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Variation in twilight predicts the duration of the evening emergence of fruit bats from a mixed-species roost

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This study investigated how variation in twilight duration affects the evening emergence of two species of fruit bat, the black flying-fox, *Pteropus alecto*, and the grey-headed flying-fox, *Pteropus poliocephalus*, from a mixed-species colony in New South Wales, Australia. Because there are threshold illuminances that accompany the onset and end of emergence activity, I predicted that the duration of the colonywide emergence should vary with twilight duration. Because the duration of twilight varies both with season and with latitude, emergence duration should vary correspondingly. As expected, emergence duration correlated with seasonal changes in twilight duration and was independent of meteorological and ecological variables. Furthermore, *P. alecto* showed a wider distribution of individual emergence times than *P. poliocephalus*, which corresponded with the different latitudinal distributions of the two species. This study shows that seasonal and latitudinal variation in activity timing in bats may merely be a by-product of the underlying circadian mechanism, which may confound studies that seek adaptive ecological explanations for inter- and intraspecific variation in the timing of activities around dawn and dusk.

Keywords: Chiroptera; emergence timing; fruit bats; latitudinal variation; *Pteropus alecto*; *Pteropus poliocephalus*; seasonal variation; twilight duration

The evening emergence of bats from their day roost as they leave to forage during the night is one striking manifestation of a circadian rhythm. Such rhythms are ubiquitous phenomena in the animal kingdom as they enable organisms to exploit the temporal structure in their environment and organize their daily lives correspondingly (e.g. Takahashi et al. 2001). Bat emergences provide convenient systems for illuminating proximate questions about circadian rhythms because they entail very predictable events that may involve thousands of individuals (e.g. Erkert 1978, 1982).

Many studies have shown that, in accordance with the nearly universal nocturnal lifestyle of bats, emergence activity is correlated with the timing of sunset (Venables 1943; Prakash 1962; Jacobsen & DuPlessis 1976; Erkert 1978; Zack et al. 1979; Swift 1980; McAney & Fairley 1988; Korine et al. 1994; Catto et al. 1995; Kunz & Anthony 1996; Lee & McCracken 2001). This is probably because one major cost of emerging early is the increased risk of predation by diurnal avian predators (Speakman 1991, 1993; Fenton et al. 1994), whose acuity diminishes rapidly with decreasing illumination intensity (e.g. Fox et al. 1976; Reymond 1985). Much of the variation in emergence activity is thought to reflect adaptations to variation in predation (Kunz 1974; Swift 1980; McWilliam 1989; Speakman 1991; Fenton et al. 1994; Speakman et al. 1999; Duvergé et al. 2000; Petrzelkova & Zukal 2003; Welbergen 2006), food availability (Lee & McCracken 2001), or social context of emerging individuals (Welbergen 2006). However, proximate factors also underlie variation in emergence timing. Bats, like most terrestrial organisms, use changes in the quantity of illuminance around dawn and dusk as cues to synchronize their circadian rhythms to the 24-h day (e.g. Erkert 1982; Usui et al. 2000). There are usually specific lower threshold illuminances of dusk twilight that trigger the onset of activity (e.g. Isaac & Marimuthu 1993). Accordingly, in several species the evening emergence is advanced when ambient illuminance is lower due to cloud cover (Prakash 1962; Kunz 1974; McWilliam 1989; Shiel & Fairley 1999; Welbergen 2006).

It has not been considered previously that when individual bats use specific threshold illuminances to trigger

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the onset of their emergence activity, the resulting interindividual variation in emergence times should depend on the rate of change in illuminance during twilight, and the duration of the colonywide emergence should therefore be positively correlated with twilight duration (Fig. 1). Twilight duration shows a bimodal annual pattern with maxima at the solstices (~21 December and ~21 June) and minima at the equinoxes (~20 March and ~22 September) and a unimodal latitudinal pattern with maxima at the poles and minima at the equator (e.g. McFarland & Munz 1975). Most bat species are active during most of the year and consequently subjected to marked seasonal variation in the duration of twilight. Thus, for such species it can be predicted that the duration of their emergence activity should be longer nearer the solstices than nearer the equinoxes. In addition, many bat species have large distributions covering several degrees of latitude (Nowak & Walker 1994) and consequently are subjected to marked latitudinal variation in the duration of twilight. In highly mobile species, such as bats, local adaptation of the circadian system is unlikely to occur because it will tend to be counteracted by gene flow from the centre of the species' range (e.g. Mayr 1963; Lenormand 2002). Thus, such species should show longer emergence duration at higher latitudes than at lower latitudes within their range. Despite the long-held interest in emergence timing in bats, no study to date has looked at the effects of season and latitude on emergence duration. Such studies are important because seasonal and latitudinal variation in twilight may confound studies that seek adaptive explanations for variation in emergence timing in bats.

In this study, I examined how seasonal and latitudinal variation in twilight duration affects the emergence timing of two closely related species of fruit bat, the black flying-fox, *Pteropus alecto gouldi* (Temminck 1837), and the grey-headed flying-fox, *Pteropus poliocephalus* (Temminck 1825). *Pteropus alecto* has a current latitudinal distribution that ranges from southern New Guinea (±8°S) (Mickleburgh et al. 1992) into eastern Australia where it has extended its range by several degrees of latitude during the past 75 years: Ratcliffe (1932) placed the southern latitudinal distribution limit at the Mary River (25°S), in Queensland; however, reproductive groups have recently been recorded as far south as Port Macquarie (31°S) in New South Wales (P. Eby, personal communication). In contrast, *P. poliocephalus* is endemic to the southeastern forested areas of Australia, principally east of the Great Dividing Range (Ratcliffe 1931; Mickleburgh et al. 1992; Hall & Richards 2000). Its latitudinal distribution ranges from Rockhampton (23°S) in Queensland to Melbourne in Victoria (38°S) where it extends into higher latitudes than any other pteropodid (Mickleburgh et al. 1992; Hall & Richards 2000). Both species are long-lived placental mammals, are among the largest species of bats (Hall & Richards 2000) and have many aspects of their life history and behaviour in common (e.g. Nelson 1965; Hall & Richards 2000). Both species are considered essentially panmictic, showing a lack of genetic subdivision between populations that is typical for migratory birds (Webb & Tidemann 1996). Between Rockhampton and Port Macquarie *P. alecto* and *P. poliocephalus* share mixed-species colonies among the foliage and branches of canopy trees (e.g. Nelson 1965; Webb & Tidemann 1996; Tidemann 1999; Welbergen 2005) and at dusk both species emerge from these colonies simultaneously in search of pollen, nectar, fruit and blossom (personal observation; Fujita & Tuttle 1991; Spencer et al. 1991; Eby 1995, 1996).

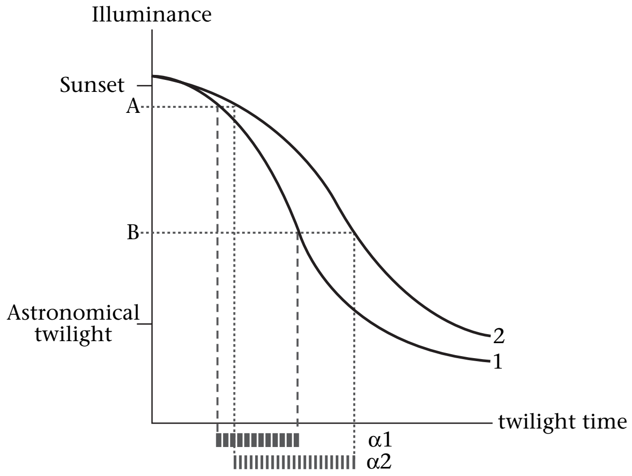

Figure 1. Emergence duration (α) as a function of illuminance change during twilight. Curve 1 represents illuminance change during twilight at lower latitudes or near the summer solstices; curve 2 represents illuminance change during twilight at higher latitudes or near the equinoxes. A represents the specific illuminance at which the first bat emerges from a colony; B represents the illuminance at which the last bat emerges from the same colony.

To investigate how seasonal and latitudinal variation in twilight duration affects individual emergence timing, I examined the dynamics of the emergence from a mixed-species colony in northern New South Wales, Australia, the area where the latitudinal distributions of *P. alecto* and *P. poliocephalus* currently overlap (Welbergen et al., in press). First, I looked at how the duration of the colonywide emergence related to the duration of twilight. I predicted that the duration of the colonywide emergence would be correlated with the duration of twilight. Second, I compared the distribution of the emergence times of *P. poliocephalus* individuals with that of *P. alecto* individuals. Since *P. alecto* and *P. poliocephalus* have the centres of their distributions at lower and higher latitudes, respectively, I predicted that, at the intermediate latitude where the study was conducted, the variance in the distribution of the emergence times of *P. alecto* individuals would be greater than that of *P. poliocephalus* individuals.

METHODS

Study Site

The study was conducted in and near the Dallis Park colony (−28.332°S, 153.384°E) near Murwillumbah, New South Wales, Australia. The colony was on a 2-ha strip of swampland covered by trees such as paperbark (*Melaleuca* spp.) and eucalypts (*Eucalyptus* spp.). The colony contained between 26 000 and 29 000 *P. poliocephalus* and *P. alecto* (Welbergen 2005; P. Eby, personal communication).

This colony was the focus of a study on the social organization of *P. poliocephalus* (Welbergen 2005) between December 2000 and July 2003. During these periods, two field assistants and I were working in the colony between four and six times per week. The bats were quickly habituated to our presence early during the field seasons as evidenced by our ability to move about in the colony without causing them to leave their roosting positions.

Astronomical Data

Astronomical data on sunset and astronomical twilight times were obtained from Geoscience Australia (http://www.ga.gov.au/). The 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 astronomical twilight is defined as the instant in the evening when the centre of the sun is at a depression angle of 18° below an ideal horizon. Twilight duration is defined as the time interval between the sunset and the end of astronomical twilight. 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 and astronomical twilight can be taken as relative measures of local illuminance under ideal meteorological conditions.

Colony Emergence Data

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

The onset and the end of the emergence from the Dallis Park colony were recorded on 62 and 46 occasions, respectively, from January to July during 2002 and 2003. Phase angle differences (Ψ) for the onset and end of emergence activity were calculated following the method of Kenagy (1976), whereby Ψ is defined as the time interval between the sunset and the onset or end of activity (positive if advanced and negative if delayed with respect to sunset). Annual variation in Ψ usually indicates the existence of an adaptation process in the circadian timing mechanism. Usage of Ψ facilitates meta-analyses of behavioural studies that seek adaptive explanations for variation in the timing of activities around dawn and dusk. To maximize repeatability and to exclude those single bats that were only temporarily venturing away from the colony, the onset of the emergence (Ψ_{oe}) was defined as the time interval between the sunset and the moment when 10 bats could be seen flying above the colony canopy. The end of the emergence (Ψ_{ee}) was defined as the time interval between the sunset and 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 duration of the colonywide emergence (α) was defined as the interval between Ψ_{oe} and Ψ_{ee} (Isaac & Marimuthu 1993). The data from 2002 and 2003 were pooled in the analyses because there was no year effect on either Ψ_{oe} or Ψ_{ee} ($t = 0.76$, $P = 0.451$, $df = 59$; $t = -1.95$, $P = 0.059$, $df = 35$, respectively).

Emergence Stream Composition Data

Changes in the proportions of emerging *P. poliocephalus* and *P. alecto* in emergence streams were assessed on six nights in 2002 and 2003 from two observer stations located under the main emergence streams. From the start of each emergence a Sony trv110 Digital8 Camcorder (running in 'Nightshot' mode) was filming the emerging stream against the background sky to keep track of the absolute number of bats in the stream. At the same time, I determined the species of ~25% of individuals flying continuously overhead with the aid of a high-powered spotlight (750 000 candle powers) strapped to a set of 10 × 50 Cat-Eye binoculars, and this was vocally recorded on the Camcorder. *Pteropus poliocephalus* is easily distinguishable from *P. alecto* by its collar of orange/brown fur that fully encircles the neck, by its generally frizzled grey appearance and by the presence of fur right down the legs to the toes (Hall & Richards 2000). Using the above combination of binoculars and spotlight, these characteristics could readily be observed. These recordings enabled me to determine the median emergence time ($\Psi_{(median)}$) of the two species and changes in relative proportions of individuals of the two species in the emergence stream.

Weather Data and Ecological Variables

Because previous analyses had shown that meteorological variables and the presence of a predator affected the onset of the emergence (Welbergen 2006), these variables were included in the analysis of the relationship between the duration of the colonywide emergence and the duration of twilight.

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 millimetres), maximum temperature in 24 h after 0900 hours (in °C), minimum temperature in 24 h before 0900 hours (in °C), air temperature at 1500 hours (in °C), dew point temperature at 1500 hours (in °C), wet bulb temperature at 1500 hours (in °C), relative humidity at 1500 hours (in percentage), wind speed at 1500 hours (in km/h) and total cloud cover at 1500 hours (in eighths).

The white-bellied sea eagle, *Haliaeetus leucogaster*, and the wedge-tailed eagle, *Aquila audax*, are both predators of *P. poliocephalus* and *P. alecto* (personal observation; Ratcliffe 1932; Nelson 1965). Data on their presence were collected opportunistically: whenever a potential predator was sighted within or above the colony, the date, time, location and species were recorded. A predator was sighted during 22 of 62 of the afternoons that I was present in the colony before emergence time was recorded. 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 was not possible to estimate the probability of observing a predator if one was present; however, missed recordings of the presence of a predator would lead only to an underestimation of any effect of the presence of a predator on emergence duration.

Another variable that may affect emergence duration is colony size. The available methods for estimating the size of *Pteropus* spp. colonies are extremely labour intensive (e.g. Eby et al. 1999; Westcott & McKeown 2004), and regular assessments of colony size were therefore beyond the scope of this study. However, in a previous study no relationship was found between the emergence duration and the size of 16 *Pteropus* spp. colonies in New South Wales, Australia (Eby et al. 1999). In addition, there are no indications that the size of the Dallis Park colony underwent substantial changes during the 2002 and 2003 study periods: four extensive counts of the Dallis Park colony 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, personal communication), and we did not notice any significant fluctuations in the density, area or size of the colony during our regular work in Dallis Park from January to July in 2002 and 2003. It appears safe therefore to assume that colony size did not confound variation in emergence duration in this study.

Statistical Analysis

Statistical tests were carried out using Minitab for Windows (v. 13.0; Minitab. Inc., State College, PA, U.S.A.). All tests were two tailed and significance was set at $\alpha < 0.05$.

A principal components analysis (PCA) was conducted on the nine weather variables (24 h precipitation, maximum temperature and 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 generalized linear model (GLM) inappropriate. The first four components of the principal component analysis on the weather variables were retained because they had eigenvalues greater than 0.96 and together explained 94.9% of the total variance.

In summary, the first component of the PCA on the weather variables, PC1 (44.9% variance), had moderately positive loadings from 24 h maximum and minimum temperature and 1500 hours air temperature, dew point and wetbulb; PC2 (27.9% variance) had strongly positive loadings from relative humidity and cloud cover; PC3 (11.4% variance) had a strongly negative loading from 24 h precipitation; PC4 (10.7% variance) had strongly negative loading from 1500 hours wind speed (for details see Table 1 in Welbergen 2006).

To examine the relationship between α and the duration of twilight, weather variables and the presence of a predator, a GLM was used with α as the dependent variable, the presence of a predator as a factor (present versus absent) and time of sunset, time of year and the retained four principal components as covariates. To examine whether Ψ_{oe} or $\Psi_{ee,}$ was related to twilight duration, I used Ψ_{oe} and Ψ_{ee} as respective dependent variables in the same GLM as above.

A logistic regression was used to demonstrate the temporal difference in the emergence timing of *P. alecto* and *P. poliocephalus* during a typical sampling occasion (i.e. Fig. 3). However, because of outliers in some of the distributions of the individual emergence times of *P. alecto* and *P. poliocephalus*, the condition of normality could not always be met; therefore Mood's median test (e.g. Siegel & Castellan 1988) was used to test the equality of $\Psi_{(median)}$, and Levene's test (e.g. Neter et al. 1996) was used to determine differences in the variance of the distributions of individual emergence times.

RESULTS

Timing and Duration of the Emergence from the Colony

The emergence started between 3 and 30 min after sunset and lasted on average 21:24 ± 06:13 (min:s).

None of the principal components and neither the presence of a predator, time of sunset or time of year significantly explained variance in α (GLM: PC1: $F_{1,45} = 0.25$, $P = 0.623$; PC2: $F_{1,45} = 0.13$, $P = 0.724$; PC3: $F_{1,45} = 0.31$, $P = 0.579$; PC4: $F_{1,45} = 0.44$, $P = 0.512$; presence of predator: $F_{1,45} = 0.57$, $P = 0.455$; time of sunset: $F_{1,45} = 0.23$, $P = 0.632$; time of year: $F_{1,45} = 0.01$, $P = 0.950$); however, as expected, the duration of twilight did have a significant positive effect on α ($F_{1,45} = 19.77$, $P < 0.0001$; Fig. 2).

The relationship between twilight duration and α was due mainly to the effect of twilight duration on Ψ_{ee} and

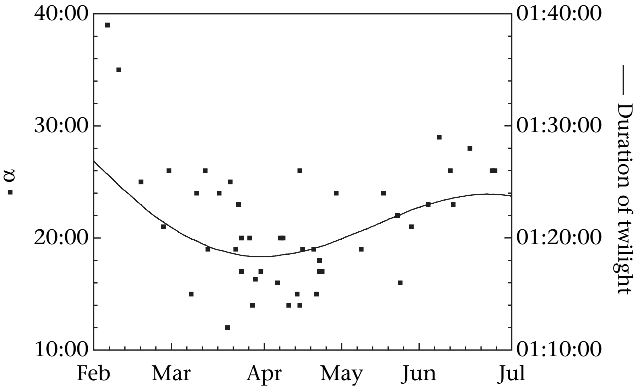

Figure 2. Duration of the colonywide emergence (α) in min:s versus duration of twilight (i.e. end of astronomical twilight; time of sunset in h:min:s) at the latitude where the study was conducted (−28.000°S). Note that the maximum twilight duration is shorter during the austral winter solstice (21 June) than during the austral summer solstice (21 December).

not on Ψ_{oe} because only Ψ_{ee} was correlated with the duration of twilight when substituted for α in the above GLM (Ψ_{oe}: GLM: PC1: $F_{1,61} = 0.03$, $P = 0.870$; PC2: $F_{1,61} = 28.06$, $P < 0.001$; PC3: $F_{1,61} = 0.32$, $P = 0.571$; PC4: $F_{1,61} = 0.76$, $P = 0.387$; presence of predator: $F_{1,61} = 5.60$, $P = 0.022$; time of sunset: $F_{1,61} = 2.82$, $P = 0.099$; time of year: $F_{1,61} = 0.42$, $P = 0.520$; duration of twilight: $F_{1,61} = 0.01$, $P = 0.910$; Ψ_{ee}: GLM: PC1: $F_{1,45} = 0.85$, $P = 0.362$; PC2: $F_{1,45} = 5.38$, $P = 0.026$; PC3: $F_{1,45} = 0.07$, $P = 0.798$; PC4: $F_{1,45} = 0.26$, $P = 0.611$; presence of predator: $F_{1,45} = 0.77$, $P = 0.385$; time of sunset: $F_{1,45} = 4.42$, $P = 0.042$; time of year: $F_{1,45} = 1.94$, $P = 0.172$; duration of twilight: $F_{1,45} = 33.71$, $P < 0.001$). The significant effects of PC2 and presence of a predator on Ψ_{oe} are similar to those reported in Welbergen (2006).

Temporal Distribution of Emergence Streams

The proportion of *P. poliocephalus* relative to *P. alecto* decreased significantly as the emergence progressed (Fig. 3; logistic regression: $G = 257.91$, $df = 1$, $N = 785$, $P < 0.001$). This general pattern held across emergence streams and across dates: $\Psi_{(median)}$ of *P. alecto* was significantly later than that of *P. poliocephalus* in five of six emergence stream composition assessments (Table 1). However, as expected, the distribution of individual emergence times of *P. alecto* had a significantly larger interquartile range than that of the *P. poliocephalus* in five of six emergence stream composition assessments (Table 1), indicating that a given number of *P. alecto* took more time on average to leave the colony than a similar number of *P. poliocephalus*.

DISCUSSION

This study demonstrates that the duration of the emergence activity of bats can vary with twilight duration. Twilight periods contain important photic temporal information that allows animals to maintain their synchrony with the rhythmically changing environment (Kavanau 1962); however, relatively few studies have examined how the transitional phases affect variation in activity timing (e.g. Kavanau 1962; Kavanau & Peters 1976; Usui et al. 1989; Roenneberg & Foster 1997; Tang et al. 1999).

As expected, the duration of emergence activity of *P. poliocephalus* and *P. alecto* was positively correlated with seasonal variation in twilight duration. A similar pattern has been reported in a lemur, the Verreaux's sifaka, *Propithecus verreauxi*, which shows more variation in the timing of their daily activities around solstices than around equinoxes (Erkert & Kappeler 2004). In a previous study (Welbergen 2006), I showed that the onset of the colonywide emergence was correlated with the timing of sunset, the cloud cover, and the presence of a diurnal predator. However, in this study, these variables did not explain variance in emergence duration. One variable that correlates with emergence duration in some microchiropteran species is colony size (e.g. Avery 1986). However, colony size does not correlate with emergence duration in *P. poliocephalus* (Eby et al. 1999). In species that roost in enclosed structures, such as caves, buildings and tree cavities, the rate of individuals emerging can be limited by the size of exits (e.g. Kunz & Anthony 1996). Species that roost among the branches of canopy trees do not have such limitations, and therefore it is less likely that colony size would have an important impact on emergence duration in species such as *P. poliocephalus*

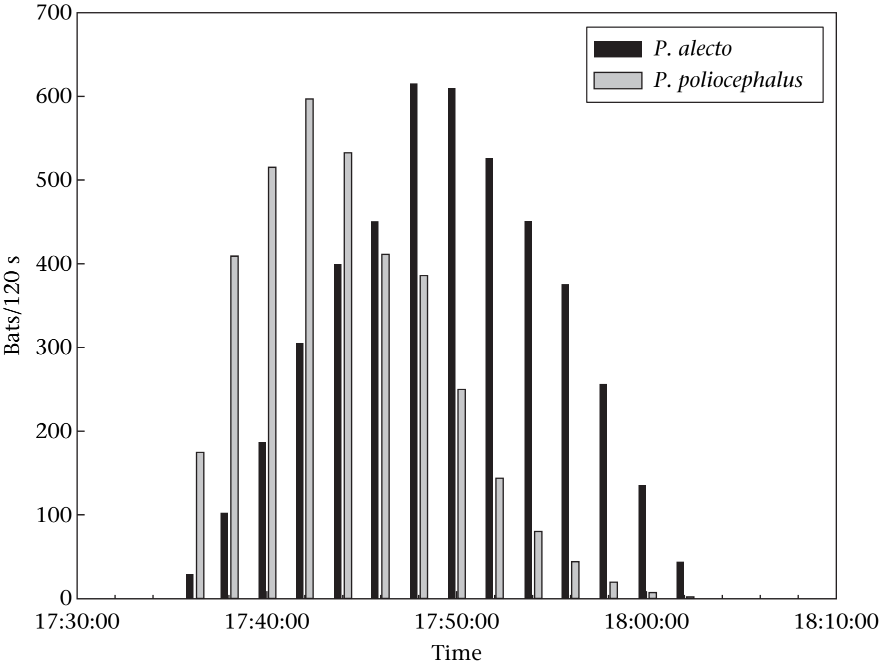

Figure 3. Rate of emergence (i.e. number of bats/120 s) separated by species during the bat emergence from the Dallis Park colony on a typical sampling occasion (20 May 2003) at station 2.

Table 1. Temporal aspects of the species composition of the emergence streams

					Moods median test†		Levene's test‡ for equality of variances	
Station	Date	Number of bats sampled (% *P. alecto*)	*P. poliocephalus* $\Psi_{(median)}$±interquartile range*	*P. alecto* $\Psi_{(median)}$±interquartile range	Chi-square (df=1)	*P*	Test statistic	*P*
1	20 May 2002	361 (84.8%)	−34:15±06:28	−37:40±06:14	10.14	<0.01	1.49	0.22
2	16 June 2002	431 (76.6%)	−32:42±05:09	−38:59±05:52	106.53	<0.01	6.67	0.01
1	1 May 2003	334 (41.9%)	−33:44±05:20	−35:09±07:11	3.49	0.06	6.72	<0.01
1	20 May 2003	785 (56.4%)	−39:09±05:20	−46:58±09:33	198.16	<0.01	68.49	<0.01
2	2 June 2003	618 (60.0%)	−36:39±05:27	−47:25±08:02	192.62	<0.01	24.97	<0.01
2	18 June 2003	774 (70.9%)	−32:03±05:30	−40:32±06:03	154.45	<0.01	7.34	<0.01

*$\Psi_{(median)}$ is the median time of emergence in min:s relative to sunset (negative when later than sunset).

†Significance under Mood's median test indicates a significantly later $\Psi_{(median)}$ of *P. alecto* than of *P. poliocephalus*.

‡Significance under Levene's test for equality of variances indicates a significantly larger interquartile range in the distribution of individual emergence times of *P. alecto* than of *P. poliocephalus.*

and *P. alecto*. It is difficult to think of any other (seasonal) phenomena that could affect emergence duration because the duration of twilight is hypobolic from austral summer (i.e. 21 December) to austral winter (i.e. 21 June) (Fig. 2).

Twilight duration explained variance only in the end of emergence and not in the onset. There are at least two possible reasons for this. First, the end of the emergence should be more sensitive to changes in twilight duration than the onset because, relative to time of sunset, the timing of lower illuminances will vary more between twilight regimes than the timing of higher illuminances (e.g. compare $A_{1,2}$ versus $B_{1,2}$ in Fig. 1). Second, the timing of bats that leave early during the emergence is likely to be under stronger selection from diurnal predators (e.g. Speakman 1991, 1993; Fenton et al. 1994) and foraging needs (e.g. Lee & McCracken 2001) than the timing of bats that leave later. Therefore, ecological factors, such as predation and food availability, are likely to account for a greater proportion of variance in the onset than in the end of the emergence.

As expected, the duration of emergence activity of *P. alecto* and *P. poliocephalus* corresponded with the different latitudinal distributions of the species. *Pteropus alecto* and *P. poliocephalus* have their centre of their species range at lower and higher latitudes, respectively, than the intermediate latitude where the study was conducted. Since both species are considered essentially panmictic (Webb & Tidemann 1996), it is unlikely that local adaptation of their circadian systems has occurred. Therefore, their respective species-specific emergence duration should reflect the twilight conditions that prevail at the latitudes near the centre of their respective species range. Indeed, I found that, at the intermediate latitude where the study was conducted, the variance in the distribution of the emergence times of *P. alecto* individuals was greater than that of *P. poliocephalus*. This general pattern held across emergence streams and across years.

The median emergence time of *P. alecto* was significantly later than that of *P. poliocephalus* in five of the six emergence stream composition assessments. Such interspecific variation in emergence time is thought to be the result of different species-specific trade-offs between the risk of predation and the foraging needs (e.g. Jones & Rydell 1994). This idea is largely corroborated by cross-species analyses of emergence times (Jones & Rydell 1994; Rydell et al. 1996). As predicted, relatively large and fast-flying species of bats, which are presumably less vulnerable to diurnal avian predators, usually emerge earlier than smaller and slower species (Jones & Rydell 1994); species that can feed independently of the dusk peak in dipterans and as consequence have a lesser need to forage earlier tend to emerge later from their roosts (Jones & Rydell 1994; Rydell et al. 1996). However, there are no obvious adaptive reasons to suspect that emergence timing should differ between *P. alecto* and *P. poliocephalus*: both species have many aspects of their behaviour and life history in common, and where they co-occur they compete for identical floral resources and suffer from the same predators (Hall & Richards 2000; Welbergen 2006).

However, in mobile species with large latitudinal distributions, emergence timing is unlikely to be adaptive throughout the species' range, and therefore the later emergence of *P. alecto* may simply be an artefact of *P. alecto*'s more tropical distribution. Tropical bats tend to emerge earlier relative to time of sunset than temperate species (Jones & Rydell 1994). Illuminance at a given time interval after sunset is much lower at tropical than at temperate latitudes; therefore, relatively earlier emergence at more tropical latitudes does not necessarily entail an increased risk of predation by diurnal avian predators. In fact, it remains to be established that tropical species emerge at illuminance similar to that of temperate species. Little foraging time can be gained during twilight at tropical latitudes compared to temperate latitudes. Therefore, selection for emergence at higher light intensities should be weaker in tropical than in temperate species, and consequently the former are likely to emerge at lower light intensities than the latter. Further investigation is required to evaluate this speculation.

The present study indicates that part of the variation in activity timing may merely be a by-product of the underlying circadian mechanism and not an outcome of certain ecological adaptations. Therefore, it is important to account for seasonal and latitudinal variation in twilight duration because these may confound studies that seek adaptive explanations for inter- and intraspecific variation in the timing of activities around dawn and dusk.

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