

Dark butterflies camouflaged from predation in dark tropical forest understories

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Abstract. 1. Morphological characteristics, especially coloration, are related to thermoregulation and camouflage, both of which are crucial for species survival and fitness. In cool environments such as the understory of closed rainforests, darker organisms have thermal advantages and may be able to absorb heat more efficiently. However, such habitats are also suitable for darker organisms with respect to camouflage, making it difficult to elucidate whether the association of dark-coloured organisms with shady environments is a consequence of thermal stress or predation pressure, or both.

2. In this study, butterfly communities were surveyed and artificial butterflies (mealworms attached to plastic sheeting to mimic adult butterflies) used to test whether differences in wing luminance are related to predation rates within open and closed habitats in monsoonal tropical forests of southwestern China.

3. Using artificial butterflies, significantly lower predation rates were found for dark-coloured artificial butterflies within closed habitats, whereas such relationships were not found within open habitats. It was found that actual butterfly communities were also significantly darker in closed than in open habitats.

4. These results demonstrate that darker colours may have the effect of reducing predation rates in shady environments and that different habitat types can have contrasting effects on luminance and therefore predation risk.

Key words. Artificial butterfly, morphology, predation, tropical rainforest, wing luminance.

Introduction

Morphology is one of the key functional traits that determines the performance and fitness of an organism, and therefore may affect distribution and diversity patterns (Kingsolver & Huey, 2008; Bishop *et al.*, 2016). Among insects, morphological functions such as mimicry, camouflage and thermoregulation are used to adapt to variable environments, which present multiple selection pressures via biotic (e.g. predation) and abiotic processes (e.g. thermal regimes) (Chai & Srygley, 1990; They & Gomez, 2010). These multiple selection pressures may complicate the mechanisms through which morphological characteristics have been shaped (Marden & Chai, 1991; Eilers *et al.*, 2003; Hegna *et al.*, 2013).

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The luminance (luminous intensity of light reflected from a given area) of insects may present multiple morphological functions which could ultimately influence their fitness and survival (Watt, 1968; Brakefield, 1987; Wilson *et al.*, 2001; Trullas *et al.*, 2007; Hegna *et al.*, 2013). One well-known function of luminance is heat absorption from solar radiation. Under constant solar radiation, dark organisms can gain more heat than can light organisms, which is important especially for diurnal insects such as butterflies whose activities are largely dependent on external heat (Watt, 1968; Brakefield & Willmer, 1985; Bishop *et al.*, 2016). Being able to heat up and reach optimum body temperatures quickly could increase mobility and minimise predation risk for insects in cool habitats (Lederhouse *et al.*, 1987). In open and hot habitats, however, light-coloured organisms may benefit from minimising the risk of overheating and expanding activity time (Schmitz, 1994; Forsman *et al.*, 2002). These advantages could lead to evolutionary adaptations through which individuals found in cooler closed habitats are

generally darker, and those found in hotter open habitats are lighter in colour. Consequently thermoregulatory advantages are frequently proposed to explain organisms exhibiting different luminance patterns along thermal gradients (Zeuss *et al.*, 2014; Bishop *et al.*, 2016; Xing *et al.*, 2016).

On the other hand, coloration can also provide aposematic signals or camouflage against predators (Endler & Greenwood, 1988). For example, species that best imitate their microhabitats would be better camouflaged against predators, and dark environments would then favour darker-coloured morphs that lower its contrast with surroundings and minimise visually cued predation (Williams, 2007; Karpestam *et al.*, 2012). Dark habitats such as closed canopy forests are also cooler due to reduced solar radiation (Endler, 1993), and the abundance of dark-coloured individuals in such habitats are often attributed to thermal benefits (; Pereboom & Biesmeijer, 2003; Brisson *et al.*, 2005; Xing *et al.*, 2016). However, the importance of visual cues and predation pressures in selecting levels of luminance is rarely examined, although they are potentially of similar importance. Only a few studies have reported conflicts between thermal and camouflage benefits (Lindstedt *et al.*, 2009; Hegna *et al.*, 2013).

Previous studies demonstrated that larger prey sizes generally suffer from higher predation rates, but the predation rate may or may not vary according to the morphological (coloration) characteristics in a given environment (Remmel & Tammaru, 2009; Karpestam *et al.*, 2014). Hence, we also considered different prey sizes and their interaction effects on the effectiveness of camouflage.

Butterflies are one of the best-studied insect groups, and their luminance is known to be important in both thermoregulation and camouflage (Robbins, 1981; Kingsolver, 1983). In addition, many studies have reported morphological plasticity of butterfly wing coloration in response to changes in thermal environments and other selection pressures (Van Dyck & Wiklund, 2002; Talloen *et al.*, 2004; Otaki, 2008). Darker butterfly species have been reported to occur in dark environments such as closed-canopy rainforests (Xing *et al.*, 2016), hence making butterflies an ideal insect group to test these hypotheses.

Lepidoptera mimicking models have been widely used in predation experiments examining camouflage and other anti-predator strategies (Cuthill *et al.*, 2005; Stevens *et al.*, 2007; Stevens *et al.*, 2008), although such artificial butterflies lack some characteristics (e.g. Stevens *et al.*, 2008).

In this study we used artificial butterflies of varying wing luminance (black and white) and size (large and small) to test: (i) the differences in predation rate between open and closed habitats; and (ii) whether wing luminance and size influence predation risks in open and closed habitats. The predation rates in open and closed habitats were expected to be similar, but darker and smaller butterflies were expected to be well camouflaged in closed habitats, resulting in lower predation rate. In contrast, in open habitats, darker and larger butterflies were expected to suffer a higher predation rate. We also tested whether the results of artificial butterflies match with those of actual butterfly communities by testing differences in wing luminance and size of butterfly species caught in open and closed habitats.

Materials and methods

Study sites and habitats

Our work was carried out in Xishuangbanna Nature Reserve in southernmost Yunnan, China (latitude 21.5°N, 100.5°E), in May 2016. Three locations were selected: Xishuangbanna Tropical Botanical Garden (BG, ~560 a.s.l.), the '55K' Plot (ZK, ~750 a.s.l.), and Bubeng Ecological Station (BB, ~700 a.s.l.) (Fig. 1a,b). Open and closed habitats were selected within each location. Closed habitats were all within the secondary forest interiors aged 60 years or more, whereas open habitats included tea plantations, nurseries, and forest edges. We established a 1-km transect in each habitat area.

Artificial butterflies and predation experiments

Each artificial butterfly was made with one piece of 0.5-mm-thick rectangular plastic sheeting, representing wings. A freshly killed mealworm was attached under the plastic sheeting with a 0.8-mm-diameter metal wire (which was poked through the mealworm to minimise the chance of losing it as a result of rain or wind) with approximately one-third of the body part exposed from the plastic sheeting (similar to Stevens *et al.*, 2008, see Fig. 1). Black and white plastic sheeting was used to represent dark- and light-coloured wings. Large (8 × 5 cm) and small (5 × 4 cm) pieces of sheeting were prepared as these two sizes represented commonly encountered species in both forest and open habitats. Mealworm length was selected to be proportionally similar to wing sizes (large model, 25–30 mm; small model, 15–20 mm) (Fig. 1c,d).

Artificial butterflies were fastened around twigs 1.5 m above ground along each transect. Artificial butterflies were placed at least 5 m apart with alternate treatment arrangements (i.e. black, large; white, small; black, small; white, large) to avoid autocorrelation of each predation event. In all, 40 artificial butterflies were used for each of the four treatments at two locations (BG, ZK). At BB, however, only 20 artificial butterflies were used for each treatment due to the small size of the open habitat. Hence a total of 320 artificial butterflies were used in each of BG and ZK (40 models × two habitats × two wing sizes × two coloration treatments) and 160 in BB, making a total of 800 artificial butterflies deployed.

The experiment was carried out in the dry season from 6 May to 2 June 2016 with negligible rainfall over that period. Each artificial butterfly was checked for predation, and mealworms were replaced every 24 h consecutively for 6 days. Tangle foot was spread around the twigs above and below the artificial butterflies to avoid ant predation. As the mealworms were firmly attached to the plastic sheeting by a thin wire, missing mealworms were considered to have been predated by vision-cued predators (birds, lizards, see Shapiro, 1974; Ehrlich & Ehrlich, 1982). We excluded predation by other insects (as they may or may not rely on vision cues alone), such as cockroaches and wasps (these generally leave parts of caterpillars behind with saw-like laceration), and predatory bugs (*viz.* Reduviidae, the exoskeleton of mealworms will be intact). Two data loggers (HOBO UA-002-64-; Onset Computer, Bourne, Massachusetts)

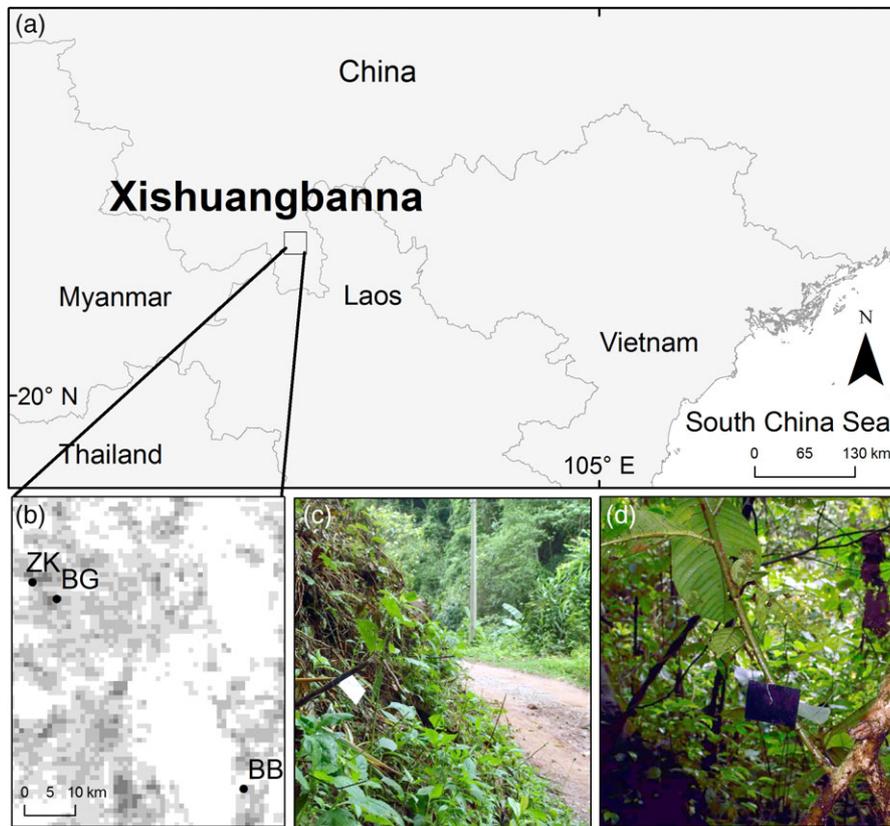


Fig. 1. A map showing the location of Xingshuangbanna Nature Reserve (a) with the three sampling locations (b), and photos of our artificial butterflies (c, open habitat; d, closed habitat). BG, Xishuangbanna Tropical Botanical Garden; ZK, '55K' Plot; BB, Bubeng Ecological Station. Greyscale pixels in the map (b) indicate the gradient from natural (grey, primarily forested areas) to human transformed areas (white, primarily agricultural and rubber plantation), based on 1-km-resolution global land cover maps (Tuanmu & Jetz, 2014). [Colour figure can be viewed at wileyonlinelibrary.com].

were placed at the height of our artificial butterflies (1.5 m) along each transect (at least 400 m away from each other) to record temperature ($^{\circ}\text{C}$) and light intensity (lux) every 5 min for 6 days for the duration of the experiment.

Butterfly community colour and size

To investigate dorsal and ventral wing luminance as well as wingspan of actual butterfly communities, we conducted a 30-min butterfly survey following the 'Pollard Walk' protocol (Pollard, 1977) each day after replacing mealworms along each transect. We conducted a total of 36 daily Pollard Walk surveys (six daily surveys \times three locations \times two habitats). We caught one individual for each of the species recorded from the surveys, and mounted them into specimens for colour analysis. Specimens were photographed from a fixed distance (45 cm) using the same camera (Nikon D5300) with standardised settings (ISO 125, aperture $f/16$, shutter speed $1/60\text{s}$). Photographs were further analysed with Adobe PHOTOSHOP CC 2014 software. Each specimen was transferred into greyscale using the *blur* function and all pixels covering dorsal and ventral wings were averaged for luminance [a value from 0 (dark) to 255 (white)]. Wingspans were also measured with a 0.01-mm caliper and represented body size. For some uncaptured species (i.e. no specimens),

luminance and wingspans of congeneric species or species of the same mimicry chain were used.

Statistical analysis

Daily predation rate was calculated by dividing the number of predation events by the total available artificial butterflies for that specific treatment at each location on that specific day. Each daily predation rate was based on 40 models deployed at BG and ZK, or 20 models at BB. A total of 144 observations (six daily predation rates \times three locations \times two habitats \times two wing sizes \times two coloration treatments) were used for statistical analysis. A generalised linear mixed-effects model (GLMM) using the package *nlme* was fitted to analyse the effects of habitat type, luminance, body size and the three-way interaction on artificial butterfly predation (Zuur *et al.*, 2009). Location was treated as a random factor in our model.

To test the effect of habitat types on morphological characteristics of actual butterfly communities, we averaged dorsal and ventral wing luminance as well as wingspan of the species caught from each of the daily Pollard Walk samples ($n = 36$). We fitted GLMM to test the effect of habitat types with locations as a random factor. Differences in temperature and light intensity between the two habitat types were tested using *t*-tests. All the analyses were conducted in R 3.2.3 (R Core Team 2014).

Results

Study sites and habitats

We found significant differences in daily temperature ($P < 0.01$) and light intensity ($P < 0.01$) between open and closed habitats, with open habitats having higher temperatures (means of 29.44 and 24.90 °C in open and closed habitats, respectively) and greater light intensities (23 546.7 and 3191.8 lux, respectively).

Artificial butterflies and predation experiments

Across all locations, predation rate was significantly higher in closed (0.14 ± 0.01 ; mean \pm SE) than open habitats (0.10 ± 0.01) ($P < 0.01$, Fig. 2). While we found no significant effects of wing luminance ($P = 0.165$) and size ($P = 0.551$), interaction between artificial butterfly colour and habitat was significant ($P = 0.031$). This was because the predation rate of black artificial butterflies (0.12 ± 0.02) was lower than that of white butterflies (0.16 ± 0.02) in closed habitats, whereas no differences were observed in open habitats (Fig. 3).

Butterfly community colour and size

Pollard Walk surveys yielded a total of 99 butterfly species in closed habitats and 81 in open habitats. Across all locations, dorsal wings of butterfly species were significantly darker ($P < 0.01$) in closed (129.09 ± 2.34) than open habitats (138.22 ± 1.38) (Fig. 4). Similarly, ventral wings were significantly darker ($P < 0.01$) in closed (148.06 ± 2.74) than in open habitats (159.84 ± 1.21). Unlike wing coloration, we found no significant differences in butterfly wingspan ($P = 0.12$; closed, 47.67 ± 1.32 mm; open, 44.20 ± 1.62 mm; Fig. 4).

Discussion

Our findings suggest that dark-winged butterflies are subject to lower predation rates than are light-coloured butterflies within closed habitats, whereas both dark- and light-coloured butterfly models suffer similar predation rates in open habitats. In open habitats, where light intensity is generally higher, simple dark and light colour differences may not affect their conspicuousness to predators (Endler, 1987). The results of our butterfly community and predation experiments support our hypothesis that camouflaging plays a role in shaping luminance either separate from or in addition to thermoregulatory advantages in darker, closed habitats. Despite a large bias in the studies of wing coloration towards its thermoregulation roles, our experimental study addressed the importance of camouflaging in certain types of habitat.

We also considered that butterfly size may interact with wing coloration, affecting predation rates. A larger body size could increase detectability by predators (Rommel & Tammaru, 2009; Karpestam *et al.*, 2014), whereas increased body size could limit the size of their predators or, for aposematic species, magnify the warning signals to deter predators (Nilsson & Forsman, 2003). However, we found no significant size effect on predation rate.

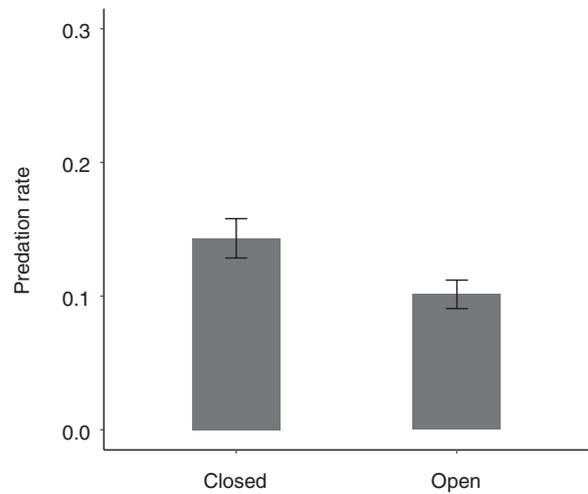


Fig. 2. Mean daily predation rates (\pm SE) of artificial butterflies in closed and open habitats.

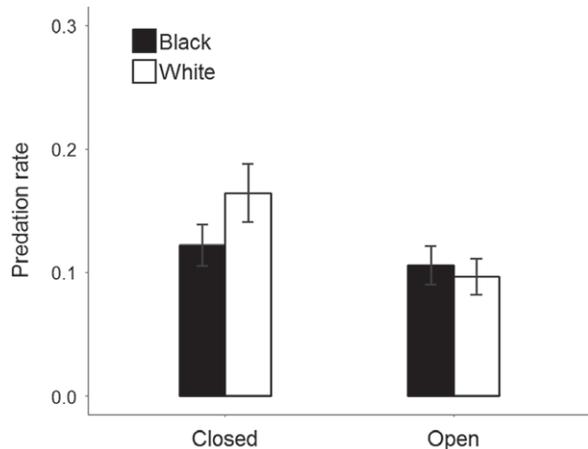


Fig. 3. Mean daily predation rates (\pm SE) of artificial butterflies with black and white wing colorations within closed and open habitats.

This could potentially explain why our community comparison found no differences in wingspan between open and closed habitats. The lack of size effects may be explained by the interplay among body size, wing coloration and habitat complexity, which ultimately determines the strength and direction of size effects on predation rate. Mänd *et al.* (2007) conducted a manipulative experiment to measure predation rate on artificial larvae with varying body sizes, which were placed in enclosures with 'simple' (green fill) or 'complex' (plant picture) backgrounds. They found that, for camouflaged individuals, detectability was unrelated to body size. For conspicuous individuals, however, they found that detectability was only positively related to size when individuals were placed under 'simple' backgrounds, whereas detectability was unrelated to 'complex' backgrounds. This may be related to our observations, as the natural habitats used in our study can be considered as 'complex' background.

The pattern of higher predation rates in closed habitats is in contrast to other studies in the tropics which have used caterpillar models (made from green-coloured plasticine) to

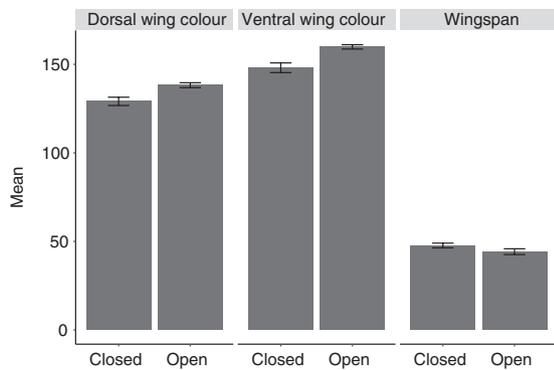


Fig. 4. Mean (\pm SE) dorsal and ventral wing luminance (larger values indicate lighter wing colour) and wingspan of butterfly species found in open and closed habitats.

quantify predation rates within forest interiors and open habitats (Posa *et al.*, 2007; Seifert *et al.*, 2015), habitat edges (Richards & Coley, 2007) and forest fragments (Ruiz-Guerra *et al.*, 2012), in which predation rates were found to be lower in more closed habitats. These differences may be explained by the predation by ants, as these omnipresent, generally thermophilic predators were not excluded in the highlighted studies. Ants are natural enemies of caterpillars, but not for healthy adult butterflies (Shapiro, 1974; Floren *et al.*, 2002). Vision-cued predators of adult butterflies commonly found in our closed forest habitats include birds, such as hill blue flycatcher (*Cyornis banyumas*), white-rumped shama (*Copsychus malabaricus*), crow-billed drongo (*Dicrurus annectans*), and ashy drongo (*Dicrurus leucophaeus*), as well as lizards, such as *Calotes emma* and *Acanthosaura lepidogaster*. However, in open habitats, only *D. leucophaeus* and *C. emma* were regularly observed (W. Cheng, pers. obs.).

Air temperature was much higher in open than in closed habitats. Average air temperature in the open habitats (29.5 °C) was close to the optimum body temperatures typical of tropical butterflies (30–40 °C; Chai & Srygley, 1990), suggesting that overheating may readily occur if thermoregulation is not effective (Wasserthal, 1975). Light-coloured butterfly assemblages primarily found in hot open habitats are therefore likely to be attributable to thermoregulation purposes other than predation avoidance (Pinkert *et al.*, 2016; King *et al.*, 2016). In the face of global warming, our findings suggest that changes in the wing colour of butterfly individuals (as many butterfly species possess morphological plasticity; Gotthard & Nylin, 1995; Kingsolver, 1995) may reduce their thermal risks without affecting predation risks. However this is applicable only within the open habitats, and predation rate may increase if changes towards lighter coloration occur within closed habitats.

Although we were unable to test the thermal benefit hypothesis within closed habitats, it is likely that darker organisms benefit from absorbing more solar radiation. This may have implications for the impacts of climate change, as possible trade-offs between predation risks and thermoregulation (by lightening their colour) could rise as a result of climate change (Hegna *et al.*, 2013). Morphological shifting to lighter colours has already been observed in various insect groups in Europe.

Ladybird beetles (Brakefield & de Jong, 2011), butterflies and dragonflies (Zeuss *et al.*, 2014) were all found to be lighter compared with their historical records. This could also have serious implications for forests under selective logging. Although selective logging may not affect organisms directly, it could change light environments inside the forest and indirectly disrupt their camouflage effectiveness (Koh, 2007).

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SX originally conceived the idea; WC, SX and TB developed the methodology; WC, YC, and RL conducted the fieldwork; WC performed statistical analyses; and WC, SX, and AN wrote the manuscript. Other authors provided editorial advice.

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