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Diurnal activity in the Samoan flying fox, *Pteropus samoensis*

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Speakman and co-workers suggested the diurnal Samoan flying fox, *Pteropus samoensis*, may be at risk of hyperthermia when flying during the day, particularly at high levels of insolation. We monitored activity of this bat and climate simultaneously at two different sites and four times of year in American Samoa. Flight activity varied significantly with time of day, between days, study sites and seasons. Out of the six data sets collected, the four with the highest mean levels of insolation showed a significant decrease in bat numbers with increasing temperature and sunlight. When each individual activity count was directly compared to the predictions of Speakman and co-workers' biophysical model, 85–95% of bat flight activity was found to be in conditions the model suggested would not pose a risk of hyperthermia. This supports the suggestion that in extreme conditions the animals would not fly as they risked overheating. The 5–15% of counts in which animals were seen to fly in conditions the model predicted they should not may be explained by erroneous assumptions underlying the model predictions.

Keywords: *Pteropus samoensis*; hyperthermia; diurnality; flight

1. INTRODUCTION

The fact that bats (Chiroptera) are almost entirely nocturnal, along with possible explanations for this phenomenon, has been well-documented recently (Speakman 1990; Thomas *et al*. 1991; Rydell & Speakman 1994; Speakman *et al*. 1994). A total of three hypotheses have been proposed to explain the lack of chiropteran diurnality: (i) competition from diurnal birds; (ii) predation by diurnal birds; and (iii) the risk of hyperthermia (Speakman 1995). Despite occasional observations of interactions between bats and diurnal birds (see, for example, Ollason *et al*. 1992) there is little evidence that competition is an important factor influencing activity patterns of insectivorous or frugivorous bats (Speakman 1995). However, there are many examples of diurnal birds preying on Microchiroptera (Black *et al*. 1979; Rautenbach *et al*. 1990; Yosef 1991). Predation risk may therefore be a more significant factor, particularly for small insectivorous bats living in the temperate zone (Speakman 1991).

Predation may also be a constraint on diurnal activity in larger frugivorous bats. For example, White *et al*. (1988) suggested *Pteropus* species might be an important food source for Peregrine falcons (*Falco peregrinus*) in Fiji, however other factors may also be important for these bats. Thomas *et al*. (1991) showed that the body temperature of different species of bats in flight was close to the upper lethal body temperature for resting bats, and Reeder & Cowles (1951) suggested that bats were forced to adopt a nocturnal lifestyle so their highly vascularized wings would not be exposed to additional heat loads from solar radiation. By constructing a biophysical model, Speakman *et al*. (1994) predicted that the risk of fatally overheating during daylight flight might constrain diurnality, especially for bats weighing over 900 g that live between 40° N and 40° S such as large flying foxes (Pteropodidae). Hyperthermia may thus be the primary factor restricting the activity of large tropical bats.

Despite these potential constraints there are several species of bats which are active in the day. Study of these unusual species may provide an insight into the factors which more routinely constrain bat activity to the night. For example, the insectivorous Azorean bat (*Nyctalus azoreum*), endemic to the Azores archipelago where there are no avian predators likely to prey on bats, has been known to be diurnal since at least the 1890s (Moore 1975). Speakman & Webb (1992) have shown that although this species is more active in daylight hours than most species, it is actually more active, and over a larger area, at night. A lull in the activity of this bat in mid-afternoon when the ambient temperature was highest was also observed (Speakman 1995) suggesting that risk of hyperthermia may also play a role in the activity patterns of this species.

Nocturnal tropical fruit bats may forage during the day after cyclones when there are food shortages following the destruction of vegetation. For example, the Insular flying fox, *Pteropus tonganus*, and the Samoan flying fox, *Pteropus samoensis*, in Samoa (Grant *et al*. 1997, 1998; Pierson *et al*. 1996), the Greater Mascarene flying fox, *Pteropus niger*, on Mauritius (Cheke & Dahl 1981) and the Marianas flying fox, *Pteropus mariannus*, in the Mariana Islands (Wiles & Glass 1990). Furthermore, there are several reports of diurnal activity in fruit bats even in the absence of cyclones. Many of these come from oceanic islands that are free of potential predators, for example, *Pteropus melanotus* on Christmas Island (Tidemann 1987), *P. tonganus*

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in Tonga (Mosley 1879, in Baker & Harris 1957), the Island flying fox, *Pteropus hypomelanus*, in the Maldive Islands (Phillips 1958) and the Comores lesser fruit bat, *Pteropus seychellensis*, in the Comores (Cheke & Dahl 1981). Interpreting diurnality in these bats as being caused by release from predation however is complicated by the existence of sympatric nocturnal species on some islands, e.g. *P. tonganus* in Samoa (Morrell & Craig 1995). A further problem is the difficulty defining diurnality. Many sightings of 'diurnally active' bats refer only to activity within arboreal roosts, or movements between roost sites (see, for example, Lekagul & McNeeley 1977) which could be responses to disturbance. In some instances, however, reports refer specifically to more prolonged foraging activity (see, for example, Mosley 1879).

One clear example of a diurnally foraging bat is the Samoan flying fox. Its conspicuous diurnal behaviour was first reported by Peale (1848). Cox (1983) observed bats soaring on thermals high above the forest and foraging on rainforest fruits and flowers throughout the day. A sub-species of *P. samoensis* occurs in Fiji where it is thought also to be diurnal, but behaves more cryptically, not soaring high above the forest canopy as it does in Samoa (White *et al*. 1988; Wilson & Engbring 1992). Peregrine falcons, are found in Fiji but not in Samoa, hence the observed differences in flight behaviour between island groups may be at least partly explained by a risk of predation. Speakman *et al*. (1994) suggested that as maximum ambient air temperatures in Samoa span the predicted critical temperatures, beyond which this species should not fly in daylight because of risk of hyperthermia, there should be daily and seasonal variation in this bats' activity, related to variation in environmental factors that are likely to influence its heat balance, such as ambient temperature and input of solar radiation. Several previous studies have reported diurnal variation in activity in the Samoan flying fox, however, there are discrepancies regarding the actual activity pattern. Cox (1983) reported a midday peak in activity. In contrast, Wilson & Engbring (1992) and Morrell & Craig (1995) found a midday lull in activity. These variations might reflect seasonal differences in climate conditions and how these vary with time of day, but none of these previous studies simultaneously logged climate variables while also monitoring flight activity.

The aim of the present study was to establish the diurnal activity of *P. samoensis* at two different sites at different times throughout the year, while making simultaneous climate measurements, to establish relations between climate and bat activity. A second aim was to calculate the critical air temperatures at which activity in this bat would be constrained by hyperthermia, by using the model of Speakman *et al*. (1994), and thus to establish whether any lulls in activity of this bat corresponded to times when the observed air temperature exceeded the critical air temperature.

2. METHODS

(a) *Predictions of climate conditions producing hyperthermia*

Speakman *et al*. (1994) stated that in January the range of ambient air temperatures in Samoa spanned a critical value (T_{acrit}), predicted from their biophysical model, above which *P. samoensis* should not be able to fly during the day without experiencing hyperthermia. Many factors affect this critical temperature. Physical factors include, the angle of the sun, cloud cover and whether the bat was flying in sun or shade. Biological factors include, body mass, flight speed and albedo of the wings (Speakman *et al*. 1994). Estimates for most of these variables for Samoa were based on unverified assumptions. We therefore aimed to generate more realistic and detailed predictions for *P. samoensis* by reparameterizing the same model using data obtained from the field.

The model required values for the following variables: body mass, wing span, wing area, flight speed, wing albedo, sun angle, percentage cloud cover, proportion of wing exposed vertically through a wing beat, maximum wing temperature, ground albedo and ground temperature. Estimates of body mass for adult *P. samoensis* captured in Western and American Samoa were taken from Richmond *et al*. (1995). Wing span and area were generated from these masses by using allometric equations (Norberg & Rayner 1987). We estimated flight speed by measuring the time it took ten individuals to fly between points of known distance apart. The proportion of light absorbed into the wing was initially set at 0.82 (after Speakman & Hays 1992), but as the albedo of *P. samoensis* is unknown we subsequently allowed it to vary between 0.1 and 1.0. The angle of the sun was varied between 90° and 30° (below this angle the sun disappeared below the valley ridges). Cloud cover was set at 56.7%, which was the mean of all measurements made at both sites (range 0–100%). During flapping the proportion of wing exposed was set at 0.7 (Speakman *et al*. 1994), but as *P. samoensis* often soars (Wilson & Engbring 1992) we varied this between 0.7 and 1.0. The last three factors, maximum wing temperature, ground albedo and ground temperature, were set at 315 K, 0.12 and 303 K respectively, after Speakman *et al*. (1994). The critical temperatures (T_{acrit}) above which *P. samoensis* should not be able to fly because of hyperthermia were generated by using the above values for a bat flying in direct sun and a bat flying in identical conditions but in cloud shade.

(b) *Study site*

Flight activity of *P. samoensis* was observed at two sites on the steep volcanic island of Tutuila, American Samoa in the South Pacific (14° S, 170° W). Tutuila is the largest island in the American Samoan group with a total land area of 137 km^2. We selected two valleys with good viewing area and different densities of bats: Amalau and Nu'uuli. The Amalau valley had the greatest number of *P. samoensis* on Tutuila, in the early 1990s, whereas the Nu'uuli valley had comparatively few. Amalau was a semi-circular 14.4 ha valley forested with mature native trees. It extended from a coastal road to the Malaugoa ridge, 452 m high, and was rimmed by a 244 m ridge. In comparison the Nu'uuli valley covered 21 ha at the base of Matafoa peak and was surrounded by 125 m high ridges. The floor of this valley was residential with cleared land, secondary growth and banana plantations. Almost all of the mature trees there had been destroyed by three cyclones during the previous seven years.

(c) *Counting methods and species identification*

The number of bats in flight was obtained by counting the number of individual *P. samoensis* in flight, in three ten-minute periods each hour from dawn to dusk. Minimum numbers of *P. samoensis* observed during each ten-minute period were recorded. To avoid counting the same individuals repeatedly, we divided the viewing area in each valley into sections of approximately 200 m along the ridgetops. More than one individual was recorded per section only when more than one bat was seen simultaneously in that section. In both valleys bats were easily visible, by using binoculars, throughout the whole valley up to the top of all the ridges. A total of five separate full day counts were completed within a two-week period at each site and time of year. To determine whether diurnal behaviour varied with time of year, counts were made at Amalau four times during 1994–1995: first in December 1994, when temperature and daylength were greatest; in March 1995; in June 1995, when daylength was shortest and the temperature and rainfall lowest; and in October 1995. At the Nu'uuli valley counts were made twice; in March 1995, and October 1995. Although bats were seen flying for varying amounts of time, we were concerned only with the number of bats in flight in each count period. During early morning, and late afternoon, *P. tonganus* could often be seen flying in the same valleys. By using binoculars, even from a distance, differences between the two species—for example in wing shape and flight behaviour—enabled identification of *P. samoensis* (see Wilson & Engbring (1992) for a full description of both species in flight). On 12 out of the 30 days, surveys were done (three days from Nu'uuli in October 1995, and nine days from Amalau: four in June 1995 and five in March 1995), we counted numbers of *P. tonganus* simultaneously.

(d) *Climate measurements*

Before the start of each ten-minute count the following variables were recorded at the observation site: shade temperature, by using a data logger (Grant Squirrel) or a mercury thermometer—positioned under vegetation, sheltered from wind. A probe was also positioned in the sun to give an indication of levels of insolation. Wind speed was measured by using a portable anemometer or estimated visually by using the Beaufort scale. Percentage cloud cover was estimated visually. Furthermore, any rainfall was noted, as well as angle of sun and whether it was shining directly, partly obscured (shining through thin cloud) or completely covered by dense cloud. Shade temperatures for every count were subtracted from corresponding exposed probe (sun) temperatures to give an indication of intensity of insolation as light readings were not always obtained. An ordinal index was also created to describe the amount of sunshine (sun cover) by allocating a value of zero to counts where the sun was totally covered by cloud, one to counts where the sun was partly covered and two to counts where there was direct sunshine.

(e) *Statistical analyses*

Analysis of variance was used to establish variation in bat activity and climate variables between sites and time of year. Two-way ANOVAs were then used on each five-day data set individually, to look for significant variation in each variable with day, and time of day. As many of the climate variables were closely correlated it was unsuitable to use them as independent predictors of bat activity, so a principal component analysis was done on the climate data from each five-day set of data to redefine the climate as a series of orthogonal axes. To define the factors explaining most of the variability in observed bat numbers, the scores for each axis extracted ($n=4$–7) were then used as independent predictors in a stepwise multiple regression analysis (for the method see Jolliffe (1982)).

(f) *Comparison of model predictions to observed bat activity*

We compared the revised predictions from the biophysical model to the flight behaviour of bats during the day. Each count from 25 days of data (comprising five, five-day sets of data—it was not noted whether the sun was covered by cloud or shining directly at Amalau in June, so this data set could not be analysed), was individually compared with predictions from the model in the following way: for each measure, observed percentage cloud cover, the angle of the sun and whether the bat was flying in sun or shade were used to calculate a critical temperature from the model, keeping all other variables at the mean settings listed here. We then measured the difference between actual shade temperature measured at that time, and the corresponding critical temperature.

3. RESULTS

(a) *Reanalysis of model predictions*

A total of six of the factors in the biophysical model were varied within a range of values relevant to conditions for *P. samoensis* in Samoa. In each case, the model generated much higher predicted temperatures above which the bats would not be able to fly without risking overheating (T_{acrit}) for animals flying in the shade of cloud than for those flying in direct sunlight but with otherwise identical conditions (see figure 1*a*–*f*). This was particularly so for manipulations of mass, flight speed, angle of sun and percentage of wing exposed (figure 1*a*,*b*,*d*,*f*). In all manipulations except cloud cover, a much larger range of T_{acrit} was generated by varying conditions for bats flying in the shade of clouds. Varying mass and percentage of wing exposed had a relatively small effect on T_{acrit} for these bats (figure 1*a*,*f*). However, varying the other four factors had a much more profound effect, particularly wing albedo and cloud cover which resulted in changes in T_{acrit} of 25 °C and 15 °C, respectively (figure 1*c*,*e*). The total range of critical temperatures generated by the model manipulations both for animals flying in direct sun and in shade was 18.6–46.6 °C.

(b) *Activity patterns*

Bat numbers were higher in all four Amalau data sets than for either of the data sets from Nu'uuli. Numbers at both sites were lowest in March with peak numbers observed at Amalau in January (table 1). There were significant differences in mean number of bats between sites and between seasons (table 2). The number of bats also varied significantly between days in all data sets except Nu'uuli in March (ANOVA: table 3). At each site and time of year bat activity varied significantly with time of day, except at Amalau in January (ANOVA: table 3).

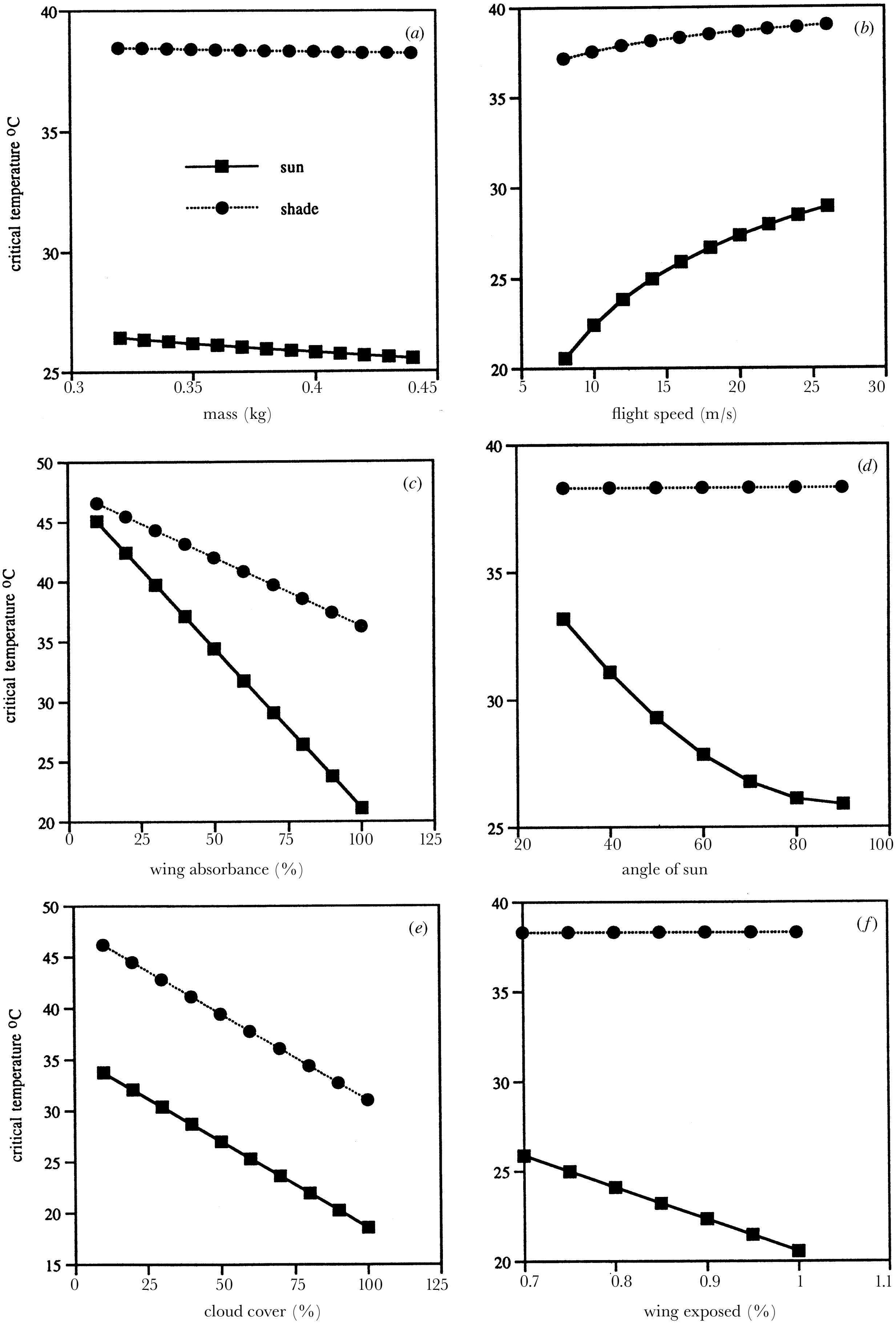

Figure 1. Results of model analysis showing the effect of varying (*a*) mass, (*b*) flight speed, (*c*) wing albedo, (*d*) angle of sun, (*e*) percentage cloud cover, and (*f*) percentage wing exposed. Shown here are temperatures at which the model predicted that flight would incur a risk of hyperthermia for bats flying in direct sunlight (filled circles) and in the shade of clouds (filled squares).

Table 1. *Mean (standard deviation) number of bats and each climate variable, averaged across all ten-minute counts across each five-day period of data collection*

	Amalau				Nu'uuli	
	January	March	June	October	March	October
number of bats	10.84 (3.86)	5.81 (2.69)	8.86 (6.0)	7.0 (4.04)	1.91 (1.37)	2.57 (1.98)
shade temperature in °C	27.77 (1.22)	28.49 (1.99)	27.27 (1.42)	27.08 (1.96)	28.12 (2.02)	26.79 (1.73)
temperature in sun in °C	—	33.39 (6.57)	30.44 (3.65)	32.63 (5.83)	31.64 (5.48)	29.96 (4.88)
insolation	—	4.83 (4.97)	3.17 (2.78)	5.55 (4.28)	3.53 (3.85)	3.17 (3.59)
sun coverage	0.34 (0.65)	0.96 (0.95)	—	0.67 (0.84)	0.57 (0.82)	0.38 (0.7)
cloud cover in %	81.88 (20.1)	40.95 (30.3)	34.16 (29.6)	53.37 (25.0)	54.65 (27.2)	72.46 (25.3)
wind speed in knots	0.96 (0.99)	0.5 (0.92)	2.08 (1.68)	0.64 (1.0)	0.43 (0.7)	1.34 (1.44)

Table 2. *F-values and significance levels from analysis of variance on number of bats and climate variables, examining the effect of time of year and site*

	time of year		site	
	F-value	significance level	*F*-value	significance level
number of bats	4.21	$p<0.001$	320.21	$p<0.001$
shade temperature	110.56	$p<0.001$	22.72	$p<0.001$
temperature in sun	67.26	$p<0.001$	103.4	$p<0.001$
insolation	46.32	$p<0.001$	100.69	$p<0.001$
sun coverage	152.6	$p<0.001$	60.29	$p<0.001$
cloud cover	52.6	$p<0.001$	78.25	$p<0.001$
wind speed	81.56	$p<0.001$	12.97	$p<0.001$

Table 3. *F-values and significance levels resulting from analysis of variance on number of bats and climate variables examining effect of time of day (first value) and day (second value), for each five-day set of data*

	Amalau				Nu'uuli	
	January	March	June	October	March	October
number of bats	0.36^{c}	33.32^{b}	1.62^{a}	4.63^{b}	10.28^{b}	3.14^{b}
	3.47^{b}	6.33^{b}	1.88^{b}	1.23^{c}	2.93^{b}	2.71^{a}
shade temperature	10.42^{b}	2.8^{c}	17.06^{b}	1.05^{c}	5.86^{b}	7.12^{b}
	21.9^{b}	2.09^{c}	6.65^{b}	12.58^{b}	2.19^{b}	20.21^{b}
temperature in sun	—	—	6.37^{b}	6.03^{b}	10.58^{b}	2.32^{c}
	13.35^{b}	1.09^{c}	7.04^{b}	9.2^{b}	4.17^{b}	9.94^{b}
insolation	—	—	3.84^{b}	7.94^{b}	6.16^{b}	5.09^{b}
	7.18^{b}	1.35^{c}	6.12^{b}	6.2^{b}	4.19^{b}	6.22^{b}
sun coverage	2.06^{b}	6.74^{b}	4.72^{b}	5.35^{b}	—	—
	3.15^{b}	7.12^{b}	2.58^{b}	10.51^{b}	1.63^{a}	6.32^{b}
cloud cover	0.8^{c}	17.65^{b}	0.47^{c}	21.76^{b}	0.64^{c}	9.63^{b}
	0.55^{c}	9.31^{b}	0.45^{c}	71.46^{b}	1.11^{c}	27.09^{b}
wind speed	0.23^{b}	19.91^{b}	0.87^{c}	4.98^{b}	0.71^{c}	63.3^{b}
	0.86^{c}	11.07^{b}	1.58^{a}	1.66^{c}	0.43^{c}	54.18^{b}

[a] $p<0.01$.
[b] $p<0.001$.
[c] Not significant.

Mean number of bats was plotted against time of day for each of the five-day sets of data (figure 2*a*–*d*, Amalau and 2*e*,*f*, Nu'uuli). Data collected from Amalau in March, June and October (figure 2*b*,*c*,*d*) and from Nu'uuli in March and October (figure 2*e*,*f*) exhibited similar patterns with a pronounced lull in bat numbers at around 10.00 to 11.00 h, and a peak in activity around 16.00 to 18.00 h. This pattern is most clearly demonstrated in the

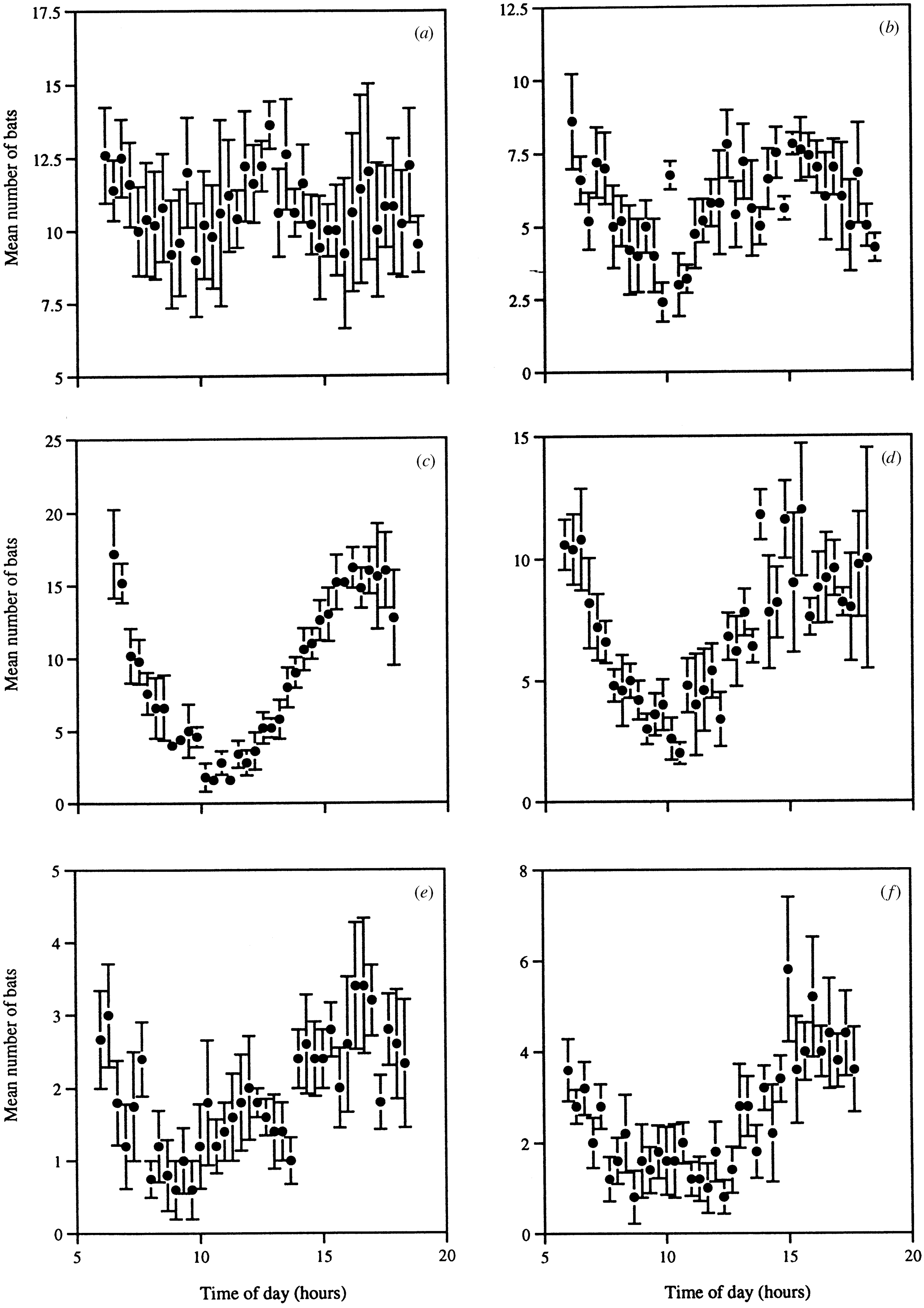

Figure 2. Changes in observed bat numbers over time of day at Amalau in (*a*) January, (*b*) March, (*c*) June and (*d*) October, and at Nu'uuli in (*e*) March and (*f*) October. Each point represents the mean with standard error of a ten-minute count at a given time over five days of counts.

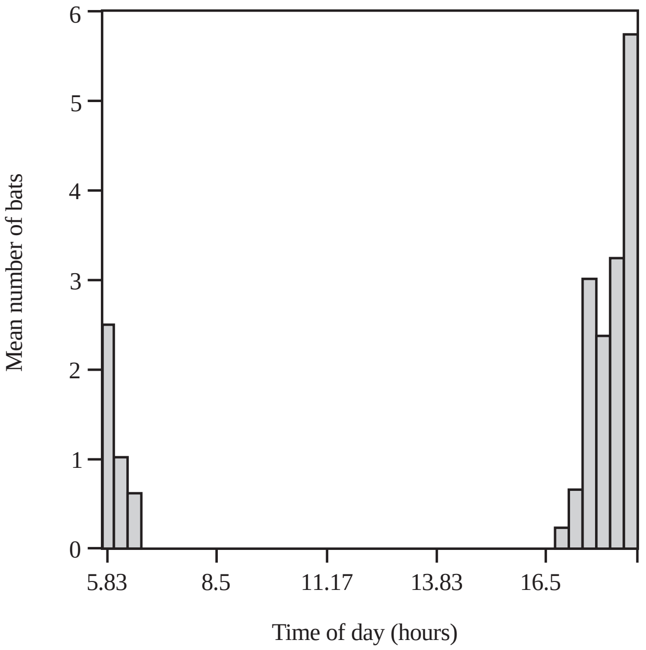

Figure 3. Mean number of *P. tonganus* over time of day, counted on 12 separate days (nine days at Amalau, three at Nu'uuli).

data set collected at Amalau in June (figure 2*c*). In all of these data sets there was one or more individual day that did not conform to this mean pattern. Data collected at Amalau in January (figure 2*a*) were not consistent with the general pattern seen in the other five data sets with a slight peak occurring at midday rather than later in the afternoon. Standard errors in this data set were also much larger indicating a higher day-to-day variation in bat numbers.

Mean numbers of *P. tonganus* counted over 12 days were also plotted against time (figure 3). In contrast to *P. samoensis*, no *P. tonganus* were counted on any of the 12 days between 06.30 and 16.50 h. Small numbers of bats were counted around 06.00 h at the start of counting. The animals reappeared around 17.00 h with numbers starting to build up at 18.00 h as light was beginning to fade.

(c) *Variation in climate*

Each climate variable was significantly different between sites and time of year (table 2). Amount of sunshine and temperature, as indicated by the index of sun cover and sun minus shade temperature, were highest at Amalau and Nu'uuli in March, cloud cover was highest at Amalau in January and Nu'uuli in October and lowest at Amalau in June, wind speed was highest at Amalau in June and at Nu'uuli in October and lowest at both sites in March (table 1). Shade temperature, sun temperature, insolation (as measured by sun−shade temperature) and sun coverage all showed highly significant variation with time of day for all data sets (ANOVA: table 3). The same four variables were also significantly variable between days except for shade temperature at Amalau in January, March and October, sun temperature at Amalau in June and insolation at Amalau in October (table 3). Cloud cover did not vary significantly with time of day in any data set but did show highly significant variation between days for all data sets (table 3). Wind speed showed significant changes with time of day only at Amalau in January and Nu'uuli in March but varied significantly between days in all data sets except Nu'uuli in March (table 3).

(d) *Relation between bat activity and climate variables*

Measurements of humidity, by using a probe linked to the data logger, and light level, by using a light meter, were made in some data sets only and these data were included in the principal components analysis. High correlations were found between many of the climate variables (see, for example, table 4). In each data set the first principal component (PC1) explained between 49.1% and 63.4% of the observed variation. In every case the main factors affecting PC1 were the climate variables associated with insolation i.e. a combination of shade and sun temperature, sun minus shade temperature, sun coverage and light level. (Table 5*a*–*f* shows the eigenvectors resulting from principal component analysis on each data set.) This PC was clearly an indicator of insolation. Interpretation of the other PCs was less straightforward and they were not consistent across sites or time of year.

Bat activity in three of the data sets, collected at Amalau, in March, June and October was significantly affected by PC1 ($p<0.05$, $p<0.01$ and $p<0.01$, respectively). Average cloud cover was lower in all three of these collection periods than in the other three, whereas temperature and amount of sunshine were high. At Nu'uuli in March there was also low cloud cover and high levels of insolation but PC1 did not have a significant effect on activity, although there was a negative effect of sunshine, reflected by a relation with PC5 ($p<0.01$). In the other two data sets (Amalau in January and Nu'uuli

Table 4. *Correlations between climate variables (Amalau, October)*

(All data are significant ($p<0.05$) correlation coefficients, except those highlighted in bold.)

	shade temperature	temperature in sun	wind speed	sun cover	cloud cover	insolation
temperature in sun	0.854	—	—	—	—	—
wind speed	0.25	0.215	—	—	—	—
sun cover	0.586	0.694	0.388	—	—	—
cloud cover	−0.228	−0.313	−0.313	−0.426	—	—
insolation	0.706	0.971	**0.179**	0.689	−0.326	—
light level	0.77	0.792	0.238	0.682	**−0.167**	0.726

Table 5*a–f*. *Results of principal component analysis of variation in all the climate variables in each data set*

(Eigenvalues and proportion of variation explained and eigenvectors for the first four PCs are presented. Dominant variables influencing each PC are highlighted in bold (eigenvectors greater than 0.4 and less than −0.4). The first PC in each case is clearly influenced by the variables reflecting insolation.)

	PC1	PC2	PC3	PC4
(*a*) *Amalau in January*				
eigenvalue	2.126	0.885[a]	0.597	0.393
proportion	0.531	0.221[a]	0.149	0.098
eigenvectors				
shade temperature	−0.579	0.172[a]	0.23	**0.763**
cloud cover	0.387	**0.779**[a]	**0.493**	−0.03
wind speed	−0.459	**0.59**[a]	−0.591	−0.303
sun cover	−0.552	−0.125[a]	**0.596**	−0.57
(*b*) *Amalau in March*				
eigenvalue	4.19[a]	1.039	0.836[a]	0.55
proportion	0.599[a]	0.148	0.119[a]	0.079
eigenvectors				
shade temperature	−0.434[a]	−0.121	0.28[a]	−0.183
humidity	0.363[a]	0.32	−0.127[a]	**0.726**
wind speed	−0.155[a]	−0.76	−0.547[a]	0.294
cloud cover	0.246[a]	−0.508	**0.706**[a]	0.261
sun cover	−0.434[a]	0.132	−0.187[a]	0.082
sun temperature	−0.464[a]	0.079	0.212[a]	0.281
sun–shade temperature	−0.438[a]	0.154	0.168[a]	**0.447**
(*c*) *Amalau in June*				
eigenvalue	2.457[a]	1.149[a]	0.916	0.477
proportion	0.491[a]	0.23[a]	0.183	0.095
eigenvectors				
sun temperature	−0.631[a]	−0.026[a]	−0.133	0.082
shade temperature	−0.511[a]	0.179[a]	0.242	−0.749
cloud cover	−0.081[a]	**0.782**[a]	**0.475**	0.396
wind speed	−0.115[a]	−0.583[a]	**0.781**	0.191
sun–shade temperature	−0.566[a]	−0.126[a]	−0.297	**0.49**
(*d*) *Amalau in October*				
eigenvalue	4.289[a]	1.227	0.664	0.385
proportion	0.613[a]	0.175	0.095	0.055
eigenvectors				
shade temperature	−0.426[a]	−0.182	−0.147	**0.445**
sun temperature	−0.46[a]	−0.181	0.107	0.208
wind speed	−0.18[a]	**0.67**	−0.65	0.205
sun cover	−0.40[a]	0.17	−0.011	−0.805
cloud cover	0.211[a]	−0.622	−0.672	−0.157
sun–shade temperature	−0.442[a]	−0.169	0.201	0.099
light level	−0.417[a]	−0.202	−0.23	−0.184
(*e*) *Nu'uuli in March*				
eigenvalue	4.438	1.038	0.806	0.406
proportion	0.634	0.148	0.115	0.058
eigenvectors				
sun temperature	−0.46	0.041	−0.167[a]	0.178
shade temperature	−0.435	0.133	−0.049[a]	−0.509
humidity	**0.433**	−0.043	0.032[a]	**0.551**
wind speed	−0.224	0.316	**0.906**[a]	0.167
cloud cover	0.088	**0.917**	−0.314[a]	0.106
sun cover	−0.413	−0.195	−0.068[a]	0.308
sun–shade temperature	−0.427	−0.012	−0.212[a]	**0.521**
(*f*) *Nu'uuli in October*				
eigenvalue	3.661	1.332[a]	1.09	0.585
proportion	0.523	0.19[a]	0.156	0.084
eigenvectors				
shade temperature	−0.43	**0.404**[a]	−0.021	−0.036
sun temperature	−0.497	0.075[a]	−0.158	−0.318
wind speed	−0.031	−0.54[a]	**0.666**	−0.436
sun cover	−0.343	−0.468[a]	−0.034	**0.638**
cloud cover	−0.134	**0.542**[a]	**0.672**	0.173
sun–shade temperature	−0.465	−0.106[a]	−0.209	−0.422
light level	−0.464	−0.123[a]	0.186	0.305

[a] PC that regression analysis showed to be significantly correlated with bat numbers.

in October), characterized by high cloud cover and corresponding low levels of sunshine, activity was not related to PC1 (increasing insolation). At Nu'uuli in October, where mean shade temperature was low, bat numbers increased with increasing temperature (as shown by a significant influence of PC2, $p < 0.001$). The other dominant variable observed to have a significant effect on numbers in some of the data sets was cloud cover. Bat activity at Amalau in January, March and June and at Nu'uuli in October increased significantly with increasing cloud cover (as reflected by relations with PC2, $p < 0.01$; PC3, $p < 0.01$; PC2, $p < 0.01$; and PC2, $p < 0.01$; respectively, all of which were dominated by cloud cover). At Amalau in January, and Nu'uuli in October, these were the primary PCs correlated with bat numbers and during both these collection periods mean cloud cover was much higher than in the other four. Wind speed also sometimes affected activity, but here the relation was more variable. PC2 influenced activity at Amalau in January ($p < 0.01$) which indicated a positive relation with wind, as did PC3 which influenced numbers at Nu'uuli in March ($p < 0.05$), whereas increasing wind speed had a negative impact on numbers at Amalau in June (PC2, $p < 0.01$). The highest mean wind speed was also measured at Amalau in June.

(e) *Comparison of model predictions to observed bat activity*

For each of the five data sets analysed, in most of the situations when bats were seen flying, the observed shade temperature was less than the critical temperature at which bats would experience hyperthermia predicted by the model. Nevertheless, in 5–15% of situations bats were observed in flight when the shade temperature exceeded the critical temperature at which the model had predicted these bats would be unable to fly because of the risk of hyperthermia. The mean difference between observed shade temperature and corresponding critical predicted temperature across five days of measurements has been plotted along with mean bat activity for all five data sets analysed (figure 4*a*–*e*). Increasing temperature and insolation resulted in a decrease in the mean difference between shade temperature and T_{acrit} in the middle of the day in all five data sets. The extent of this decrease varied, ranging from Nu'uuli in October where all mean shade temperature measurements were lower than T_{acrit} (figure 4*e*) to Amalau in January, where for a three-hour period the shade temperature came close to or exceeded T_{acrit} (figure 4*a*). Despite five out of six data sets demonstrating a general decline in flight activity during the middle of the day, the relation between temperature difference and bat numbers was not consistent. At Amalau in January there was a peak in bat numbers at the time when shade temperature exceeded T_{acrit} i.e. when the model suggested there was a risk of hyperthermia (figure 4*a*). Similarly, bat numbers were near their peak at Amalau in March when the model suggested the risk of heat stress was greatest (figure 4*b*). In contrast, at Nu'uuli in March and October bat numbers were lowest at times when the difference between shade temperature and T_{acrit} was small i.e. when predicted risk of hyperthermia was high (figure 4*d*,*e*).

4. DISCUSSION

Speakman *et al.* (1994) calculated a range in T_{acrit} for *P. samoensis* in Samoa of 28.1–31.5 °C. The range of temperatures generated by the modified and more extensive manipulations for *P. samoensis* here was far greater, spanning temperatures that are both lower and much higher than would normally be found in Samoa at any time of year. As this new range of temperatures does still span the range of observed air temperatures in Samoa we predicted, as Speakman *et al.* (1994) originally suggested, that there could indeed be a risk of hyperthermia under certain combinations of climate conditions, for example, high percentage cloud cover while the sun is uncovered by cloud, and therefore we should expect significant variation in this species' diurnal activity.

The day-to-day variation in the pattern of activity recorded here might explain the inconsistencies in previous attempts to describe activity patterns of the Samoan fruit bat (see, for example, Cox (1983), peak in activity 11.00–14.00 h; Morrell & Craig (1995), lull in activity 10.00–14.00 h; Wilson & Engbring (1992), activity peaks in early morning and late afternoon). We found that bat activity varied significantly between sites, the time of year, and day-to-day. Therefore observed diurnal activity patterns will vary according to the time of year, day and site chosen. Discrepancies in described activity are further exacerbated by the fact that none of the previous studies attempted to measure activity continuously through the day, but amalgamated data from segments of activity information collected over separate days.

Consistently fewer bats were counted in the Nu'uuli valley than at Amalau. This can probably be explained by differences in vegetation between the two areas i.e. Nu'uuli has more secondary growth. Most of the animals counted at Nu'uuli were passing over the valley, few bats were seen roosting or foraging in the valley itself. In contrast, although Amalau also acts as a corridor for bats travelling into neighbouring areas of forest, in all seasons bats could also be seen roosting and foraging in the valley. The Amalau valley has a high density of *Syzygium inophylloides* of which the flowers and fruit are a preferred food source for *P. samoensis* (Pierson *et al.* 1996). Peak flowering time for this species was in December 1994 and January 1995. At this time large numbers of *P. samoensis* were seen foraging around the trees which may explain the high mean numbers of bats counted at this time of year as well as the lack of a lull in activity around midday when insolation was high. It was beyond the scope of this study to account for the length of time in flight of individual animals. However, it is probable that time in flight is a key factor affecting the risk of hyperthermia at times when insolation is intense. It is possible that the high numbers of bats seen in flight at midday at Amalau in January were primarily engaged in short foraging flights as opposed to commuting longer distances and were therefore less at risk of overheating.

Temperature and sunshine were negatively correlated with bat flight activity at Amalau in three of the four times of year that measurements were made. When insolation was generally high, increases in sunshine and temperature were correlated with reduced bat activity, but when cloud cover was high and there was less direct

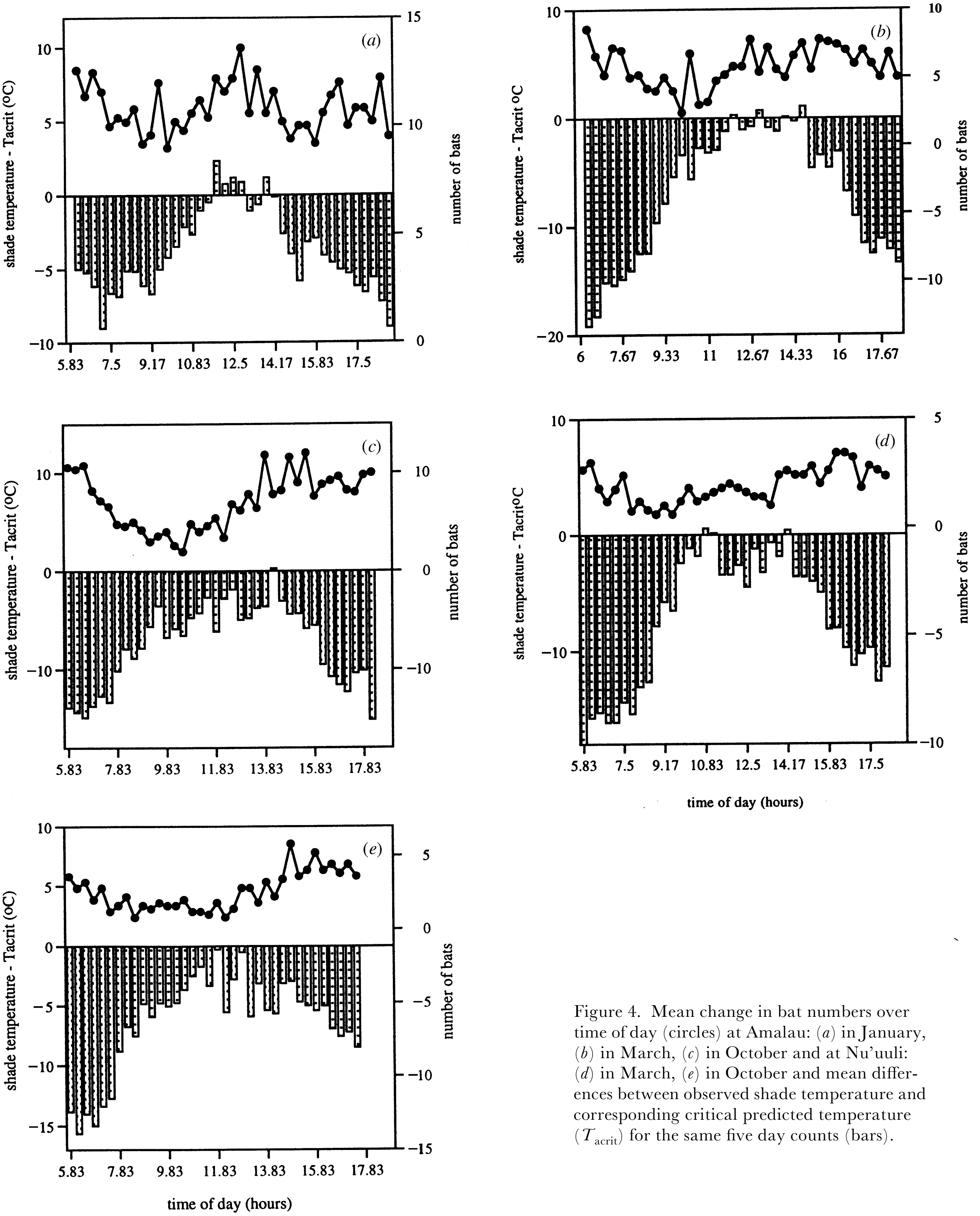

Figure 4. Mean change in bat numbers over time of day (circles) at Amalau: (*a*) in January, (*b*) in March, (*c*) in October and at Nu'uuli: (*d*) in March, (*e*) in October and mean differences between observed shade temperature and corresponding critical predicted temperature (T_{acrit}) for the same five day counts (bars).

sunshine, this relation did not occur. At Nu'uuli in October, although increasing amounts of sun and light levels were found to be related to decreased bat numbers, increasing shade temperature was actually correlated to increased activity. This may be explained by the low mean shade temperatures at this time. The percentage of time that there is direct sunshine is probably a key factor and is supported by the biophysical model predictions. In every manipulation, T_{acrit} predictions were at least 10–15 °C lower for bats flying in direct sun than for bats flying in shade.

Bat activity in four of the six data sets was found to significantly increase with increasing cloud cover. This directly contradicts the predictions of Speakman and co-workers' (1994) biophysical model which suggests that T_{acrit} is much lower when cloud cover is high. However, a key factor affecting the model predictions is whether the bats are flying in direct sunlight or in the shade of clouds; as cloud cover increases, the probability of the sun being shaded also increases. Whether the sun is covered by cloud or not has a greater affect on T_{acrit} than changing cloud cover in either condition. Wind speed only significantly decreased flight activity when wind speeds were high, i.e. at Amalau in June. When wind speeds were over three knots we often observed bats being buffeted about and struggling to fly over ridges. At other times, when mean wind speed was lower, either no relation or a positive relation between wind speed and bat numbers was found.

Most of our results conform to the suggestion that diurnal activity in *P. samoensis* will pose a risk of hyperthermia when ambient shade temperatures and solar radiation are high (Speakman *et al*. 1994). Whereas the most of observations of bats in flight were within the conditions predicted by the model, up to 15% of bats observed were flying when the model predicted they should not owing to the risk of hyperthermia. Furthermore, when bat activity patterns were directly compared with the critical temperatures predicted by the model, as often as not, high levels of activity were observed at times the model predicted maximum risk of overheating. However, although we have generated revised estimates of T_{acrit} from the model, we have still greatly simplified an extremely complex situation and many assumptions were still made. For example, we used a value of 0.82 for wing albedo (after Speakman & Hays 1992) taken from measurements made on the wing membrane of mostly insectivorous bats in the visible spectrum only. No measurements of the albedo of *P. samoensis* wings have been made yet, and it is possible that even in insectivorous bats the wing membranes are less absorbent in the ultraviolet and infrared areas of the electromagnetic spectrum. According to the model manipulations made in this paper, decreasing wing absorbance by only 10% would increase T_{acrit} by approx 5 °C. This factor alone would mean that almost all the observations of animals flying above T_{acrit} would fall within the constraints of the model. Another complicating factor is the transient nature of many of the climate variables we measured. Cloud cover and consequently sun coverage often changed very rapidly. Most of the bats counted as flying beyond T_{acrit} were flying in direct sunlight, but under conditions of fast moving cloud the sun was often quickly covered soon after climate measurements were made, instantly lowering T_{acrit} at that time by at least 10 °C. It is possible that often bats were counted in very different climate conditions to those measured just ten minutes previously. Our data support previous reports that in Samoa *Pteropus samoensis* is active throughout the day and that high levels of insolation may inhibit its activity.

Data recently collected from radio tracking two young male *P. samoensis* showed that there was nocturnal, as well as diurnal, activity but the extent of this activity is not known (Brooke 1996). In contrast to *P. samoensis*, the sympatrically occurring *P. tonganus* did not behave in the same way but restricted their foraging activity to the hours of darkness. Although *P. tonganus* are slightly larger than *P. samoensis* (A. P. Brooke, unpublished data), their size falls well within the mass range used in the model manipulations and we found that altering the mass had little effect on T_{acrit}. Therefore we might predict that the same constraints applied to both species and in identical conditions *P. tonganus* should have been able to fly during the day at times when *P. samoensis* was seen to be active. *P. samoensis* has a longer history of living in isolation than *P. tonganus*. Perhaps *P. tonganus* has not yet had time to evolve diurnality on Samoa. Diurnal activity may also be related to population density and fruit availability. Considerable overlap in activity in the two species was seen before cyclones recently devestated the islands (Pierson *et al.* 1996). After the cyclones, *P. tonganus* numbers dropped by 80–90%. The more strictly nocturnal behaviour we observed may be a consequence of reduced numbers and abundant food supply (Pierson 1993).

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