Transparency improves concealment in cryptically coloured moths

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Mónica Arias[1]*, Marianne Elias[2], Christine Andraud[3], Serge Berthier[4], Doris Gomez[1,4]

[1] CEFE, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[2] ISYEB, CNRS, MNHN, Sorbonne Univ., EPHE, Univ. Antilles, Paris, France

[3] CRC, CNRS, MNHN, Paris, France

[4] INSP, Sorbonne Univ., CNRS, Paris, France

*Correspondence author email: moarias@gmail.com

Running title

Transparency enhances terrestrial camouflage

Abstract

Predation is a ubiquitous and strong selective pressure on living organisms. Transparency is a predation defence widespread in water but rare on land. Some Lepidoptera display transparent patches combined with already cryptic opaque patches. A recent study showed that transparency reduced detectability of aposematic prey with conspicuous patches. However, whether transparency has any effect at reducing detectability of already cryptic prey is still unknown. We conducted field predation experiments with free avian predators where we monitored and compared survival of a fully opaque grey artificial form (cryptic), a form including transparent windows and a wingless artificial butterfly body. Survival of the transparent forms was similar to that of wingless bodies and higher than that of fully opaque forms, suggesting a reduction of detectability conferred by transparency. This is the first evidence that transparency decreases detectability in cryptic terrestrial prey. Future studies should explore the organisation of transparent and opaque patches in animals and their interplay on survival, as well as the costs and other potential benefits associated to transparency on land.

Keywords

Predation, communication, vision, butterfly, camouflage

Introduction

Predation is ubiquitous and exerts a strong selection on living organisms. Often, prey sport cryptic colour patterns that reduce detectability by visual predators, rendering prey hardly distinguishable from their background. Crypsis is achieved if colour patterns represent random samples of background colouration (Endler, 1981). This is challenging, as backgrounds are often complex combinations of elements that can move and that vary in colour and pattern (Ruxton *et al.*, 2004). Background matching is efficient only if sufficient number of aspects perceived by predators (e.g., colour, brightness, polarization) are matched (Endler, 1978; Ruxton *et al.*, 2004). Moreover, perception of prey coloration can vary between predators with different visual systems as suggested by the different colours displayed by the dwarf chameleon *Bradypodion transvaalense* when hiding from snakes or from birds (Stuart-Fox *et al.*, 2006). Given the intimate dependence between prey survival and background colouration, cryptic colourations constrain prey movements, and potentially hinder "risky" activities such as foraging, which are associated to an increase in predation risk (Stamp & Wilkens, 1993; Bernays, 1997; Gotthard, 2000). By contrast, dynamic colour changes (Hanlon *et al.*, 1999) or transparency (Johnsen, 2014) can free prey from background dependency, improve survival in visually heterogeneous environments, and foster vital activities such as foraging. Notably, transparency can minimize detectability against virtually any background (Johnsen, 2014).

Transparency maximises light transmission, minimising reflection and absorption at all angles and for all wavelengths seen by predators. Transparency is rare on land, with the notable exception of insect wings. Among insects, Lepidoptera (moths and butterflies) typically have opaque wings covered by coloured scales involved in intraspecific communication (Jiggins *et al.*, 2004), and antipredator defences such as aposematism (i.e. advertisement of unpalatability, Mallet & Singer, 1987), masquerade (i.e. imitation of inedible objects, Suzuki *et al.*, 2014) and camouflage (Stevens & Cuthill, 2006). Yet, wing transparency has evolved independently in multiple Lepidoptera families often in combination with opaque elements. By comparing detection of four real species of

aposematic butterflies by predators, Arias *et al* (2019) recently showed that even if all offered high visual contrast and were conspicuous to predators, fully opaque species were more detectable than species with transparent elements. In this case, transparency may help reducing detection in the first place, but if detected, butterflies may benefit from advertising their unpalatability with highly contrasting patches (McClure *et al.*, 2019). However, in many species, transparency has evolved in already cryptic butterflies, as in the Neotropical moth *Neocarnegia basirei* (Saturniidae) or the Malaysian *Carriola ecnomoda* (Erebidae), where transparent wing areas are surrounded by brownish patches frequent in their visual background. Whether transparency can decrease detectability of already cryptically coloured prey remains unknown. We here test for the first time whether transparency decreases detectability on already cryptic terrestrial prey, by conducting field predation experiments by free avian predators and using artificial moths.

Materials and Methods

Field experiments

We performed predation experiments in May 2018 in southern France, in La Rouvière forest, (43.65°N, 3.64°E) for one 1-week session and at the Montpellier zoo (43.64°N, 3.87°E) for the subsequent two 1-week sessions. According to the local bird-watcher website www.faune-lr.org insectivorous species reported for the zoo and its surroundings are more numerous. However, predator communities are rather similar between sites in spring (Table S2). Great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), predators of artificial prey in previous similar studies (Rowland *et al.*, 2008; Stevens *et al.*, 2008), were seen every morning while monitoring artificial prey at both locations. Additionally, diurnal insectivorous birds such as the Eurasian jay (*Garrulus glandarius*), the common chaffinch (*Fringilla coelebs*), the golden oriole (*Oriolus oriolus*) and the European robin (*Erithacus rubecula*) have also been seen in both localities. We followed the previously validated protocol (Rowland *et al.*, 2008; Stevens *et al.*, 2008) for monitoring artificial prey survival from

predation by bird communities. Artificial prey (body and wings) were pinned on green oak *Quercus ilex* tree trunks (>10cm in diameter, with few or no moos cover), every 10m in the forest cover. To minimise ant attacks, artificial prey were one centimetre away from the trunk. Additionally, this space was covered by 0.4 cm of Vaseline and 0.6 cm of sticky double-faced transparent tape. Vaseline and tape could be seen from the side, but not when facing the artificial moth. We randomly placed artificial moths with edible body, and three types of wings: fully opaque grey wings (C form), wings with grey contour and large transparent windows (T form), and no wings (B form) as a control of body attractiveness (Fig. S1). Prey were disposed vertically to the ground and mostly facing north to reduce direct sunlight reflection. We monitored prey survival once per day for the following four consecutive days after placing them on trunks, and removed them afterwards.

Artificial moths

As in other similar experiments (Cuthill *et al.*, 2005; Stevens *et al.*, 2006, 2008), artificial moths consisted of paper wings and an edible body, made of flour and lard in this case. Triangular shaped moths (triangle 25x36mm, surface of 450mm²) did not mimic any real local species, but resembled a generic resting moth (examples in Fig. S1). We designed moths that bore a constant crypsis level by displaying poor visual contrast (chromatic and achromatic) against the average trunk colouration of the highly abundant green oaks.

First, we took reflectance spectra of green oak trunk colouration (Fig. S2) and laminated grey paper. We then computed colour and brightness contrasts between paper and trunk as perceived by birds, by using Vorobyev and Osorio's discriminability model (Vorobyev & Osorio, 1998). This model reconstructs the difference in colour and brightness between two colour patches (here butterfly and trunk), as seen by a predator under a given light environment. Contrasts are expressed in JNDs (just noticeable differences) and 1 JND is commonly assumed as the threshold below which two colours are indistinguishable. We found that Grey155 (i. e., in a RGB scale (Red, Green, Blue) from 0 (black) to 255 (white), R=G=B=155), printed with a HP officejet pro 6230 printer on Canson® sketch paper, was

chromatically indistinguishable but lighter than oak trunks (Table S1), and was chosen as it allowed us testing transparency as a crypsis enhancer on moths bearing a colour that conferred the same imperfect level of crypsis to all artificial prey (see ESM for contrast calculation details). We built the "T" form by cutting two triangular windows (total area of 234 mm^2) in the laminated grey triangle, and putting a transparent film (3M for inkjet, chosen for its high transparency even in the UV range see ESM, Fig S2) underneath the remaining parts. On top of moth wings, we added an artificial body made from pastry dough (428g flour, 250g lard, and 36g water, following Carrol & Sherratt (2013)), dyed grey by mixing yellow, red and blue food dyes (spectrum in Fig. S2, contrast values in Table S1). Such malleable mixture allowed us to register and distinguish marks made by bird beaks from insect jaws. We finally computed the visual contrasts produced in the eyes of bird predators (for details see ESM extended materials and methods): C was cryptic (chromatic contrast < 1JND, achromatic contrast ≤ 1.64 JND) and more conspicuous than T and B forms (Table S1).

Data collection and analysis

We hereafter report all measures, conditions and data exclusions of our experiment, as well as how we determined our sample sizes. As it has been done in previous similar studies, prey were considered as attacked only when artificial moths showed V-shaped or U-shaped marks on their body, or when a prey was missing without signals of invertebrate attacks (i.e. no body scraps left on wings or around the butterfly on the trunk, Carroll & Sherratt, 2013; Hossie *et al.*, 2015). We monitored hundreds of prey models within a few hours and decided as a group whether marks we observed on these models represented valid attacks. Because the observers were aware of the hypothesis, there was the opportunity for bias in the interpretation of marks on models. However, we believe this bias was minimized because we made decisions as a group, most marks were unambiguously attributable or not attributable to birds, and we were focused on the more difficult task of finding models in the field and thus were distracted from the hypothesis when assessing marks on models. We removed all remains of artificial moths attacked by birds, but replaced them

when attacked by invertebrates or fully missing. Non-attacked prey were considered as censored data. We started with a sample size of 100 prey items per treatment, as reported on similar studies (Schaefer & Stobbe, 2006; Stevens, 2007). We increased the experimental effort until statistical clarity was reached while keeping similar sample sizes per treatment (see Amrhein *et al.*, 2019 and Dushoff *et al.*, 2019 for discussion on statistical clarity versus statistical significance). One hundred and fifty artificial moths placed in a frequently visited zone of the zoo were excluded from the experiment dataset. In this zone too many moths were completely removed (body, wing, and pin) and it was impossible to determine whether birds as magpies or humans took them. Therefore, all artificial prey from this zone (those that disappeared and those that had not) were removed from the analyses. We analysed prey survival using Cox proportional hazard regression (Cox, 1972), with type of prey, week and their interaction as explanatory variables. By including "week", the first contrast tests for time and place (by comparing week 1 at La Rouvière, and weeks 2 and 3 at the zoo), while the second contrast test for 'time' at the zoo (Table 1). Overall significance was measured using a Wald test. Statistical analyses were performed in R (R Foundation for Statistical Computing, 2014) using *survival* package (Therneau & Lumley, 2009).

Results

492 artificial moths including 165 C moths, 163 T moths and 169 B moths were analysed. 70 of these moths were attacked (predation rate: 14.08%, see Fig. S3 for an example of an attacked prey). Survival strongly differed between forms (Wald test =24.35, df = 8, $p = 0.002$): wingless bodies and butterflies with transparent windows were similarly attacked ($z = 1.51$, $p = 0.13$) and both were less attacked than opaque butterflies ($z = 3.98$, $p < 0.001$, Fig. 1, Table 1). Differences between attacks registered at La Rouvière (where 151 moths were displayed on week 1) and attacks at the zoo appeared small (hazard ratio = 0.96) and statistically unclear (pooling weeks 2 and 3 together, $z = -0.04$, $p = 0.71$, Table 1). At the zoo, more attacks were registered on week 2 (with 154 analysed moths and closer to blue and great tit reproduction peak) than on week 3 (with 192 analysed moths,

153 z = 0.55, p = 0.003). No statistically clear interaction between prey form and time or prey form and
154 place was detected (Table 1).

155 **Discussion**

156 Using artificial prey mimicking resting moths with and without transparent elements, exposed to a
157 natural community of avian predators, we show for the first time that transparency confers survival
158 benefits in already cryptically-coloured terrestrial prey. Transparent butterflies were attacked as little
159 as wingless bodies and less than opaque butterflies, suggesting that transparent windows reduce
160 detection. This study is the first to investigate the benefit value of transparency in cryptic terrestrial
161 prey, and to experimentally isolate the effect of transparency from other aspects (as patch colour or
162 patch size). Whether the position and the size of transparent windows, as well as the intrinsic optical
163 properties of the transparent surface (levels of transmission and reflection briefly explored by Arias
164 *et al* (2019) and McClure *et al* (2019)) and its interaction with the ambient light (Johnsen & Widder,
165 1999) influence transparency efficiency also remains untested for terrestrial prey.

166 Although repeatedly proven useful to evaluate predation pressure in the wild (Cuthill *et al.*, 2005;
167 Stevens *et al.*, 2006; Merrill *et al.*, 2012; Carroll & Sherratt, 2013), artificial prey experiments as ours
168 have several limitations (Irschick & Reznick, 2009). Those include the lack of predator species
169 identification, sampling a subset of all possible interactions between prey and predators (i.e. prey
170 detection but not attack, attack of the same prey by different predators), and excluding prey
171 movement, a feature that can facilitate detectability by predators. Camera traps have been useful to
172 get more information on artificial prey predation (Akcali *et al.*, 2019). However, they have provided
173 little information when studying artificial insect predation so far (Low *et al.*, 2014; Ho *et al.*, 2016),
174 most likely because camera traps are less efficient at capturing birds than other predators such as
175 mammals (Ho *et al.*, 2016; Akcali *et al.*, 2019). Other options as DNA analyses on preyed items could
176 be of better help at identifying avian predator species in future studies (Rößler *et al.*, 2018).

Crypsis can incur costs related to thermoregulation (Carrascal *et al.*, 2001), intraspecific communication (Dunham & Tierney, 1983), and, more importantly, mobility (Stamp & Wilkens, 1993; Ruxton *et al.*, 2004), thereby hindering foraging and looking for mates. While costs of transparency in terms of thermoregulation and communication have been unexplored so far, transparency can potentially reduce detectability in virtually all backgrounds, reducing the mobility costs associated to crypsis, and enlarging habitat exploitation as reported for the transparent form of the *Hippolyte obliquimanus* shrimp (Duarte *et al.*, 2016). However, if camouflage is maximal when including transparency and offers additional benefits in terms of mobility, the low representation of transparency in land, especially in Lepidoptera, is puzzling. As it has been hypothesised for benthic habitats, transparency may be more costly than pigmentation (Johnsen, 2001). In Lepidoptera, scales are involved in several physiological adaptations (communication, water repellency, thermoregulation) (Miaoulis & Heilman, 1998; Jiggins *et al.*, 2004; Wanasekara & Chalivendra, 2011). Whether transparent wings may incur communication, hydrophobic or thermal costs remains to be studied to better understand the costs associated with the evolution of transparency on land and explain its rarity.

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Competing interests

Authors have no conflict of interest to declare.

Ethical statement

No animal was intentionally harmed during this experiment and most artificial prey were found and collected, avoiding leaving wastes in the forest.

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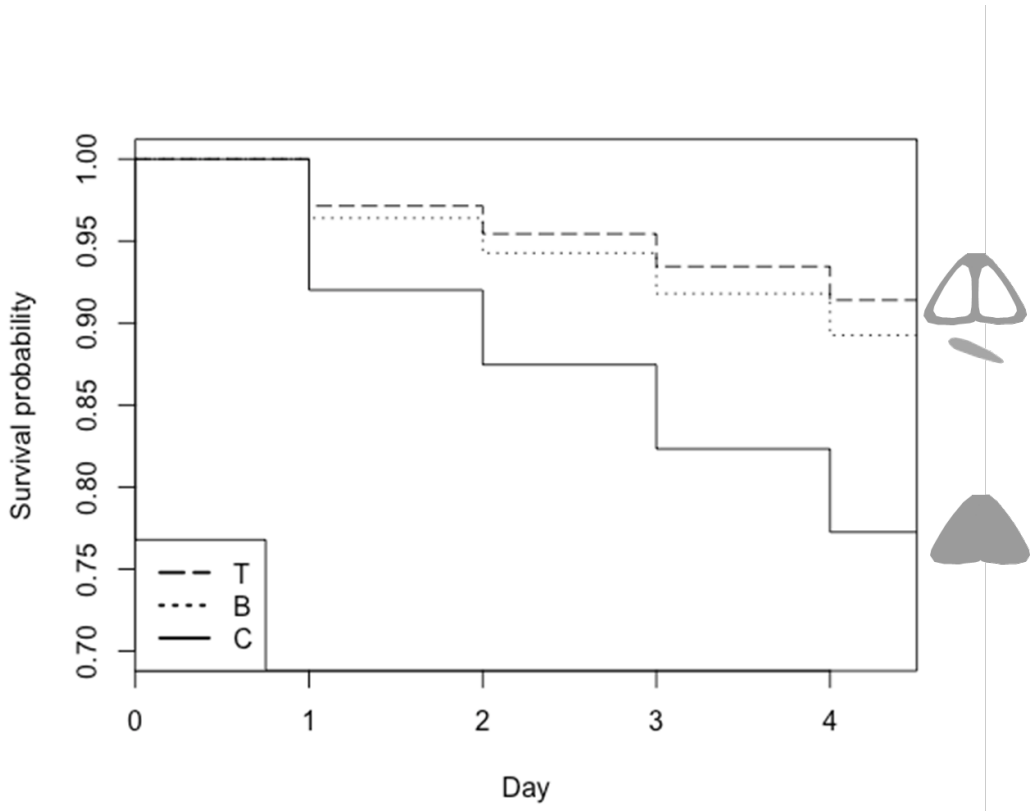

296

297 Figure 1. Survival of artificial prey with (T) transparent elements on their wings, (B) bodies without
298 wings, and (C) fully coloured opaque butterflies. Artificial butterflies were placed on tree trunks and
299 monitored for their 'survival' every day for 4 days. Data from the three weeks during which the
300 experiment was conducted are pooled together.

301

Table 1. Cox regression analyses for attacks on artificial butterflies.

	Coefficient	Exp. Coef	SE	*z*	*p*
Form. C > T +B	-0.34	0.71	0.09	-3.98	<0.001***
Form. B > T	-0.01	0.99	0.20	-0.03	0.9750
Rouvière w1 < Zoo w2 & w3	-0.04	0.96	0.10	-0.38	0.7061
Zoo w2 > Zoo w3	0.55	1.73	0.18	3.01	0.003 **
Form C > T +B: Rouvière w1 < Zoo w2 & w3	-0.04	0.96	0.06	-0.63	0.5289
Form. B > T : Rouvière w1 < Zoo w2 & w3	0.01	1.01	0.14	0.06	0.9505
Form. C > T +B: Zoo w2 > Zoo w3	0.11	1.11	0.11	0.99	0.3219
Form. B > T: Zoo w2 > Zoo w3	-0.35	0.71	0.26	-1.36	0.1729

Explanatory variables are: form (fully coloured 'C', with transparent windows 'T', and wingless bodies 'B'), week (w1, w2, w3), place (Rouvière and zoo) and their interactions. Notice that the experiment was performed only at Rouvière on w1 and only at the zoo on w2 and w3. Therefore, the contrast " Rouvière w1 < Zoo w2 & w3 " tests both time and place simultaneously. *z* corresponds to the values from the Wald z test used to test for factor significance, Exp. Coeff. to exponentiated coefficients or hazard ratios and SE to standard errors. Symbols: ** $p < 0.01$, *** $p < 0.001$.