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White and clear wings in bats (Chiroptera)

J. Rydell, M.B. Fenton, E. Seamark, P.W. Webala, and T.C. Michaelsen

Abstract: White or clear ("whitish") wings are a distinct feature in about 30 species of tropical insectivorous bats (Mammalia: Chiroptera) belonging to three families (Emballonuridae, Molossidae, and Vespertilionidae). Such wings may provide camouflage against the sky at dusk and dawn, when bats commute to and from the roost and are vulnerable to aerial predation from birds. We tested this hypothesis by comparing the contrast of black, white, and transparent plastic models against the evening sky. Compared with normally dark wings, white and particularly transparent wings indeed reduce the contrast against the sky and may also prevent overheating in bats flying in daylight. Whitish wings could facilitate earlier evening emergence and later morning return, increasing access to crepuscular or diurnal insects as food. But whitish wings become maladaptive near artificial lights, where they are highly visible when illuminated against the dark sky. Pale but colored (not whitish) wings and reticulated patterns on translucent wings in some African and south Asian bats may be variations on the same theme, functional as camouflage against a lit background of vegetation and shades.

Key words: aeroecology, bats, camouflage, Chiroptera, open air, overheating, predation, tropics.

Résumé : Des ailes blanches ou transparentes (« blanchâtres ») constituent un caractère distinctif chez quelque 30 espèces de chauves-souris (mammifères : chiroptères) insectivores tropicales appartenant à trois familles (emballonuridés, molossidés et vespertilionidés). De telles ailes pourraient tenir lieu de camouflage sur le ciel au crépuscule et à l'aube, quand les chauves-souris se déplacent en provenance et en direction de leur dortoir et sont vulnérables à la prédation aérienne par des oiseaux. Nous avons vérifié cette hypothèse en comparant le contraste de modèles en plastique noir, blanc et transparent avec le ciel du soir. Comparativement à des ailes normalement sombres, les ailes blanches et, en particulier, transparentes réduisent effectivement le contraste avec le ciel et pourraient aussi prévenir la surchauffe des chauves-souris volant à la lumière du jour. Les ailes blanchâtres pourraient faciliter l'émergence plus précoce en soirée et le retour plus tardif le matin, accroissant l'accès aux insectes crépusculaires ou diurnes comme source de nourriture. Les ailes blanchâtres sont toutefois mésadaptées à proximité de lumière artificielle, où elles sont très visibles dans le ciel obscur lorsqu'elles sont illuminées du bas. Des ailes pâles, mais colorées (pas blanchâtres) et des motifs réticulés sur des ailes translucides chez certaines chauves-souris africaines et sud-asiatiques pourraient constituer des variations sur le même thème, qui tiennent lieu de camouflage sur un arrière-plan illuminé de végétation et d'ombres. [Traduit par la Rédaction]

Mots-clés : aéroécologie, chauves-souris, camouflage, chiroptères, air libre, surchauffe, prédation, tropiques.

Introduction

Animal coloration has long fascinated biologists, perhaps more so than other morphological features (e.g., Darwin 1859, 1871; Bates 1862; Wallace 1879; Poulton 1890; Cott 1940; Wickler 1968; Caro 2005). The subject continues to attract a diversity of researchers. For example, recent studies reveal how the evolution of coloration and color vision may co-evolve, driven by sexual selection (Twyman et al. 2016), and how the stripes protect zebras from blood-sucking flies (Egri et al. 2012).

Adaptive coloration often is associated with concealment, by camouflage and (or) countershading (Thayer 1909; Kiltie 1988; Endler 2006). Other functions include interspecific communication such as warning and predator confusion (Powell 1982), social signaling (Gerald 2001), or regulation of physiological processes such as thermoregulation (Speakman and Hays 1992; Horváth et al. 2018). In mammals, studies of adaptive coloration have mainly focused on conspicuous, diurnal species such as primates (Gerald 2001) and ungulates (Egri et al. 2012). Bats have received relatively little attention from this perspective, but they provide an interesting counter-example because they are small and nocturnal and tend to depend more on echolocation than on vision (Fenton and Simmons 2014; Eklöf and Rydell 2018).

In appearance, wings of the more than 1400 species of living bats are quite uniform, as are the supporting skeletons, already obvious in the earliest known fossil bats (Simmons et al. 2008). Consistency of wing structure is apparent in other flying animals, from insects to birds and pterosaurs, probably reflecting the extraordinary demands of flight (Alexander 2015). The wing membranes of most species of bats are uniformly dark in color, usually brownish or blackish. They do not, for the most part, have spectacular color patterns typical of many species of birds and insects, but sparse evidence suggests that some bats use coloration for

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Table 1. Bats (Chiroptera) with "whitish" wings by geographical occurrence and taxonomic affinity.

Region	Emballonuridae	Vespertilionidae	Molossidae
Latin America	*Diclidurus albus* Wied-Neuwied, 1820[a,b,c] (northern ghost bat) *Diclidurus ingens* Hernández-Camacho, 1955[c] (greater ghost bat) *Diclidurus isabellus* (Thomas, 1920)[c] (Isabelle's ghost bat) *Diclidurus scutatus* Peters, 1869[c] (lesser ghost bat) *Peropteryx leucoptera* Peters, 1867[c] (white-winged dog-like bat; fig. 1) *Peropteryx pallidoptera* Lim, Engstrom, Reid, Simmons, Voss and Fleck, 2010[c] (pale-winged dog-like bat; fig. 1)	None	None
Africa and Madagascar	*Taphozous mauritianus* E. Geoffroy, 1818[d,e] (Mauritian tomb bat) *Taphozous hildegardeae* Thomas, 1909[d] (Hildegarde's tomb bat; fig. 1) *Taphozous nudiventris* Cretzschmar, 1830[d] (naked-rumped tomb bat) *Taphozous perforatus* E. Geoffroy, 1818[d,e] (Egyptian tomb bat) *Coleura afra* (Peters, 1852)[f] (African sheath-tailed bat)	*Neoromicia rendallii* (Thomas, 1889)[d,e] (Rendall's serotine) *Neoromicia tenuipinnis* (Peters, 1872)[d,e] (white-winged serotine; fig. 1) *Neoromicia isabella* Decher, Hutterer and Monadjem, 2015[k] (Isabelline white-winged serotine) *Glauconycteris kenyacola* Peterson, 1982[d] (Kenyan wattled bat) *Glauconycteris variegata* (Tomes, 1861)[d,e] (variegated butterfly bat; fig. 2) *Glauconycteris gleni* Peterson and Smith, 1973 (Glen's wattled bat) *Scotoecus albofuscus* (Thomas, 1890)[e] (light-winged lesser house bat) *Mimetillus moloneyi* (Thomas, 1891)[d,e] (Moloney's flat-headed bat)	*Myopterus whitleyi* (Scharff, 1900)[e] (bini free-tailed bat) *Chaerephon chapini* J.A. Allen, 1917[e] (Chapin's free-tailed bat) *Chaerephon nigeriae* Thomas, 1913[d] (Nigerian free-tailed bat) *Chaerephon pumilus* (Cretzschmar, 1826)[d] (little free-tailed bat; fig. 1)
Asia and Australia	*Saccolaimus saccolaimus* (Temminck, 1838)[i,j] (naked-rumped pouched bat)	*Hypsugo macrotis* (Temminck, 1840)[i] (big-eared pipistrelle) *Hypsugo vordermanni* (Jentink, 1890)[g] (Vordermann's pipistrelle) *Kerivoula pellucida* (Waterhouse, 1845)[i] (clear-winged woolly bat) *Kerivoula hardwickii* (Horsfield, 1824)[h] (Hardwicke's woolly bat) *Myotis macrotarsus* (Waterhouse, 1845)[g] (pallid large-footed myotis)	None

Note: The wings of *Glauconycteris* spp. from Africa and *Kerivoula* spp. and *Myotis macrotarsus* from Asia are not strictly "whitish" but are described as "almost translucent" or "semi-translucent" (Payne et al. 1985; Monadjem et al. 2010). *Glauconycteris gleni* has translucent patagia and transparent wings (P.W. Webala, unpublished data) and *G. variegata* has a superimposed reticulated pattern on otherwise translucent wings (Lanza et al. 2015: fig. 4). The wings of *Diclidurus* are "pinkish", but the bodies are all white (Ceballos and Medellín 1988).

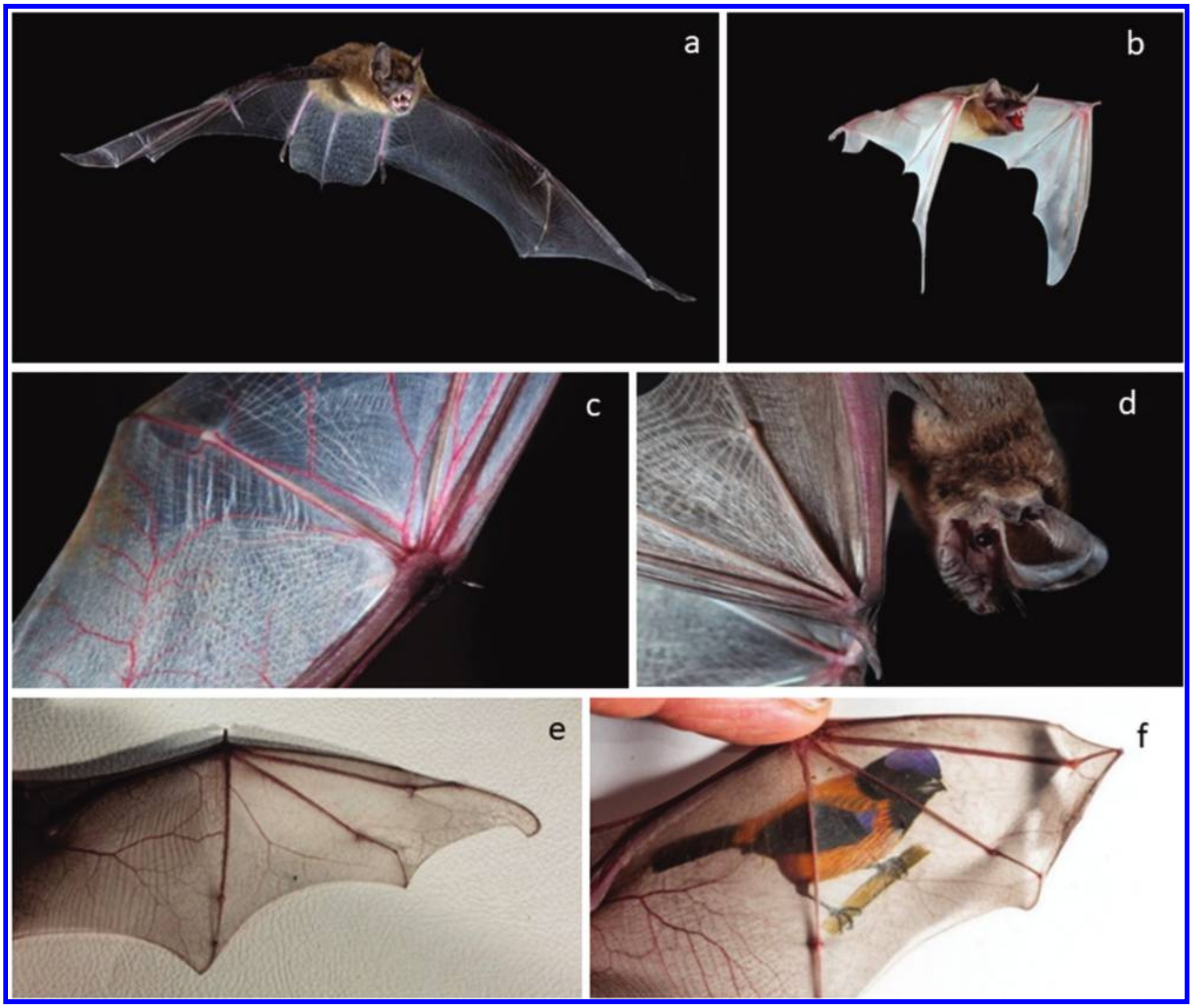
[a]Reid (1997).
[b]Gomes and Reid (2015).
[c]López-Baucells et al. (2018).
[d]Lanza et al. (2015).
[e]Monadjem et al. (2010).
[f]Garbutt (2007).
[g]Payne et al. (1985).
[h]Bates and Harrison (1997).
[i]Francis (2008).
[j]Menkhorst and Knight (2011).
[k]Decher et al. (2017).

communication (Chaverri et al. 2018). Consistently dark-colored wings coincide with the generally nocturnal behavior of bats. About 30 species of tropical insect-eating bats have white, translucent, or transparent wings. They belong to three families of mostly open-air foraging bats (Table 1; Figs. 1*a*–1*f*). Why do some species of bats have white or clear wings?

We found no explanations or interpretations of how whitish or translucent wings might confer an adaptive advantage to bats. Intuitively, such wings could be maladaptive and increase visibility to predators, resulting in high predation rate. This is the case in some white, visually displaying crepuscular insects (Andersson et al. 1998).

Bats vary in wing color from brown to black, from whitish to clear (Figs. 1*a*–1*f*). White or clear wings reflect a drastic reduction in pigmentation of the membranes. In some cases, such membranes are partly covered by weakly pigmented fur, making them

Fig. 1. Wing colors in bats. Included are a "typical" dark-winged bat ((*a*) *Eptesicus fuscus* Beauvois, 1796; photograph by M.B. and S.L. Fenton) and four species of "whitish winged" bats ((*b*) *Taphozous hildegardeae* (photograph by J. Rydell), (*c* and *d*) *Chaerephon pumilus* (photographs by J. Rydell), (*e*) *Peropteryx pallidoptera* (photograph by S.L. Fenton), and (*f*) *Peropteryx leucoptera* (photograph by M.B. Fenton)). Color version online.



more or less opaque. Here, we use "whitish" consistently to describe a variable combination of unpigmented or sparsely pigmented membranes, sometimes partly covered with white or very light-colored fur.

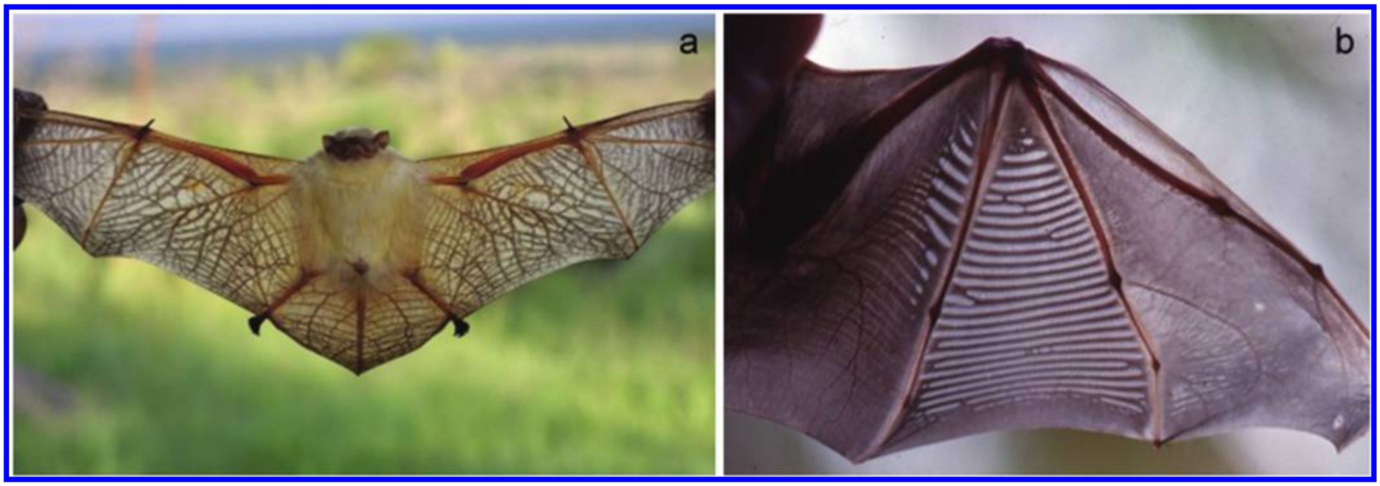
We assume that whitish wings have no relevance in darkness, and we focus our attention on lighting at dusk and dawn. For example, whitish wings could be an anti-predator adaptation, useful under the specific light conditions that prevail in the evening and early morning. This is when many bats commute to and from the roost, and therefore are vulnerable to predation by aerial-hawking birds (Fenton et al. 1994; Jones and Rydell 1994; Mikula et al. 2016), including specialized bat predators, e.g., the Bat Hawk (*Macheiramphus alcinus* Bonaparte, 1850) (Black et al. 1979; Hartley and Hustler 1993).

We tested predictions arising from our hypothesis that whitish wings minimize the contrast (visibility) of a bat flying against dusk and dawn skies. We expect to find whitish wings predominantly in bat species that (*i*) live in open habitats, such as savannas, where shadows and other protective places are relatively sparse, (*ii*) fly in the open air, where they are likely to be noticed by predators from below (against the sky), and (*iii*) emerge relatively early in the evening, when light is still bright enough for raptorial birds to see. The main result of the study was substantiated using flight activity data from clear- and dark-winged bats monitored acoustically in a community of bats in Kenya.

Literature survey

We assessed the incidence of bats with whitish wings using data presented in field guides and our collective experience with captured and free-flying bats. In the literature, we looked for pictures or specific comments about wing color (Table 1). The extent of pigmentation and presence of fur on "whitish" wing membranes can vary considerably among individuals within a species and on different parts of the same wing, but the significance of this variation is unclear. Species listed in Table 1 have some individuals with whitish, translucent, or transparent wings (Figs. 1*a*–1*f*). Sometimes wings have darker areas, particularly where they join the body. Lanza et al. (2015) illustrate variation in the wings of *Taphozous mauritianus* (Emballonuridae) and *Chaerephon pumilus* (Molossidae). Taylor et al. (2009) noted that in *C. pumilus* there are dark- and light-winged individuals which may correspond to different "species", but Jacobs et al. (2004) showed that differences in wing color do not necessarily reflect different genotypes.

Fig. 2. (*a*) The reticulated pattern on translucent wings in *Glauconycteris variegata* (photograph by B.P. Patterson) and (*b*) the right wing of a *Centurio senex* showing a translucent window at the front of the wing (the dactylopatagium minus) and an area with translucent stripes (on the plagiopatagium and the dactylopatagium major) (photograph by M.B. and S.L. Fenton). Color version online.



There also is considerable geographic variation in wing color in some other species. For example, the wings of *Mimetillus moloneyi* (Vespertilionidae) vary from "deep brownish between the forearm and the 5th finger but over the rest whitish or transparent" (Koopman 1994 cited in Lanza et al. 2015, p. 363) or more uniformly dark (Monadjem et al. 2010). *Coleura afra* (Emballonuridae) has "very pale brown and translucent" wings in Madagascar (Garbutt 2007) and southern Africa (Monadjem et al. 2010). The wings of these bats are "light brown" (not translucent) in East Africa (Lanza et al. 2015). The wings of *Taphozous perforatus* (Emballonuridae) are "mostly white" (Monadjem et al. 2010) or "light brown to whitish" (Lanza et al. 2015) in Africa but "light brown" and non-translucent in India (Bates and Harrison 1997). Finally, *Saccolaimus saccolaimus* (Emballonuridae) has "translucent" wings in Southeast Asia (Francis 2008) but "olive brown" wings in Australia (Menkhorst and Knight 2011).

Some species in Table 1 have "yellowish" rather than "whitish" or translucent wings, described as "pale", e.g., *Glauconycteris kenyacola* from Africa (Lanza et al. 2015) and *Kerivoula pellucida* from southeast Asia (Francis 2008), or "almost translucent", e.g., *Kerivoula hardwickii* from India (Bates and Harrison 1997). The membranes of the ghost bat genus *Diclidurus* from the Neotropics are described as "pink" or "pinkish" (Reid 1997; López-Baucells et al. 2018). The function of weak wing pigmentation is probably qualitatively the same as in more strictly "whitish" wings, but perhaps is suited for slightly different habitats. For example, according to Francis (2008), the South Asian emballonurid *Taphozous melanopogon* Temminck, 1841 (black-bearded tomb bat) has "wings pale, appearing whitish in flight". The African *Glauconycteris variegata* (Vespertilionidae) has a dark reticulated pattern on translucent yellowish wings (Fig. 2*a*).

In some species, whitish coloration extends beyond the wings onto the venter, probably combining camouflage and countershading (Endler 2006). More extreme is *Diclidurus albus* and its congeners (Emballonuridae), which are entirely white, except for wings and ears. These bats forage high in the open air (Gomes and Reid 2015). Body fur color influences the overall impression of white- and clear-winged bats. For example, white wings of *Neoromicia tenuipinnis* contrast sharply with jet black fur. The differences are less striking in other species, such as whitish wings and golden-colored fur in the closely related *Neoromicia rendallii*.

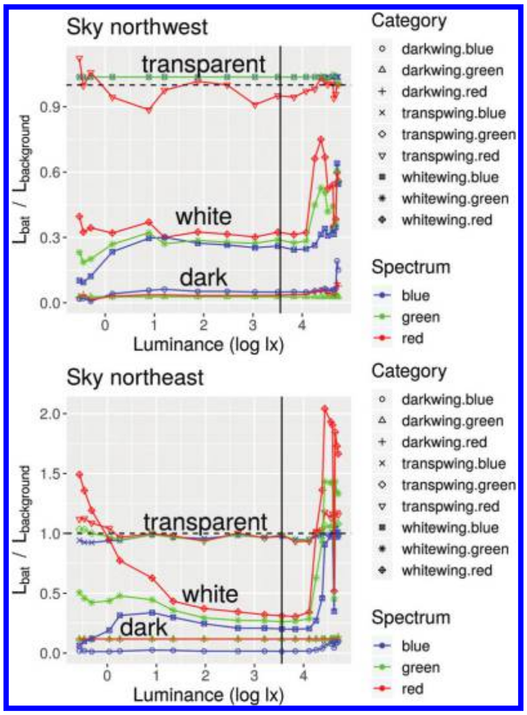
The occurrence of whitish winged bats is spatially dependent. They are found exclusively in tropical parts of the major biogeographical regions (Neotropics, Ethiopian, and Oriental or Australian), but not in Europe and the Middle East (Dietz and Kiefer 2014), China (Smith and Xie 2008), Taiwan (Cheng et al. 2012), or North America (Barbour and Davis 1969). Taxonomically, whitish wings occur in Emballonuridae, Vespertilionidae, and Molossidae in the Old World tropics but are restricted to Emballonuridae among Neotropical bats.

Species with whitish wings range in size from very small (3–4 g in *N. tenuipinnis* and *Hypsugo vordermanni*; Monadjem et al. 2010; Payne et al. 1985) to large (40–50 g in *S. saccolaimus*; Francis 2008), and the trait does not seem to be associated with body size. Rather, whitish wings are most frequent in species with relatively long and narrow wings, typical in the majority of the families and genera concerned. Such a wing form facilitates straight and fast flight (Norberg and Rayner 1987) and is associated with high-intensity echolocation and long-range detection of insects in open air space (Barclay 1985).

Some whitish winged species of the genera *Glauconycteris*, *Kerivoula*, and *Myotis* (Vespertilionidae) do not conform to this pattern of wing design because they are relatively slow fliers with intermediate wing loadings and low aspect ratios. They use a hovering, butterfly-like flight and generally forage near the ground and among vegetation, rather than in the open air (Francis 2008; Monadjem et al. 2010). There are no whitish winged bats with big erect ears, which would have indicated a gleaning or flutter-detecting lifestyle.

Although dark-colored wings prevail in Phyllostomidae, there are transparent small "windows" on otherwise dark wings in three frugivores (*Centurio senex* Gray, 1842 (wrinkle-faced bat) (Fig. 2*b*), *Sphaeronycteris toxophyllum* Peters, 1882 (visored bat), and *Ectophylla alba* H. Allen, 1892 (Honduran white bat)). *Diaemus youngi* (Jentink, 1893) (white-winged vampire bat) has white wing tips, but the rest of the wings are dark (Reid 1997; López-Baucells et al. 2018). In addition, transparent "windows" on otherwise dark wing membranes are also found in *Pteropus capistratus* Peters, 1876 (Bismark masked flying fox) (Pteropodidae) from New Guinea (Bonaccorso 1998). Chaerephon (ca. 470–400 BC) was a friend and follower of Sokrates and mentioned in the writings of Aristophanes. Characterized as pale (whitish) and malnourished, like a living corpse, Chaerephon was nicknamed "the bat" because of his consistently nocturnal habits and bony appearance. Therefore, when naming the bat taxon *Chaerephon*, Dobson (1874) may have referred to the whitish appearance of some of the species.

Fig. 3. The contrast of the bat models against a clear sky in the northwest and northeast around dusk for a transparent-winged, a white-winged, and a dark-winged bat model. The contrast is lowest near $L_{bat}/L_{background} = 1$, which is marked with a broken horizontal line. Below the line, the bat models appear increasingly darker than the background (the sky). The RGB (red, green, and blue) colors were plotted separately. Time of sunset (2020 Central European summer time) is indicated by a vertical solid line at L = 3600 lx. Color version online.



Materials and methods

Light measurements

To test predictions from our hypothesis that whitish wings mask their appearance against the sky, we designed a simple experiment. We made three bat models of roughly natural size (25 cm wingspan) from a transparent PVC-plastic sheet. One was painted very dark grey and one was painted white, using semi-matt water-soluble paint. The third was left unpainted and with a semi-gloss surface, typical of transparent-winged bats. We mounted the models next to each other on a stick and photographed them in the evening against (*i*) clear sky towards the northwest (direction of sunset) and (*ii*) clear sky towards the northeast (90° east of sunset), respectively. We made exposures at 10 min intervals from 1 h before sunset to 1 h after sunset. We used a Canon 5D Mk IV camera with a 24 mm f/2.8 Canon lens on a tripod. The settings were "Av" mode, f = 2.8–8, and ISO 1250. Before analysis, the original RAW files were converted to JPG format (quality 12) at 300 dpi, but they were left unedited. The photographs were taken in a semi-natural setting (J.R.'s garden) in Sweden (57°N) on 14 and 15 April 2019.

We used the pipette tool in Adobe Photoshop CS2 to measure the brightness (luminance) of the bat models and the background from the photographs. For each photograph, we made five readings each of background, dark bat, transparent bat, and white bat. The mean values were used for the plots shown in Fig. 3. The "contrast" between the bat and the background was obtained by dividing the two measures of luminance ($L_{bat}/L_{background}$), thus giving a dimensionless value. We used RGB (red, green, blue) color space and analyzed the colors separately. We assume that contrast measured in this way is closely correlated with the visual detectability of a flying bat. We also measured the luminance of the sky directly, using an analog Gossen Mastersix light meter, immediately after each bat exposure. Three such readings were taken each time and the middle one was used for the analysis and in the plots.

Bat activity monitoring

To investigate if dark-winged and whitish winged bats differed in their patterns of daily flight activity, we used the data from an acoustic survey made by one of us (P.W.W.) in the Meru area in central Kenya in April 2019. Four static bat detectors (Song Meter SM4BAT FS & ZC; Wildlife Acoustics, Inc., Maynard, Massachusetts, USA) were deployed at each of four independent sites (1–4) during one night per site. At each site, the four detectors (D1–D4) were placed 100 m from each other along a transect.

The species were identified from their echolocation calls, using BatSound version 4 (Pettersson Elektronik AB, Uppsala, Sweden; available from https://batsound.com) and a partly published call library of bats from Kenya (Webala et al. 2019) and unpublished data. We recognized 10 species of aerial-hawking bats including three (*Chaerephon pumilus*, *T. mauritianus*, and *Coleura afra*) that have whitish wings (Table 1). We excluded occasional observations of other bats, mostly gleaners (e.g., *Lavia frons* (E. Geoffroy, 1810) (yellow-winged bat)) and flutter detectors (e.g., horseshoe bats *Hipposideros* spp. and *Rhinolophus* spp.).

Statistics

A Wilcoxon's signed-rank test (V) was used to test for differences in activity patterns between whitish winged and dark-winged bats. The paired test alternative signifies that comparisons were made only between observations from the same locality and the same night. To ensure a reasonable sample size, we only included species with $N > 30$ observations each night, and we included only species with at least 10 such pairwise comparisons. The analysis was carried out in R version 3.5.1 (R Core Team 2018).

Results

Photographed against a clear sky (Fig. 3), the transparent bat model always showed the lowest contrast, regardless of ambient light intensity and time after sunset. The dark model always showed the highest contrast and the white model was always intermediate. The figure shows the result for two different (consecutive) evenings with the models photographed against the northwest, i.e., the direction of sunset where the sky is lightest, and against the northeast, i.e., 90° east of sunset, where the sky is darker, respectively. The result was qualitatively the same in both cases.

There were more or less distinct peaks notably in the red and the green at log luminance > 4. This is because the models were temporarily exposed to direct sunlight before sunset. The peak particularly in the red at log luminance < 1 is an effect of local light pollution from residential high-pressure Na (orange) street lights in the vicinity (>100 m away). This illustrates that the contrast between the white model and the sky increases in artificial light as the sky darkens. In the figure, this is particularly obvious against the darker sky in the northeast. We did not attempt any statistical test in this case, because of the potentially confounding effect of the streetlights.

Monitoring echolocation calls of bats at four sites in Kenya indicated that three whitish winged species of Emballonuridae and Molossidae consistently emerged and foraged earlier in the evening than any of seven dark-winged species (belonging to the same families and Vespertilionidae). Hence, regardless of taxonomic affinity, the whitish winged bats seemed to be more crepuscular than the dark-winged ones in this area (Fig. 4).

Four of the species monitored had a sufficient number of observations for reliable statistical testing. The white-winged *Chaerephon pumilus* spent more time hunting during the first hour of the night

Fig. 4. Variation in nightly activity (bat passes; untransformed mean ± SE) of whitish winged bats (*Chaerephon pumilus*, *Coleura afra*, and *Taphozous mauritianus*) and darker winged bats (*Nycticeinops schlieffeni* (Peters, 1860) (Schlieffen's twilight bat), *Pipistrellus rueppellii*, *Scotophilus andrewreborii*, *Neoromicia capensis* (A. Smith, 1829) (Cape serotine), *Mops condylurus*, and *Otomops harrisoni* Ralph, Richards, Taylor, Napier and Lamb, 2015 (Harrison's large-eared giant mastiff bat)) in Meru area, central Kenya, in April 2019. Note that the *y* axes have different scales.

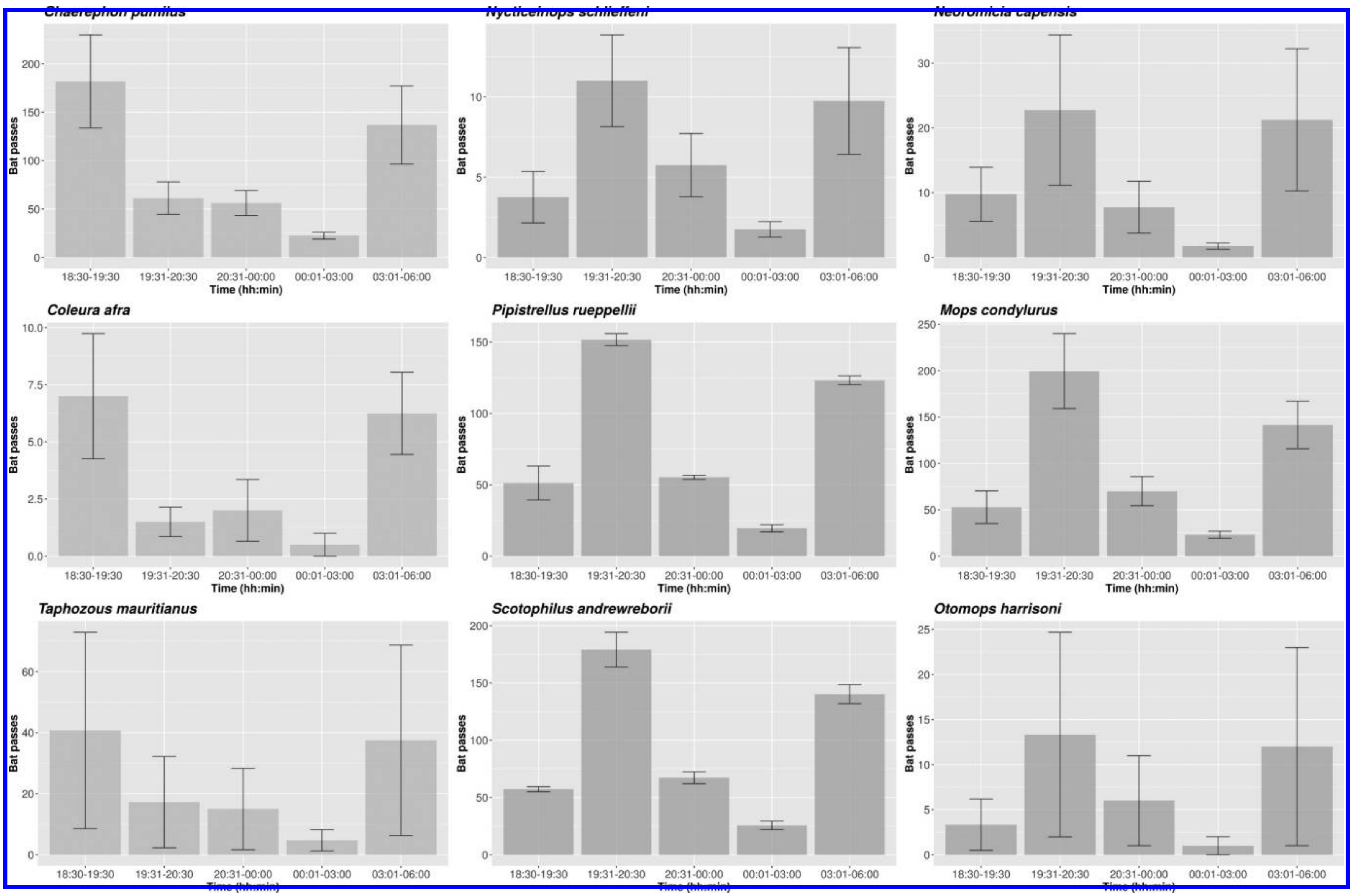
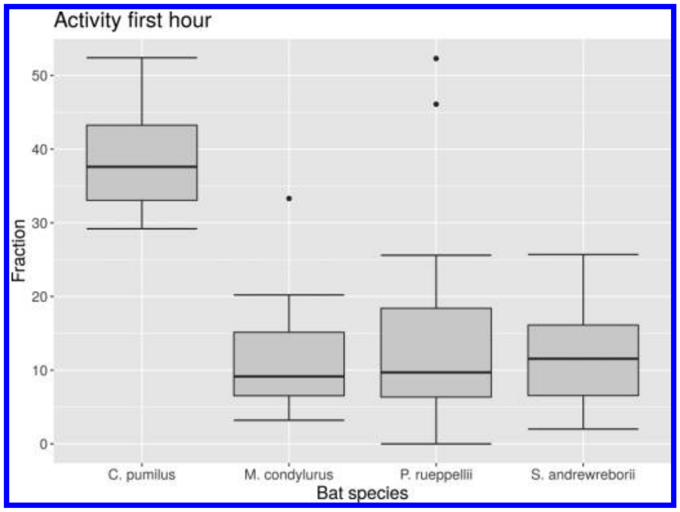


Fig. 5. Box plot showing the difference in crepuscular activity (in % activity during the hours of 1830–1930) between the white-winged species *Chaerophon pumilus* and the three dark-winged species *Pipistrellus rueppellii*, *Scotophilus andrewreborii*, and *Mops condylurus*. Boxes represent the medians (thick horizontal lines) and quartiles, whereas whiskers show the extremes within 1.5 times the interquartile range.



(median = 40%) compared with the three dark-winged species *Pipistrellus rueppellii* (J. Fischer, 1829) (Rüppell's pipistrelle) (median = 8%; $V = 102$, $p < 0.0007$, $n = 14$), *Scotophilus andrewreborii* Brooks and Bickham, 2014 (Andrew Rebori's house bat) (median = 12%; $V = 105$, $p < 0.0002$, $n = 14$), and *Mops condylurus* (A. Smith, 1833) (Angolan free-tailed bat) (median = 9%; $V = 105$, $p < 0.0002$, $n = 14$). In contrast, there was no significant difference between the three dark-winged species ($p > 0.32$ in all comparisons, $n = 16$). The result is shown graphically in Fig. 5.

Discussion

Whitish wings may provide camouflage against the evening sky, thereby facilitating earlier emergence and foraging in some tropical bats. Early-evening emergence (and late-morning return) can expose foraging bats to large populations of crepuscular insects (as opposed to strictly diurnal or nocturnal ones), particularly swarming flies (Diptera) (Rydell et al. 1996; Russo et al. 2011; Malmqvist et al. 2018). However, it can be risky, because some birds of prey are active and forage at this time of the day (Black et al. 1979; Fenton et al. 1994).

We predicted that whitish wings in bats would be associated with open habitats and species that fly relatively fast in the open air. This seems to be the case in general and regardless of the taxonomic affinity, and this supports our idea.

However, some specific cases do not agree with our predictions about the occurrence of white wings in bats, as the species do not live in dry, open habitats and (or) are rather slow, fluttering flyers, typically moving near the ground. At least two whitish winged vespertilionid species *N. tenuipinnis* (Rosevear 1965; Monadjem et al. 2010) and *Neoromicia isabella* (Decher et al. 2017) occur in rain forest but may forage in open areas, gaps in the canopy, or above the canopy. Two of us (J.R. and P.W.W.) have observed *N. tenuipinnis* in a relatively dry and open woodland on the shores of Lake Victoria in Kenya. These bats emerged early and flew at canopy height, in accordance with our prediction. On the other hand, the very similar *N. rendallii* has frequently been captured when flying near the ground in Zambia by one of us (E.S.). Two small white-winged *Hypsugo* species (Vespertilionidae) from Malaysia occur in mangrove forest (Payne et al. 1985; Francis 2008), but probably forage in openings and above the canopy rather than within the forest.

Contrary to our prediction, two whitish winged species of the butterfly bat genus *Glauconycteris* (Vespertilionidae) in Africa emerge early but typically fly slowly and flutter near the ground (Nowak 1999; Lanza et al. 2015, p. 349). The wings of *Glauconycteris gleni* are transparent, whereas those of *G. kenyacola* are pale or slightly translucent (but not white). The wings of *G. variegata* are dominated by a fine reticulated pattern (Fig. 2*a*). Likewise, the wooly bats *K. pellucida* and *K. hardwickii* (Vespertilionidae) of southern Asia also are relatively slow-flying forest bats, although their wings are "semi-translucent" (Bates and Harrison 1997; Francis 2008).

The white coloration of the aerial-hawking and insectivorous ghost bat genus *Diclidurus* (Emballonuridae) is strikingly similar to that of the fruit-eating *E. alba* and *Mesophylla macconnelli* Thomas, 1901 (MacConnell's bat) (Phyllostomidae), two Neotropical rainforest species. However, like *Diclidurus*, *E. alba* and *M. macconnelli* roost under large leaves (Rodríguez-Herrera et al. 2008). The similarity suggests that white coloration may have other functions in bats beyond camouflage in the sky, perhaps associated with roosting. Vaughan (1970) proposed that translucent windows in the wings of some fruit-eating phyllostomid bats allow them to see their surroundings without revealing their eyes while roosting in the vegetation.

Dark wing membranes increase absorption of solar radiation and could make bats prone to overheating (Speakman and Hays 1992; Speakman et al. 1994). This could mean that once bats had evolved dark wing membranes, they were "trapped in the darkness of the night" (Voigt and Lewanzik 2011). Nocturnality in bats probably evolved in a predator–prey context (Rydell and Speakman 1995), but it is not obvious that the dark wing membranes did the same. In fact, our results suggest that transparent or white wings would have been better options initially, as it provides good camouflage at least against the sky regardless of light conditions and also may prevent overheating.

Whitish wings that confer camouflage can be a disadvantage when bats hunt insects attracted to artificial lights. When *Taphozous* spp. fly around a strong light, the white wings are highly visible and could increase vulnerability to predators. In this way, a sophisticated adaptation, such as whitish wings, becomes useless and even dangerous, as environmental change, in this case introduction of artificial light, signifies novel demands. A winner in the evolutionary arms race may quickly become a loser.

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