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Doris Gomez, Mónica Arias, Marina Dhennin, Thomas G Aubier, Christine Andraud, Pascal Barla, Marianne Elias

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Title :

Transparency, the ultimate camouflage? Background dependency and influence of ambient light intensity

Authors :

Gomez D^{1†}, Arias M^{1,2}, Dhennin M¹, Aubier T³, Andraud C⁴, Barla P⁵, Elias M^{6,7}

Affiliations :

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

² PHIM, Univ Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

³

⁴ CRC, CNRS, MNHN, Sorbonne Univ., EPHE, Univ. Antilles, Paris, France

⁵ LABRI, INRIA, Bordeaux, France

⁶ ISYEB, CNRS, MNHN, Sorbonne Univ., EPHE, Univ. Antilles, Paris, France

⁷ Smithsonian Tropical Research Institute, Gamboa, Panama

[†] corresponding author: dodogomez@yahoo.fr

Abstract

The role of transparency in camouflage is understudied, particularly in terrestrial animals. What level of protection can intermediate levels of transparency offer? Does this protection depend on light conditions or background characteristics? Does transparency more protective than background-matching uniform coloration? Can transparency free animals from background dependency? Using a computer-based predation experiment, we asked human subjects to locate a butterfly (with uniformly opaque, semi-opaque, or transparent wings) hidden against different background (vegetation, soil or trunk). Our results confirm for the first time experimentally that intermediate transparency levels offer better protection in dimmer light conditions. Butterflies appearing smaller (either smaller in size or seen from a greater distance) or with more edge-disruption markings were more protected, especially when transparent. Butterflies closer to the predator's focal point or on poorly-contrasted background were less protected, unless more transparent. As the game went through, participants learned to find butterflies more frequently and quickly, with more significant progress for more transparent butterflies. Brighter light facilitated learning. Younger participants improved their reaction times while older participants increased their likelihood of finding the butterflies. Overall, transparency outperforms uniform coloration, whether generalist across several backgrounds or specialist of one background. This suggests that transparency, due to its high fidelity to the background, helps free prey from background dependency. The limited prevalence of transparency in Lepidoptera might be due to potential trade-offs that require further investigation.

Keywords:

transparency, concealment, detection, predator, visibility, background-matching, ambient light

Introduction

Transparency is abundant in water while it is rare on land. Consequently, the vast majority of studies have focused on transparency in water and repeatedly shown that transparency provides a camouflage role (Johnsen 2001, 2014, Bagge et al. 2016, Bagge 2019). Unevenly distributed across the phylogeny and likely gained multiple times independently, transparency is mostly influenced by habitat characteristics and abundant in groups dominated by pelagic existence at depths with enough solar radiation for vision (Johnsen 2001). In pelagic environments, highly transparent organisms can be found at the top of the water column, while less transparent organisms are found at the bottom (Johnsen, 2001, 2014). At the bottom of the water column, in dim light conditions, visual performance is poor and a high minimum contrast threshold between the prey and its surrounding is needed for predators to detect the prey (Anthony 1981); hence, low levels of transparency already provide an effective camouflage. On the other hand, near the surface, in bright light conditions, vision performs better and the contrast threshold is lowered; hence, only high levels of transparency provide an effective camouflage (Johnsen & Widder 1998). The protection of prey with intermediate levels of transparency against visually-hunting predators is thus closer to that of opaque prey in bright light than in dim light. Although this theoretical prediction has been established long ago based on observations on zooplankton (Johnsen & Widder 1998), this prediction has never been tested experimentally. As in water, the visual performance of predators on land is higher in bright than in dim light conditions, notably in birds (Hodos et al. 1976; Kassarov 2003; Lind et al. 2013) and in humans (Blackwell 1946). Transposing the predictions established by Johnsen & Widder (1998) for aquatic organisms to terrestrial habitats and terrestrial light environments, we can predict that semi-opaque prey should be closer in protection to opaque prey in bright light than it should be in dim light (Fig 1).

In terrestrial habitats, the evolution of coloration, and especially background-matching prey, has been largely studied to date, both through theoretical and experimental studies (Merilaita et al. 1999, 2001, Merilaita 2003, Dimitrova and Merilaita 2012). In visually-heterogeneous microhabitats, a 'generalist' prey (showing an average in coloration between the different microhabitats) can perform overall better than 'specialist' prey: background-matching colorations can be really cryptic on their specialised background but quite conspicuous on the backgrounds they are not the specialist of, and this trade-off can be costly. Conversely, being a generalist prey can be advantageous, as shown by predation experiments on birds (Merilaita et al. 2001). Whether generalist or specialist forms are advantageous not only depends on habitat visual heterogeneity, but also on other parameters. Given that transmitting light from the background offers the ultimate camouflage as it can reproduce any background faithfully, we expect transparency to be an efficient camouflage in all habitats and to perform better than a compromise generalist coloration. It can effectively help prey free from background-dependency.

To test Johnsen & Widder's hypothesis (1998) concerning intermediate levels of transparency and the hypothesis that transparency could free prey from background dependency, we designed a computer-based experiment involving human participants that had to find a butterfly hidden resting on natural backgrounds, where we carefully manipulated butterfly pattern (level of transparency, similarity to background), ambient light intensity, butterfly size (as proxy of predator-prey distance) and background type.

Methods:

We tested our hypothesis using an online citizen-science game based on photographs in which human participants had to detect a single hidden butterfly as fast as possible. Computer experiments, often used in studies relating to camouflage (Bond and Kamil 2002, Fraser et al. 2007, Egan et al. 2016, Toh and Todd 2017) combine several advantages: a precise control of prey features and background appearance, an a priori quantification of prey detectability by predators and background complexity, large amount of rapidly-collected data, all criteria allowing to test complex questions with precise predictions. Even though humans and birds differ in vision (for instance in UV detection or in photoreceptors involved in colour or brightness detection (Bennett et al. 1994, Kelber et al. 2003)),

prey detection experiments often show similar results with humans or birds (Xiao and Cuthill 2016, Arias et al. 2019), likely because both are vertebrates and share similar neuronal mechanisms for visual signal analysis.

Image elaboration

For this game, we used 3 '*background types*' that host butterflies in natural habitats: vegetation, trunk and soil (ESM Fig S1). For each background type, we took 8 different sets of HD photographs in the wild or in public gardens, using a 7.6cm square paper as a scale object in the photo, and a mobile phone (Moto G5, Android 8.1.0) and a photo stand. Each set contained photographs at 5 different levels of exposure, which were then used to reconstruct a High-Dynamic Range (HDR) image using the LuminanceHDR software (v2.6, using Profile 1 for automatic reconstruction). Each HDR image was then exported to the EXR format, and used to create three levels of lighting (ESM Fig S2).

For the entire game, we used a single butterfly silhouette, that of a *Pseudoscada erruca* (Nymphalidae) seen from above with extended wings. We manually identified an opacity mask in Gimp, corresponding to the thin-black contours of the butterfly, and we never modified this contour. The inner wing coloration was modified using the complement of the opacity mask to generate 3 uniformly-coloured specialist butterfly types, each specialized in each background type (inner wing coloration = average of RGB values for the 8 photographs of that background type) and a uniformly-coloured generalist butterfly type (inner wing coloration = average of RGB values over all 24 photographs). Hence, we defined the '*butterfly type*' as a variable with four levels (soil, vegetation, trunk, generalist ESM Fig S4). We defined '*butterfly transparency*' as a variable with three levels: opaque, semi-opaque wings (opacity divided by 50%), and transparent (85% transparent, a higher transparency level introduces the weird impression of an absent surface ESM Fig S4). A transparency mask was constructed by multiplying the complement of the opacity mask by the transparency level (ESM Fig S4) Since transparency was common to all butterfly types, we generated only one transparent butterfly, thus creating 9 different butterfly forms (ESM Fig S4, S5C). In addition to the opacity and transparency masks, we also generated a normal map image (using <https://cpetry.github.io/NormalMap-Online/>), which is required to produce plausible shading as described later on (ESM Fig S4). We maintained butterfly real size to have a 5cm wing span, thus adapting its apparent size to the zoom of the photograph and distance of the position where it was placed in the photograph. Finally, we defined a variable called '*butterfly background similarity*': it was true when a butterfly type was similar to the background type (a soil butterfly on a soil background, a trunk butterfly on a trunk background, or a vegetation butterfly on a vegetation background), or false otherwise.

In each photograph, we defined 3 alternative '*positions*' where one butterfly could be placed and realistically integrated it in the photograph using a purpose-made process common to all HDR images. The butterfly was first mapped to a plane and slightly rotated by hand to visually conform to the orientation of the surface supporting it. The next step to integrate the butterfly visually into the background was to shade it with a plausible lighting environment (ESM Fig S3). The diffuse lighting was then used to shade the butterfly wings according to the normals to its surface stored in the normal map image (ESM Fig S4, S5). A faint shadow was finally added to the background to realistically anchor the butterfly in the photo. This was done by filling the butterfly opacity mask with black and blurring it using a wide Gaussian filter (ESM Fig S5). Even though the whole process required manual intervention, we stress that the same choices were applied to all butterflies placed at a given position in a given image. Each photograph containing a hidden butterfly was then modified to present 3 different brightness levels (a bright level, an intermediate level where pixel brightness was divided by $\sqrt{2}$ relative to the bright, a low level where pixel brightness was divided by $\sqrt{2}$ relative to the intermediate, ESM Fig S2). Since the whole process was applied to a HDR image, modifying its brightness did not create over- or under-exposed images. In total, we generated an image library containing 1944 images (3 background types * 8 images per background type * 3 brightness levels * 3 positions * 9 butterfly forms).

Image analysis

The average $L^*a^*b^*$ value of the 72 background photographs without butterfly (24 background photos * 3 brightness levels) did not vary much for soil, varied on the a^* axis for trunk, while it varied on the b^* axis for vegetation (ESM, Fig S6). We measured *'image complexity'* of these images using the R package *imagefluency* (Mayer 2024). This measure gives the ratio between the compressed image and the uncompressed image. The closer to 1, the more complex the image. We then computed the average luminance over the entire image, that we called *'Ambient light intensity'*. We also computed the local contrast between the butterfly and its immediate surrounding background, by computing the RGB values for the inner wing colouration of a butterfly, and the RGB average value for the background on an area of a body length around the butterfly. These values were then converted into the $L^*a^*b^*$ CIELAB human vision system to compute the contrast along each axis separately (in a first approximation, we can consider that a^* contrasts green against red, and that b^* contrasts blue against yellow). We computed the *'overall local contrast'* as the contrast combined over the three axes (L^* , a^* , and b^*). The higher the value, the more contrasted was the butterfly against its background. Finally, we computed a quantitative measure of detectability by computing the GabRat index (Troscianko et al. 2017). The GabRat index quantifies the ratio between the number of false edges (edges perpendicular to the animal contour) and the number of true edges (edges parallel to the animal contour). Prey with greater GabRat values – with more edge disruption markings – were less detectable, being a good proxy of detectability (Troscianko et al. 2017). We computed this measure using the *GabRat_plugin2* in ImageJ for each of the 1944 images, a sigma value of 2, and for each axis L^* , a^* , and b^* separately. *'GabRat_a'* and *'GabRat_b'* quantified chromatic disruption markings while *'GabRat_L'* quantified achromatic disruption markings.

Image presentation in a game

Over the course of a game, a single participant was only exposed sequentially to 72 images randomly sampled from the generated image library using a purpose-built R script, so that each of the 3 butterfly positions was presented only once in each of the 24 different background images. Each participant saw the same amount of each transparency level: 24 opaque, 24 semi-opaque, and 24 transparent butterflies and the same amount of each exposure levels (low, medium, high). Each participant saw all background images and 3 times each (one for each position). Conversely, the number of images containing a given butterfly type (soil, vegetation, trunk, generalist) was not equal for all butterfly types within a game. Finally, the order of presentation of the images within a game was random.

As the game was online, we made it as standardized as possible for all participants by asking them to follow several simple steps before the test. Participants were asked to hold a credit card to a bar on the screen and enter the apparent size in cm of their credit card. This enabled us to consider *'image size'* as a factor in further analyses. Participants were asked to sit one arm-length distance away from their computer screen in order to ensure a consistent viewing distance across images seen by a given participant. Participants always wearing glasses were asked to keep their glasses on. Participants were requested to concentrate on the yellow circle between images to stay focused and concentrated throughout the whole test and to keep interruptions at a minimum level. They were asked to look carefully at the images to minimize false negatives. In addition, they were asked to fill a small questionnaire (*'Age'* category (9 possible categories [1-9],[10-19],[20-29],[30-39],[40-49],[50-59],[60-69],[70-79],[80-89]), non-corrected vision default (yes/no), first time they played that game (yes/no), *'Entomological knowledge'* (yes/no) or habit of *'Searching in nature'* (yes/no)) to control for these factors in subsequent analyses. Data were anonymously collected.

Once presented with an image, the participant had to click on the position of the hidden butterfly as quickly as possible. The butterfly was considered as not found if no click was made for 20 sec, or not in an area corresponding to an imaginary circle surrounding the butterfly. After the click (or after 20 sec), a yellow circle appeared around the butterfly on the image, then the image disappeared but the yellow circle remained on a black background, to serve as a focus for the participant gaze. The distance between this circle and the position of the hidden butterfly in the next image was included in the

analyses as '*Distance to Reference Point*'. At the end of the game, we collected the information of the questionnaire, the image identity, the order of presentation (trial number from 1 to 72), the time taken to click and the position of the click. The position of the click was then compared with the position of the butterfly (known for each image) in order to determine whether the participant had found the butterfly.

Statistical analyses

We restricted the analysis to naïve players, no uncorrected visual impairment, older than 20 years old as children had lower performance and including them made variation of Found or Time with age parabolic and not linear. We obtained a total of 127 440 observations for 1770 players that we could analyse. Unfortunately, we could not use cox-regression mixed models to analyse simultaneously (butterfly found (no/yes) and time to find it) as the dependent variables of a survival model, because running such models could not handle many factors nor interactions. Conversely, we used generalized linear mixed models to analyse separately the butterfly found (yes/no, binary error distribution) and the time to find the butterfly (when found, gaussian error distribution) as dependent variables. We selected models for random variables, finally retaining player ID, photograph (24 different) and the position within a photograph (1, 2 or 3) as random variables. Since only one transparent morph had been generated irrespective of the butterfly morph (vegetation, trunk, soil), we wrote an R-routine to randomly assign a morph (vegetation, trunk, soil, generalist) to the transparent morph, in order to separate the transparency level (transparent, semi-opaque, opaque) and the butterfly type (vegetation, trunk, soil). We tested as fixed factors in the models: age (7 categories, as a quantitative variable), entomological knowledge (yes/no), nature search experience (yes/no), ambient light intensity (as a quantitative variable), image size, image complexity, image background type (soil, trunk, vegetation), image number (1 to 72 as a quantitative variable), distance to reference point, butterfly transparency level (opaque, semi-opaque, transparent), butterfly type (soil, vegetation, trunk, generalist), butterfly size, butterfly chromatic and achromatic disruption markings (GabRat_a, GabRat_b, GabRat_L) overall local contrast, and butterfly-background similarity (yes/no, yes when butterfly type and background type were identical). We tested all relevant two-way interactions. All continuous variables were centred and scaled to compare effect size. Training followed an asymptotic evolution, hence image number was log-transformed in all models. The best model was selected based on the minimisation of the Akaike criterion (AICc). We ran the models 20 times for 20 different random assignments to examine the impact of this random assignment on model AICc ranking and model coefficients.

Bond and Kamil (2006) found no relationship between accuracy of prey capture and latency to capture in parallel search (when detection task was easy) and a negative relationship for serial search (when the detection task was difficult and no time limit imposed on search). Using the mixed model approach and the same random factors as before, we tested the relationship between the delay to click (whether the prey was found or not) and the probability to find the butterfly (yes or no). Although there was a time limit imposed in our experiment, we thought this would help characterizing the level of difficulty of the detection task.

Results

Randomly assigning transparent butterflies to one background type did not change the best model (identical in all 20 models for both variables). Hence, we hereafter only present the results concerning one random assignment. We found a strong negative relationship between the probability of finding a butterfly (yes or no) and the latency to click (in milliseconds, whether the butterfly was found or not, estimate=- 3.722E-04±2.5E-06, $p < 0.0001$) showing that searching a butterfly hidden in an image was a serial task needing an important visual attention.

Effect of butterfly colour pattern on butterfly protection

Globally, transparent butterflies were more protected (less likely found, and less quickly found if found) than semi-opaque butterflies (transp<SO effect positive for Found, negative for Time, Table 1 row 2, Table 2), which in turn were more protected than opaque butterflies (SO<O effect positive for Found, negative for Time, Table 1 row 3, Fig 2, Table 2).

Butterflies were more protected (less likely found and less quickly found when found) when they had more edge disruption markings (GabRat_a and GabRat_b negative for Found, GabRat_a, GabRat_b, GabRat_L positive for Time Table 1 row 20, 21, 22, Table 2, Fig 3). The differences in protection between transparent, semi-opaque, and opaque butterflies increased when the butterflies got more complex relative to their surroundings (transp<SO x GabRat_a positive for Found, negative for Time Table 1 row 53 54, transp<SO x GabRat_L and SO<O x GabRat_L positive for Found, negative for Time Table 1 row 51 52 Fig 3, Table 2). Conversely, the differences in protection between transparent, semi-opaque, and opaque butterflies increased when the butterflies got less complex relative to their surroundings for GabRat_b (transp<SO x GabRat_b negative for Found, transp<SO x GabRat_b and SO<O x GabRat_b positive for Time Table 1 row 55 56 Fig. 3, Table 2). While opaque butterflies were similarly protected irrespective of their complexity relative to their surroundings, semi-opaque butterflies and more importantly transparent butterflies were less likely and less quickly found when more complex relative to their surroundings (Fig 3, Table 2).

Overall and irrespective of the background they rested on, specialist butterflies were less protected than generalist butterflies (ButType Gen<Spe positive for Found, negative for Time Table 1 row 4). Likewise, irrespective of the background they rested on, trunk-specialists were more protected than soil or vegetation specialists (ButType trunk<(soil,vegetation) positive for Found, negative for Time Table 1 row 5). Participants needed more time to find soil specialists compared to vegetation specialists (ButType soil<veg negative for Time Table 1 row 6).

As expected, specialist butterflies were more protected when they were similar to their background than when they were dissimilar (ButBackSimilarity yes<no positive for Found, negative for Time Table 1 row 7, Fig 4). The difference in protection between butterflies similar to their background and butterflies dissimilar to their background was greater for opaque than for semi-opaque, and for semi-opaque than for transparent butterflies, for which being similar or dissimilar was assigned at random and resulted in equivalent protection (Transp<SO x ButBackSimilarity yes<no and SO<O x ButBackSimilarity yes<no positive for Found and negative for Time Table 1 row 26 27, Table 2). The difference in probability to be found did not depend on ambient light intensity (ButBackSimilarity x Ambient Light Intensity not significant for Found Table 1 row 28). Conversely, the difference in time to find similar versus dissimilar butterflies faded with increasing light intensity (ButBackSimilarity x Ambient Light Intensity positive for Time Table 1 row 28). The gain in protection – probability to be found and time to be found – offered by being similar to the background was slightly higher for vegetation than for trunk (ButBackSimilarity yes<no x BackType trunk<vegetation positive for Found, negative for Time Table 1 row 24, Fig 4) and higher for trunk than for soil (ButBackSimilarity yes<no x BackType soil<trunk positive for Found, negative for Time Table 1 row 23). The gain in protection offered by being similar to the background increased as image complexity increased (ButBackSimilarity yes<no x Image Complexity positive for Found, negative for Time Table 1 row 25).

Effect of light conditions

Hidden butterflies were less protected (more likely to be found, and more quickly found when found) in bright than in dim light (Ambient Light Intensity effect positive for Found, negative for Time Table 1 row 8, Fig 5AB). In brighter conditions, the protection of the different levels of transparency got more similar (Transp<SO x Ambient light intensity and SO<O x Ambient light intensity negative for Found, positive for Time Table 1 row 32 33, Table 2, Fig 5AB). When scaling the protection of transparent and opaque butterflies to maximal and minimal values respectively, the protection of semi-opaque butterflies got more similar to that of opaque butterflies in brighter light, both in terms of probability and time to be found (Fig 1 and Fig 5CD).

Learning (change in probability to find a butterfly throughout the game) was similar in bright and dim light (Ambient light intensity x Image Number not retained for Found in the best model Table 1 row 48) but progresses in time to find the hidden butterfly were greater in bright than in dim light (Ambient light intensity x Image Number negative for Time Table 1 row 48). Increasing ambient light intensity had a greater effect on the probability to find a butterfly for older than for younger participants (Ambient light intensity x Age positive for Found Table 1 row 44) while it had a greater effect on the time needed to find a butterfly for younger than for older participants (Ambient light intensity x Age positive for Time Table 1 row 44).

Size and its interaction with light and transparency

Smaller butterflies were more protected (in relative size (Butterfly Size effect positive for Found, negative for Time Table 1 row 9, Table 2, Fig 6AB) or in absolute size (Image size effect positive on Found, negative on Time Table 1 row 18, Table 2). Butterflies that were further away from the reference point fixed by participants between any two images were also more protected (Distance to Reference Point effect negative for Found, positive for Time Table 1 row 15).

Butterflies were easier to find at lighter conditions independently of their relative or absolute size (Ambient light intensity x But Size and Ambient light intensity x Image Size not significant for Found Table 1 row 45 46). Yet, the gain in time to find a butterfly in under brighter light conditions was higher when butterflies were smaller (either relative to the image size or in absolute: Ambient light intensity x But Size and Ambient light intensity x Image Size positive for Time Table 1 row 45 46).

The difference in protection (probability to be found, time to be found when found) between the different levels of transparency decreased as butterfly size increased within the image (transp<SO x Butterfly Size and SO<O x Butterfly Size negative effect for Found, SO<O x Butterfly Size positive for Time Table 1 row 36 37, Table 2, Fig 6AB) or as image size increased in absolute (SO<O x image Size negative effect for Found, transp<SO x Image Size and SO<O x image Size positive for Time Table 1 row 38 39). When scaling the protection of transparent and opaque butterflies to maximal and minimal values respectively, the protection of semi-opaque butterflies got more similar to that of opaque butterflies for bigger butterflies, in terms of time to be found but not in terms of probability to be found, which remained stable whatever the butterfly size (Fig 6CD). Finally, being close to the reference point fixed by the participant helped reveal the butterfly, more for opaque than for semi-opaque, and more for semi-opaque than for transparent butterflies; transparent butterflies were similarly protected whatever the distance to the reference point fixed by participants (transp<SO x Distance to Reference Point and SO<O x Distance to Reference Point interaction effects negative for Found, positive for Time Table 1 row 30 31, Table 2).

Background effect

There was no significant difference between background types in terms of protection overall (Back Type soil<trunk and Back Type trunk<vegetation not significant for Found or Time Table 1 row 16 17). The difference in time to find the hidden butterfly between soil and trunk or trunk and vegetation decreased as image size increased (Back Type soil<trunk x Image Size and Back Type trunk<vegetation x Image Size positive for Time Table 1 row 57 58) or as image complexity increased (Back Type soil<trunk x Complexity and Back Type trunk<vegetation x Complexity positive for Time Table 1 row 59 60).

Overall, the probability to find a hidden butterfly did not vary with image complexity or image contrast (either local around the butterfly or global) but when the butterfly was found, it took more time to find it in a more complex image or in an image with a higher local contrast (Image Complexity and Overall Local contrast effect positive for Time Table 1 row 10, 19). As ambient light intensity increased, a complex image became more protective for butterflies: it reduces the probability to find the butterfly or increased the time needed to find it when it was found (Ambient light intensity x Image Complexity negative for Found, positive for Time, row 47).

The differences in protection between transparent, semi-opaque, and opaque butterflies decreased for more complex images (transp<SO x Image Complexity and SO<O x Image Complexity positive for Found and negative for Time Table 1 row 49 50, Table 2) and for images with higher overall local contrast (SO<O x Overall local contrast negative for Found, transp<SO x Overall local contrast and SO<O x Overall local contrast positive for Time Table 1 row 42 43, Table 2).

Effect of "predator" learning and other characteristics

As the game went through, participants learned to find butterflies, they found butterflies more often and more quickly (ImageNumber effect positive for Found, negative for Time, Table 1 row 11, Fig 7). Relative to the situation at the beginning of the game, learning yielded better relative progresses in protection for the hidden butterfly for transparent butterflies compared to semi-opaque butterflies, and in time to capture the hidden butterfly for semi-opaque butterflies compared to opaque butterflies (transp<SO x ImageNumber positive for Found and positive for Time Table 1 row 40, SO<O x ImageNumber positive for Time Table 1 row 41, Fig 7).

In general, younger participants performed better than older participants: they were more likely to find a hidden butterfly and they were faster in locating it (Age effect negative for Found and positive for Time Table 1 row 12). Through training, older participants made greater progresses in capture probability compared to younger participants, while younger participants made greater progresses in the time to find butterflies compared to older participants (ImageNumber x Age effect positive for Found, positive for Time Table 1 row 29).

Semi-opaque and transparent butterflies were more similar in protection (probability to be found, time to be found) for older than for younger participants (transp<SO x Age negative for Found, positive for Time Table 1 row 34, Fig 8AB). Semi-opaque and opaque butterflies were more similar in protection (time to be found) for older than for younger participants (SO<O x Age positive for Time Table 1 row 35, Fig 8B). When scaling the protection of transparent and opaque butterflies to maximal and minimal values respectively, semi-opaque butterflies got more similar in protection to that of transparent butterflies as participants got older, especially for the probability to find a butterfly (Fig 8CD).

Finally, whatever the images, participants with naturalist experience performed better: they were more likely to find butterflies when they were used with searching items in nature or knew insects (Entomological Knowledge and Searching in Nature positive for Found Table 1 row 13 14) and they found butterflies more quickly when they were used to searching items in nature (Searching in Nature negative for Time Table 1 row 13).

Discussion

In this computer-based predation experiment, more transparent prey were overall more protected, in agreement with previous predation experiments with birds in cages (Arias et al. 2019) or with bird predator community in the field (Arias et al. 2020).

Our study provides the first experimental support for the theoretical prediction made by Johnsen & Widder (1998) that a given level of transparency would be more protective in dim light and less protective in bright light. We established that the relative protection offered by the intermediate level of transparency was more similar to that of opaque butterflies in bright light (both in terms of probability to find a butterfly and time to find it) and relatively more similar to that of transparent butterflies in dim light. This confirms that the protective effect of intermediate levels of transparency is contextual of ambient light intensity. Even low levels of wing transparency can be protective, and this trait may have evolved in species flying in forest cover, especially in understory. In tropical rainforests, only 2% of the light illuminating the canopy reaches the ground (Bazzaz and Pickett 1980)

and understorey clearwing butterflies and moths should have lower levels of transparency on their wings than their canopy counterparts, an hypothesis that remains to be studied.

More generally, easing the detection task decreases the relative degree of protection of intermediate levels of transparency, a conclusion that we can infer from two results and that echoes the effect of increasing ambient light intensity. First, the higher similarity in protection between semi-opaque and opaque butterflies in younger participants compared to older participants can be interpreted in the same way. With increasing age, the human visual system undergoes physiological changes such as impaired spatial contrast sensitivity, prolonged dark adaptation, and decreased visual processing speed (Owsley 2016). The decline in visual performance of older people under low illumination implies the need for more light to maintain similar visual performance to young adults (Oweley 2016). Hence, being young in age has similar effects as increasing light intensity. Second, the protection of semi-opaque butterflies got more similar to that of opaque butterflies for butterflies bigger in size.

Butterflies apparently smaller in size (through butterfly size or image size) are more difficult to detect, an intuitive result if we consider that smaller apparent size is related to greater predator viewing distance. That prey are more protected from predators at a higher viewing distance has been repeatedly supported in theoretical approach, observation or experiments, including computer-based experiments (Endler 1978, Ruxton et al. 2004, Tullberg et al. 2005, Arias et al. in print). The novel result here is that transparency enhances the protective effect of decreasing apparent size, as if it increased the distance at which predators viewed their prey. Moreover, even when close to predators' attention point, transparent static butterflies remain difficult to detect, an additional asset when predator approach. In other words, transparency partially offsets the benefits that predators classically derive from approaching opaque prey, at large distance (size) and at close distance (distance to attention point).

Learning yielded progresses in capturing all types of butterflies, whatever their degree of transparency. Yet, progresses were smaller for opaque butterflies, likely because of a high capture probability from the beginning of the experiment, around 90%, which left little room for improvement. Conversely, progresses through learning were largest for transparent butterflies. In a context of a small number of prey types, predators can form a search image, an internal representation of the prey species, or some characteristics of the prey species used to help detection (Lawrence & Allen 1983 cited dans Troscianko 2009). In predation experiments, jays have shown an improvement in their capture ability with successive encounters with one prey type consistent with the formation of a search image (Pietrewicz and Kamil 1979). By contrast, they have shown no improvement in capture ability with successive encounters with two prey types, suggesting they did not form a search image when facing several types of prey. Because they allow light to pass through, transparent butterflies have the appearance of the background. As a result, much of the surface area of their wings varies in appearance from one image to the other. A predator facing transparent prey find itself in conditions similar to those of jays confronted with several types of prey. If transparency itself were used as a key feature for detection, learning should not bring much improvement. Yet, we observe an improvement in the capture ability of transparent butterflies. This result is consistent with the results of experiments on jays only if we consider that constant characteristics (wing contour, butterfly abdomen, position of the head upwards which are identical from one image to another) and not transparency itself (whose appearance varies greatly) are used for detection and the formation of search images.

Overall, the level of prey protection heavily depended on background complexity. Increasing background complexity increased the time needed to find the hidden butterfly. Although we here use a relatively coarse and imprecise descriptor of background complexity, results on background

complexity and at the edge between animal and background are largely congruent. In all cases, our experiment involved a serial visual detection task as latency and accuracy were negatively correlated, as found in experiments with jays and complex backgrounds (Bond and Kamil 2006). The protective effect of background complexity has been repeatedly shown in previous studies (Kono et al. 1998, Merilaita 2003, Dimitrova and Merilaita 2012, 2014). Complex backgrounds elicit a slow visual search (Bond and Kamil 2006) and complex backgrounds contain more visual information to be processed, making the detection task more difficult (Merilaita 2003). The accentuation of complexity protective effect in brighter light is likely due to more details being accessible to visual inspection and acting as potential distractors slowing down the prey detection task. Butterflies with more achromatic edge disruption markings and more chromatic edge disruption markings were more protected, as previously found (Troschianko et al. 2021). Butterflies with more edge disruption markings and more transparency were even more protected (in the transparent patch, the background becomes visible, which likely adds edge disruption markings), showing that multiple visual traits ensuring low detectability can act together (Arias et al. 2021) and have synergistic effects, as shown for defence traits (Kikuchi et al. 2023). The result that transparency increases the protective effect of background complexity, likely through edge disruption markings, is novel. Future research should focus on deciphering which aspects of background and butterfly interplay in the detection of transparent butterflies.

Habitats were visually heterogeneous in our experiment: specialised butterflies were highly cryptic on their matching background, and highly detectable on the mismatching backgrounds. This resulted in a lower overall survival probability of specialised butterflies compared to the generalist butterfly. Similar outcomes had been found in predation experiments with tits: the generalist prey had lower predation risk than the specialised matching colorations in a heterogeneous habitat consisting of two microhabitats (Merilaita et al. 2001). Whether specialist or generalist coloration is more beneficial depends on the level of crypsis provided by the coloration in the different microhabitats, on the probability that the prey frequents the different microhabitats and on the probability it may encounter a predator in each of these different microhabitats (Merilaita et al. 1999). Moreover, our results show that transparent butterflies are as efficiently hidden on all background types and more efficiently than uniform colorations, be they specialist or generalist of several backgrounds. In the shrimp *Hippolyte obliquimanus*, uniformly coloured morphs are habitat-specialists and highly habitat-dependent, they are poor swimmers but they can change colour. Conversely, the transparent morph (transparent with dark stripes) frequents different habitats and this good swimmer shows little habitat-dependency but has no ability to change colour (Duarte et al. 2016). These observations suggest that transparency can simultaneously efficiently free prey from background visual dependency and maintain a high degree of crypsis on all types of backgrounds. A recent field experiment exploring avian predation of artificial butterflies showed that predation was slightly contingent on background for opaque but not for transparent butterflies, suggesting transparency helped enlarging protection (Yeager et al. 2024).

Another argument comes from theoretical considerations. Simulations have shown that antipredator warning colorations are more likely to invade a population of cryptic prey when the prey frequented microhabitats that were highly different visually, rendering impossible the evolution of a camouflage efficient for both microhabitats (Merilaita and Tullberg 2005). Although the topic of warning coloration is complex, transparency may have also evolved as an efficient alternative to background-dependent matching colorations. Whether transparent species have larger range sizes and lower habitat dependency than opaque cryptic species remains an open question.

Why is the prevalence of transparency – so efficient in terms of concealment – so limited in Lepidoptera? In opaque butterflies and moths, scales are involved in multiple vital functions ranging

from flight enhancement, communication, thermoregulation, or water repellency. Recent studies show that transparency entails costs in terms of water repellency, with more transparent butterflies and moths being less able to repel water (Gomez et al. 2021). Likewise, transparent patches are less efficient to heat up than opaque patches, be they dark or light in coloration and entail potential costs for thermoregulation (Ossola et al. 2023). Similarly, opaque patterns have been repeatedly shown to serve courtship communication in opaque butterflies (Kemp and Rutowski 2011). It is reasonable to think that in transparent lepidopteran species, coloration may have a lower relevance for communication with conspecifics or other species. These elements may explain why transparency is not so common in Lepidoptera.

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Data availability:

All data used for the game (images, in-between black images with a yellow circle, code to randomly choose the order of images presented to a participant, code to put the game online, data collected, code to clean, analyse the data and make the table and the graphs are available at the following DOI:

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Table 1 : Results of the best mixed models (one random assignment) for the probability to find the hidden butterfly (Found) and the time to find it when found (Time). Fixed factors are listed and row numbers help locating the factors. The symbol – indicates a factor not retained in the best model. Significant effects are indicated in bold: ~p<0.1, * p<0.05, **p<0.01, ***p<0.001.

Nb	Effect	Found (yes or no)			Time (in ms)		
		Estimate	t-value	p-value	Estimate	t-value	p-value
1	(Intercept)	3.44 ± 0.249	13.8	<0.001***	8.41 ± 0.0483	174.14	<0.001***
2	ButTransp.T<SO	1.11 ± 0.0372	29.92	<0.001***	-0.223 ± 0.000144	-1551.45	<0.001***
3	ButTransp.SO<O	1.3 ± 0.0373	34.76	<0.001***	-0.264 ± 0.000118	-2231.29	<0.001***
4	ButType.Gen<Spe	0.0764 ± 0.00714	10.7	<0.001***	-0.0217 ± 3.04e-05	-715.98	<0.001***
5	ButType.trunk<(soil,veg)	0.134 ± 0.013	10.3	<0.001***	-0.026 ± 5.34e-05	-486.2	<0.001***
6	ButType.soil<veg	0.0775 ± 0.0237	3.27	0.00108**	-0.0266 ± 1e-04	-265.55	<0.001***
7	ButBackSimilarity.yes<no	0.113 ± 0.0168	6.75	<0.001***	-0.0235 ± 6.43e-05	-365.82	<0.001***
8	Ambient Light Intensity	0.599 ± 0.143	4.18	3e-05***	-0.119 ± 0.000657	-181.86	<0.001***
9	ButSize	1.19 ± 0.269	4.42	1e-05***	-0.213 ± 0.0519	-4.1	4e-05***
10	Image Complexity	-0.197 ± 0.165	-1.19	0.23351	0.0404 ± 0.000749	53.99	<0.001***
11	Image Number	0.526 ± 0.0112	46.81	<0.001***	-0.081 ± 4.71e-05	-1720.25	<0.001***
12	Age	-0.877 ± 0.0305	-28.75	<0.001***	0.196 ± 0.00552	35.55	<0.001***
13	Searching in Nature.no<yes	0.142 ± 0.0365	3.9	1e-04***	-0.0224 ± 0.00597	-3.76	0.00017***
14	Knowledge.no<yes	0.0874 ± 0.0336	2.6	0.00926**	-	-	-
15	Distance To Reference Point	-0.0459 ± 0.0128	-3.57	0.00035***	0.0506 ± 4.78e-05	1058.07	<0.001***
16	Back Type.soil<trunk	0.459 ± 0.374	1.23	0.21917	-0.0954 ± 0.0727	-1.31	0.18962
17	Back Type.trunk<vegetation	0.324 ± 0.366	0.885	0.37633	-0.0577 ± 0.0713	-0.809	0.41871
18	Image Size	0.387 ± 0.031	12.47	<0.001***	-0.0428 ± 0.00126	-34.1	<0.001***
19	Overall Local Contrast	-0.0196 ± 0.0311	-0.632	0.52746	0.00777 ± 0.000117	66.48	<0.001***
20	GabRat_L	0.175 ± 0.0491	3.56	0.00037***	0.0131 ± 0.000187	70.45	<0.001***
21	GabRat_a	-0.272 ± 0.0229	-11.84	<0.001***	0.0436 ± 9.31e-05	468.37	<0.001***
22	GabRat_b	-0.276 ± 0.0262	-10.52	<0.001***	0.0585 ± 0.000108	543.3	<0.001***
23	ButBackSimilarity.yes<no:Back Type.soil<trunk	0.135 ± 0.0259	5.2	<0.001***	-0.023 ± 0.00011	-209.58	<0.001***
24	ButBackSimilarity.yes<no:Back Type.trunk<vegetation	0.0808 ± 0.0266	3.04	0.00237**	-0.0308 ± 0.000112	-274.48	<0.001***
25	ButBackSimilarity.yes<no:Image Complexity	0.035 ± 0.0128	2.73	0.00641**	-0.0104 ± 9.53e-05	-109.16	<0.001***

26	ButTransp.T<SO:ButBackSimilarity.yes<no	0.0571 ± 0.0189	3.03	0.00248**	-0.00839 ± 7.87e-05	-106.71	<0.001***
27	ButTransp.SO<O:ButBackSimilarity.yes<no	0.102 ± 0.0239	4.27	2e-05***	-0.024 ± 8.12e-05	-295.23	<0.001***
28	ButBackSimilarity.yes<no:Ambient Light Intensity	-	-	-	0.00586 ± 9.56e-05	61.34	<0.001***
29	Image Number:Age	0.0255 ± 0.00949	2.68	0.00727**	0.00178 ± 4.78e-05	37.38	<0.001***
30	ButTransp.T<SO:Distance To Reference Point	-0.0417 ± 0.0159	-2.63	0.0085**	0.0162 ± 6.47e-05	250.84	<0.001***
31	ButTransp.SO<O:Distance To Reference Point	-0.0443 ± 0.0205	-2.16	0.0306*	0.0203 ± 6.73e-05	301.71	<0.001***
32	ButTransp.T<SO:Ambient Light Intensity	-0.363 ± 0.0297	-12.2	<0.001***	0.0562 ± 0.000144	391.24	<0.001***
33	ButTransp.SO<O:Ambient Light Intensity	-0.423 ± 0.0355	-11.92	<0.001***	0.065 ± 0.000136	479	<0.001***
34	ButTransp.T<SO:Age	-0.036 ± 0.0148	-2.44	0.01483*	0.0128 ± 6.62e-05	193.12	<0.001***
35	ButTransp.SO<O:Age	-0.000945 ± 0.0176	-0.0537	0.9572	0.00884 ± 6.5e-05	136.1	<0.001***
36	ButTransp.T<SO:ButSize	-0.158 ± 0.0218	-7.24	<0.001***	-0.0194 ± 8.7e-05	-223.16	<0.001***
37	ButTransp.SO<O: ButSize	-0.176 ± 0.0274	-6.43	<0.001***	0.00756 ± 8.82e-05	85.69	<0.001***
38	ButTransp.T<SO:Image Size	-0.0373 ± 0.0166	-2.25	0.02448*	0.00929 ± 6.53e-05	142.3	<0.001***
39	ButTransp.SO<O:Image Size	-0.0679 ± 0.0214	-3.17	0.00153**	0.00834 ± 6.75e-05	123.57	<0.001***
40	ButTransp.T<SO:Image Number	0.0312 ± 0.0143	2.17	0.02976*	0.00782 ± 6.73e-05	116.1	<0.001***
41	ButTransp.SO<O:Image Number	0.0309 ± 0.0172	1.79	0.07307~	0.00703 ± 6.76e-05	103.97	<0.001***
42	ButTransp.T<SO:Overall Local Contrast	-0.0669 ± 0.0354	-1.89	0.05916~	0.000286 ± 0.000143	2.01	0.04485*
43	ButTransp.SO<O:Overall Local Contrast	-0.0904 ± 0.0325	-2.79	0.00533**	0.024 ± 0.000117	205.91	<0.001***
44	Ambient Light Intensity:Age	0.0248 ± 0.0109	2.28	0.02265*	0.00191 ± 4.63e-05	41.36	<0.001***
45	Ambient Light Intensity: ButSize	-0.0218 ± 0.0152	-1.43	0.15246	0.00346 ± 6.58e-05	52.66	<0.001***
46	Ambient Light Intensity:Image Size	0.021 ± 0.0122	1.72	0.08485~	0.00203 ± 4.7e-05	43.11	<0.001***
47	Ambient Light Intensity:Image Complexity	-0.111 ± 0.0404	-2.74	0.00608**	0.0211 ± 0.000176	119.71	<0.001***
48	Ambient Light Intensity:Image Number	-	-	-	-0.00485 ± 4.71e-05	-102.84	<0.001***
49	ButTransp.T<SO:Image Complexity	0.402 ± 0.0303	13.25	<0.001***	-0.058 ± 0.000147	-393.59	<0.001***
50	ButTransp.SO<O:Image Complexity	0.381 ± 0.0374	10.2	<0.001***	-0.0635 ± 0.000142	-446.63	<0.001***
51	ButTransp.T<SO:GabRat_L	0.312 ± 0.0258	12.09	<0.001***	-0.103 ± 1e-04	-1023.15	<0.001***
52	ButTransp.SO<O:GabRat_L	0.262 ± 0.0322	8.15	<0.001***	-0.0774 ± 0.000104	-745.63	<0.001***
53	ButTransp.T<SO:GabRat_a	0.251 ± 0.0219	11.47	<0.001***	-0.00319 ± 9.46e-05	-33.69	<0.001***
54	ButTransp.SO<O:GabRat_a	0.28 ± 0.025	11.19	<0.001***	-0.00728 ± 8.93e-05	-81.54	<0.001***
55	ButTransp.T<SO:GabRat_b	-0.123 ± 0.0281	-4.38	1e-05***	0.0358 ± 0.000114	312.88	<0.001***
56	ButTransp.SO<O:GabRat_b	-0.0545 ± 0.0283	-1.92	0.05443~	0.0284 ± 9.84e-05	288.54	<0.001***

57	Back Type.soil<trunk:Image Size	-	-	-	0.00463 ± 6.53e-05	70.8	<0.001***
58	Back Type.trunk<vegetation:Image Size	-	-	-	0.000311 ± 6.5e-05	4.78	<0.001***
59	Back Type.soil<trunk : Image Complexity	-	-	-	0.00879 ± 8.84e-05	99.48	<0.001***
60	Back Type.trunk<vegetation : Image Complexity	-	-	-	0.0114 ± 8.73e-05	130.15	<0.001***

Table 2: summary of the main results concerning transparency (interaction effect)

Increased camouflage for	effect greater/lower for more transparent butterflies
greater wing transparency <i>(rows 2 and 3)</i>	-
dimmer light conditions <i>(row 8)</i>	greater an intermediate level of transparency is already protective in dimmer light <i>(rows 32 and 33)</i>
butterfly apparently smaller (butterfly smaller in size or at a greater prey-predator distance) <i>(row 9 and row 18)</i>	greater smaller butterflies are even more camouflaged when transparent, as if seen from further away than in reality <i>(rows 36 and 37, rows 38 and 39)</i>
more complex backgrounds* <i>(row 10)</i>	greater on complex backgrounds, butterflies benefit from being transparent (simpler backgrounds are relatively not so detrimental to uniform colorations) <i>(rows 49 and 50)</i>
more edge disruption markings L*, a in the butterfly pattern <i>(rows 20 and 21)</i>	greater background pattern (visible through transparent butterflies) adds edge disruption markings hindering the detection of transparent butterflies <i>(rows 51, 52, 53, and 54)</i>
more edge disruption markings b in the butterfly pattern <i>(row 22)</i>	lower hinders more the detection of uniformly-opaque butterflies on the b chromatic component <i>(rows 55 and 56)</i>
greater colour similarity of the butterfly to its background <i>(row 7)</i>	lower the advantage of similarity exists more for opaque than for semi-opaque butterflies, does not exist for transparent butterflies <i>(rows 26 and 27)</i>
butterfly further away from attention point <i>(row 15)</i>	lower butterflies close to attention point benefit from being transparent; whatever the distance, transparent butterflies are always difficult to spot <i>(rows 30 and 31)</i>
backgrounds with higher local overall contrast* <i>(row 19)</i>	lower high overall contrast is detrimental for uniformly- opaque butterflies; transparent butterflies are always difficult to spot <i>(rows 42 and 43)</i>

In italics the rows it refers to from Table 1. In Table 1, if the sign of the effect changes in Found and/or Time from the simple effect to the interaction, it means transparency amplifies the effect; otherwise it attenuates it. *Effect on time only.

Figure 1:

Predictions on the level of protection – probability to be found (A) and time to be found (B) – of semi-opaque prey relative to that of opaque prey (minimal protection) and fully transparent prey (maximal protection), following Johnsen & Widder's theoretical prediction (Johnsen & Widder 1998). The protection of semi-opaque prey is expected to be more similar to that of opaque prey in bright light than it would be in dim light.

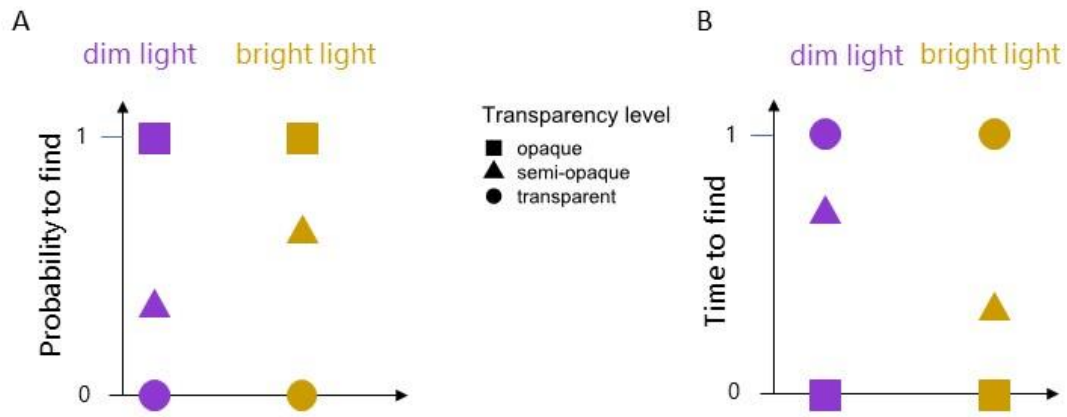


Figure 2:

Predicted probability to find a butterfly (A) and the predicted time to find it (B) in relation to transparency levels, opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle).

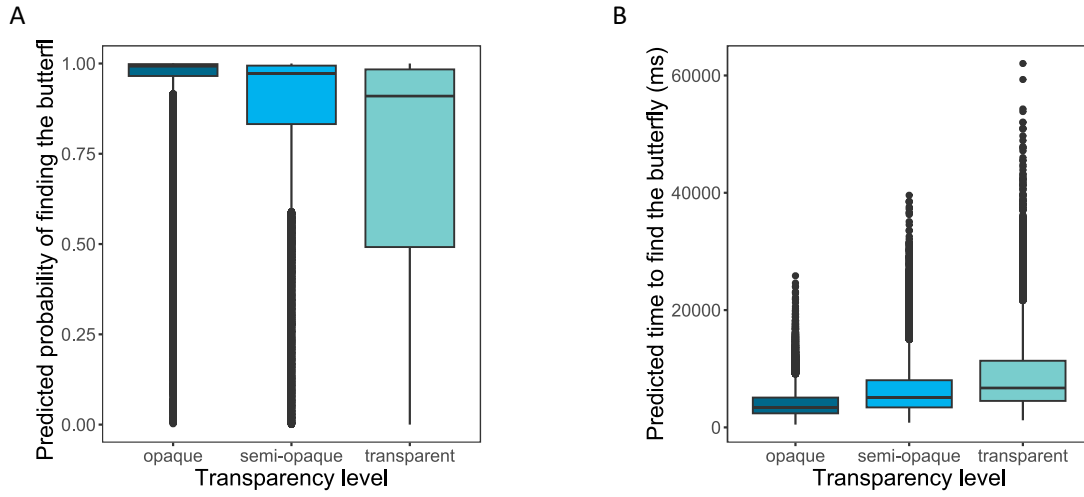


Figure 3:

Predicted probability to find a butterfly (A,C,E) and the predicted time to find it (B,D,F) in relation to butterfly chromatic complexity GabRat_a (A,B), GabRat_b (C,D) and achromatic complexity GabRat_L (E,F), for the three transparency levels, opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle). Predicted values around the quartiles along with standard errors are plotted, and may be not evenly distributed depending on the variable distribution.

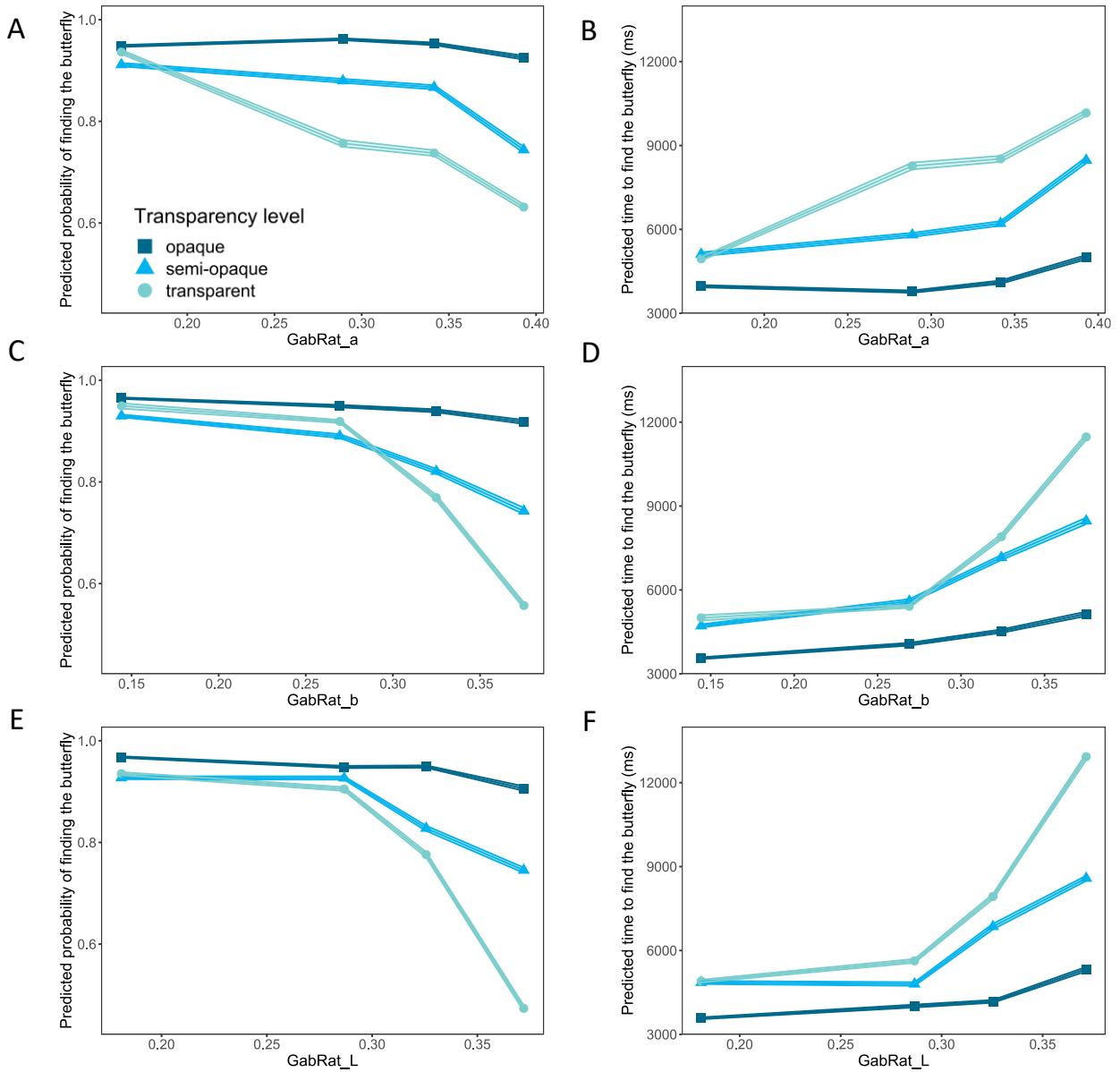
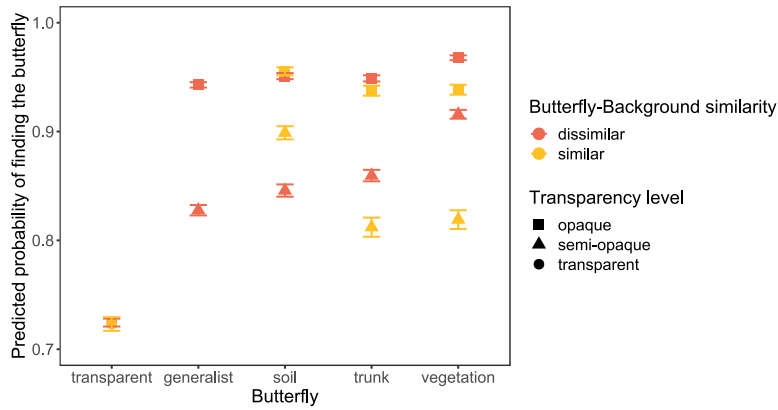


Figure 4:

Predicted probability to find a butterfly (A) and the predicted time to find it (B) in relation to butterfly similarity to its background (similar yellow, dissimilar red), for different transparency levels : opaque (square), semi-opaque (triangle), and transparent (circle). Transparent butterflies were randomly assigned to being of a background type (soil, trunk, vegetation) and thus randomly assigned to being similar or dissimilar. Generalist butterflies were always dissimilar to the background.

A



B

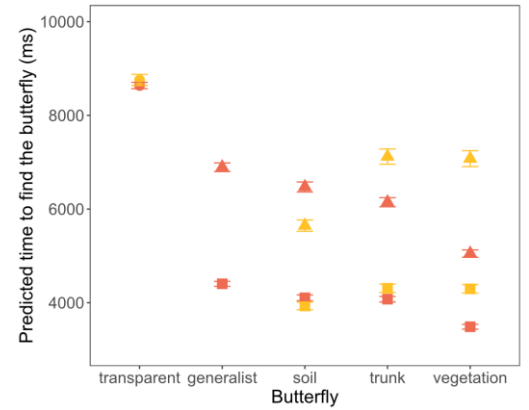
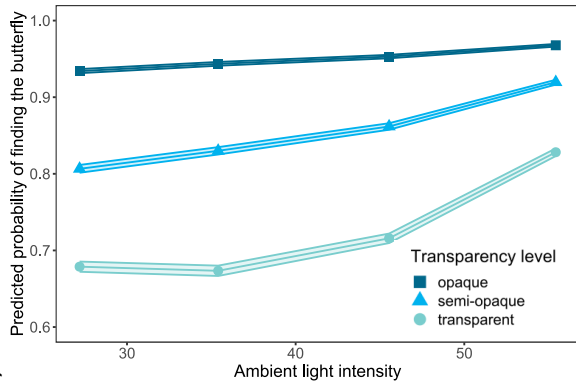


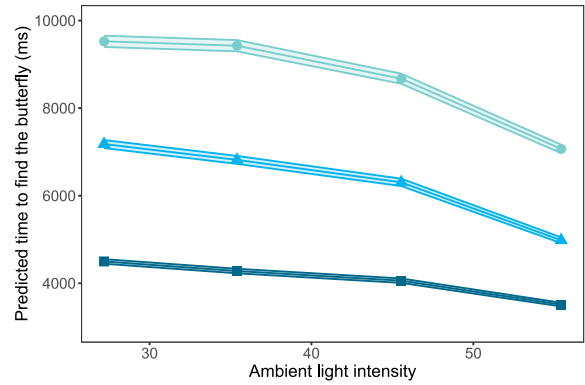
Figure 5:

Predicted probability to find a butterfly (A) and the predicted time to find it (B) in relation to ambient light intensity levels. Scaling the values of opaque and transparent levels to minimal and maximal protection respectively, the protection of semi-opaque butterflies is plotted relatively to the others, for the probability to find a butterfly (C) and the time to find it (D). Transparency levels are opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle). Predicted values around the quartiles along with standard errors are plotted, and may be not evenly distributed depending on the variable distribution.

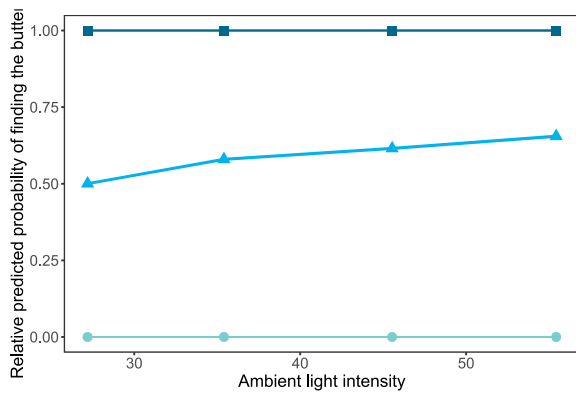
A



B



C



D

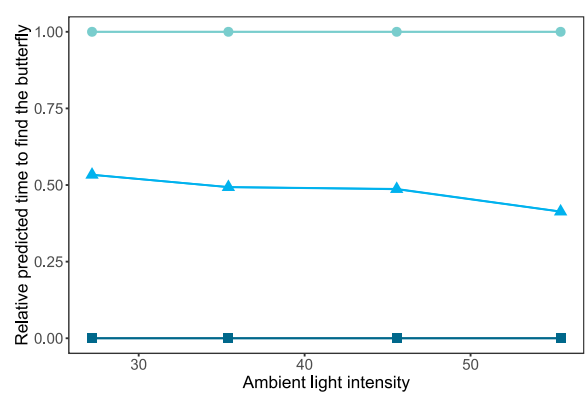


Figure 6:

Predicted probability to find a butterfly (A) and the predicted time to find it (B) in relation to butterfly size within an image. Scaling the values of opaque and transparent levels to minimal and maximal protection respectively, the protection of semi-opaque butterflies is plotted relatively to the others, for the probability to find a butterfly (C) and the time to find it (D). Transparency levels are opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle). Predicted values around the quartiles along with standard errors are plotted, and may be not evenly distributed depending on the variable distribution.

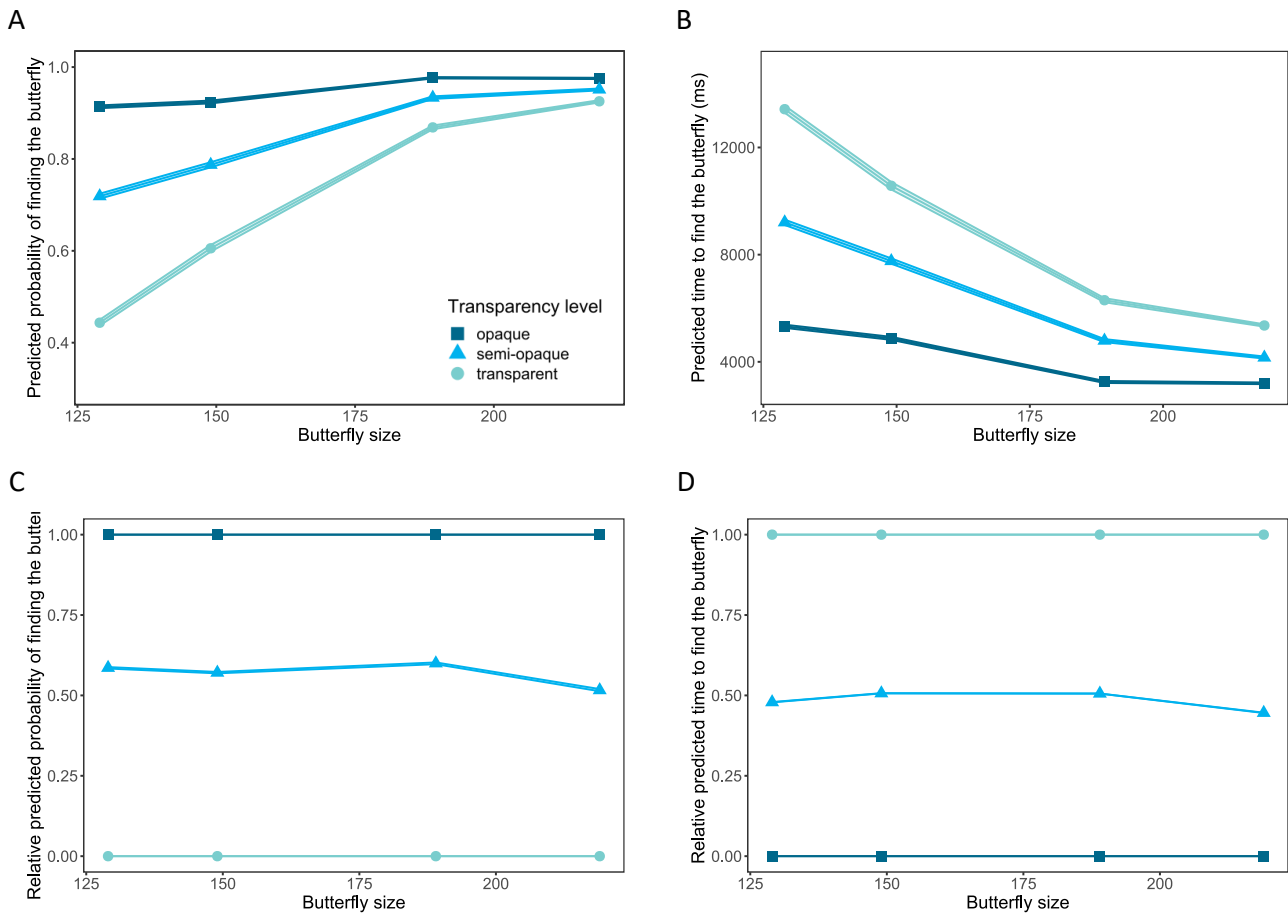


Figure 7:

Evolution of the predicted probability to find a butterfly (A) and the predicted time to find it (B) with image number (from 1 to 72) throughout a game. Transparency levels are opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle). Mean values are plotted along with standard errors. Notice that in analyses, we took $\log(\text{image number})$ as the variable in the models, which explains the asymptotic relationship in the plots below.

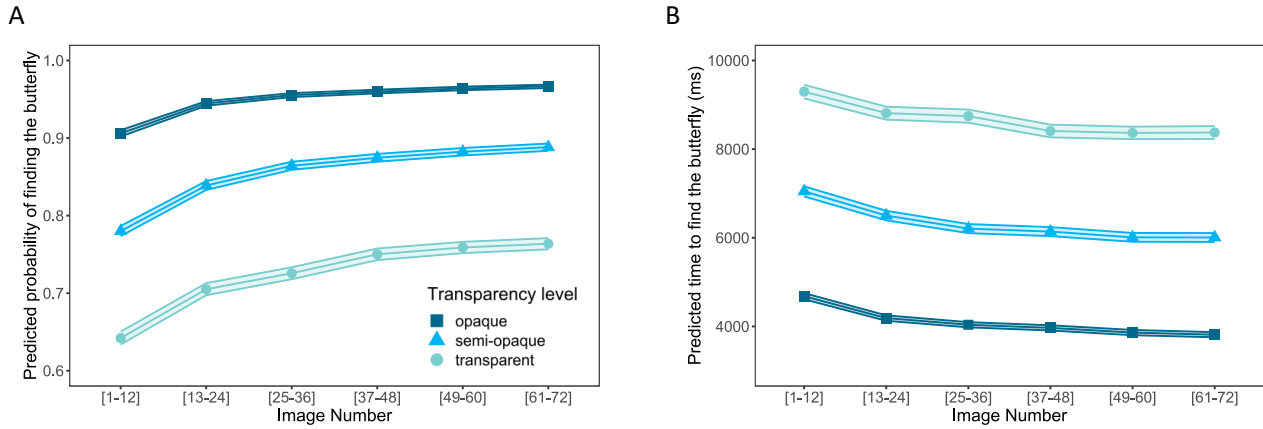
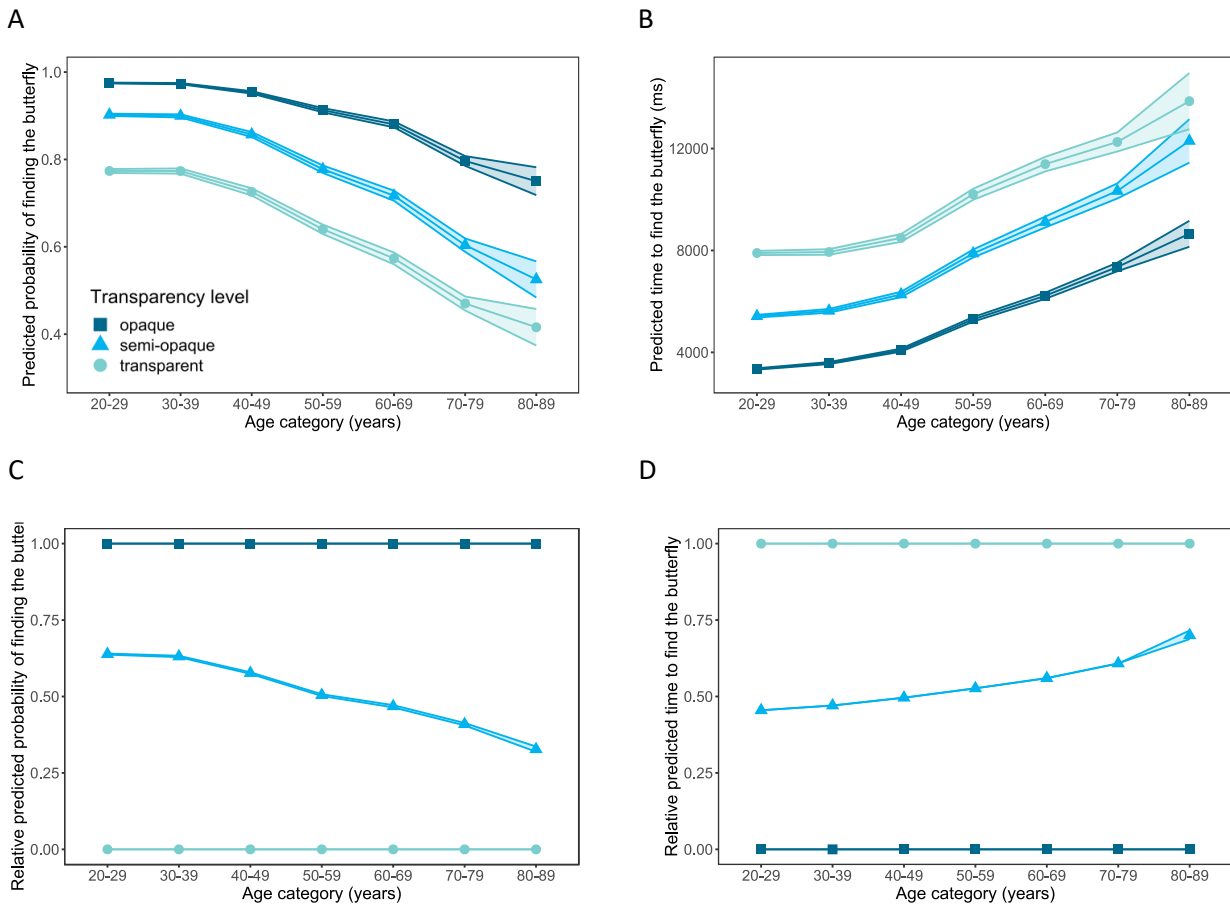


Figure 8:

Predicted probability to find a butterfly (A) and the predicted time to find it (B) in relation to age categories for adult players. Scaling the values of opaque and transparent levels to minimal and maximal protection respectively, the protection of semi-opaque butterflies is plotted relatively to the others, for the probability to find a butterfly (C) and the time to find it (D). Transparency levels are opaque (dark blue, square), semi-opaque (mid blue, triangle), and transparent (light blue, circle). Mean values are plotted along with standard errors (larger for the last age category less represented in the dataset).



Electronic Supplementary Material

Supplementary methods

Image elaboration process

The image elaboration process works in three main steps. First, the background image is used to estimate an environment lighting required to integrate the butterfly image. Second, we use the same input image of a butterfly (*Pseudoscada erruca*) to create several masks required to compose the butterfly on top of the background. Last, we integrate the image of the butterfly in the background with plausible lighting and shadowing. This process is not fully automatic, and we explicitly indicate the manual adjustments that we have made at each step. However, we emphasize that all manual adjustments are kept unchanged between butterfly morphs, which allows for their comparison.

We photographed 8 background images for each of the type of environment (vegetation, soil and trunks, see Figure S1). Each background is photographed at 5 different levels of exposure. These 5 photographs are used to reconstruct a High-Dynamic Range (HDR) image using the LuminanceHDR software (v2.6, using Profile 1 for automatic reconstruction). The resulting HDR image called B (for “Background”) is stored in the EXR format, which allows for variations of intensity levels (see Figure S2). The first step of the image elaboration process is to extract an environment lighting from B . To this end, we follow the approach introduced by Khan et al. (2006), whereby B is projected orthogonally on both the front and back side of a sphere inscribed in the image (see Figures S3A-B). The resulting spherical image is blurred angularly to reproduce the appearance of a perfectly diffuse sphere reflecting the estimated environment, called an irradiance environment map (Figure S3B). This is efficiently done through a projection on Spherical Harmonic bases restricted to order 2, as described in the seminal work of Ramamoorthi et al. (2001). The resulting image L_b corresponds to a sphere that looks as if it were visually integrated in the background environment (see Figure S3C). We perform two manual adjustments per irradiance environment map: we optionally reduce color saturation, and we add a diffuse white light reflection to mimic reflection from the sun, which is given by:

$$L_s(\mathbf{n}) = I_s \left(\frac{\mathbf{n} \cdot \mathbf{l} + 1}{2} \right)^{\gamma_s},$$

where I_s in $[0,1]$ controls the reflection intensity, γ_s controls its spread, and the reflection is maximal when the unit normal \mathbf{n} (i.e., a point on the sphere) is aligned with \mathbf{l} , a manually chosen light source direction (i.e., a unit vector). Figures S3D-E show examples of reconstructed diffuse lighting images with different choices for γ_s in L_s . The irradiance environment map is then simply given by:

$L(\mathbf{n}) = L_b(\mathbf{n}) + L_s(\mathbf{n})$. The next step consists in creating the images M_i of the butterfly morphs for four butterfly colors ($i \in \{1,2,3,4\}$ for generalist, soil, trunk, and vegetation morphs respectively), their opacity masks \bar{W}_k for three butterfly transparency levels ($k \in \{O, SO, T\}$ for opaque, semi-opaque and transparent respectively), and their shadow masks S_k . They are all necessary for a plausible integration into the background image. We take as input the image of a *Pseudoscada erruca* butterfly, which is white-balanced to yield a reflectance image R (see Figure S4, bottom left). We then manually identify an initial opacity mask W in Gimp, corresponding to the thin-black contours of the butterfly (see Figure S4, bottom middle). For each butterfly morph color i , we modify the reflectance image R to manually color its wings to yield R_i , using $1-W$ (the complement of the opacity mask) to identify wing pixels. The opacity mask is also manually modified to yield \bar{W}_k for each of the three opacity levels (100%, 45% and 15% opacity). In addition, we estimate a normal map image N from R (using <https://cpetry.github.io/NormalMap-Online/>), which encodes variations of surface orientation by

storing a unit normal vector at each pixel via an RGB encoding (see Figure S4, bottom right). Since the background photographs may be slightly blurry, we need to blur the image of the butterfly morph and of its transparency mask. To this end, we use a Gaussian filter g_I that blurs an image according to a standard deviation σ_I , which we manually choose to approximate the level of blur found in background photographs (it is equal to 4 pixels for most backgrounds). The butterfly morph images and opacity masks are then given by:

$$M_i(\mathbf{p}) = g_I(R_i(\mathbf{p}) \cdot L(\mathbf{n})),$$

$$\bar{W}_k(\mathbf{p}) = g_I(W_k(\mathbf{p})),$$

where \mathbf{p} is a 2D vector of pixel coordinates, and $\mathbf{n} = N(\mathbf{p})$ is the normal (i.e., a 3D unit vector) at pixel \mathbf{p} . Hence the M_i store the blurred lit butterfly images, and \bar{W}_k the blurred opacity masks. In Figure S4, we show all combinations of butterfly images and opacity masks, composited onto a striped background.

We also use a shadow mask, obtained by applying a very large Gaussian filter g_S of standard deviation $\sigma_S = 400$ pixels to the opacity masks \bar{W}_k followed by a gamma non-linearity to avoid the darkest tones:

$$S_k(\mathbf{p}) = g_S(W_k(\mathbf{p}))^{0.8}.$$

All three images are manually positioned at the desired location in the background image, and scaled down to match the size of the post-it placed in the photograph as a reference. The shadow mask is then slightly offset in a direction opposite to the estimated sun direction \mathbf{l} projected in the image plane.

In the last step, we first compute the HDR color image C_{ik} of a butterfly of a given color i and transparency level k . Note that for fully transparent morphs, the color i has no visual impact on the result. C_{ik} is created by compositing the butterfly morph image M_i over the background image B pre-multiplied by the butterfly shadow mask S_k , using the opacity mask \bar{W}_k as a mixing weight:

$$C_{ik}(\mathbf{p}) = \bar{W}_k(\mathbf{p}) \cdot M_i(\mathbf{p}) + (1 - \bar{W}_k(\mathbf{p})) \cdot B(\mathbf{p}) \cdot S_k(\mathbf{p})$$

The final color image \bar{C}_{ik} is obtained by applying a tone mapping operator that brings pixel color coefficients to the [0,1] range for display on a conventional monitor:

$$\bar{C}_{ik}(\mathbf{p}) = \varepsilon \cdot C_{ik}(\mathbf{p})^{1/2.2}$$

where ε is an exposure parameter, and $1/2.2$ is a conventional gamma correction for RGB display. The three brightness conditions used in the experiment are obtained by setting ε to 1, $1/\sqrt{2}$ and $1/2$.

Figure S5 shows the visual impact of each stage of the image elaboration process. When the butterfly image is composited on the background by merely using its reflectance and transparency (Figure S5A, S5D), it does not look naturally integrated in the background. Using the estimated irradiance map for relighting the butterfly image (Figure S5B, S5E) significantly improves integration; yet, the butterfly appears as disconnected from the background. Adding the cast shadow component (Figure S5C, S5F) anchors the butterfly image to elements of the background, making it look as part of the environment.

Supplementary references

Khan, E.A., Reinhard, E., Fleming, R.W., Bühlhoff, H.H., 2006. Image-based material editing. *ACM Trans. Graph.* 25, 654–663. <https://doi.org/10.1145/1141911.1141937>

Ramamoorthi, R., Hanrahan, P., 2001. An efficient representation for irradiance environment maps, in: *Proceedings of the 28th Annual Conference on Computer Graphics and Interactive Techniques. Presented at the SIGGRAPH01: The 28th International Conference on Computer Graphics and Interactive Techniques*, ACM, pp. 497–500. <https://doi.org/10.1145/383259.383317>

Figure S1 :

Background images used in the computer-based experiment, for vegetation (upper row), soil (middle row) and trunk (bottom row). All players saw all of these images with a hidden butterfly three times during the experiment, each with a butterfly hidden in a different position.



Figure S2:

Examples of backgrounds used to control for ambient light intensity levels. For each background image of the three types vegetation (upper row), soil (middle row) and trunk (bottom row), we took five photographs at different expositions to build HDR images. This then allowed us to recreate three levels of exposure in post-process: low (left), intermediate (middle), and high (right) exposure. The intermediate level was the high level divided and square root of 2, and the low level was the high level divided by 2. We then computed the continuous variable called 'ambient light intensity' as the mean brightness over the entire image.

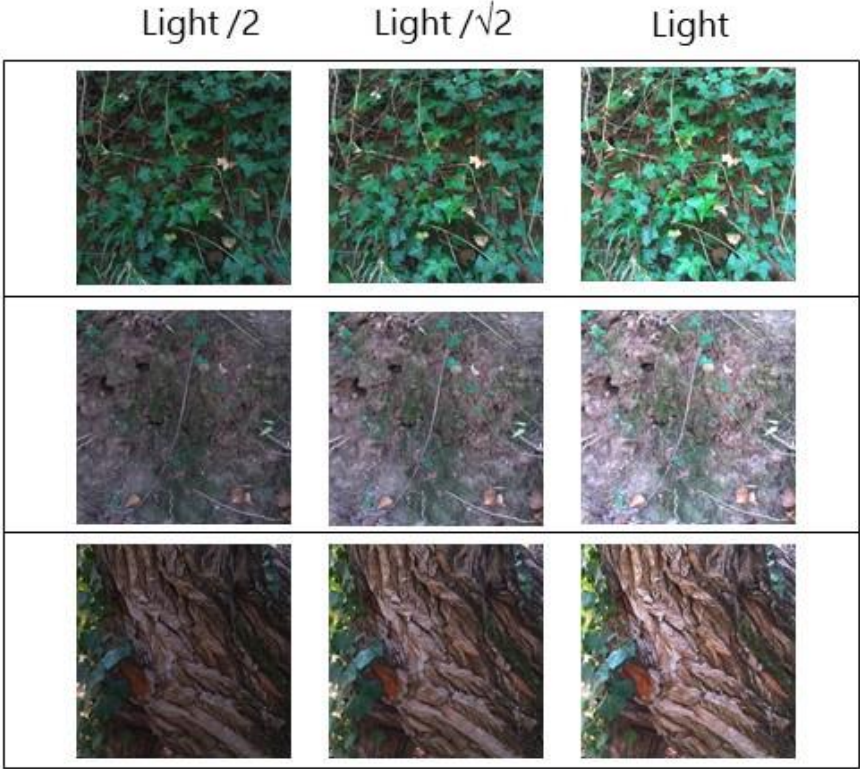


Figure S3:

Construction of an irradiance environment map L from an input HDR background image B . (A) A circular region is cut from the background image. (B) It is mapped on a sphere (top) then blurred angularly (Ramamoorthi and Hanrahan, 2001) to yield an irradiance environment map (bottom). (C) Placing the image of the sphere on the original background B makes it look as if it were integrated into it. (D) A diffuse white light reflection is added manually with a small spread ($\gamma_s = 20$). (E) The spread is manually adjusted ($\gamma_s = 6$) to yield a better integration.



Figure S4:

Illustration of the different morphs (one butterfly color per row, one opacity per column) placed on top of a synthetic stripped background. We use a single transparent morph (T) as shown in the last column, since the butterfly color (here we use the generalist color) has little impact with such a low opacity. The opacity percentages indicate the average opacity over wing regions; we avoid a zero opacity for the transparent morph as we found such an extreme transparency makes wings look holed. At the bottom, we show the input reflectance image R , opacity mask W , and normal map N .

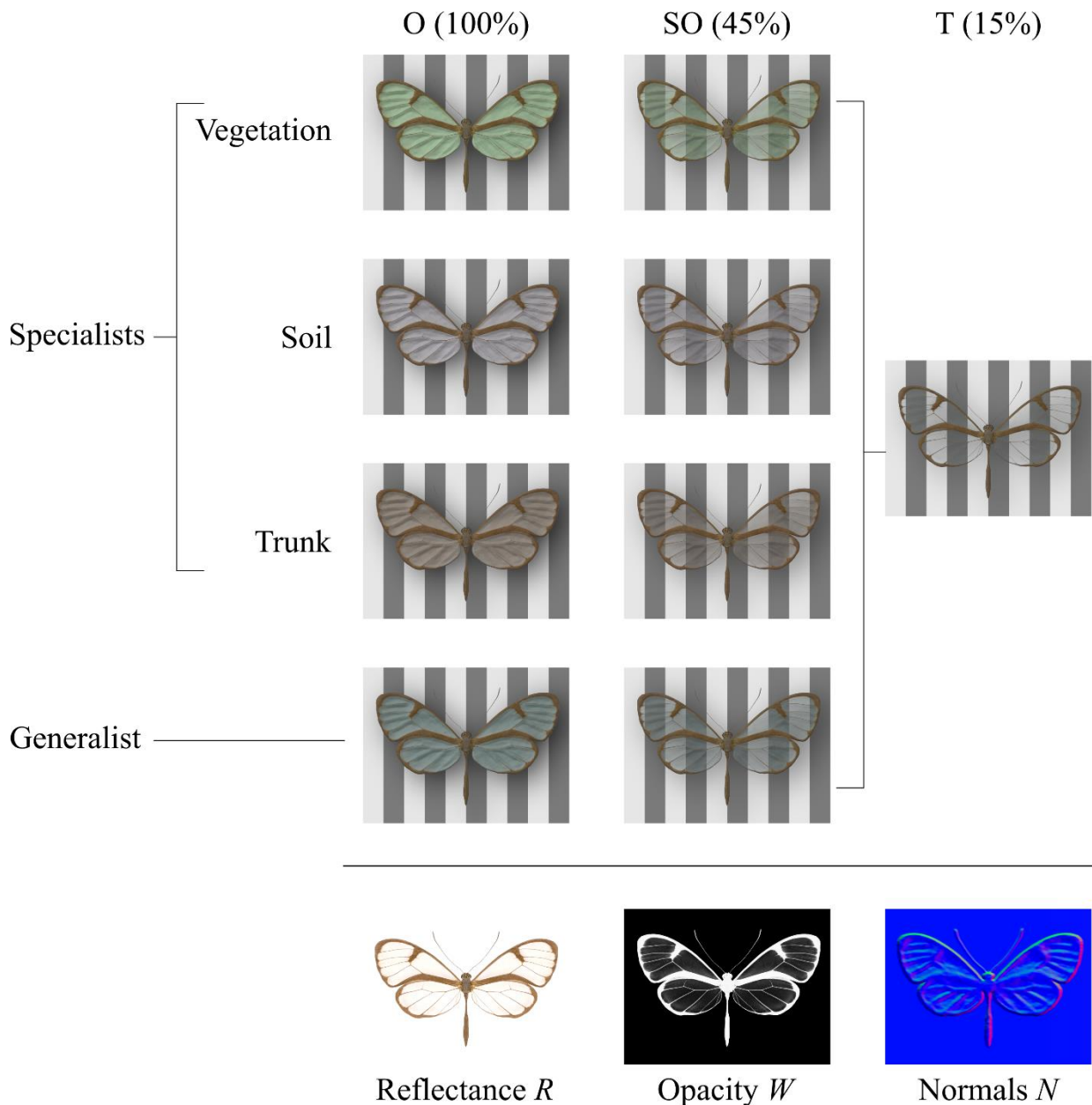


Figure S5:

Compositing of the butterfly image on a background (top row: full image; bottom row: zoom on butterfly). (A,D) The butterfly is composited without shading nor shadow, using only reflectance and transmittance masks. It seems disconnected from the background as it is not lit properly and does not cast any shadow on leaves. (B,E) Using the estimated irradiance environment map to relight the butterfly yields a better image integration in terms of colors; yet the butterfly still appears to float in front of the leaves. (C,F) Adding a soft cast shadow subtly anchors the butterfly image to the background.

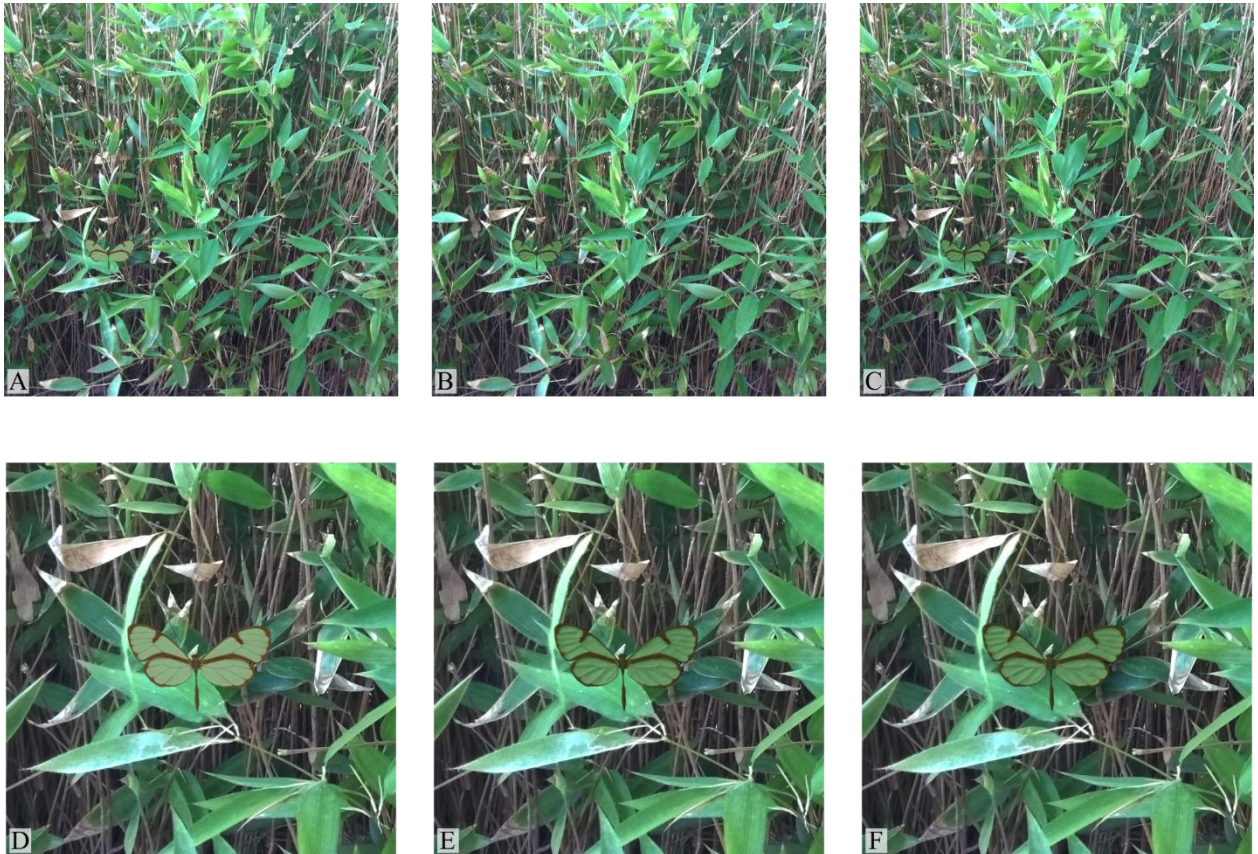


Figure S6:

L*a*b* coordinates of the average value of all pixels of the background images used in the game, in relation to the environment type and the ambient light level. While soil images show little chromatic variation, variation lies on a* (from green to red) for trunk backgrounds and on b* (from blue to yellow) for vegetation backgrounds.

