



Original Article

Positioning behavior according to individual color variation improves camouflage in novel habitats

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Behavior can play a key role in adaptation, especially in novel environments. Here, we study how ground-perching grasshoppers that colonized street pavements as novel habitats behaviorally manage their detection rates by predators. We found that grasshoppers positioned themselves aligned with the spaces between adjacent bricks more than expected by chance. By performing a virtual predation experiment, we confirmed that this positioning behavior decreases the predation rate. Surprisingly, individuals with a poorer cryptic coloration made greater use of this positioning behavior, whereas individuals with a better cryptic coloration relied more on background color matching. Additionally, positioning behavior interacted with other anti-predation behaviors, individuals that were positioned on the space between bricks allowed potential predators to get closer before fleeing. These results indicate that these grasshoppers showed adaptive flexibility in camouflage and escape behaviors as a function of both individual and environmental variation. Such behavioral flexibility should allow organisms to cope better with novel environments, which deserves more study especially in the current context of global change.

Key words: behavior, background matching, behavioral flexibility, camouflage, novel environment, urban adaptation.

INTRODUCTION

How organisms adapt to novel environments has become a key question due the increasing rate of rapid human-induced changes to natural habitats (Sih et al. 2011). Urbanization is one of such changes, causing major habitat transformation. Even though urban expansion into natural areas generally has a negative effect on biodiversity, for some species it promotes new opportunities to exploit new ecological niches (Diamond 1986). However, it is still unclear why and how these species are able to adapt to urban settings (Carrete et al. 2011). Behavioral changes can allow organisms to benefit from the new opportunities arising (Sol et al. 2011), including the decision to move to novel habitats when these provide a better match between phenotype and environment (Edelaar et al. 2008; Duckworth 2009; Carrete and Tella 2010; Karpestam et al. 2011). Thus, behavior may play an important role in how organisms cope with novel conditions, often being an essential component of the rapid responses necessary to deal with environmental changes or novel habitats (Holway and Suarez 1999).

Adaptation to a certain habitat through camouflage is a common strategy in nature. The prevention of detection, called crypsis, is probably the most studied camouflage strategy with numerous examples across taxa and ecosystems. There are numerous strategies to achieve crypsis like background matching (matching the color, lightness, and/or pattern of a background), disruptive coloration (creating the appearance of false edges), countershading (showing dark colors on body parts exposed to light and light colors on parts usually shaded), and several others (Stevens and Merilaita 2009). There are also forms of camouflage that are different from crypsis, such as masquerade (ensuring that organisms are misidentified once they have been detected; Skelhorn et al. 2010) or motion dazzle (markings that hinder the estimation of speed and trajectories; Stevens and Merilaita 2009; Hogan et al. 2016). Animal behavior can interact with all these strategies and forms of camouflage and could, therefore, be very important in their optimization. There are several studies that have investigated the relationship between camouflage and behavior for crypsis (De Ruiter 1956; Edmunds and Grayson 1991; Wilkens 1993; Webster et al. 2009; Kang et al. 2012; Lovell et al. 2013; Wilson-Aggarwal et al. 2016) or other forms of camouflage like masquerade (Skelhorn et al. 2011; Skelhorn and Ruxton 2013). Nonetheless, in general, we are just starting to appreciate how important animal behavior is in

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enhancing camouflage strategy; so, more research effort is needed in this area (Hensley et al. 2015; Wilson-Aggarwal et al. 2016), especially in the context of rapid environmental change.

In this study, we focus on a natural colonization of a recently urbanized area by ground-perching grasshoppers, and on the individual responses to this novel habitat in the context of behavior–camouflage interactions. These grasshoppers appear to enhance camouflage through background color matching as well as by a positioning behavior involving perching site choice and body orientation. There is, however, a trade-off between background matching and this positioning behavior after movement (e.g., a short escape flight): background matching requires immobility to avoid detection by movement, whereas behavioral positioning requires some adjusting local movement. We might, therefore, expect that individuals make different choices depending on their variation in color. Specifically, we test: 1) if a positioning behavior strategy improves survival, 2) if grasshoppers use the positioning behavior strategy more than that would be expected at random, 3) if a greater level of camouflage provided by background matching (in color and luminosity) reduces the use of a positioning behavior, and 4) how the camouflage strategy used affects the escape behavior of individuals.

METHODS

Study system

We studied the adaptation of the Azure Sand Grasshopper (*Sphingonotus azurescens*). This is a ground-perching grasshopper that normally lives on natural open soils and does not climb into plants. We recently found it colonizing novel urban-like habitats at Dos Hermanas (province of Seville, Spain; 37.306° N, 5.932° E). These novel habitats are pavements (streets) in an abandoned housing area that is closed off to traffic. The streets are composed of 4 different types of pavement: dark asphalt, paths made of brown bricks, paths of grey bricks, and sidewalks of pale tiles. The streets surround large blocks of little-vegetated natural soils, where grasshoppers are common. Because of the low level of use and maintenance of the pavements, some colonizing food plants are growing in-between the bricks and tiles, allowing grasshoppers in turn to colonize these streets as alternatives to natural soils. The fact that these pavements are acceptable habitats is confirmed by

the presence of many individuals, adult males that are displaying, recaptures of marked individuals, observations of copulations and egg deposition, and the presence of nymphs in spring.

Individual grasshoppers vary in a continuous manner in body coloration from very pale to almost black, and from bluish-gray to orange-brown. Their coloration normally resembles that of the local substrate on which they occur. This color match thus provides camouflage via the background color matching strategy. However, initial observations suggested that on the urban pavements grasshoppers sometimes align their body with the lines that arise where 2 tiles or bricks meet (Figure 1).

Data collection

To test for the differential use of positioning behavior by grasshoppers in urban habitats, we searched for individuals perched on gray bricks (Figure 1). Each individual ($n = 35$) was disturbed 10 times such that it jumped up and flew a few meters away to another spot. We noted their position after each escape (aligned/not aligned with lines, i.e., use of positioning behavior or not), 10 s after each landing, to allow individuals to move a bit in order to better align their body with the lines, if they wanted to. At the end, we caught the grasshoppers using a net to determine sex, take a photograph (see below for details on color measurement), and measure the length of the individual.

In addition, we systematically surveyed all 4 pavements types in the study area for grasshoppers. Any grasshopper detected was captured and was individually marked with a combination of 3 letters on the posterior part of both fore wings (which already have some irregular dark markings), using a black permanent marker pen (Staedtler permanent Lumocolor, resistant to water and UV light). All individuals were photographed and then released at the location of first encounter. For each individual, we recorded sex, day of capture, type of substrate on which it was found, the initial perching position (on a line or not), the flight initiation distance, and the distance flown. The flight initiation distance (FID) is the distance at which an organism begins to flee an approaching threat; it is an important component of the antipredatory behavior and thought to be an indicator of an animal's perception of threat (Blumstein et al. 2003; Gotanda et al. 2009; Carrete and Tella 2010). The entire study area was searched regularly for marked and new, unmarked adult grasshoppers from June to October of 2016, covering the entire period when adults are common.

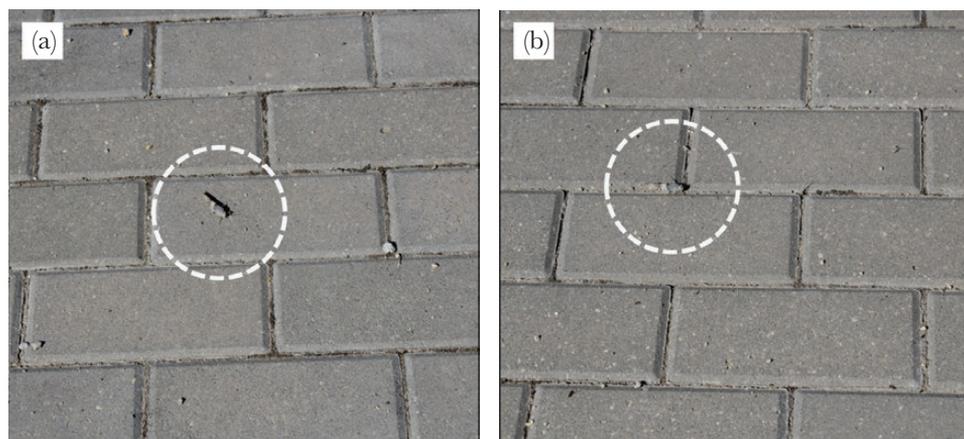


Figure 1

Camouflage strategies used by grasshoppers in urban habitats (white circles show the position of individuals). (A) Background color matching. (B) Positioning behavior by the alignment of the body with the line between 2 bricks.

Virtual predation experiment

We tested the survival rate of grasshoppers according to their camouflage strategy. We performed a predation experiment using humans as predators. Humans adopt a similar search pattern to birds (one of the more commonly observed potential predators of the Azure Sand Grasshopper at our study site) when looking for prey on a computer screen (Ruxton et al. 2005), have comparable information processing capabilities (Dukas and Ellner 1993; Dukas and Kamil 2001; Dukas 2002; Xiao and Cuthill 2016), and the results obtained using humans are comparable to those of analogous studies using birds (Cooper 1984; Beatty et al. 2005; Fraser et al. 2007; Knill and Allen 2010; Karpstam et al. 2013; Stevens et al. 2013; Xiao and Cuthill 2016). For this virtual predation experiment, we used photos of 16 different backgrounds in our study area (10 of pavements and 6 of natural open soils), taken at a distance of 1.5 m perpendicular to the ground. We also used photos of 40 grasshoppers (26 males and 14 females), in which we removed the background of the photo (see “Image taking and processing” for details on image capture and color measurement). We developed a computer program written in JavaScript in which the 16 different backgrounds appear on screen in a random order. On each of these background images, we placed the images of 2 to 4 random grasshoppers (out of the set of 40) that appeared in a random location with a random orientation. On the same background, we also placed another 2 to 4 random grasshoppers, but these appeared randomly within a finite set of previously fixed locations and orientations such that they aligned with the elements of the background (sticks for natural soils and lines between bricks for pavements). We presented these different combinations on a touch screen with a resolution of 1920 × 1080 pixels as a computer game to 261 human participants. Participants were instructed to find and touch (“capture”) as many grasshoppers as possible in a total of 160 s for the 16 different screens. An example screen was provided before the start for instruction and training, and people could move to the next screen when they wanted (i.e., when no more grasshoppers were seen by them). The program recorded the following data: the identity (self-created nickname), age and gender of the human participant, the identity of the background used, the number, identity and sex of grasshoppers placed, the position of each grasshopper (aligned or not), and if the grasshopper was captured or not.

Image taking and processing

To quantify background color matching in the field, grasshoppers and backgrounds were photographed in situ with a Canon 1200D camera mounting a 18–55 mm Canon lens (locked at 55mm) using fixed camera settings of $f/12$ aperture, 1/50 shutter speed, ISO 200. Pictures were taken in RAW format and included an 18% reflectance gray standard. Following Troscianko and Stevens (2015), we linearized the images and converted these from camera color space to the relative photon catches of the relevant predator. The grasshoppers might be predated on by a wide range of visual predators (mammals, birds, lizards, insects, and spiders) with very different visual systems, but we used the spectral sensitivity of the blue tit, *Cyanistes caeruleus* (cone ratios from Hart (2001)), because birds appear to be the most abundant visual predators in the area (all authors personal observation). As grasshoppers and backgrounds do not reflect ultraviolet radiation (as checked by spectrophotometry), we did not include the UV cone types into the analysis, performing a trichromatic color analysis (Stevens et al. 2007). For the virtual predation experiment involving human predators, we

instead used the spectral sensitivity of humans (Hofer et al. 2005). The color measures in grasshoppers were made on a pre-defined diamond-shaped area in the dorsal part of the metazone of the pronotum, which is representative for the overall body color. Next, we quantified color contrasts between photon catches of grasshoppers and photon catches of backgrounds according to a log-linear form of the color discrimination model, which assumes that visual discrimination is limited by receptor noise (Vorobyev and Osorio 1998), and using a Weber fraction value of 0.05 for the most frequent cone type. We also quantified luminance contrasts using a version of the model based on achromatic differences (based on blue tit double cones and human luminance, i.e., perceived lightness, respectively). These color and luminance contrasts were expressed in “just-noticeable-differences” (JND) whereby values between 1.0 and 3.0 indicate difficult discrimination, whereas values increasing above 3.0 indicate increasingly improved discrimination (Siddiqi et al. 2004).

Statistical methods

Analyses were performed in R version 3.2.3 (R Core Team 2015). As a partial test of whether grasshoppers use positioning behavior as a camouflage enhancement technique on urban pavements, we tested if they perched on the lines between 2 bricks more often than expected by random placement. To obtain this random expectation, we first determined the available proportion of a brick that could be considered as part of the line between 2 bricks to be 16.4% (i.e., the surface area close to the edges of a brick). As the pavement has a regular pattern, this value is the same for all bricks. We then used a binomial process to determine the percentage of times that an individual would be perched on a line if it was positioned randomly 10 times (the number of data per individual in the field), repeated this for 35 hypothetical individuals (our sample size in the field), and calculated the average (population) percentage of line use. Finally, we repeated this procedure 100 000 times to obtain a distribution of this percentage for the population. Then, we compared the observed average value of the use of lines in the field with the expected distribution for random space use.

Using this same data set of field observations, we tested if their color might influence the differential use of positioning behavior by grasshopper individuals (background color matching vs. positioning). We fitted a generalized linear model, modeling the use of positioning with background lines as the dependent variable (scored as yes or no, modeled using a binomial error structure; 10 observations for each individual, individual identity included as a random effect). Fixed effects were fitted for differences between grasshopper and the whole area background in color and luminosity (for the blue tit visual model, in JND units), grasshopper sex (male/female) and length, and day of observation (2 different days). We also tested if perching on lines could actually be explained as a micro site choice to achieve greater background matching in the color and luminosity components (because these components could be different between the central surface of the brick and the lines due to the presence of lichens, moss, dirt, etc.). For this, the same model structure was fitted, but using the differences in color and luminosity between the grasshopper and the lines between bricks instead of the surface of the gray brick, as measured from the images.

To test if there was an effect of grasshopper position on its escape behavior when a potential predator is approaching, we analyzed the escape data by fitting a Bayesian generalized linear bivariate mixed model using the *MCMCglmm* R-package (Hadfield 2010). This approach allowed us to fit a bivariate mixed model, which is

better than fitting 2 separate models for FID and distance flown since these variables were correlated ($r = 0.31$). We used the flight initiation distance (FID) and the distance flown as response variables ($n = 345$), using a Gaussian family error distribution. Fixed effects were fitted for the use of positioning behavior (aligned with lines: yes/no), type of habitat (four different types of pavement), sex (male/female), and color and luminosity differences between grasshopper and background (for the blue tit visual model, in JND units). We also included day (33 different days) and individual identity (211 individuals) as random effects. The joint posterior distribution for the model was estimated from 1 100 000 Markov Chain Monte Carlo iterations sampled at 1000 iteration intervals after an initial burn-in period of 100 000 iterations (leaving 1000 uncorrelated effective samples), using weakly informative parameter-expanded priors for the variance components; the degree of belief parameter (ν) was 2 for the random effects and 0.002 for the residuals. Convergence of models was verified by visually inspecting output plots following Hadfield (2015) and model convergence diagnostics (autocorrelation, Gelman and Rubin 1992).

The data from the virtual predation experiment was analyzed to test what determines the probability of survival of the grasshoppers. For this, we used generalized linear mixed-effects models specified in the lme4 R-package (Bates et al. 2015). We used the capture of the grasshopper individual (captured or not, $n = 14910$) as dependent variable. Fixed effects were fitted for sex of the grasshopper (male/female), gender of the observer (male/female), type of background (natural soil/ pavement—binary), alignment with items (aligned or not, i.e., a test for positioning behavior), density of grasshoppers on the screen, ranging from 2 to 8), and color and luminosity differences between grasshopper and background (for human visual model, in JND units; i.e., a test for background matching on their color and luminosity components). As random effects, we fitted the identity of the observer, the identity of the grasshopper, and the identity of the background photo as we had repeated data for each of these.

RESULTS

Grasshoppers clearly use the positioning behavior by perching more often on the line that arises where two grey bricks meet than expected by random chance (Figure 2). On average, grasshoppers were about twice as likely to perch on a line as expected. Moreover, there was a striking effect of the grasshopper-background color difference on this probability: individuals with a poorer cryptic coloration were more likely to perch on a line (Figure 3, Table 1). Use of the line for perching was independent of grasshopper sex or size, and it did not depend on the luminance difference (Table 1). The same effects were found when we used the line instead of the surface of the brick to calculate background-grasshopper color and luminance differences (Supplementary Table S1).

The virtual predation experiment confirmed that the positioning behavior (perching near a line) significantly increases survival by 39% (36.7% survival rate for aligned locations vs. only 26.4% for random locations across backgrounds). The mixed model yielded significant effects for alignment with items (Estimate (aligned yes) = -0.421 ± 0.097 SE, $P < 0.0001$) and JND difference in color (Estimate = 0.120 ± 0.051 SE, $P = 0.019$) confirming that background matching (in color) and positioning behavior decrease predation (the effect for background matching in luminosity was very weak and nonsignificant: $P = 0.092$). We also found a mild but significant effect of the density of grasshoppers

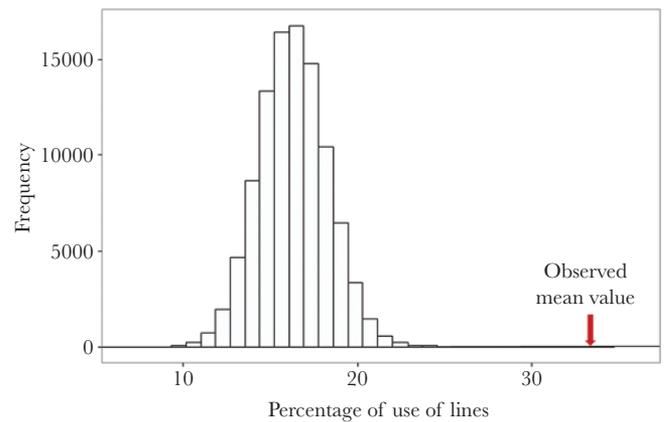


Figure 2

Grasshoppers perch on lines more often than expected. The distribution is the expected mean percentage of use of lines between 2 bricks if the usage of the pavement were random (based on 100 000 simulations of a random binomial distribution involving 10 trials for 35 individuals each, random probability of line use 16.4%). The observed mean value in the field (arrow, based on 10 observations for 35 individuals each) does not overlap with 95% of the distribution for random space use.

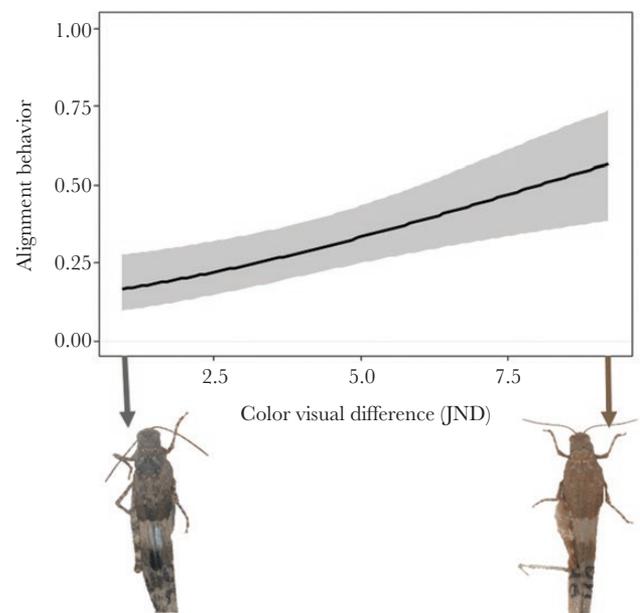


Figure 3

Cryptically colored grasshoppers mostly use background color matching, whereas less cryptically colored grasshoppers increasingly use the positioning behavior. Shown is the relationship between the color difference (between grasshoppers and gray brick urban pavement for the Blue tit visual model, in JND units) and the alignment with the lines between bricks for perching. The black line is the model prediction and the grey shadow is its 95% confidence level. Also shown are the images of the grasshoppers with the best (0.95 JND units) and the worst (9.21 JND units) background matching in color, with respect to gray bricks (shown in Figure 1).

decreasing the predation rate (Estimate = -0.061 ± 0.019 SE, $P = 0.002$). The rest of the fixed effects (sex of grasshopper and gender of observer, type of background) were not significant ($P > 0.05$) whereas all random effects (identities of observers, grasshoppers and backgrounds) were significant ($P < 0.0001$ for each one; Supplementary Table S2).

Table 1**Overview of effects on the probability to perch on a line and their statistical support (generalized linear model, binomial family)**

	Estimate	SE	z value	P value
(Intercept)	-0.929	3.076	-0.302	0.763
JND Background—grasshoppers color difference	0.204	0.068	3.000	0.003
JND Background—grasshoppers luminance difference	-0.046	0.055	-0.836	0.403
Sex (male)	-0.370	0.633	-0.585	0.559
Day (2nd day)	-0.190	0.239	-0.794	0.427
Size	-0.001	0.012	-0.074	0.941

The coefficient for the reference categories (not listed) is always zero. Significant effects ($P < 0.05$) are highlighted in bold.

When grasshoppers are already aligned with lines upon first approach by an observer, they have a shorter flight initiation distance (posterior mean = -0.58, Credible Interval = -1.03 to -0.15; Table 2, Supplementary Table S3). Females flew a greater distance than males; but for the other fixed effects, the posterior 95% credible intervals overlapped with 0. Both random effects (individual identity and day) had clear effects (Table 2, Supplementary Table S3).

DISCUSSION

We found in our virtual predation experiment that grasshoppers that exhibit a positioning behavior (perching close to objects such as sticks or lines between bricks) have an increased survival (Supplementary Table S2). In the urban study site, grasshoppers perch on lines between bricks more often than expected (Figure 2). They do so especially when their degree of background matching (in color) is worse (Figure 3 and Table 1), and this effect is not because the lines provide better background matching in color (Supplementary Table S1). Finally, when they are perched on a line, they allow a potential predator to approach more closely before fleeing (Table 2). All these results support that grasshoppers are actively using positioning behavior to increase camouflage and thereby reduce predation risk. In general, individuals who exhibit an alignment behavior benefit from an improvement in their camouflage. This may be due to several mechanisms. The first one could be background matching in pattern as, jointly, lines between bricks make up a regular pattern in the background; so, by aligning with this pattern, the individuals resemble a scene's overall pattern more than that if the grasshopper is perched out in the open, away from the lines. We also have to note that background complexity increases dramatically around the lines, which is known to interfere with detection and, therefore, improve camouflage (Xiao and Cuthill 2016). Other effects also could explain this camouflage improvement, like self-shadow concealment (Thayer 1896; Cott 1940; Kiltie 1988) or the concealing of 3D surface disruption, since the area between 2 bricks is a bit lower than the surface of the bricks (Stevens and Merilaita 2009). Masquerade could also be an explanation for this improvement of camouflage, with aligned grasshoppers masquerading as a line between bricks and being initially detected but subsequently misclassified by predators. Confirming masquerading requires a focus on the responses of predators, by manipulating their experience with putative models and prey (Skelhorn et al. 2010).

Irrespective of how exactly camouflage is increased, individual grasshoppers face a trade-off: positioning behavior requires small-scale movements to align with other objects (like brick lines), whereas crypsis benefits from immobility in order to prevent detection by movement. Figure 3 indicates that variation among

Table 2**Posterior distributions for fixed effects (mean and its 95% credible interval) and random effects (mean for the variance and its 95% credible interval) on flight initiation distance (FID) and distance flown**

FID	Posterior mean	95% credible interval
Fixed effects		
Aligned with lines (yes)	-0.580	-1.026 to -0.147
Random effects		
Individual	0.511	0.147 to 0.897
Day	0.026	3.845×10^{-08} to 0.096
Distance flown		
Fixed effects		
Sex (male)	-0.579	-1.095 to -0.058
Random effects		
Individual	0.988	0.344 to 1.733
Day	0.110	2.296×10^{-06} to 0.363

Effects with 95% Credible Intervals overlapping zero are not shown (but provided in Supplementary Table S3).

individuals in color and, therefore, in the relative benefit of background color matching results in a shifting balance between camouflage strategies: positioning behavior is used more frequently when background color matching is lower. Evaluation of to what extent these results may vary with predator characteristics like visual system, foraging behavior (we assumed aerial views by an avian predator) or viewing distance (Skelhorn and Ruxton 2014) would need further testing.

Camouflage by crypsis implies a match between phenotype and environment, but environments can exhibit a great variation in color, brightness, or pattern in space and time. One of the solutions to environmental variation in general is the evolution of genetic polymorphisms via divergent natural selection (Bond and Kamil 2006; for which we have some evidence in our system (Edelaar et al. 2017)), but in the absence of habitat choice this has a large demographic cost (selective mortality) and does not deal well with rapid changes or very heterogeneous habitats. Improving the organism's appearance through phenotypic plasticity is a more flexible strategy (well developed in our immature grasshoppers; Edelaar et al. 2017). However, the changes in the environment with which an organism has to match (because of environmental changes and/or individual movements across different environments) could be faster than the ability of individuals to change their appearance. Even though some organisms like cephalopods or chameleons have the ability to develop rapid color changes and patterns, in general slow color changers (which need from days to months to change, like our grasshoppers (Edelaar et al. 2017; Peralta-Rincon et al. 2017) are likely to be more widespread in nature (Stevens 2015). In these cases, only adaptive behavior that

tries to match the environment to the phenotype can provide a rapid response to environmental heterogeneity in time or space. In the absence of the ability of grasshoppers to change the local environment (e.g., its color) where they currently are, they can only increase this match by selecting and if necessary moving to environments that provide them with greater camouflage (a form of nonrandom dispersal (Edelaar et al. 2008; Karpestam et al. 2011; Edelaar and Bolnick 2012)). Here, we have demonstrated how indeed grasshoppers respond behaviorally to local environments depending on the match between their phenotype and the environment: if the color match is good, they stay on the gray bricks that enhances background matching in color; but if the color match is poorer, they move and adjust their body orientation with the lines between bricks, which also enhances camouflage. Such a flexible behavior and adaptive selection of their environment at a small scale in general increases performance, and here would still allow grasshoppers with a less-matching color to successfully colonize novel habitats.

The grasshoppers change their antipredatory behavior, in this case the flight initiation distance, in a flexible way depending on the camouflage strategy used. They also showed behavioral flexibility in the use of different camouflage strategies depending on their level of camouflage provided by background matching in color. This could imply a level of cognition by the individuals in a broad sense, perceiving the environment, learning, classifying, and making decisions (Shettleworth 2001; Shettleworth 2010; Rowe and Healy 2014; Skelhorn and Rowe 2016) that enable them to evaluate their degree of phenotypic matching to the environment (in this case camouflage). In this way, organisms can have a beneficial behavioral response to environmental changes, which provides a better adjustment to the environment very quickly, almost instantly. Due to the important ecological and evolutionary implications that these interactions between cognition, behavior, and camouflage could have in our study system and presumably in many other ecological systems, more research on this topic is necessary (Stevens 2015; Skelhorn and Rowe 2016). A few recent studies have explored this, like FID in ground nesting birds depending on the level of camouflage (Wilson-Aggarwal et al. 2016), moths that select a resting position to improve their camouflage (Kang et al. 2012; Kang et al. 2015), or cuttlefish that change between camouflage strategies (Buresch et al. 2011). Overall, such behavioral interactions can provide a rapid adaptive response and might be key in understanding how individuals can cope with natural or human-caused rapid changes in the environment, or how native and nonnative, invasive organisms can colonize new habitats.

CONCLUSION

We found that Azure sand grasshoppers, adapting to a novel urban environment, use the lines between bricks more than expected by chance. A virtual predation experiment suggests that such a positioning behavior results in a reduction in the predation rate. However, individuals use different camouflage strategy depending on their cryptic coloration, as less cryptic individuals made greater use of positioning behavior whereas more cryptic individuals relied more on background color matching. Additionally, individuals using positioning behavior showed shorter flight initiation distances. Together, our results support an adaptive flexibility in camouflage and escape behaviors as a function of individual and environmental

variation, allowing grasshoppers to cope better with traditional as well as novel environments.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Baños-Villalba et al. (2017).

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