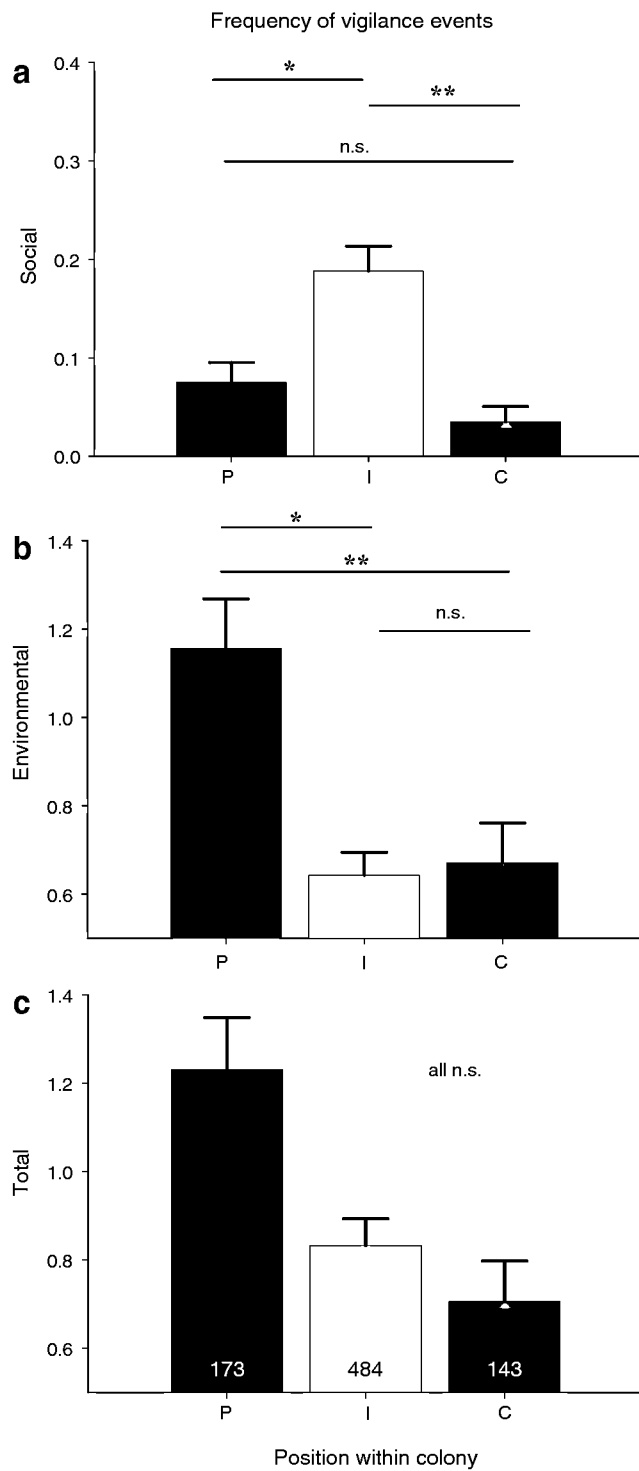


Fig. 2 Differences in the frequencies of vigilance in flying-foxes occupying peripheral (P), intermediate (I), and central (C) areas within a colony. Frequencies are presented for **a** social, **b** environmental, and **c** total frequency of vigilance. Each bar represents the mean±SEM. Sample sizes are identical for all parts of the figure and indicated in **c**. Graphically, significances are indicated as $P < 0.05$ and < 0.01 with one or two asterisks, respectively

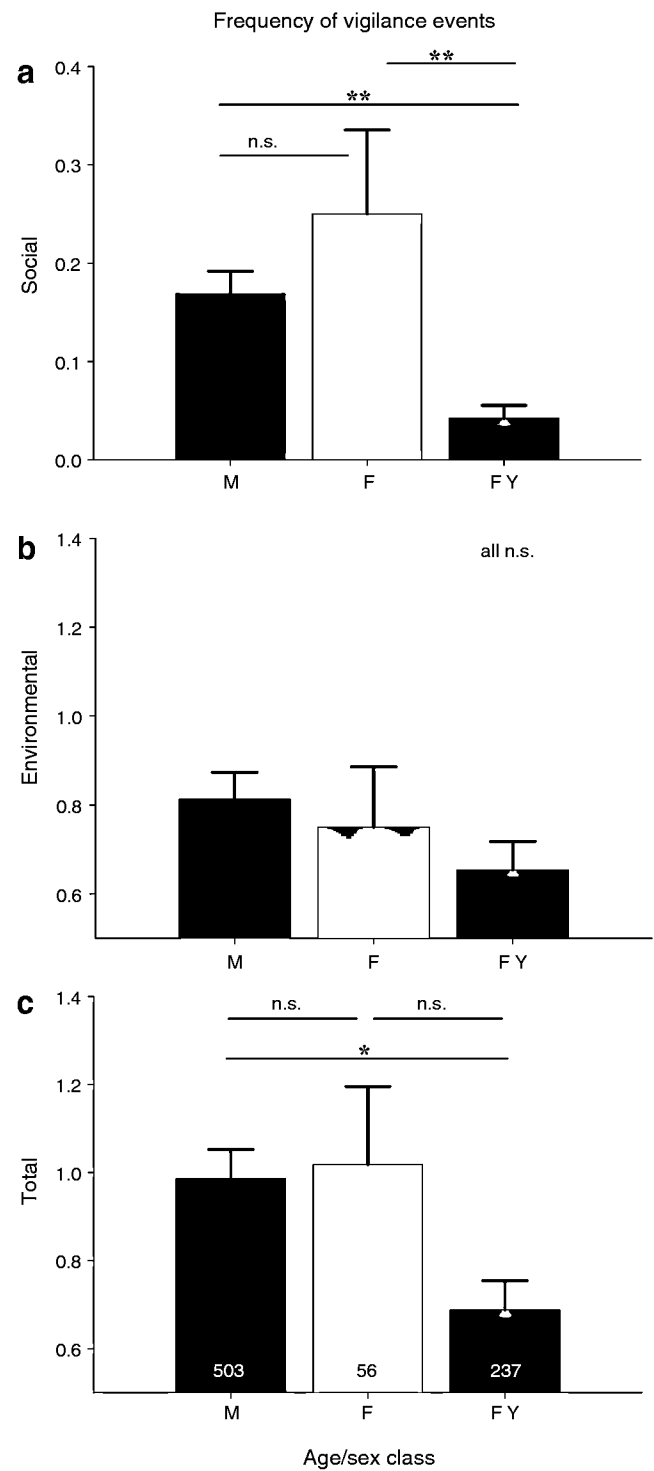


Fig. 3 Age/sex differences in the frequencies of social vigilance for males (M) and females without young (F) as well as females with offspring (FY). Each bar represents the mean±SEM. Sample sizes are identical for all parts of the figure and indicated in **(c)**. Graphically, significances are indicated as $P < 0.05$ and < 0.01 with one or two asterisks, respectively

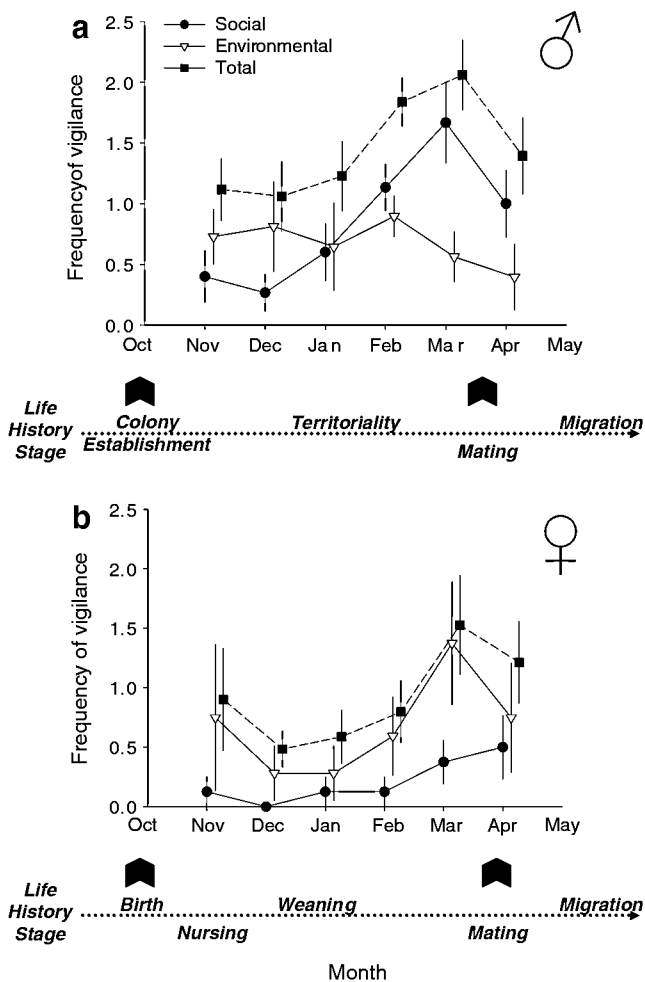


Fig. 4 Frequencies of environmental and social vigilance of centrally and intermediately located individual **a** males ($n=15$ for all months) and **b** females ($n=8$ for all months; initially with young) over the course of the study period. Frequency of total vigilance is indicated by the dashed line. Main life history events are assigned to months for orientation at the bottom of each graph for the respective sex (following Pinson 2009). Each bar represents the mean \pm SEM

the risk of predation would be infinitesimally small for members of large flying-fox colonies. One possible explanation would be the reliability of antipredator information: it is always more reliable for an individual to gather its own information than to rely on others to first detect and then communicate their knowledge. Another explanation could be that predators target nonvigilant individuals; however, it is very difficult for predators to approach flying-foxes without being detected.

Overall, flying-foxes displayed very low levels of vigilance across time, space, and the sexes, compared to other terrestrial mammals previously studied such as roe deer (San Jose et al. 1996), elk (Childress and Lung 2003), and kangaroos (Pays and Jarman 2008), which exhibit up to five times the frequency of vigilance (about 6.5, 3.0, and 5.5 vigilant bouts per 300 s, respectively). Very low

vigilance frequencies have been found, however, in very large mammals such as giraffes (Cameron and Du Toit 2005). This finding is in support of a potential group size effect in flying-fox colonies. One major difference between our study and those done on vigilance in other mammals is that we studied vigilance during the day while flying-foxes were generally asleep, rather than when they were foraging. This may partly explain the very low levels of vigilance displayed by our study animals. Also, individuals consistently devoted more effort to environmental than to social vigilance. While we cannot exclude the possibility that environmental or/and antipredatory information is gathered indirectly from a social vigilance events as suggested by previous studies (Treves 2000), or vice versa, we can assume that if the primary target of vigilance is identified, a distinction between the types of vigilance may assist our understanding of the nature and dynamics of vigilance behavior better than considering only overall vigilance, as has been suggested by Hirsch (2002). In our study, both spatial and temporal effects would have been masked by studying overall vigilance alone, a problem identified previously in the study of vigilance (Beauchamp 2001). Fruit bat colony sites tend to be topographically very variable and nonhomogeneous, and the social organization of colonies often undergoes substantial seasonal changes. This may potentially result in data which are difficult to interpret; thus, careful methodology appears crucial for future research.

Flying-fox colonies are highly structured and have a complex social organization (Welbergen 2005). This sets the stage for an equally fascinating safety organization. It would be interesting to study vigilance in flying-foxes in essentially predator-free island environments, as is the case in *P. tonganus* in American Samoa (Grant and Banack 1994). We speculate that the vigilance architecture of flying-fox colonies may require colonies of a certain minimum size and suitable structural characteristics to provide effective safety benefits to individuals. Krause and Ruxton (2002) conclude that in a foraging context, species seem to benefit by being able to reduce antipredatory vigilance when in the company of others, which may, in their opinion, explain why nuclear species tolerate satellite species in multispecies groups. Flying-fox colonies on the Australian east coast, which *P. poliocephalus* increasingly share with rising numbers of the invading *P. alecto* (Welbergen et al. 2008), may equally provide safety benefits and thus allow a more effective and rapid invasion by *P. alecto*, a ‘foothold’ hypothesis that warrants further study.

Finally, from a conservation perspective, safety from predation and stability of social organization should be considered high priorities for recovery of a long-lived ecological keystone species with complex social organization. In the context of sustainably and successfully

managing human–wildlife conflicts involving flying-foxes (Hall 2002; Thiriet 2005) and to reverse decline of the species, a more detailed understanding of the group safety dynamics in *P. poliocephalus* appears to be of major importance.

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References

- Balmford A (1991) Mate choice on leks. *Trends Ecol. Evol.* 6:87–92
- Balmford A, Rosser AM, Albon SD (1992) Correlates of female choice in resource-defending antelope. *Behav Ecol Sociobiol* 31:107–114
- Bart J, Earnst SL (1999) Relative importance of male and territory quality in pairing success of male rock ptarmigan (*Lagopus mutus*). *Behav Ecol Sociobiol* 45:355–359
- Beauchamp G (2001) Should vigilance always decrease with group size? *Behav Ecol Sociobiol* 51:47–52
- Blumstein DT, Daniel JC, McLean IG (2001) Group size effects in quokkas. *Aust J Zool* 49:641–649
- Boinski S (1988) Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behav Ecol Sociobiol* 23:177–186
- Brooke AP, Solek C, Tualalelei A (2000) Roosting behavior of colonial and solitary flying foxes in American Samoa (Chiroptera: Pteropodidae). *Biotropica* 32:338–350
- Bumann D, Krause J, Rubenstein D (1997) Mortality risk of spatial positions in animal groups: The danger of being in the front. *Behaviour* 134:1063–1076
- Burger J, Gochfeld M (1994) Vigilance in African mammals—differences among mothers, other females, and males. *Behaviour* 131:153–169
- Cameron EZ, Du Toit JT (2005) Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Anim Behav* 69:1337–1344
- Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago
- Cheney DL, Seyfarth RM (1981) Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76:25–61
- Childress MJ, Lung MA (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim Behav* 66:389–398
- Colagross AML, Cockburn A (1993) Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus*. *Aust J Zool* 41:325–334
- Di Blanco Y, Hirsch BT (2006) Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position. *Behav Ecol Sociobiol* 61:173–182
- Domenech J, Senar JC (1999) Are foraging serin (*Serinus serinus*) females more vigilant than males? The effect of sex ratio. *Ardea* 87:277–284
- Ebensperger LA, Hurtado MAJ, Ramos-Jiliberto R (2006) Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology* 112:879–887
- Eby P, Lunney D (2002) Managing the grey-headed flying-fox *Pteropus poliocephalus* as a threatened species: a context for the debate. In: Eby PLD (ed) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, pp 1–15
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Ginnett TF, Demment MW (1997) Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* 110:291–300
- Grant G, Banack S (1994) Predation on *Pteropus tonganus* by a barn owl in American Samoa. *Aust Mammal* 18:77–78
- Hall L (2002) Management of flying-fox camps: what have we learnt in the last twenty five years? In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, pp 215–224
- Hall L, Richards G (2000) Flying foxes: fruit and blossom bats of Australia. University of New South Wales Press, Sydney
- Hamilton W (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Hirsch B (2002) Social monitoring and vigilance behaviour in brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol* 52:458–464
- Hirsch BT (2007) Costs and benefits of within-group spatial position: a feeding competition model. *Q Rev Biol* 82:9–27
- Hovi M, Alatalo RV, Hoglund J, Lundberg A, Rintamaki PT (1994) Lek centre attracts black grouse females. *Proc R Soc Lond, B* 258:303–305
- Jones ME (1998) The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. *Anim Behav* 56:1279–1284
- Koenig A (1998) Visual scanning by common marmosets (*Callithrix jacchus*): functional aspects and the special role of adult males. *Primates* 39:85–90
- Krause J (1994) Differential fitness returns in relation to spatial position in groups. *Biol Rev Camb Philos Soc* 69:187–206
- Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford
- Kunz TH, Robson SK, Nagy KA (1998) Economy of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. *J Mammal* 79:631–642
- Martin PR, Bateson P (1996) Measuring behaviour, 2nd edn. Cambridge University Press, Cambridge
- Nelson J (1965) Behaviour of Australian Pteropodidae. *Anim Behav* 13:544–557
- Pavey CR, Smyth AK, Mathieson MT (1994) The breeding season diet of the powerful owl *Ninox strenua* at Brisbane, Queensland. *Emu* 94:278–284
- Pays O, Jarman PJ (2008) Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo? *Behav Ecol Sociobiol* 62:757–767
- Pinson D (2009) The flying fox manual, 2nd edn. Stickeebatz Publishing, Murwillumbah, New South Wales, Australia
- Price TD (1984) Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. *Evolution* 38:327–341

- Prins HHT, Iason GR (1989) Dangerous lions and nonchalant buffalo. *Behaviour* 108:262–296
- Ratcliffe F (1932) Notes on the fruit bats (*Pteropus* spp.) of Australia. *J Anim Ecol* 1:32–57
- Rattenborg NC, Lima SL, Amlaner CJ (1999) Half-awake to the risk of predation. *Nature* 397:397–398
- Roberts G (1996) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Roithmair ME (1994) Male territoriality and female mate selection in the dart-poison frog *Epipedobates trivittatus* (Dendrobatidae, Anura). *Copeia* 1:107–115
- Rose LM (1998) Behavioural ecology of white-faced capuchins (*Cebus capucinus*) in Costa Rica. PhD thesis, Washington University, St. Louis
- Rose LM, Fedigan LM (1995) Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim Behav* 49:63–70
- San Jose C, Lovari S, Ferrari N (1996) Temporal evolution of vigilance in roe deer. *Behav Processes* 38:155–159
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Steenbeek R, Piek RC, van Buul M, van Hooff J (1999) Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. *Behav Ecol Sociobiol* 45:137–150
- Thiriet D (2005) The relocation of flying-fox colonies in Queensland. *Environmental Planning and Law Journal* 22:231–239
- Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722
- van Schaik CP, van Noordwijk MA (1989) The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav Ecol Sociobiol* 24:265–276
- Waite A (1987) Vigilance in the white-breasted nuthatch: effects of dominance and sociality. *Auk* 104:429–434
- Welbergen JA (2005) The social organisation of the grey-headed flying-fox (*Pteropus poliocephalus*). PhD thesis. University of Cambridge, Cambridge, UK
- Welbergen JA (2006) Timing of the evening emergence from day roosts of the grey-headed flying-fox, *Pteropus poliocephalus*: the effects of predation risk, foraging needs, and social context. *Behav Ecol Sociobiol* 60:311–322
- Welbergen JA (2008) Variation in twilight predicts the duration of the evening emergence of fruit bats from a mixed-species roost. *Anim Behav* 75:1543–1550
- Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc R Soc, B* 275:419–425
- Wilkinson G (1995) Information transfer in bats. *Symp Zool Soc Lond* 67:345–360