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The escape artist: deimatic behavior in a South American grasshopper, Paramastax nigra

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Abstract

Prey have developed a diverse set of antipredator defenses that increase survival. However, when primary defenses (e.g., camouflage) fail, some organisms implement a deimatic display as a secondary defense. This display acts as a signal that causes an attacking predator to hesitate or withdraw its attack, increasing the prey's chance to escape. The *Paramastax nigra* grasshopper, a member of the monkey grasshopper family (Eumastacidae), exhibits a unique display when approached closely by exposing its conspicuous white hindwings, which remain extended while vibrating at high speed, causing it to resemble a fuzzy white sphere. The overall function of this display is unknown, however, this could be a deimatic behavior. First, we investigate whether individuals are more visually discriminable to avian predators in terms of body luminance when found on unmatched backgrounds. We found that individuals were significantly more discriminable on unmatched backgrounds. We then investigated whether *P. nigra* initiates its putative deimatic display at a greater distance when individuals are positioned on backgrounds that do not match their body coloration. We found that the display initiation distance of *P. nigra* is dependent on whether they are on surfaces that match their body color. Our results suggest that the conspicuous white coloration displayed when *P. nigra* leap away may be a deimatic behavior used as a secondary defense when their primary defense, camouflage, fails.

Introduction

The three billion year arms race between competitors, predators, and prey is a quintessential example of natural selection that ultimately impacts the diversification and complexity of organismal traits (Dawkins and Krebs 1979; Dawkins 1982; Vermeij 1994; Levy 1999). Under these selection pressures, prey have developed a diverse set of antipredator defenses that promote survival by reducing the risk of detection, increasing the likelihood of escaping predation, or deterring potential predators through physical, behavioral, or chemical means (Merilaita et al. 2017; Caro and Ruxton 2019; Rubio et al. 2024a). The form and function of antipredator defense mechanisms can be placed into three main categories: mechanisms that facilitate avoiding detection (e.g., (Poulton 1890; Cott 1940)), mechanisms that facilitate avoiding attack after detection (e.g., (Tilson and Norton 1981; Brown et al. 1999; Brown 2013)), and mechanisms that facilitate the deception of predators (e.g., (Blest 1957; Gochfeld 1984; Miller 1991)). Antipredator strategies are traditionally divided into primary and secondary defenses. Primary defenses function to prevent an encounter from occurring by facilitating the avoidance of detection, such as through camouflage (Endler 2006). If these initial strategies fail and the prey is detected, it may then employ a secondary defense to discourage the predators (Edmunds 1974). These second tactics are generally categorized as flight reaction, where prey automatically flee once detected, or a fight reaction, where prey animals use mechanisms that injure or frighten predators (Ruxton et al. 2004).

Deimatic behavior, a secondary fight reaction, hinders or delays the impulse of predators to attack by startling them with a sudden display. Such behavior promotes survival, as a startled predator may hesitate, delay, or completely terminate its attack. Prey animals use several different deimatic strategies, which can be classified as either a pre-emptive defense, where a display confuses or shocks an

approaching predator, or a counter-defense, where a display is executed after physical contact (Davis 1984; Koch and Schnitzler 1997; Friedel 1999; Umbers et al. 2015). Deimatic behavior can be exhibited through vibratory, acoustic, or visual sensory channels (Dunning 1968; Johnson and Brodie 1975; Koch and Schnitzler 1997; Friedel 1999). Visual deimatic displays are common in nature and are often quite similar across taxa. For instance, the sudden appearance of a conspicuous 'eyespot' pattern on a prey animal can startle an approaching or attacking predator, causing a delay or cessation of its attack (Maldonado 1970; Lenzi-Mattos et al. 2005; Stevens 2005; Hanlon and Messenger 2018). Another common feature is the sudden exposure of bright color patches on a cryptic body after physical contact, which is meant to warn predators that they are toxic and therefore unpalatable (Johnson and Brodie 1975; Brodie 1983; Umbers and Mappes 2015).

Insects in the order Orthoptera, which is composed of the crickets, katydids, and grasshoppers, are commonly cryptic (Stevens and Merilaita 2011). Members in this order are equipped with enlarged and modified hind legs, which may increase the distance covered when jumping from an approaching or attacking predator. Some Orthopterans possess bright or high contrast colors or patterns that are normally hidden that serve as antipredator defenses (Loeffler-Henry et al. 2019) observed in some species after crypsis fails (Umbers et al. 2015). For example, the mountain katydid is highly cryptic, however, when disturbed, it reveals hidden deimatic conspicuous coloration signaling that they are chemically defended (Umbers and Mappes 2015). This study highlights the significance of deimatic displays in Orthoptera, suggesting they are a core component of their defensive strategies. Nevertheless, further empirical research is essential to fully understand the evolutionary and ecological implications of these behaviors.

Predators of orthopterans include a range of visually oriented animals such as birds, reptiles, and small mammals, as well as arthropod predators like mantises and spiders (Mook and Davies 1966; Cherrill and Begon 1989; Nickle and Heymann 1996; Kok and Louw 2000; Redinger and Gifford 2022). In tropical forest environments, visually hunting birds are particularly relevant, as they rely on movement and contrast to detect prey among complex foliage. Visually hunting birds possess highly developed visual systems capable of detecting both chromatic and luminance contrasts (Kelber et al. 2003). However, for prey detection, particularly in complex textured backgrounds, luminance contrast is often more salient than color information (Osorio et al. 1999).

The *Paramastax nigra* grasshopper, a member of the monkey grasshopper family (Eumastacidae), native to South America, is typically found on hanging leaves. Obvious morphological features include a metallic green and black colored head, thorax and forewings, white colored hindwings, a bright yellow-green colored abdomen, and a black ovipositor (Figure 1) (Supplementary Video 1) (video has been slowed to 1/8x). When closely approached, the grasshopper leaps straight up into the air, and lifts its forewing and extends its hindwings. This action exposes its conspicuous white hindwings, which remain extended while vibrating at high speed, covering most of the grasshopper and causing it to resemble a fuzzy white sphere while it descends (Supplementary Video 2) (video has been slowed by 1/8x). This

transforms the metallic green grasshopper into an entirely different looking entity: a bright, fuzzy, blurry ball of white in mid-air. Upon landing, the white blur vanishes, and grasshoppers sit perfectly still.

The overall function of this display is unknown, however, it may function as a deimatic behavior designed to startle or confuse predators. The sudden exposure of high-luminance hindwings in *P. nigra* may be especially effective at disrupting visual tracking or eliciting a startle response in avian predators. In the midst of confusion, the exact location in which the *P. nigra* grasshopper lands after its deimatic leaping display may be unknown to the predator, enhancing its survival prospects. If the sudden appearance of conspicuous white coloration serves as a deimatic display, and thus as a secondary defense, it should occur mainly when predators are in close proximity. Furthermore, if this behavior serves as a secondary defense, grasshoppers should use it less frequently, and be more reluctant to abandon it, when on surfaces that match their body color, since crypsis would serve as their primary means of avoiding detection.

In this study, we investigated the integrated antipredator strategy of *P. nigra* examining the interplay between primary camouflage and secondary deimatic display. First, we evaluated *P. nigra's* primary defense by testing the hypothesis that *P. nigra* exhibits background matching for crypsis. We predicted that their body coloration corresponds to the substates on which they are typically found, and that individuals exhibit a behavioral preference for landing on matching backgrounds. Second, we investigated the driver behind the transition to a secondary deimatic display. If the sudden appearance of conspicuous white coloration serves as a deimatic defense, it should be deployed strategically based on the efficacy of the primary camouflage. Therefore, we hypothesized that the grasshopper would rely on crypsis when safely matched to their substrate, but switch to a deimatic display when conspicuous or detected. We predicted that flight initiation distance upon implementing the deimatic display would be significantly lower when grasshoppers are on matching surfaces than on non-matching surfaces, reflecting a reluctance to abandon active crypsis. Finally, because deimatic displays are presumably energetically costly, we hypothesized that *P. nigra* would prioritize primary crypsis over repeated secondary displays as physiological resources deplete. We predicted that flight initiation distance would decrease with successive individual encounters as individuals exhaust their energy stores, independent of the background color on which they were initially found.

Materials and Methods

Study Site, Study Species, and Experimental Procedures

We sampled areas in Tarapoto, Peru that consisted of walking trails surrounded by old-growth forest on either side**.** We walked until we found grasshoppers on the trail itself or on green leaves to the side of the trail. We documented *P. nigra* grasshoppers as being on an "unmatched background" if they were found on walking trails or bare soil, which were light to dark brown in coloration, or on a "matched background" if they were found on green background (e.g., green leaves or vegetation). Once *P. nigra* grasshoppers were found, we approached them until they initiated their deimatic display of white conspicuous

coloration while they leapt away. At that point, we measured the distance (cm) from the observer to the grasshopper's initial location before the deimatic display, as well as the distance the grasshopper traveled. In addition, we recorded the location the *P. nigra* grasshopper was originally found and the location the grasshopper landed (e.g., trail, leaf). We repeated this process for each grasshopper until they could no longer be followed.

Background matching: color and luminance

The use of smartphone photography as an accessible tool for studying animal coloration has been made possible by advancements in quantitative color analysis software (van den Berg et al. 2020). We took photographs of 12 grasshoppers using a Calibrite ColorChecker Passport Photo 2 and an Apple iPhone 14 Pro Max set to capture RAW images. For each grasshopper, we also captured images of matched backgrounds (green leaves) and unmatched backgrounds (trail, soil) near where the grasshopper was found. Images were processed using the MicaToolbox package (Troscianko and Stevens 2015) implemented in ImageJ v.1.54. To quantify how closely each grasshopper matched the color and luminance of its background, with grasshopper coloration defined by whole-body color, we used the logarithmic version of a predator visual discrimination model (Vorobyev and Osorio 1998). This model estimates the just noticeable difference (JND) between two stimuli, in this case, the grasshopper and its background, based on receptor noise–limited vision (Kemp et al. 2015; de Alcantara Viana et al. 2023). JND values represent the perceptual distance between the two stimuli as seen by a predator – a value of 1 JND corresponds to the threshold of discriminability, meaning the two stimuli are predicted to be indistinguishable under ideal conditions. Values greater than 1 indicate increasing perceptual contrast and thus greater detectability. In the context of background matching, higher JND values therefore reflect poorer camouflage against the corresponding background. We first converted RAW images into linearised and standardized multispectral image stacks. We then created a cone catch model using the spectral sensitivities of the peafowl (*Pavo cristatus*), a visual system widely utilized in orthopteran predation studies (e.g., (Heinze et al. 2022), omitting the ultraviolet (UV) cone given a dearth of evidence showing UV coloration in grasshoppers. Based on established estimates of receptor noise in the peafowl, we used cone proportions of LW = 0.92, MW = 1.00, and SW = 0.81 and Weber fractions of 0.1 and 0.2 for color and luminance models, respectively (Hart 2002). We measured cone catch values of each grasshopper by selecting a region of interest (ROI) including the head, thorax, and abdomen and excluding the legs and antennae. For each background image, we randomly selected ten ROI's of roughly 300 x 300 pixels to get an average cone catch value per background image. We then derived an average color and luminance JND for each grasshopper to each of the two habitat types.

Statistical Analysis

To test whether deimatic display initiation distance increases when *P. nigra* grasshoppers are not on surfaces matching their body color, we built a linear mixed-effects model (LMM) with log-transformed flight initiation distance as the response, background color upon flight (e.g., matched and unmatched) and what number flight it was in the event of successive encounters in a row (e.g., first flight, second

flight, third flight) as fixed effects, and individual *P. nigra* grasshopper ID as a random effect to account for repeated measures within individuals. We also estimated repeatability by dividing the amount of variation explained by individual ID by the total variance explained by individual ID and residuals (V_{ID} / V_{ID} + V_R; (Nakagawa and Schielzeth 2010). To test whether initiation of a deimatic display is more likely to be initiated by physical contact when *P. nigra* grasshoppers are on surfaces matching their body color as opposed to surfaces not matching their body color, we used a Firth-penalized logistic regression with a binomial error distribution. In addition, to test whether *P. nigra* grasshoppers land on surfaces that match their body color following the initiation of a deimatic display, we built a generalized linear mixed model (GLMM) with background color (e.g., matched and unmatched) as the binary response variable and individual *P. nigra* grasshopper ID as a random effect. To test whether distance traveled decreases after each deimatic display, we built a linear mixed-effects model with flight distance as the response, what number flight it was as a factored fixed effect, and individual *P. nigra* grasshopper ID as a random effect. To determine if background type predicted JND values, we used a linear mixed-effects model with either chromatic or luminance JND as the response variable, background type as a fixed effect, and grasshopper ID as a random effect. We used the R package lmerTest (Kuznetsova et al. 2017) for our linear mixed-effects model and generalized linear mixed model. We performed all analyses in R version 4.4.2 “Pile of Leaves” (R Core Team 2024).

Results

Our avian visual model showed that *P. nigra* individuals were not significantly different in chromatic contrast between matched and unmatched backgrounds (Fig. 2A). By contrast, grasshoppers had significantly higher luminance JND values on unmatched backgrounds compared to grasshoppers on matched backgrounds (t-value = 2.435, p-value ≤ 0.05; Fig. 2B). A majority of both chromatic and achromatic JND values exceeded the perceptual threshold of 1, the minimum JND for hypothetical discrimination under perfect lighting conditions, indicating that most grasshoppers are visually distinguishable from their backgrounds. Luminance-based JNDs were consistently higher against unmatched backgrounds, suggesting that grasshoppers are more conspicuous to avian predators under these conditions.

We observed an average of 2.52 (SD = 1.06) deimatic display events per individual across 17 grasshoppers. Observations were maintained until grasshoppers could no longer be tracked. We found strong evidence that *Paramastax nigra* grasshoppers that were on surfaces matching their body color show lower deimatic display initiation distance compared to those not on surfaces matching their body color (t-value = -8.315, p-value < 0.001; Fig. 3A). In other words, observers could get closer to grasshoppers before flight when grasshoppers were on surfaces matching their body color. Repeatability of flight initiation distance based on individual ID only explained around 3.58% of the total variance in the residuals, suggesting that the variation in our outcome variables cannot be explained by differences between individuals. Physical contact was never necessary to initiate a deimatic display when grasshoppers were on unmatched backgrounds, however, physical contact was necessary 64.5% of the

time to initiate a deimatic display when *P. nigra* grasshoppers were on matched backgrounds (Firth-penalized logistic regression: X^2 = 16.15, df = 1, p-value < 0.001; Fig. 3B; Supplementary Video 3). We found that *Paramastax nigra* grasshoppers are more likely to land on a background that matches their body color than a background that does not (e.g., walking trail, ground) (SE = 3.219, z-value = 3.156, p-value = 0.0016). Finally, we found that *P. nigra* grasshoppers traveled shorter distances as the number of initiated deimatic displays increased (df = 33.43, t-value = -3.433, p-value < 0.05).

Discussion

Natural selection drives adaptive evolution by favoring genetic variants with phenotypes that maximize fitness (Williamson et al. 2007; Bonner 2020; Rubio and Summers 2022; Rubio et al. 2024b). Predation is a strong force driving selection, causing prey animals to evolve a diverse set of antipredator defenses (Caro 2005; Kikuchi et al. 2023). Although antipredator defenses have been extensively studied, relatively little research has focused on understanding the behavioral mechanisms behind deimatic displays, impeding investigation into how the mechanisms of antipredator defenses evolve. Visual deimatic displays are a secondary antipredator strategy that often couples conspicuous coloration with startle behaviors to frighten predators, allowing displayers to escape predation when primary defenses, such as background matching, are unsuccessful (Edmunds 1974). The *P. nigra* grasshopper exhibits a metallic green and black colored head, thorax and forewings, a bright yellow-green colored abdomen, and black ovipositor; however, when closely approached or touched, this grasshopper leaps straight up into the air and exposes its conspicuous white hindwings, which remain extended while vibrating at high speed before landing. Our results suggest that this is a deimatic display and is used as a secondary defense when the primary defense, crypsis, fails.

We found that grasshoppers are significantly more discriminable to avian predators in terms of luminance when located on backgrounds that do not match their own luminance compared to those that do. Visually hunting birds possess highly developed visual systems that can detect both chromatic and luminance contrasts (Kelber et al. 2003). However, under natural, complex visual conditions, luminance contrast often plays a more dominant role in prey detection than color (Osorio et al. 1999). Therefore, when a grasshopper's body luminance more closely matches that of leaves on which it is found, it may decrease the likelihood of being detected by avian predators. This reliance on background matching may also explain why *P. nigra* grasshoppers tended to land on leaves that matched their body coloration following a deimatic display. By returning to a cryptic background, individuals may reduce their visibility to predators after revealing themselves during the display, thereby enhancing the effectiveness of crypsis as a post-display defense. Grasshoppers are equipped with compound eyes composed of multiple ommatidia, each containing photoreceptor cells that enable them to discriminate between colors (Vukusic and Chittka 2012). Studies suggest that grasshoppers can perceive and respond to color differences in their environment. For instance, Bernays and Wrubel (1985) found that nymphs of *Melanoplus sanguinipes* can learn to associate food with visual cues such as color or light intensity. Similarly, Camacho et al. (2020) found that *Sphingonotus azurescens* grasshoppers prefer habitats that

enhance background matching. The ability of grasshoppers to perceive and respond to color differences may explain how *P. nigra* grasshoppers are more likely to land on surfaces that match their body color following the initiation of a deimatic display.

In addition, we found that the display initiation distance of *P. nigra* grasshoppers, which might be a deimatic display, depends on the color of the surfaces they occupy. When grasshoppers were on surfaces that did not match their body color, they initiated deimatic displays at greater distances than individuals on matching surfaces. We also found that physical contact was often necessary to initiate the deimatic display of grasshoppers when they were on surfaces matching their body color, whereas physical contact was never necessary when grasshoppers were on surfaces not matching their body color. Delayed initiation of deimatic displays until after physical contact has been observed in other organisms that rely on crypsis as a primary defense (Umbers et al. 2015). As a secondary defence for cryptic organisms, deimatic displays may be favored only after contact because premature displays can be energetically costly and may reveal the organism's presence to predators that had not yet detected it. For example, the mountain katydid is highly cryptic but, when disturbed, reveals conspicuous hidden coloration that signals it is chemically defended (Umbers and Mappes 2015). Similar behavioral patterns may explain our results in *P. nigra* grasshoppers. Because *P. nigra* is not known to be chemically defended, a flash of white coloration is a dishonest signal, as they are actually palatable. This may be part of why crypsis serves as the primary defense of *P. nigra* grasshoppers, when background coloration matches their body color, whereas deimatic displays function as a secondary defense. In addition, our results show that *P. nigra* grasshoppers tend to land on surfaces matching their body color following the initiation of a deimatic display, and that grasshoppers traveled shorter distances as the number of initiated deimatic displays increased. The reduction in distance traveled across successive flights suggests that deimatic displays are energetically costly and should therefore be initiated only when necessary. This provides a contributing hypothesis for why crypsis is preferred as the primary defense. Shorter, more abrupt movements may also reduce a predator's ability to maintain accurate tracking of the prey during pursuit.

The white coloration of the secondary display of *P. nigra* may be adaptive. White coloration reflects nearly all wavelengths of visible light, creating a high luminance contrast with darker colors like green, which absorbs a significant amount of light. As a result, white coloration is highly visible in forested environments, especially in the understory, and is more easily detected by predators with visual systems capable of recognizing white coloration (Endler 1993). The sudden appearance of a high luminance color in a low-light environment when *P. nigra* grasshoppers are either approached too closely or touched may startle predators and delay their attack, allowing the grasshopper to escape. In addition to startling predators, the sudden display of white coloration while *P. nigra* grasshoppers evade an attack may provide misleading information about their true resting color; this may confuse and impair predator ability to locate them once they settle on a surface that allows them to continue their cryptic antipredator strategy. Finally, the highly visible white coloration of the hindwings may closely resemble the bright coloration of aposematic insects such as butterflies, potentially eliciting avoidance response in predators that associate conspicuous white signals with unpalatable prey. Indeed, *P. nigra* is sympatric

with the ghost yellow butterfly (*Eurema albula*) at our study locality, which exhibits white colored hind and for wings. While studies suggest that some grasshoppers can be distasteful or toxic to predators, often as a result of sequestering plant-derived chemicals through their diet (Sword 2001), this form of defense varies across species and is not known from *P. nigra*. If *P. nigra* also lacks such chemical defenses, the hindwing display may instead represent a form of dishonest signalling or Batesian mimicry..

Conclusion

Deimatic defensive displays are a fascinating yet understudied aspect of animal behavior. Our results demonstrate that *P. nigra* grasshoppers integrate crypsis and deimatic behavior as complementary antipredator defenses. When on backgrounds that match their body coloration, individuals rely primarily on crypsis and often delay initiation of a deimatic display until predators approach closely or make physical contact. In contrast, individuals on nonmatching backgrounds initiate displays at greater distances, suggesting that the loss of effective crypsis alters defensive decision-making. We also found that grasshoppers preferentially return to color-matching backgrounds following displays, reinforcing the importance of background matching in their antipredator strategy. Together, these findings provide evidence that the initiation and deployment of deimatic displays are context dependent and closely linked to the effectiveness of primary defenses. Future studies can assess the generality of these results by investigating whether similar results can be found in other habitat types. For example, the impact of the sudden appearance of white coloration may have been amplified in the dim lighting of old–growth forests, however this effect might be reduced in open grasslands, which *P. nigra* grasshoppers also occupy. It is possible that the initiation distance of the deimatic display of *P. nigra* grasshoppers may vary depending on the ambient light levels of the environment. Our work highlights how prey animals dynamically integrate multiple antipredator strategies in response to changing environmental conditions and predation risk.

Declarations

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Ethics approval

Not applicable.

Consent for publication

All authors consent to this work being published.

Competing interests

The authors declare no competing interests.

Data availability

Codes for all analyses are available on Github (https://github.com/andreworubio/escape_artist.git)

Author contributions

Designed research: AOR, KS

Collected data: AOR, AMD, GVA

Analyzed data: AOR, MRM, JVN

Contributed to writing: AOR, MRM, AMD, JVN, GVA, AMMS, KS

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Figures

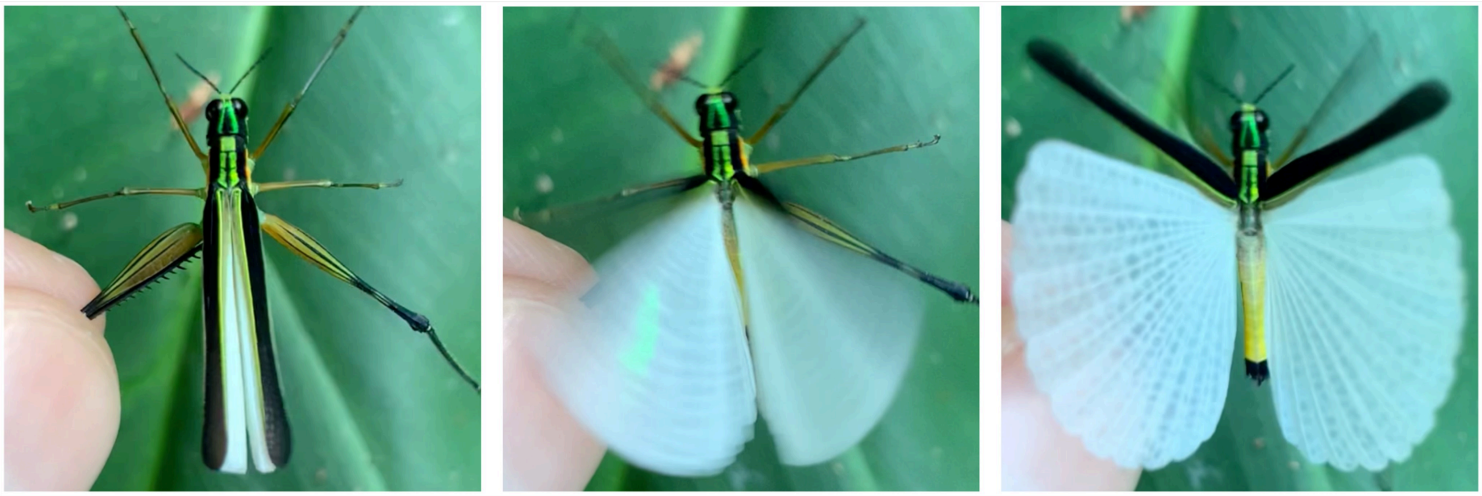


Figure 1

Deimatic display in the *Paramastax nigra* grasshopper displaying its white conspicuous posterior wing.

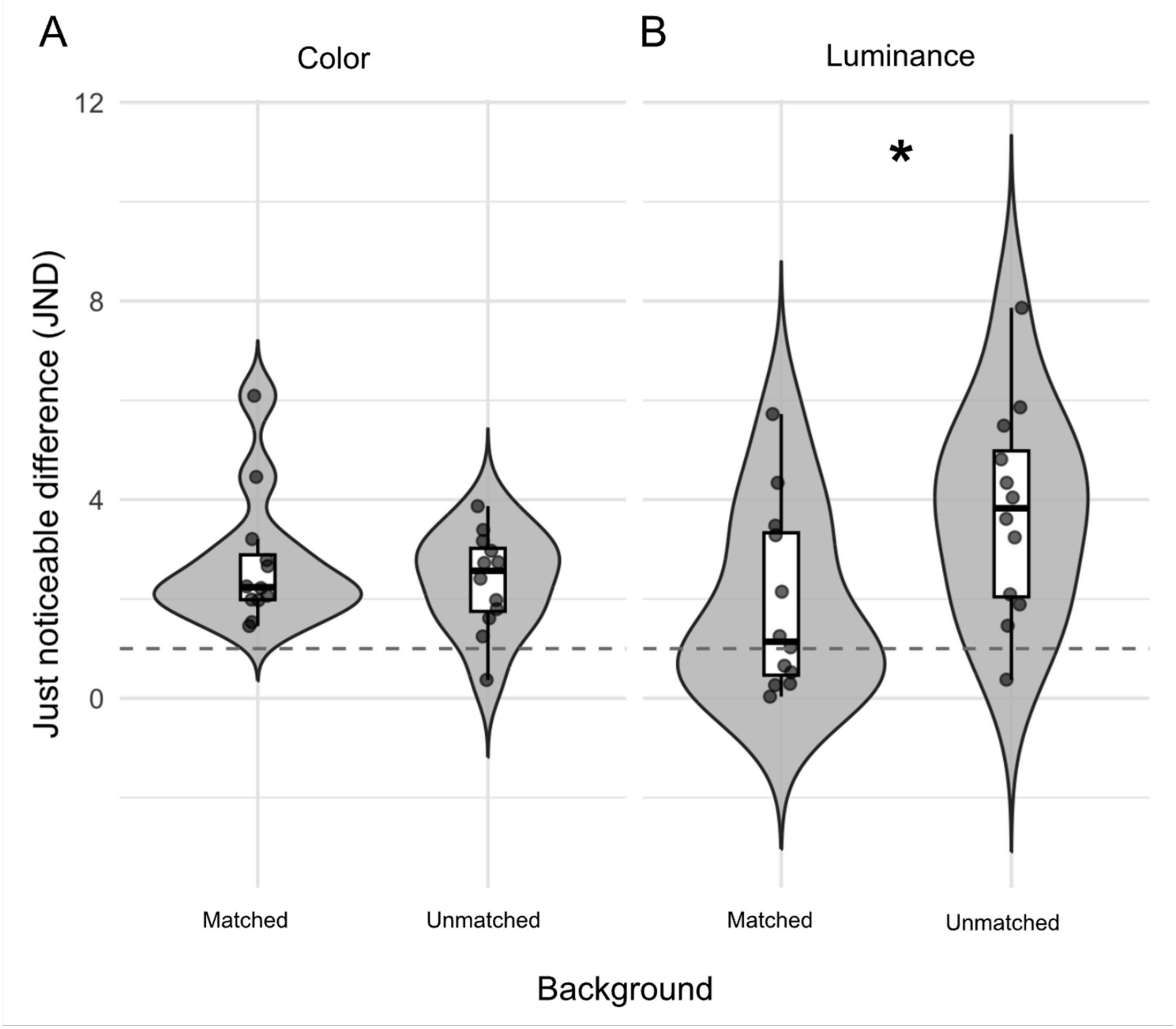


Figure 2

Discrimination values (Just noticeable differences; JND) for *P. nigra* on matched and unmatched backgrounds. JND values for A) color match and B) luminance match. The dashed line indicates the JND = 1 threshold.

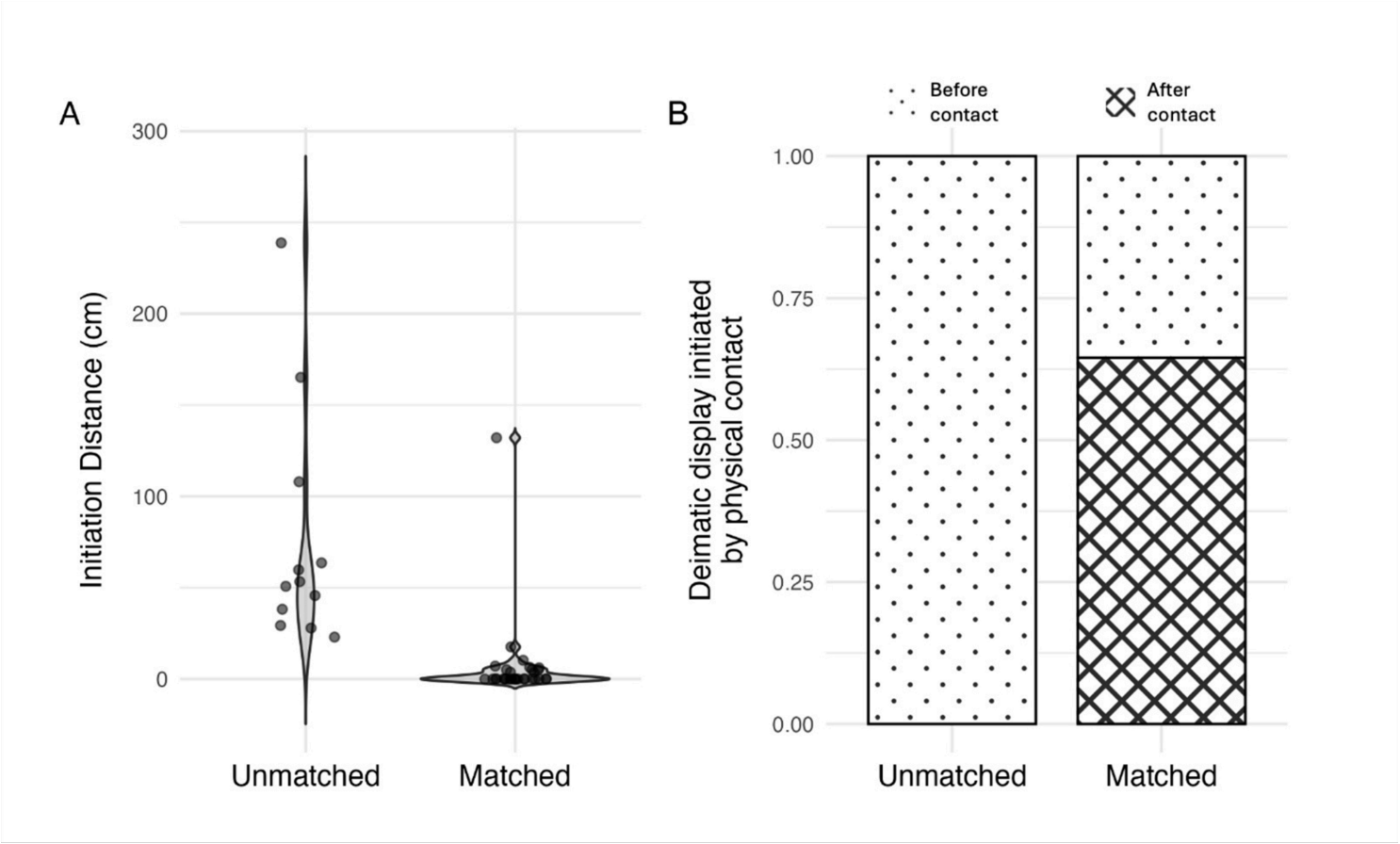


Figure 3

Initiation of deimatic display in *Paramastax nigra* grasshoppers. A) Deimatic display initiation distance when *P. nigra* grasshoppers are either on an unmatched background or matched background. Shorter initiation distances indicate that observers were able to get closer to the grasshopper. B) Proportion of deimatic display initiated by physical contact when grasshoppers are either on an unmatched background or matched background. Circle symbols represent occurrences when *P. nigra* grasshoppers initiate their deimatic display before physical contact while crosshatch represents occurrences when *P. nigra* grasshoppers initiate their deimatic display after physical contact.

Supplementary Files

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