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Absorption of visible spectrum radiation by the wing membranes of living pteropodid bats

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Abstract The wing membranes of bats present a large surface area upon which radiation might be taken up, increasing heat load to the animals. This, combined with the high amount of heat produced during flight, has been advanced as one hypothesis explaining the fact that bats are almost exclusively nocturnal. The proportion of short-wave (visible) radiation absorbed by bat wing membrane has previously been measured at between 0.7 and 0.92. These measurements were made on pieces of membrane taken from the wings of dead, mainly insectivorous bats from temperate regions. Here we examined the amount of light transmitted through and reflected off the wing membranes of four species of live pteropodid bats. There were significant differences in wing reflection between species. At 0.68, the average proportion of light absorbed into the wing membranes was lower than previously reported. This might be because we worked with live animals or because ours were tropical bats which are routinely exposed to tropical sun when roosting. Variation in wing tension strongly affected light absorption. It was predicted that the relaxed state of wing membrane through part of the wing beat cycle would increase the absorption of light into the wings of day-flying bats. The proportion of light absorbed into wings was shown to be an important factor in the heat balance of hypothetical bats flying during the day. Our results raise the predicted temperature at which bats flying during the day might experience hyperthermia by approximately 2 °C and suggest that variation in albedo of wings between species may make some species more susceptible to overheating than others.

Key words *Pteropodid* bats · Colouration · Solar radiation · Wing membranes · Thermoregulation

Abbreviations R_{zero} radiation reflected from black matt card · R_{white} radiation reflected from white card · R_{max} maximum radiation reflection · R_{wing} radiation reflected from a piece of wing tissue · R_w radiation transmitted through a section of wing · R_i radiation incident onto a section of wing

Introduction

Solar radiation is one of the most significant environmental factors affecting animal heat balance (Porter and Gates 1969). Radiation striking an animal may be reflected off, transmitted through or absorbed into its surface. Consequently the surface properties of an animal are likely to affect its heat balance. In temperate zone animals, dark colouration functions primarily to maximise absorption of solar energy (Hamilton and Heppner 1967; Cossins and Bowler 1987) thus aiding thermoregulation (Gessaman 1973). Conversely, in the tropics, dark colouration may be disadvantageous. Dark birds may need to offset their disadvantageous colouring by nesting in the shade, while their light coloured counterparts are able to nest in full sunlight (Ellis 1980).

The proportion of sun and skylight absorbed by different animals may vary from 0.2–1.0 (Porter and Gates 1969) and differences in colour may alter the temperature at which animals experience hyperthermia. When white zebra finches were dyed black, the proportion of direct and indirect solar radiation they absorbed increased from between 0.21 and 0.27 to 0.59 and meant they could withstand an air temperature of only 12.5 °C before becoming heat stressed, compared to 30 °C prior to being dyed. Kelly et al. (1954) measured the spectral reflection of pigs of different colours. They found the proportion of incident solar radiation absorbed by white pigs was 0.49, red pigs absorbed 0.75 and black pigs absorbed 0.93. This difference meant the

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black pigs experienced heat stress in full sunlight at temperatures of 10 °C whilst the white pigs did not experience hyperthermia until temperatures above 25 °C were reached. In the visible section of the solar spectrum, absorption of radiation by vertebrate skin may be very high, at over 0.9, and over the whole spectrum, fur or feathers that appear black in the visible spectrum may absorb 0.85 of the incident radiation (Gates 1980). For animals with an insulative coat of fur or feathers, a complex combination of the characteristics of their coats combined with underlying skin colour determines heat load resulting from solar radiation (Walsberg et al. 1978; Walsberg 1988). For example, two species of golden-mantled ground squirrels (*Spermophilus lateralis* and *S. saturatus*) have different coat colours and show marked differences in the amount of solar radiation reflected. Despite this, there is little difference in heat load transferred to the skin between the two species as a result of structural differences in their fur (Walsberg 1990).

In addition to exogenous heat such as solar radiation, animals must also dissipate metabolic heat generated endogenously. The energetic cost of flight has been estimated at approximately 14 times that of basal metabolism (e.g. Hudson and Bernstein 1983; Tatner and Bryant 1986; Speakman and Racey 1991; Winter et al. 1993; Winter and von Helversen 1998). For animals that fly during the day there may be a risk of hyperthermia when endogenous metabolic heat production is added to inputs from solar radiation. This has been advanced as one hypothesis to explain why most bats are nocturnal (Speakman 1990; Thomas et al. 1991; Speakman 1995). As the body temperature of bats during flight is only slightly lower than their lethal body temperature, the capacity to dissipate heat during flight may be crucial to prevent overheating (Thomas et al. 1991). It has been suggested that bats rely largely on their wings for heat exchange (Reeder and Cowles 1951), regulating their body temperatures through vascular changes (but see Lancaster et al. 1997). Thomas et al. (1991) estimated that *Phyllostomus hastatus* lost only 14% of their metabolic heat load through respiratory evaporation and suggested that cutaneous heat loss channels were therefore very important to these animals. Although bat wings appear well adapted for heat loss, they also potentially provide a large surface area for the uptake of solar radiation. Despite this potential problem there are bats that fly frequently during the day in the tropics (for example *Pteropus samoensis* in Samoa; Cox 1983; Wilson and Engbring 1992; Thomson et al. 1998 and *Pteropus seychellensis* in the Comores; Cheke and Dahl 1981). Using a biophysical model, Speakman et al. (1994) attempted to account for all heat fluxes across the wing membranes of a hypothetical bat flying during the day. The model predicted a critical temperature beyond which bats should not be able to fly without experiencing hyperthermia. This model revealed that absorption of light into the wing membrane was an important factor affecting the critical temperature: bats with wings that

had a high absorption of short wave radiation were more susceptible to overheating than bats with wings that absorbed less radiation (Speakman et al. 1994).

The mean wing absorption of sunlight for several insectivorous bats and one pteropodid bat ranged from 0.7 to 0.92 and averaged 0.82 (Speakman and Hays 1992). These results were obtained from measurements made on pieces of partially dehydrated wing membrane removed from dead bats. It is possible that reflection and transmission of light are different in live wing membranes, which are infused with blood. The first aim of the present study was to address this possibility by measuring the absorption of sunlight by the wing membranes of living bats. The insectivorous bats measured by Speakman and Hays (1992) are rarely exposed to insolation, as they roost primarily in buildings. In contrast, many large species of pteropodid bats in tropical and subtropical regions roost on the exposed branches of trees in direct sunlight and frequently make short flights in the vicinity of their roost during the day, even if they are not diurnal foragers (Lekagul and McNeeley 1977). As a consequence they are more likely to experience heat stress resulting from absorption of solar radiation. These bats could potentially reduce the risk of hyperthermia if less solar radiation was absorbed into their wing membranes. We made measurements on the wing membranes of four species of tree roosting *Pteropus*, aiming to establish whether they did absorb less short wavelength radiation than temperate zone insectivorous bats. Filters were used to see if altering the wavelength of light within the visible part of the spectrum affected reflection and transmission in two of the species. Finally, we examined the effect that changes in wing tension, similar to those that might occur during flight, had on the absorption of light into the wing.

Materials and methods

Measurements were made on the wings of four species of *Pteropus* held in captivity at the Lube Foundation in Gainesville, Florida, USA. A total of seven Rodrigues fruit bats – *P. rodricensis* (five females, two males); four little golden-mantled fruit bats – *P. pumilus* (one female, three males); six island flying-foxes – *P. hypomelanus* (all females) and five large fruit bats – *P. vampyrus* (three females, two males) were used in the experiments. All animals were adults that had been held in captivity for several years. Bats of all species were housed in single sex groups of 6–18 individuals in wire mesh enclosures that were open to insolation, with a central heated shelter. Animals were free to move between the shelter and the exposed areas of their enclosure throughout the day. Individuals were caught approximately half an hour before measurements were made and kept in a small handling cage indoors to enable them to recover from any capture stress. For both reflection and transmission measurements, all the bats were restrained by hand on a padded board in a face down position so the dorsal side of the right wing was accessible. Their wings were stretched into a fully extended position while each measurement was made, then relaxed between measurements.

Reflection measurements

Each bat's wing was held across the surface of a sealed black box with a hole 5 cm in diameter in the top. The wing was gently

pressed down so the membrane between the third and fourth digits completely covered the hole and no ambient light could leak into the box. Light from a 75 W daylight emission bulb (Daylight Studios) held inside a sealed cylinder was directed down a metal tube of 2 cm in diameter and reflected off the wing membrane where it was positioned over the black hole. The metal tube was bent at a 45° angle. It is easiest to measure transmission directly through the wing, but for reflectance the detector and emitter need to be offset and 45° is a suitable angle. Previous studies have indicated that the angle has little effect until it is very shallow. Any light reflected off the wing up the tube was measured at the top using a precision lightmeter (Gossen Mastersix) (see Fig. 1a). The precision lightmeter was the most versatile equipment available for making measurements on live animals. We could not find a spectrophotometer for measuring near infrared that did not require sampling the tissues and measuring biopsies from dead animals. The apparatus was completely sealed and all surfaces inside were coated with black matt card. Where the metal tube pressed on the wing membrane and where the light meter was attached, a soft layer of black foam was fixed to it to prevent damage to the wing

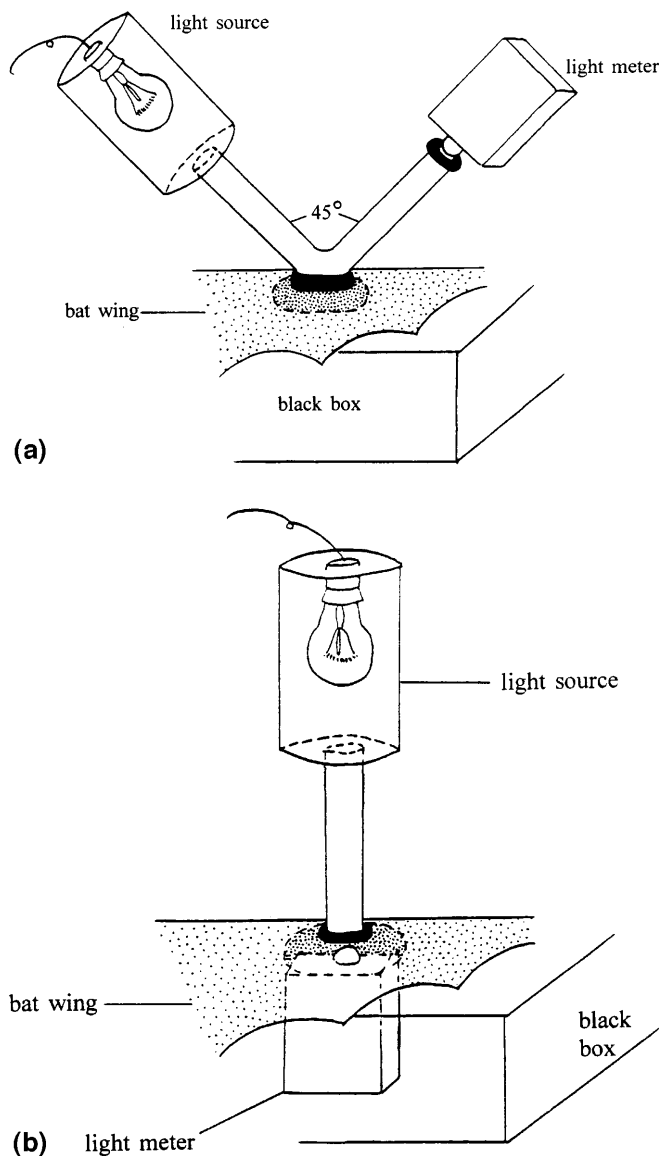


Fig. 1 Apparatus **a** used to measure reflection of light off the surface of the wing and **b** used to measure transmission of light through the wing

and stop any ambient light entering the equipment. This method assumes that reflection is mostly directional and that there is minimal diffusive reflection from the surface at angles other than 45°. This may introduce an unquantified error into the measurements. To calibrate the equipment, prior to each wing measurement a reading was taken off a piece of black matt material (zero reflection, R_{zero}) and then off a piece of white card with a known albedo (i.e. reflection) of 0.96 (R_{white}). Maximum reflection for each measurement was defined as [$R_{max} = (R_{white} - R_{zero})/0.96$]. After each wing measurement, the reflection of a piece of grey card was calculated to ensure consistency of the measurement technique. The reflection of each wing and grey card measurement was calculated by:

$$\text{reflection} = (R_{wing} - R_{zero})/R_{max} \text{ (after Speakman and Hays 1992).} \quad (1)$$

Transmission measurements

For transmission measurements, a similar setup to that described above was used, except a single straight tube was fitted to the cylinder containing the daylight bulb (Fig. 1b). The beam of light was directed vertically onto the wing. The tube was also coated with black foam to minimise leakage of ambient light into the apparatus. The lightmeter was inserted into the black box and the measuring cell positioned under the wing exactly where the light was directed. Prior to each wing reading (R_w), incident light was measured directly from the tube (R_i). This was repeated after the wing reading and if the two blank readings differed then that wing reading was rejected. Transmission was then calculated as:

$$\text{transmission} = R_w/R_i \text{ (after Speakman and Hays 1992).} \quad (2)$$

A single measure of reflection and transmission was conducted on every bat except three female *P. rodricensis* and all five *P. vampyrus*, on which two readings were taken, the mean of which was used in further analyses. On six *P. rodricensis* (four females and two males) and all four *P. pumilus* we repeated the above protocols three times in order to determine the effect of changing wavelengths of light within the visible part of the electromagnetic spectrum on wing absorption. To do this, three Kodak Wratten filters, numbers 2B, 12 and 29 were slotted in front of the daylight bulb. These filters have very rapid transition points from total absorption to total transmission and have 50% absorption/transmission points at 400, 500 and 600 nm respectively. Finally, measurements on all six *P. hypomelanus* were repeated twice with the wings held in different positions to establish the effect of changes in wing tension on absorption. The first readings were made as described above on fully extended, taut wings (i.e. with the wrist held open at 180°). Second, readings were taken with the wrist held open at an angle of approximately 160° so the wings were allowed to relax slightly. Finally, readings were repeated after the wing was further relaxed with the wrist held open at an angle of approximately 140°.

After transmission and reflection of light had been calculated for each wing measurement, the total amount of light absorbed by the wing was calculated as $1.0 - (\text{reflection} + \text{transmission})$. A paired *t*-test was used to test whether differences between the amount of light reflected and transmitted were significant. One way analysis of variance was used to test for differences in wing reflection, transmission and absorption between species and for differences resulting from changes in wing tension. Where a significant difference was obtained, a Tukey multiple comparison was applied. Two way ANOVAS were used on the combined data for *P. rodricensis* and *P. pumilus* to identify changes resulting from variation in the wavelength of light used and potential species differences. All data were arcsine-transformed before analysis.

Biophysical modelling

We used the biophysical model developed by Speakman et al. (1994) to predict the effect that changing the amount of absorption

of light into the wing membrane would have on the critical temperature above which a bat should not be able to fly without experiencing hyperthermia. The model analysis generated critical temperatures for a bat with wing absorption ranging from 10–100%, accounting for body mass (estimated from adult *P. samoensis* captured in Western and American Samoa; from Richmond et al. 1995), wing span and area and flight speed (generated from these masses using allometric equations from Norberg and Rayner 1987), sun angle (90°, i.e. directly overhead), percent cloud cover (56.7%, mean of measurements made across four seasons in American Samoa from Thomson et al., 1998), proportion of wing exposed, maximum wing temperature and ground albedo and temperature (set at 0.7, 315 K, 0.12 and 303 K, respectively; all from Speakman et al. 1994). Results were produced for a hypothetical bat, flying in the shade of clouds, and for a bat flying in direct sunlight. We used these data to assess the impact any differences in absorption found in this study, compared to mean values resulting from Speakman and Hays (1992), might have on the susceptibility of day-flying bats to hyperthermia.

Results

The maximum spectral sensitivity of the lightmeter was 400–700 nm with a peak at 550 nm. In contrast, within this range, the spectral emissivity of the light source increased between 500 nm and 700 nm. The relative sensitivity of the apparatus was calculated by combining both of the above spectral distributions (Fig. 2). The mean reflection of the standard grey card measured after each wing measurement was 0.341 ($n = 88$) with a standard deviation of 0.033.

Without exception, more light was reflected off the wing surface than was transmitted, and across all measurements this difference was significant (paired *t*-test: $T = 5.4$, $P < 0.001$, $df = 41$). For measurements without filters on fully taut wings only, mean transmission across all individuals was 0.13 ± 0.08 and mean reflection was 0.19 ± 0.08 ($n = 22$). In other words,

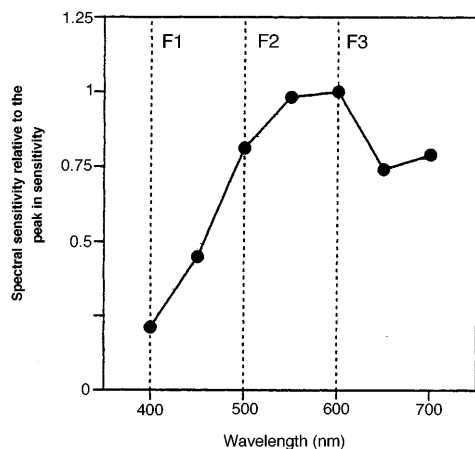


Fig. 2 Changes in the relative sensitivity of the apparatus, calculated by combining the spectral sensitivity of the light meter with the spectral emissivity of the light source, presented as a proportion of the peak in sensitivity. The filters used to block out varying wavelengths of visible light are marked; *F1* blocked out light less than 400 nm, *F2* light less than 500 nm and *F3* light less than 600 nm

6% more light was reflected off the surface of the wings than was transmitted through. When these data were combined, on average 0.68 ± 0.01 ($n = 22$) of light was absorbed into the wing. There was no relationship between transmission and reflection (regression analysis: $F = 2.02$, $P = 0.171$, $df = 1.20$, $r^2 = 4.6\%$). Wings which transmitted more light did not reflect less or more. There were significant differences between species in the amount of light reflected off the wing surface (ANOVA: $F = 3.68$, $P = 0.032$, $df = 3.18$) (Table 1). A Tukey multiple comparison test showed that *P. hypomelanus* had a lower mean reflection than *P. pumilus* (confidence interval of the mean difference assuming 5% overall error rate: 0.005, 0.114). There was no significant difference in the mean amount of light transmitted through the wing between the four species (ANOVA: $F = 1.08$, $P = 0.381$, $df = 3.18$). There was also no significant difference in mean wing absorption between the four species (ANOVA: $F = 2.18$, $P = 0.126$, $df = 3.18$) (Table 1).

Combining the *P. rodricensis* and *P. pumilus* data on reflection using filters, no significant differences were detected between the two species or as a result of changing the wavelength of light directed onto the wing surface (ANOVA: $F = 1.04$, $P = 0.315$, $df = 1.8$ and $F = 0.58$, $P = 0.631$, $df = 3.36$, respectively) (Table 2). Inserting filters did not significantly affect transmission either (ANOVA: $F = 1.18$, $P = 0.333$, $df = 3.36$) (Table 2). Higher mean values for *P. rodricensis* for all filter measurements resulted in a marginally significant effect of species difference on transmission (ANOVA: $F = 4.35$, $P = 0.045$, $df = 1.8$). However, total absorption did not vary according to species or filter used (ANOVA: $F = 3.94$, $P = 0.056$, $df = 1.8$ and $F = 0.3$, $P = 0.823$, $df = 3.36$, respectively). Mean absorption ranged from 0.55 ± 0.05 for *P. rodricensis* when filter three was used to 0.73 ± 0.05 for measurements on *P. pumilus* with no filter (Table 2).

Reducing wing tension by changing wing position in *P. hypomelanus* had a profound effect on reflection and transmission and consequently on total absorption of light into the wing membrane (ANOVA: reflection $F = 75.68$, $P < 0.001$, $df = 2.15$; transmission $F = 21.4$, $P < 0.001$, $df = 2.15$ and absorption $F = 72.69$, $P < 0.001$, $df = 2.15$). Mean reflection was reduced from over 0.13 in a fully taut wing to less than 0.02 in a relaxed wing. Correspondingly, mean transmission dropped from over 0.1 to less than 0.04. Overall, mean

Table 1 Mean \pm SE of reflection, transmission and absorption of the wing membrane of four different species of *Pteropodid* bats to the light emitted from a daylight bulb

Species	<i>n</i>	Reflection	Transmission	Absorption
<i>P. rodricensis</i>	7	0.19 ± 0.01	0.15 ± 0.01	0.66 ± 0.02
<i>P. pumilus</i>	4	0.22 ± 0.03	0.14 ± 0.02	0.64 ± 0.04
<i>P. vampyrus</i>	5	0.20 ± 0.01	0.12 ± 0.02	0.68 ± 0.03
<i>P. hypomelanus</i>	6	0.16 ± 0.01	0.12 ± 0.02	0.72 ± 0.02

Table 2 Mean \pm SE of reflection, transmission and absorption of the wing membrane of two species of *Pteropodid* bat to the light emitted from a daylight bulb, before and after passing through three different filters blocking out all light of wavelengths less than 400, 500 and 600 nm

Species	Filter	<i>n</i>	Reflection	Transmission	Absorption
<i>P. rodricensis</i>	Blank	6	0.22 \pm 0.03	0.14 \pm 0.02	0.64 \pm 0.04
	> 400 nm	6	0.24 \pm 0.04	0.13 \pm 0.01	0.63 \pm 0.05
	> 500 nm	6	0.28 \pm 0.08	0.16 \pm 0.01	0.56 \pm 0.08
	> 600 nm	6	0.27 \pm 0.05	0.18 \pm 0.02	0.56 \pm 0.06
<i>P. pumilus</i>	Blank	4	0.16 \pm 0.03	0.11 \pm 0.02	0.73 \pm 0.05
	> 400 nm	4	0.30 \pm 0.12	0.11 \pm 0.02	0.60 \pm 0.12
	> 500 nm	4	0.17 \pm 0.03	0.11 \pm 0.02	0.73 \pm 0.05
	> 600 nm	4	0.16 \pm 0.04	0.14 \pm 0.03	0.70 \pm 0.06

absorption was 0.76 ± 0.02 in taut membrane and 0.94 ± 0.01 in relaxed membrane (Table 3).

The biophysical model predicted that, for day-flying bats flying both in cloud shade and in direct sunlight, there would be a decrease in the temperature at which the animals might fly without risking over-heating with an increase in the absorbance of light into the wing membrane (Table 4). This change in critical temperature was more marked for animals flying in direct sunlight, varying from 44.5 °C when absorption was 0.1 to only 22 °C when absorption was 1.0 (Table 4).

Speakman and Hays (1992) found a mean absorbance of 0.82 in the tissue samples collected from the species they studied. This leads to a predicted critical ambient air temperature, above which flight might lead to hyperthermia under the conditions defined in the methods section, of 26.8 °C in the sun and 38.8 °C in the shade. In contrast, the estimated mean absorbance of 0.68 measured here leads to critical ambient temperatures under these conditions of 29.9 °C in the sun (about 3 °C higher than the previous estimate), and 40.2 °C in the shade (1.4 °C higher). Differences measured between the pteropodid species lead to different predicted critical ambient temperatures. Hence a hypothetical bat with a mean absorbance of 0.64 (value for *P. pumilus*) had predicted critical ambient temperatures in the sun and shade of 31.5 °C and 40.6 °C respectively, while a hypothetical bat with the same absorbance as *P. hypomelanus* (0.72) has predicted critical temperatures of 29.2 °C and 39.8 °C, respectively. Thus species-specific differences in absorbance might lead, in part, to differences in their ability to withstand hyperthermia in daylight flight.

These figures, and those we have derived previously from the biophysical model (Speakman et al. 1994), are

Table 3 Mean \pm SE of reflection, transmission and absorption of the wing membrane of *P. hypomelanus* to the light emitted from a daylight bulb with the wing membrane in three positions: (1) fully extended, (2) partially relaxed and (3) fully relaxed (see text for more details)

Wing position	<i>n</i>	Reflection	Transmission	Absorption
1	6	0.13 \pm 0.01	0.10 \pm 0.01	0.76 \pm 0.02
2	6	0.04 \pm 0.004	0.07 \pm 0.01	0.89 \pm 0.01
3	6	0.02 \pm 0.003	0.04 \pm 0.004	0.94 \pm 0.01

based on the assumption that throughout the wing beat cycle the wing membranes remain taut. We have shown here that folding the wrist joint leads to relaxation of the ptgial membranes, and in this condition they reflect and transmit significantly less light than taut membranes do. Wing-beat kinematic data for bats (Aldridge 1986) show that the wing is completely extended throughout the downstroke. However, during the upstroke the wrist and elbow are flexed so that the whole membrane is under less tension. The data derived here allow us to model the impact of these changes, which were ignored in our previous modelling.

We modelled the effects of this flexion of the wing membrane using the kinematic data from Aldridge (1986) for the greater horseshoe bat (*Rhinolophus ferrumequinum*). The exact kinematics of flight in this species may not match those of large Pteropodids, but they serve to illustrate the likely magnitude of the impact of the changes in wing membrane tension on absorbance, and thus overheating. During downstroke the ulna makes an angle of approximately 175° with the first digit. This angle changes to approximately 135° during the upstroke. We made measurements of absorbance at 180° and 140°. We assumed that the wing membrane absorbance during downstroke is equivalent to that measured with the wrist at 180°, and the absorbance during upstroke is equivalent to that measured at 140°.

Table 4 Results of analysis using biophysical model from Thomson et al. (1998) showing critical temperature (°C) beyond which a hypothetical bat flying during the day should not be able to fly without risking hyperthermia for a range of wing absorptions. Results of analysis both for a bat flying in direct sun and for one flying in cloud shade

Absorption	Critical temperature (°C)	
	In sun	In shade
0.1	44.5	46
0.2	42	45
0.3	39.5	44
0.4	37	43
0.5	34.5	42
0.6	32	41
0.7	29.5	40
0.8	27	39
0.9	24.5	38
1.0	22	37

We measured the vertically projected areas throughout a downstroke and an upstroke as a proportion of the maximally presented area at the peak of downstroke (assumed to equal actual wing area).

On average, throughout the wing-beat cycle in this species the vertically projected area averages 0.6 times the maximal projected area. During downstroke the wing area projected vertically averages 0.69 of the maximal projected area; in contrast, during upstroke the vertically projected area of the wings averages only 0.46 of the maximal projected area. If the wing was taut throughout the cycle the absorbance would average 0.72 and the vertically projected area as a proportion of the maximal area would average 0.6. Because the wing is not taut during upstroke, the absorbance increases to 0.94. Taking the products of projected area and absorbance throughout a complete wing-beat cycle and dividing the result by the average vertically projected proportion of 0.6 leads to a mean absorbance throughout the wing-beat cycle (corrected for changes in the vertically projected areas) of 0.80. The effect of changing the mean absorbance from 0.72 to 0.80 is a decrease in the critical ambient temperature at which the bats can fly in sunlight without experiencing hyperthermia by approximately 2 °C. Subtle effects therefore, not previously accounted for in the biophysical modelling (Speakman et al. 1994), may have a significant impact on the predicted critical ambient air temperatures above which bats will experience hyperthermia.

Discussion

At 0.68, the average wing absorption of all the bats we measured with fully extended wings was lower than the mean value of 0.82 recorded by Speakman and Hays (1992). There are several possible explanations for this difference. First, differences in experimental setup, such as using a different light source, may have contributed to observed differences. The daylight bulbs used in the present study are designed to imitate skylight rather than sunlight. They have a lower emission in blue wavelengths and a correspondingly higher emission in red wavelengths than indirect summer sun which was used by Speakman and Hays (1992). If the bat's wings were absorbing different amounts of light at different wavelengths this could affect net absorption. However, the data obtained from using filters (Table 2) suggested no differences with changing wavelength so this was unlikely to be important. Probably a more fundamental reason for the difference in mean absorption was the use of tissue from dead animals in the earlier study compared to live tissue in our study. Bat wing membrane is heavily vascularised (Reeder and Cowles 1951). There was no blood in the dead tissue used by Speakman and Hays (1992) and, although live wings only become perfused at high temperatures, there may still have been enough blood in the tissue we measured to potentially make a difference. Moreover, reflection and transmis-

sion are often strongly correlated with water content (Monteith and Unsworth 1990) and the tissue samples used by Speakman and Hays (1992) were partially dehydrated, particularly the sample from the pteropodid bat which came from a dry specimen (although they found no difference in absorption of light between the dry sample and the other pieces of wing membrane).

The surface of the wings of the pteropodids used here had a sheen and felt greasy to the touch. Crowley and Hall (1994) suggested that this is a lipid-based compound perhaps used to waterproof the skin. It is possible the dead tissue used by Speakman and Hays (1992) had little residual oil remaining on the surface, and the oily surface of the live bats may well have increased wing reflectance. A mean proportion of 0.19 of light was reflected off the wings of the live animals, compared to 0.05 off the dead tissue, and Speakman and Hays (1992) found more light was transmitted than reflected whereas in our study reflection was much higher. It is possible this surface protectant plays an important role in reducing the absorption of ambient light and therefore, heat stress. There may be costs and benefits associated with these animals having dark skin. As they roost in areas exposed to high levels of solar radiation dark pigments such as melanin may provide protection from damage by ultraviolet radiation. However, the dark colouration may also increase the risk of heat stress – although using a model, Walsberg (1988) showed that black skin, had one sixth the ultraviolet transmittance of lighter skin, but this increased heat load to animals by only 5%.

A final explanation for the lower mean absorptions found in this study is the use of frugivorous tree-dwelling tropical bats as compared to British insectivorous bats. Perhaps these pteropodids, exposed to high levels of solar radiation throughout the day, absorb less light into their wings to reduce heat stress, compared with the insectivores from the temperate zone, which seldom experience direct sunlight (Speakman 1990). Reeder and Cowles (1951) suggest that the exposed roosting places of many pteropodids could subject them to the risk of overheating even when not in flight. Large bats roosting in trees in tropical regions use wing fanning behaviour to increase convective and evaporative cooling (Laburn and Mitchell 1975).

Significant differences in reflection between species were observed, *P. hypomelanus* having a lower, and *P. pumilus* having a higher mean reflection than the other two species. There was no obvious explanation for the differences in reflection, as all four species are nocturnally active, roost in trees and have tropical distributions (Mickleburgh et al. 1992). However, if as suggested above, surface oils affect absorption of light into the membrane, then interspecific differences in these oils could potentially cause differences in reflection.

Our mean absorptions were slightly lower than levels suggested by Gates (1980) for vertebrates with dark colouration. However, Gates (1980) was discussing areas of vertebrates covered by feathers or fur. Smooth wing

membrane is likely to reflect more radiation which could explain the difference. The thin wing membrane of bats also transmits more radiation than the solid areas of other vertebrates measured. In addition, Gates' (1980) estimates integrated all wavelengths whereas we measured only within the visible part of the spectrum. Blocking out lower wavelengths of light did not significantly change reflection or transmission in this study. As measurements were made over a relatively small part of the solar spectrum perhaps this is not surprising. The ultraviolet part of the spectrum (150–350 nm) does not represent much of the energy from the sun (< 5%) but the near infrared region (700–1000 nm) contains almost as much energy as the visible portion. It would be interesting to examine what percent of this radiation is absorbed into bat wing membrane. Lustick (1971) and Ellis (1980) both found higher reflection in birds of different feather colour in the infrared range than in the visible. However, Porter and Gates (1969) found lower absorption at infrared wavelengths in the animals they measured. In addition, light can have peak emission at different wavelengths. For example, after going through vegetation there is a peak in the near infrared (Gates 1980), which could have implications for bats roosting in foliage. Direct sun is strong through the visible and infrared ranges, but cloud light is strong in the visible and low in the infrared range (Gates 1980) and this could affect both animals roosting in exposed areas or animals flying during the day. Depending on the level of absorption in the infrared range, cloud cover could have a significant impact on a diurnally active bat, aside from just reducing the intensity of solar radiation.

Wing membrane contains dermal papillae to enable it to stretch (Crowley and Hall 1994) and although the membrane still appears smooth when it is relaxed, it folds on a small scale and therefore thickens when the wing is folded. As bats seldom have their wings fully extended while roosting, our estimates of absorption of relaxed membrane are probably more relevant to roosting bats than those on fully taut membrane. Almost 95% of light was absorbed into relaxed wings, nearly 30% more than into extended membrane. This also has implications for animals in flight as the membrane is not fully stretched throughout the entire wing-beat cycle. Our analysis of the changes in wing membrane during flight suggests that despite the reduction in vertically projected area of wing membrane throughout a wing-beat, relaxed membrane absorbs sufficiently more radiation to result in a small decrease in the predicted temperature at which a flying bat might risk heat stress.

Using the biophysical model of Speakman et al. (1994) Thomson et al. (1998) showed that for *Pteropus samoensis*, which routinely flies during the day, changing the absorption of light into the wing membrane by just a small amount (10%) could significantly affect the temperature at which these bats would experience heat stress. Mean absorption measured in this study was over 15% lower than the value used in the model of Speak-

man et al. (1994). If this result is a more realistic estimate of wing absorption for *P. samoensis*, it is likely that the predicted temperature at which these fruit bats would experience hyperthermia is higher than initially expected. The model results suggest that for a bat of this species flying in the sun under mean conditions measured in American Samoa, the lower level of absorbance measured in this study would increase the critical temperature by approximately 2 °C. Since we have discovered interspecific differences in the absorbance of wings of nocturnal bats it would be interesting to measure the absorption of light into the wings of these diurnal bats as well as to investigate the amount of infrared light absorbed into the membrane. This might further decrease the overall absorption into the wings (Porter and Gates 1969; Lustick 1971; Ellis 1980).

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