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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

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Abstract This study addresses the functional question of how variation in foraging strategy, predation risk, and social context influence the timing of the evening emergence from day roosts of the grey-headed flying fox, *Pteropus poliocephalus*. The onset of evening emergence was expected to vary according to the relative costs and benefits of emerging early and should, therefore, reflect an optimal trade-off between predation risks and foraging needs. The onset of the colony-wide emergence was closely correlated with the time of sunset and cloud cover. However, as expected, the onset of the colony-wide emergence was delayed when a diurnal avian predator was present, whereas the onset was advanced during lactation when presumably energetic demands are higher. The trade-off between predation risks and foraging needs was further reflected in the emergence times of individual bats: adult females emerged earlier when they had higher foraging needs as indicated by their body condition; young emerged later when they were smaller and likely to be more at risk from predation due to their less developed flying skills. However, the emergence time of adult males depended on their social status: smaller bachelor males emerged from the colony earlier than larger harem-holding males who guard their harems until the last female had left. Thus, whereas the colony-wide emergence time reflected the outcome of a trade-off between predation risks and general foraging needs, on an individual level, the outcome of this trade-off depended on sex, age, body condition, and structural size and was modified by social context.

Keywords Bats · Megachiroptera · Emergence timing

Introduction

The almost synchronous emergence of great numbers of bats from their day roost can be a highly conspicuous and predictable event. Historically, the emergence of bat colonies has been studied to illuminate proximate questions about circadian rhythms (e.g., Erkert 1982), feeding ecology (e.g., Kunz 1974), and anti-predator behavior (e.g., Swift 1980; Speakman et al. 1992). Only recently has attention been directed toward the more functional question of how variation in foraging strategy and predation risk influences emergence timing between species (Jones and Rydell 1994). Few studies have examined this question within species (Duvergé et al. 2000; Lee and McCracken 2001) and we do not know how emergence timing varies with an individual's social context.

An animal's behavioral options that maximize food intake, access to mates, and so forth often expose it to an increased risk of predation (Lima and Bednekoff 1999), and natural selection is expected to favor behavioral strategies that optimize the trade-off between these conflicting demands (e.g., Lima 1998). In accordance with their nearly universal nocturnal lifestyle, bats usually emerge around dusk and this is probably because of the cost of an increased risk of predation by avian predators during the day (Speakman 1991a, 1995; Fenton et al. 1994). Against this cost are benefits that include increased foraging time and foraging opportunities (e.g., Jones and Rydell 1994; Duvergé et al. 2000; Lee and McCracken 2001), and it can be hypothesized that the exact emergence time should, therefore, be a predictable outcome of a trade-off between the risk of predation and foraging needs (e.g., Jones and Rydell 1994).

In addition to predation risk and foraging needs, social factors are also likely to affect the timing of bat emergences (Erkert 1982). Bats vary tremendously in their social organization (Altringham 1996; McCracken and Wilkinson 2000) and, consequently, there are various ways in which social factors can affect the trade-off between the relative costs and benefits of emerging early. However, these factors are expected to affect male emergence time, in

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particular, because of the difference in the factors limiting the reproduction of the two sexes: in general, male reproductive success is limited by access to mates, whereas female reproductive success is mainly limited by access to resources (Trivers 1972). If, for example, by advancing or delaying its emergence from the roost a male could increase its access to mates, then this would be expected to affect the trade-off between the costs and benefits of emerging early. There are two tentative indications for such a link: it has been suggested that the emergence time lag of male *Rousettus aegyptiacus* might be related to their defense of mating territories in the caves (Korine et al. 1994); the advanced emergence time of male *Tadarida pumila* might be related to advertisement of their presence to competitors and prospective mates outside the roost (McWilliam 1989).

In this study, I examined how predation risk, foraging needs, and social context influence emergence timing in the grey-headed flying fox, *Pteropus poliocephalus* (Temminck 1825). As *P. poliocephalus* forms large diurnal colonies that may contain tens of thousands of bats amongst the foliage and branches of canopy trees, individuals must emerge early and make long commuting flights to feed on resources that might otherwise be depleted by competing individuals (e.g., Jones et al. 1995; Kunz and Lumsden 2003). In addition, *P. poliocephalus* feeds mainly on fruit, nectar, and pollen (Eby 1995; Richards 1995) that are high in carbohydrates and relatively low in proteins and contain a high proportion of indigestible material (e.g., Kunz 1980; Erkert 1982). In contrast to the predominantly insectivorous diet of the species in which emergence timing has been studied to date, this frugi/nectarivorous diet necessitates a prolonged foraging phase to meet daily nutritional requirements (e.g., Kunz 1980). Therefore, both competition and diet put a premium on early emergence in *P. poliocephalus*. These benefits are expected to trade-off against predation costs because *P. poliocephalus* is preyed upon by two diurnal avian predators [white-bellied sea eagles (*Haliaeetus leucogaster*) and wedge-tailed eagles (*Aquila audax*) (Ratcliffe 1932; Nelson 1965a)] that may still be active around the time of emergence (J. A. Welbergen, personal observation) but whose visual acuity declines sharply with decreasing light levels (Reymond 1985). Social factors are likely to entail an additional cost of emerging early to male *P. poliocephalus* as mating is almost exclusive to the colony and harem-holding males are quickly cuckolded when prevented from guarding their harems (J. A. Welbergen personal observation; Kaiser 2004).

To investigate how trade-offs between predation, foraging needs, and social factors affect behavioral decisions within the context of this colonial vertebrate, I examined how both colony-wide and individual emergence timing varied with the relative benefits and costs of emerging early. Firstly, I looked at how colony-wide emergence timing related to astronomical and weather variables and to the presence or absence of a predator. I expected that it would be delayed when the risk of predation was higher (i.e., when the light levels at sunset were higher or when

potential predators were present). Secondly, I looked at how individual emergence time related to individual morphometric characters. In parallel with Duvergé et al. (2000), I predicted that individuals with higher energy demands and/or lower body reserves (e.g., lactating females) should emerge earlier because they should be more risk prone, whereas individuals with an increased risk of predation (e.g., young during early flight development) should be more risk averse. Finally, I looked at how individual emergence time related to an individual's social context. I predicted that as foregone mating opportunities and cuckoldry are likely to be additional costs of emerging early for a male *P. poliocephalus*, harem holders should emerge later than non-harem holders and the former should remain in their territories until the last harem female has left.

Materials and methods

Study species

P. poliocephalus is endemic to the southeastern forested areas of Australia, principally in the east of the Great Dividing Range, and it extends to higher latitudes than any other pteropodid (Ratcliffe 1931; Mickleburgh et al. 1992; Hall and Richards 2000). At night, *P. poliocephalus* flies up to 50 km to forage for fruit, nectar, and pollen (Eby 1991, 1995, 1996; Fujita and Tuttle 1991; Spencer et al. 1991), and during the day, it forms large colonies amongst the foliage and branches of canopy trees (Ratcliffe 1931, 1932; Nelson 1965a; Pierson and Rainey 1990; Mickleburgh et al. 1992; Tidemann et al. 1999).

The most likely time of conception is April (Martin et al. 1986, 1995) when there is a concomitant peak in mating activity (Nelson 1965a; Eby 1995; J. A. Welbergen, personal observation). Parturition occurs 6 months later between late September and late October (Nelson 1965a). Young are carried by their mothers during nightly foraging trips for the first 3 weeks after birth and, thereafter, are left in the colony during the night (Eby 1995; J. A. Welbergen, personal observation). Young are capable of independent flight at approximately 3 months (December to late January), at which time they start foraging outside the colony (Eby 1995; J. A. Welbergen, personal observation). Young are weaned in February and March (Nelson 1965a; Pook 1977; Martin et al. 1986, 1995; Welbergen 2005).

The mating system of *P. poliocephalus* involves seasonal mixed-sex groups (i.e., harems) that consist of single males and unstable female groups (Nelson 1965a; Welbergen 2005). From January to May, males defend 'mating territories' in the colony that are actively maintained by aggressions and scent marking (Nelson 1965a; Welbergen 2005). When territories are vacated by a resident male, the resident females are readily visited by males from elsewhere (J. A. Welbergen, personal observation; Kaiser 2004). Larger males have larger harems than smaller males and occupy the central mating territories in the colony (Welbergen 2005). The territories may contain up to five

females that mate frequently and repeatedly with the male harem holder over the course of several days. Mating outside the context of such mating territories is extremely rare as it has only been observed once (J. A. Welbergen, personal observation) despite hundreds of hours of observations on individual *P. poliocephalus* in the feeding areas by others (e.g., Nelson 1965a; McWilliam 1986; Eby 1996) and myself.

Between Rockhampton (−23.378° S, 150.513° E) and Port Macquarie (−31.432° S, 152.918° E), *P. poliocephalus* shares its range with the congeneric black flying fox, *Pteropus alecto* (Eby, personal communication; Hall 1987). *P. poliocephalus* and *P. alecto* have many aspects of their life history and behavior in common (Nelson 1965a; Hall and Richards 2000), but *P. poliocephalus* can easily be distinguished from *P. alecto* by its collar of orange/brown fur that fully encircles the neck and by the presence of fur right down the legs to the toes (e.g., Hall and Richards 2000).

Study site

The study was conducted in the Dallis Park colony (−28.332° S, 153.384° E) near Murwillumbah, New South Wales, Australia. The colony is on a 2-ha strip of swampland covered by tree species such as Paperbark (*Melaleuca* spp.) and Eucalyptus (*Eucalyptus* spp.). This colony was studied between December and July, from December 2000 to July 2003. During these periods, two field assistants and I worked in the colony all day until sunset four to six times per week. The bats were quickly habituated to our presence early during the field seasons as evidenced by the fact that we could move about in the colony without causing the bats to leave their roosting positions.

Extensive ground and emergence counts resulted in population estimates of 26,500, 28,400, 26,800, and 27,800 during January/February 2002, April/May 2002, January/February 2003, and April/May 2003, respectively (Welbergen 2005; P. Eby, unpublished). Throughout these periods, the colony had both *P. poliocephalus* (~70%) and *P. alecto* (~30%) (Welbergen 2005).

Emergence timing data

Shortly after sunset, single individuals were typically observed making small round trips over the Dallis Park colony. Some of these individuals would be venturing away from the colony for short distances and then returning again. When these individuals reached some critical density, bats no longer returned to the colony and, instead, began emerging in six continuous serpentine streams. The number and directions of the streams were stable during the entire study period.

The onset of the emergence from the Dallis Park colony was recorded on 62 occasions from January to July during

2002 and 2003. Bullock et al. (1987) considered the time when the median number of bats of a colony emerged to be the most reliable estimate of timing of the emergence of pipistrelles, *Pipistrellus pipistrellus*. However, the colony sizes of *P. poliocephalus* and *P. alecto* and their densities at emergence make accurate counting of individuals almost impossible and the estimate of median emergence time impractical (see also Nelson 1965a; Shiel and Fairley 1999; Lee and McCracken 2001). To maximize repeatability and to exclude those single bats that were only temporarily venturing away from the colony, the onset of the emergence was defined as the moment when ten bats could be seen flying above the canopy.

The end of the emergence from the Dallis Park colony was recorded on 46 occasions during January to July during 2002 and 2003. The end of the emergence was defined as the first entire minute that no bats were observed flying above the colony. This definition was chosen to avoid including occasional returning bats that could normally be observed flying above and near the colony throughout the night.

The data from 2002 and 2003 were pooled in the analyses because, relative to time of sunset, there was no year effect on either the start or the end of the emergence ($t=0.76$, $p=0.451$, $df=59$; $t=-1.95$, $p=0.059$, $df=35$, respectively).

Astronomical and weather data

Astronomical data on sunset, civil twilight, and astronomical twilight times were obtained from Geoscience Australia (<http://www.ga.gov.au/>). Sunset is defined as the instant in the evening when the upper edge of the sun's disk is coincident with an ideal horizon. The end of civil twilight and the end of astronomical twilight are defined as the instants in the evening when the center of the sun is at a depression angle of 6° and 18° below an ideal horizon, respectively. During the study at the Dallis Park colony, the azimuth of the sun at sunset moved between 243° and 297° from true north along a horizontal section of the horizon; therefore, sunset, civil twilight, and astronomical twilight can be taken as relative measures of local light intensity under ideal meteorological conditions.

Weather data were provided by the Australian Bureau of Meteorology. The data were collected by the Brays Park weather station (28.3408° S, 153.3784° E), which is located about 1.2 km from the main study site. The data consisted of precipitation in 24 h after 0900 hours (in millimeter, mm), maximum temperature in 24 h after 0900 hours (in degree Celsius, °C), minimum temperature in 24 h before 0900 hours (in degree Celsius, °C), air temperature at 1500 hours (in degree Celsius, °C), dew point temperature at 1500 hours (in degree Celsius, °C), wet bulb temperature at 1500 hours (in degree Celsius, °C), relative humidity at 1500 hours (in percentage), wind speed at 1500 hours (in kilometer per hour), and the total cloud cover at 1500 hours (in eighths).

Presence/absence of predators

Data on the presence of diurnal avian predators were collected opportunistically: whenever a potential predator was sighted within or above the colony, date, time, location, and species were recorded. Of the large Australian diurnal avian predators, only the white-bellied sea eagle and the wedge-tailed eagle were observed in the immediate vicinity of the colony. Incidentally, these are the only diurnal avian predators that are reported to prey upon *P. poliocephalus* (e.g., Ratcliffe 1932; Nelson 1965a). On several occasions, white-bellied sea eagles and wedge-tailed eagles were observed attempting to catch flying foxes by swooping into the camps. The defensive response of bats to such attacks never involves taking flight (J. A. Welbergen, personal observation) but, rather, staying in their roosting positions and flexing their wings towards the perceived source of threat (J. A. Welbergen, personal observation; Markus and Blackshaw 2002). On two occasions, a white-bellied sea eagle was observed catching flying foxes on the wing during the evening emergence of bats.

A predator was sighted during 22 out of the 62 afternoons that I was present in the colony before emergence time was recorded. No predators were observed before 1240 hours. The probability of observing a predator did not vary with time of year (binary logistic regression $G=0.021$, $df=1$, $p=0.884$). Unfortunately, it is not possible to estimate the probability of observing a predator if one was present; however, missed recordings of the presence of a predator would only lead to an underestimation of any effect of the presence of a predator on emergence time.

Morphometric data

A total of 256 bats were captured at regular intervals and at various times of the day and at night during Dec–July (2001–2003). Bats were caught with a 15×4-m mist net and a noose trap (Welbergen 2005). When bats were caught during the emergence ($n=54$; adult males $n=12$, adult females $n=28$, young $n=14$), I recorded the individual time of capture to the nearest minute, marked the bats around their thumbs with a numbered Band-Aid for temporary individual recognition, and held the bats in cloth sacks for later processing. There were no recaptures. All bats were weighed to the nearest 10 g using a 2.5-kg Pesola spring balance. Forearm length was measured to the nearest millimeter with a stainless steel ruler. In addition, thumb length, thumb claw length, and tibia length were measured to the nearest 0.1 mm with Vernier calipers. Molar wear was estimated on a 1–5 scale from a visual inspection of the teeth (1=no wear, 5=worn to gum line). The protrusion of the sternum was estimated on a 1–5 scale from a tactile inspection of the sternum (1=non-tangible, 5=sharply angular) to provide a qualitative measure of body reserves. Bats were banded on their thumbs with both a numbered metal band (Australian Bird and Bat Banding Scheme) and a unique combination of one to three colored metal bands

for permanent individual recognition. All bats were released within 2 h of capture. After that, the Dallis Park colony was regularly surveyed for the presence of banded individuals.

Filming of focal individuals

To determine the association between social context and emergence timing, a Sony trv110 Digital8 Camcorder running in “nightshot” mode was used to film groups of males and their mixed-sex group members during the emergence. A male’s territory comprises about 3.3 ± 1.6 body lengths along branches (Welbergen 2005) and mixed-sex groups are easily recognized because their members tend to form relatively tight clusters within this space. In addition, during the ~15 min before the onset of the emergence, males move about actively amongst their mixed-sex group members, scent-marking their territory by rubbing their necks along the branches (Welbergen 2005).

For the purpose of this study, ten videos were shot during the mating seasons of 2002 (five) and 2003 (five), each covering at least one banded male that was not captured during an emergence and his mixed-sex group members (if any), and between two and six other mixed-sex groups. Thus, a total of 44 groups were filmed comprising 118 individuals (adult males 42, adult females 64, adult young 12). Harem size could only be determined for 35 males (24 harem holders and 11 bachelor males) because their territories did not extend outside the frame of the video. No banded male was filmed more than once and, as the other individuals represented a very small sample of the total population, it was safe to assume that no multiple sightings of the same individuals were made during independent emergence events. Filming started approximately 1 h before dusk and was conducted from a distance of a minimum of approximately 20 m to minimize disturbances to the focal individuals. A digital clock was shown at the bottom of the frame at all times. During the first 10 min of filming, the camera was accompanied by an observer who verbally recorded the sex and age class of individuals and their location in the view. In parallel with Nelson (1965a), individuals were divided into two age classes: adult (24+ months) and young (<24 months old). During the study period (December–July), young were easily distinguished from adults from a distance by their much smaller size, their narrower shoulders relative to their head, their longer legs relative to their body length, and their larger eyes and ears relative to the area of their face (for a review, see also Holmes 2002). Adult males were distinguished from adult females by the permanent outer presence of the penis and, from December–May, also by the outer presence of otherwise regressed testes.

A still image of the first few seconds of each of the films was digitally captured and individuals that were visible in the still were identified according to their sex and age classes, using their verbally recorded location as a guide. An individual was then followed during playback until the moment (recorded to the nearest second) it flew off from its

roosting position. This process was repeated for each individual of known sex and age class until all individual emergence times were known.

Statistical analysis

A principal components analysis (PCA) was conducted on the nine weather variables (24-h precipitation, maximum temperature, minimum temperature, air temperature, dew point, wetbulb, relative humidity, wind speed, and cloud cover at 1500 hours) because multicollinearity between these variables made their use together in a general linear model (GLM) inappropriate. The first four components of the PCA on the weather variables were retained as they had eigenvalues greater than 0.96 and together explained 94.9% of the total variance.

To examine the relationship between the onset of the colony-wide emergence, weather variables, and the presence of a predator, a general linear model was used with the onset of the colony-wide emergence as the dependent variable, the presence of a predator as a factor (present vs absent), and time of sunset, time of year, and the retained four principal components as covariates.

A PCA was conducted on the morphometric data of adult males, adult females, and young (skeletal dimensions: length of forearm, tibia, thumb, and thumb claw; relative body mass; and age: molar wear), respectively, because multicollinearity between these variables made their combined use in a GLM inappropriate. The morphometric data from all individuals that were captured between Dec–July (2001–2003, $n=256$) were used to increase the sample size for the construction of the principal components. In the PCA, the body mass and sternum protrusion of adult males and females were controlled separately for time of year as these are differentially dependent on the time of year in the

two sexes (Welbergen 2005). The first two components of the PCA on the morphometric variables were retained as they had eigenvalues greater than 1 and together explained 74.9% of the total variance.

To examine the relationship between morphometrics and individual emergence timing, a GLM was used with individual emergence time (defined as the time in hh:mm from the onset of the colony-wide emergence) as the dependent variable. The models included sex and/or age class (i.e., adult vs young) as factors, the retained two principal components as covariates, and their interaction terms. As there was no difference between the individual emergence times of the banded males that were filmed ($n=10$) or captured in the net ($n=12$) during the emergence (Student's $t=0.82$, $df=14$, $p=0.428$), the filmed and captured individuals were pooled to increase the power of the analyses relating male morphometric characters to individual emergence time. As males were filmed up to 3 months after being captured, only those male morphometric variables that were not expected to change significantly during a season were used in the analyses [i.e., skeletal dimensions, relative body mass (i.e. controlled for time of year), and relative sternum protrusion (i.e. controlled for time of year)].

To examine the relationships between individual emergence time, sex/age class, and group identity (i.e., the identity shared by all members of a mixed-sex group), a GLM was used with individual emergence time (defined as the time in min:s as the onset of the colony-wide emergence) as the dependent variable, the sex/age class as fixed, and date and group identity (nested within date) as random factors, respectively.

Statistical tests were carried out using Minitab for Windows (version 13.0, Minitab) and also followed Sokal and Rohlf (1995). All tests were two-tailed and significant at $\alpha < 0.05$ unless stated otherwise. Times are presented as

Table 1 Eigenanalysis of the correlation matrix and factor loadings for the first four principal components extracted from the weather variables

Principal component	PC1a	PC2a	PC3a	PC4a
Eigenanalysis of the correlation matrix				
Eigenvalue	4.041	2.508	1.025	0.966
Percentage variance explained	44.9	27.9	11.4	10.7
Cumulative percentage variance explained	44.9	72.8	84.2	94.9
Factor loadings:				
24 hours precipitation	-0.004	0.046	-0.920	-0.354
24 hours maximum temperature	0.453	-0.220	0.049	-0.063
24 hours minimum temperature	0.410	0.257	-0.106	-0.081
1500 hours air temperature	0.423	-0.316	0.032	-0.097
1500 hours dew point	0.446	0.252	0.024	0.077
1500 hours wetbulb	0.494	0.016	0.031	0.015
1500 hours relative humidity	0.041	0.596	-0.012	0.193
1500 hours wind speed	-0.057	0.155	0.364	-0.901
1500 hours cloud cover	-0.012	0.584	0.059	-0.004

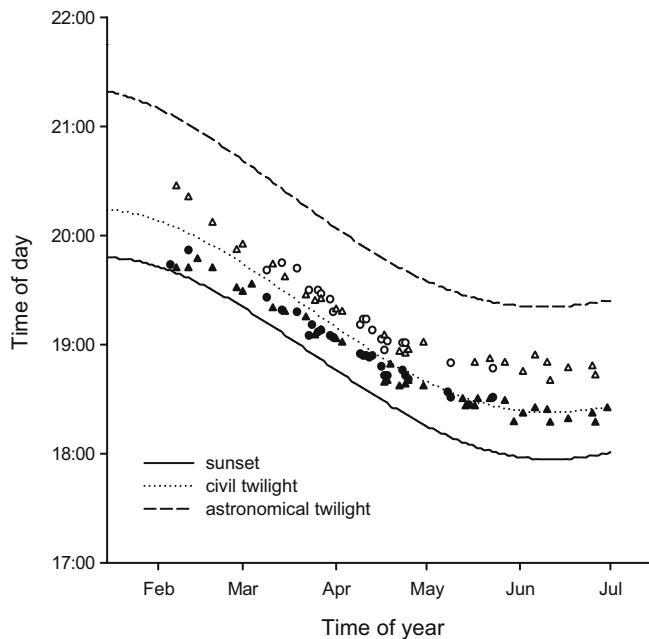


Fig. 1 Timing of onset (*closed symbols*) and end (*open symbols*) of emergence from the Dallis Park colony during 2002 (*circles*) and 2003 (*triangles*) relative to the time of sunset, civil twilight, and astronomical twilight

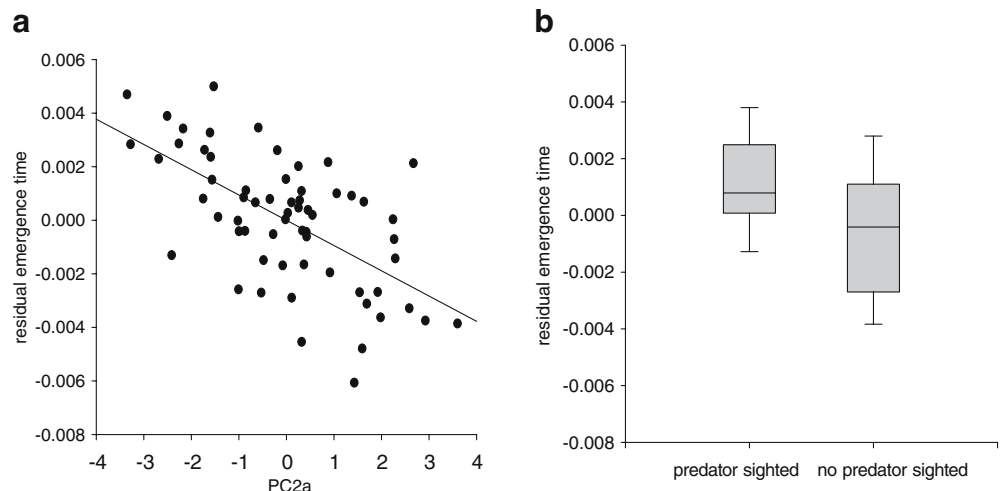
h:min:s but were converted to decimals when used in any calculations. Means are expressed as mean±one standard deviation.

Results

Timing of the emergence: astronomical variables

The emergence started between 3 and 30 min after sunset and lasted on average for 21:24±06:13 min:s (Fig. 1). The onset of the colony-wide emergence was closely associated with the time of sunset (linear regression $F_{1,61}=3,404.0$, $R^2=0.98$, $p<0.0001$). However, the emergence started and ended later relative to sunset as the season progressed from

Fig. 2 **a** (*left*) Time of the onset of the colony-wide emergence (controlled for the time of sunset and time of year) vs PC2a (see Table 1). Least-squares regression (*solid line*). **b** (*right*) Time of the onset of the colony-wide emergence (controlled for the time of sunset) on days when a diurnal avian predator was sighted vs days when no diurnal avian predator was sighted



January to mid-June, 2002–2003 ($F_{1,61}=102.7$, $R^2=0.63$, $p<0.0001$; $F_{1,45}=27.1$, $R^2=0.36$, $p<0.0001$, respectively). In addition, the onset of the colony-wide emergence occurred closer to civil twilight from January to mid-June, 2002–2003 ($F_{1,61}=77.35$, $R^2=0.56$, $p<0.001$).

Timing of the emergence: weather variables and presence/absence of a predator

Only PC2a, with strong positive loadings from humidity and cloud cover (Table 1), and the presence of a predator had a significant effect on the timing of the onset of the colony-wide emergence [PC1a $F_{1,61}=0.04$, $p=0.844$; PC2a $F_{1,61}=31.58$, $p<0.001$ (Fig. 2a); PC3a $F_{1,61}=0.33$, $p=0.567$; PC4a $F_{1,61}=0.81$, $p=0.374$; presence of predator $F_{1,61}=6.00$, $p=0.018$ (Fig. 2b); time of sunset $F_{1,61}=355.23$, $p<0.001$; and time of year $F_{1,61}=0.78$, $p=0.382$].

Individual emergence timing: the relationship with ‘relative body condition’ and ‘structural body size’

The first component (PC1b) from the PCA on the male, female, and young morphometric data had moderate to strong positive loadings from all structural variables and molar wear, whereas the second component (PC2b) had strong loadings only from relative body mass and sternum protrusion. Hence, the first component can be taken as an index of ‘structural body size’ and the second as an index of ‘relative body condition’ (Fig. 3a).

A GLM revealed that, except for the interaction between age class and sex ($F_{1,63}=4.63$, $p=0.036$), neither structural size, body condition, sex, and age class or their interactions significantly affected individual emergence time ($F_{1,63}<1.60$, $p>0.05$). However, as it was expected that relative body condition and structural size would have different effects on emergence timing depending on the age and sex of individuals, the effects of relative body

condition and structural size on individual emergence time were analyzed separately.

Effect of relative body condition on individual emergence time

Using the same model as above but this time only including age class (i.e., adult vs young) as a factor, PC2b as a covariate, and their interaction term, no effect of either age class or PC2b ($F_{1,63}=0.00, p=0.963$; $F_{1,63}=0.00, p=0.946$) was found, but their interaction had a significant effect ($F_{1,63}=5.73, p=0.020$). Examining this further, no effect of PC2b on young emergence time ($F_{1,13}=1.48, R^2=0.04, p=0.247$) was found, but there was a significant positive effect of PC2b on adult emergence time (adults $F_{1,49}=7.88, R^2=0.12, p=0.007$). Within adults, this effect was only

significant in females [males $F_{1,21}=2.42, R^2=0.06, p=0.135$; females $F_{1,27}=5.11, R^2=0.13, p=0.032$ (Fig. 3b)].

Effect of structural size on individual emergence time

Using the same model as above but this time only including age class as a factor, PC1b as a covariate, and their interaction term, no effect of either age class or PC1b ($F_{1,63}=0.73, p=0.396$; $F_{1,63}=0.75, p=0.389$) was found; however, their interaction had a significant effect ($F_{1,63}=10.64, p=0.004$). Examining this further, a significant negative effect was found of PC1b on young emergence time [$F_{1,13}=5.52, R^2=0.26, p=0.037$ (Fig. 3c)] and a significant positive effect was found of PC1b on adult emergence time (adults $F_{1,49}=6.34, R^2=0.10, p=0.015$). Within adults, this effect was only significant in males

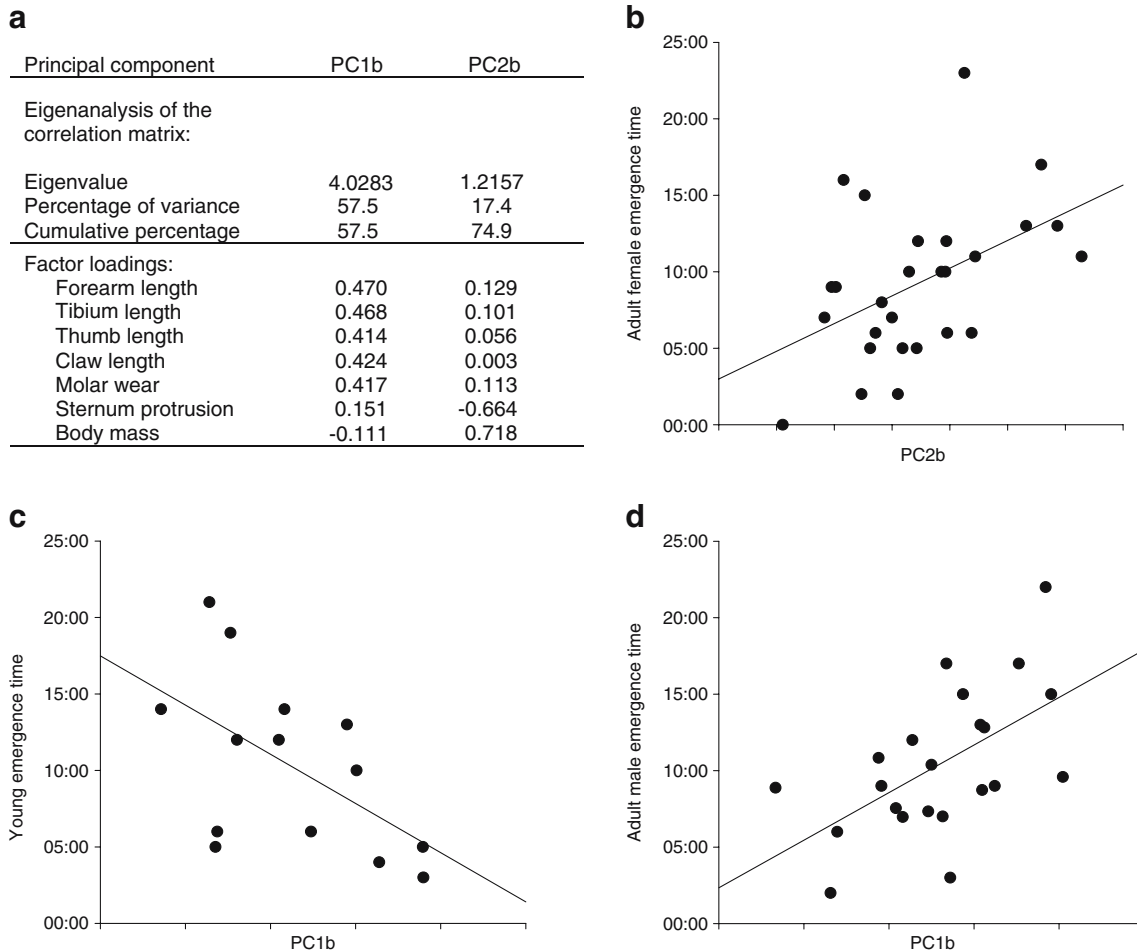


Fig. 3 The relationships between individual emergence time and ‘structural body size’ and ‘relative body condition’. **a** (top left) Eigenanalysis of the correlation matrix and factor loadings for the first two principal components extracted from the morphometric variables. Sternum protrusion and body mass controlled for time of year. **b** (top right) Adult female emergence time (in minutes as onset

of emergence) vs ‘body condition’ (PC2b) ($n=28$). **c** (bottom left) Young emergence time (in minutes after onset of emergence) vs structural size (PC1b) ($n=14$). **d** (bottom right) Adult male emergence time (in minutes after onset of emergence) vs structural size (PC1b) ($n=22$). Least-squares regressions (solid lines)

[males $F_{1,21}=9.60$, $R^2=0.29$, $p=0.006$ (Fig. 3d); females $F_{1,27}=0.58$, $R^2=0.0$, $p=0.453$].

Individual emergence timing: relationship with group identity and harem size

There was a significant effect of sex/age class and group identity on individual emergence time ($F_{2,117}=40.80$, $p<0.001$ and $F_{34,117}=4.66$, $p<0.001$, respectively), and this result held when males without harems were removed from the model ($F_{2,106}=40.80$, $p<0.001$ and $F_{23,106}=2.75$, $p=0.001$, respectively). Pair-wise comparisons revealed that males departed significantly later than females (Tukey–Kramer procedure $t=8.865$, $p<0.0001$) and young [Tukey–Kramer procedure $t=5.189$, $p<0.0001$ (Fig. 4)].

In addition, there was a positive nonlinear relationship between male emergence time and harem size [nonlinear regression $F_{1,34}=12.17$, $R^2=0.40$, $p<0.001$ (Fig. 5)]. This effect seems mainly due to the fact that bachelor males emerge earlier than harem-holding males (Student's $t=4.71$, $df=18$, $p<0.001$) as the relationship is not significant among harem-holding males (linear regression $F_{1,23}=0.56$, $R^2=0.0$ $p=0.464$).

To examine if individual emergence times were related within harems (i.e., excluding the male harem holder), the GLM analysis was repeated but this time without including the male emergence times. Sex/age class (adult female and young) no longer had a significant effect on individual emergence time ($F_{1,75}=0.28$, $p=0.603$), and neither had group identity ($F_{21,75}=1.74$, $p=0.059$), suggesting that emergence times are at best weakly related within harems. However, the individual emergence time of harem-holding males was clearly related to the emergence time of the last female in the male's harem ($F_{1,23}=18.19$, $R^2=0.44$, 17.1 , $p=0.001$). On average, males left later than their last female (paired t test, $t=5.50$, $df=23$, $p<0.001$) and, in fact, in all but one case ($n=24$), males departed only after the last female of their harem had left.

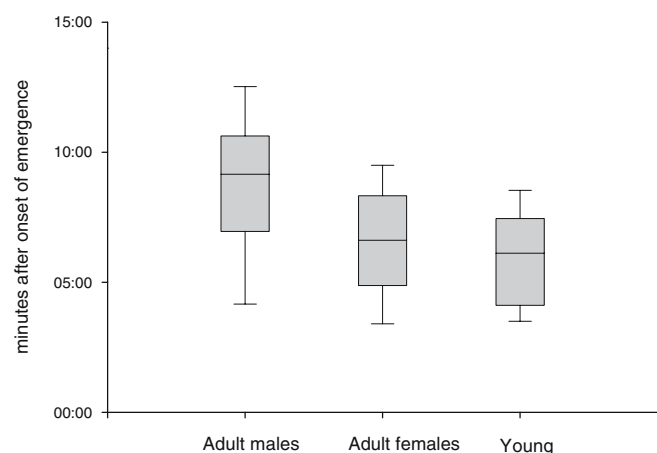


Fig. 4 Box plot showing adult male ($n=42$), adult female ($n=64$), and young ($n=12$) emergence time (in minutes after the onset of the emergence)

Discussion

In most bat species studied to date, emergence activity is correlated with timing of sunset (Venables 1943; Prakash 1962; Jacobsen and DuPlessis 1976; Erkert 1978; Zack et al. 1979; Swift 1980; McAney and Fairley 1988; Korine et al. 1994; Catto et al. 1995; Kunz and Anthony 1996; Lee and McCracken 2001). My results generally agree as colony-wide emergence timing was strongly correlated with the time of sunset but varied with time of season, meteorological variables, and potential predation risk.

The onset of emergences from the Dallis Park colony was delayed relative to sunset as the season progressed from summer into southern-hemisphere winter (see Fig. 1). The same pattern has been found in several northern-hemisphere microchiropteran species (e.g., Kunz 1974; McAney and Fairley 1988; Jones 1995; Shiel and Fairley 1999), and it has been suggested that this pattern is simply an artifact of an increase in the duration of twilight (McAney and Fairley 1988). However, I found no correlation between the duration of twilight and the onset of emergence (Welbergen 2005); rather, I found that, as the season moved into winter, the onset of the colony-wide emergence occurred closer to civil twilight (Fig. 1), suggesting that the bats emerge at progressively lower light intensities.

Food availability may affect emergence timing through its negative effects on travel distances and foraging time (e.g., Erkert 1982), and this has provided an explanation for the variation in emergence timing of some species (e.g. *Tadarida brasiliensis*, Lee and McCracken 2001). However, variation in food availability is unlikely to explain why the onset of the colony-wide emergence of *P. poliocephalus* was delayed relative to sunset towards winter because, for this species, food availability is, in fact, lowest during winter (e.g., Nelson 1965b; Eby 1991; Parry-Jones and Augee 1992).

However, the onset of the colony-wide emergence was advanced relative to sunset during late summer and early

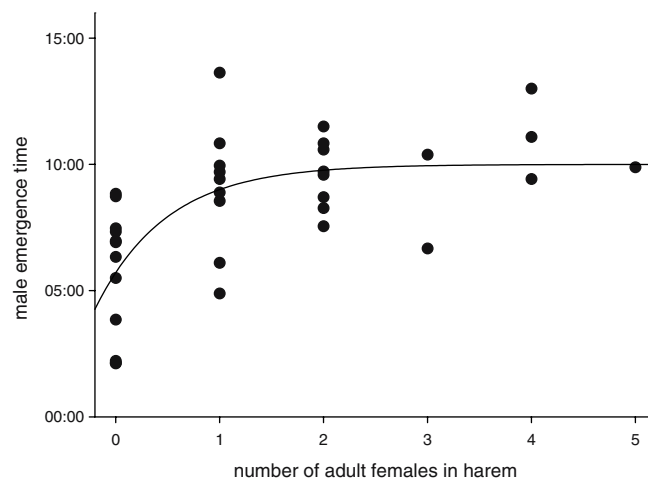


Fig. 5 Male emergence time (in minutes after onset of emergence) vs the number of females in his harem. Nonlinear least-squares regression (solid line)

autumn, which coincides with late lactation in *P. poliocephalus* (i.e., February and March, Nelson 1965a; Pook 1977; Martin et al. 1986, 1995; Welbergen 2005). Relatively earlier emergence during lactation has been reported in several microchiropterans including *Rhinolophus hipposideros* (McAney and Fairley 1988), *T. pumila* (McWilliam 1989), *Lasiurus cinereus* (Barclay 1989), *Eptesicus serotinus* (Catto et al. 1996), and *Nyctalus noctula* (Jones 1995), and it has been suggested that such relatively earlier emergence reflects an individual trade-off between extended foraging time when energy demands are highest and increased risk of predation under conditions of increased light intensity (e.g., Jones 1995; Catto et al. 1996). In bats and other mammals, lactation imposes a very high non-environmental metabolic load on the mother (e.g., Racey and Speakman 1987). Therefore, in many bat species, lactating females have increased food demands (e.g., Brody 1974; Kunz 1974; Kunz et al. 1995; McLean and Speakman 1999; Korine et al. 2004; but, see Voigt 2003) which reach a peak during late lactation (Kunz 1974; Kunz et al. 1995; Korine et al. 2004). In *P. poliocephalus*, these increased food demands are reflected in the average female body condition that reaches a minimum in March during late lactation (Welbergen 2005), suggesting that female foraging needs underlie the seasonal variation in the onset of the colony-wide emergence.

Some bat species show signs of dehydration at the beginning of their nightly foraging activity (e.g. *R. aegyptiacus*, Korine et al. 1999), suggesting that the need to drink could be a factor driving the timing of the onset of emergence. This may be particularly important for tree-roosting species such as *P. poliocephalus* that are exposed to solar radiation and potentially high temperatures all day and that have no access to water during daytime except during days with rain. Water demands will be even greater for lactating females that need water as a vehicle to deliver milk (e.g., Korine et al. 2004). However, my findings suggest that the need to drink cannot be an important factor driving the timing of the onset of the emergence because the principal components with strong loadings from 24 h maximum temperature, 1500 h air temperature (PC2a, Table 1), and 24 h precipitation (PC3a, Table 1) did not explain a significant proportion of variation in the timing of the onset of the colony-wide emergence.

The only meteorological variables that explained a significant proportion of variation in the timing of the onset of the colony-wide emergence were cloud cover and relative humidity (PC2a, Table 1). Early emergence on cloudy nights has been reported for several other species (e.g., Prakash 1962; Kunz 1974; McWilliam 1989; Shiel and Fairley 1999). Cloud cover is associated with increased relative humidity and reduces the amount of light available from the sun, and, thus, cloud cover and relative humidity are probably correlated with light intensity. Light intensity has a twofold proximate influence on bat emergence timing, serving as a Zeitgeber to synchronize endogenous circadian periodicity and exerting a direct intensity-dependent inhibitory effect on the level of activity set by the circadian rhythm (Erkert 1982). In addition, the use of a

particular light intensity as a cue for when to emerge seems adaptive with respect to predation from raptors whose visual acuity declines sharply with falling light levels (Reymond 1985).

Predation can be a major factor shaping decisions about foraging in a wide array of animal species (Lima and Dill 1990; Sih 1994). It has been suggested that many aspects of bat behavior have an anti-predator component to their function (e.g., Speakman 1991b). Predation can also have an important influence on both the timing and pattern of evening emergences (Kunz 1974; Swift 1980; McWilliam 1989; Speakman 1991b; Fenton et al. 1994; Speakman et al. 1999; Duvergé et al. 2000). In this study, I found that flying foxes emerged later when a diurnal avian predator had been sighted in the colony. To my knowledge, such a plasticity of the emergence in response to the presence of a predator has only been described in the serotine bat, *Eptesicus serotinus*, where emerging bats increased their degree of clustering in response to the presence of a nocturnal avian predator (Petrzalkova and Zukal 2003).

A relevant question is how a single diurnal avian predator can influence the onset of the colony-wide emergence which represents a collated measure of the behavior of nearly 30,000 bats. Even if predation by such predators has only minor average fitness consequences for individuals, it could have an important impact on the timing of the onset of colony-wide emergence provided there is higher predation on individuals that leave earlier than others do. Such marginal predation has been recorded in several species (reviewed in Krause and Ruxton 2002). Marginal predation is expected to select for a centripetal tendency of individuals to use each other as ‘living shields’ and can, therefore, be an important driving force behind the evolution of gregariousness, both in space and in time (Hamilton 1971). Provided there is marginal predation in time, there is selection against individual bats that leave first. This would give rise to an “after you effect” where individuals will only emerge after another individual has preceded them. As the risk from avian predators decreases with diminishing light intensity, there will be a time when, for some individual, the added predation risk due to being the first one to leave will be outweighed by the cost of forgoing more feeding opportunities.

The emergence timing of individuals was associated with social context. I found that individuals that are in the same mixed-sex group tend to have similar individual emergence times. This suggests that at least some members of a group adjust their emergence time to that of others. It is possible that individuals emerge together and that the mixed-sex groups extend into the foraging grounds (Nelson 1965a). However, this seems unlikely given that the average difference in emergence time between group members was about 01:10±01:49 (min:s). For mixed-sex group members to be able to follow each other in the dense emergence streams, they would need to depart within seconds from each other. Furthermore, I could only find conclusive evidence that males adjust their individual emergence time to that of their mixed-sex group members

(see below), suggesting that social context does not influence individual emergence time in females and young.

The emergence time of an adult female was related to her physical condition. I found that, independent of the time of year, individual adult females with a lower relative body condition left earlier relative to the onset of the emergence than individuals with a higher relative body condition. This finding supports the prediction that individuals with low body reserves should emerge before well-fed individuals because they should be more risk prone. Furthermore, it provides indirect support for the hypothesis that changes in female foraging needs underlie the seasonal variation in the timing of the onset of the colony-wide emergence.

The emergence time of a young was related to its structural size. Several studies have shown that newly volant young tend to emerge later than adults until a certain developmental stage (e.g., Audet 1990; Kunz and Anthony 1996; but, see Lee and McCracken 2001). This is explained both in terms of an increased predation risk due to lesser flight ability (Kunz 1974; Hughes et al. 1995; Kunz and Anthony 1996; Duvergé et al. 2000; Lee and McCracken 2002) and in terms of reduced foraging needs because energy needs are supplemented by milk (Jones et al. 1995; Kunz and Stern 1995). Both hypotheses are supported by my finding that larger young departed earlier relative to the onset of emergence. This study overlapped with both the time during which young were learning to fly and the weaning period, and smaller young are more likely to be less able flyers and to have their energy needs supplemented by milk from their mothers (e.g., Jones et al. 1995).

The emergence time of an adult male was associated with his social context. The individual emergence time of harem holders was positively related to the emergence time of the last female in the harem; indeed, in almost all cases, males left only after the last-departing female had left. This supports the idea that foregone mating opportunities and cuckoldry by other males are likely to be additional costs of emerging early for male *P. poliocephalus*. Males that lack a harem will not incur these costs and should, therefore, leave earlier, which was what I found. The latter may explain why adult male emergence time is positively related to structural size: as there is a positive correlation between male structural size and harem size (Welbergen 2005) and, as early emerging males tend to be bachelors, larger males will tend to emerge later. The reverse causal explanation (i.e., that harem-holding males leave later because they are larger) would be inconsistent with the finding that harem males adjust their emergence time to that of the last-departing female in his harem.

Results of this study suggest that emergence timing is a property of individuals behaving in their own self-interest, and the high degree of plasticity and structure of the emergence indicates that natural selection has had ample opportunity to act on individuals to optimize their behavior. On a colony-wide level, the onset of the emergence reflects trade-off between foraging and predation. On an individual level, this trade-off seems most relevant for females and young as the emergence timing of males is constrained by

access to females. This supports the idea that, because of the differences in factors that limit male and female reproductive success (Trivers 1972), male dispersion should primarily be influenced by dispersion of receptive females, whereas female dispersion should primarily be influenced by resource dispersion (modified by predation and the cost and benefits of social living) (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Davies 1991). As with other aspects of social organization (e.g., mating systems, Clutton-Brock 1989; Davies 1991), emergence timing follows primarily from the individual interests of females and their young.

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