



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

JUSTIN A. WELBERGEN

Department of Zoology, University of Cambridge

(Received 3 May 2007; initial acceptance 13 July 2007;  
final acceptance 1 October 2007; published online 3 December 2007; MS. number: 9382)

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.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**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

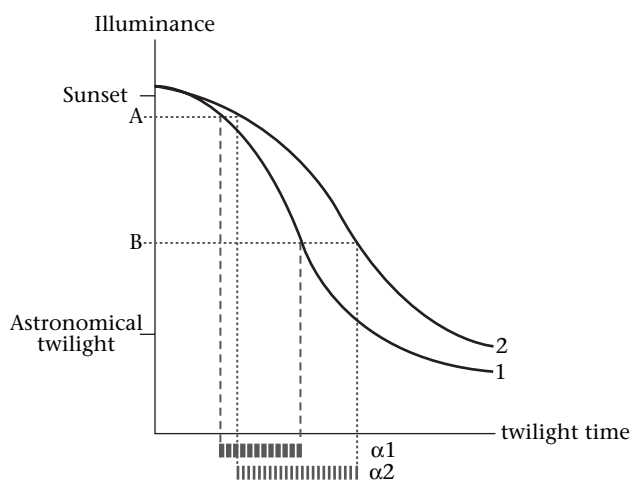
risk of predation by diurnal avian predators (Speakman 1991, 1993; Fenton et al. 1994), whose acuity diminishes rapidly with decreasing illumination intensity (e.g. Fox et al. 1976; Reymond 1985). Much of the variation in emergence activity is thought to reflect adaptations to variation in predation (Kunz 1974; Swift 1980; McWilliam 1989; Speakman 1991; Fenton et al. 1994; Speakman et al. 1999; Duvergé et al. 2000; Petrzalkova & Zúkal 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

Correspondence: Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ Cambridge, U.K. (email: [jaw44@cam.ac.uk](mailto:jaw44@cam.ac.uk)).

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



**Figure 1.** Emergence duration ( $\alpha$ ) 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.

1825). *Pteropus alecto* has a current latitudinal distribution that ranges from southern New Guinea ( $\pm 8^\circ\text{S}$ ) (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 ( $25^\circ\text{S}$ ), in Queensland; however, reproductive groups have recently been recorded as far south as Port Macquarie ( $31^\circ\text{S}$ ) 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 ( $23^\circ\text{S}$ ) in Queensland to Melbourne in Victoria ( $38^\circ\text{S}$ ) 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).

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 ( $-28.332^\circ\text{S}$ ,  $153.384^\circ\text{E}$ ) 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).

Download English Version:

<https://daneshyari.com/en/article/2417770>

Download Persian Version:

<https://daneshyari.com/article/2417770>

[Daneshyari.com](https://daneshyari.com)