



Original Article

The matador bug's elaborate flags deter avian predators

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Received 21 September 2023; revised 1 February 2024; editorial decision 4 March 2024; accepted 13 March 2024

Large, conspicuous traits frequently evolve despite increased predator attention, but in some cases, specifically to attract attention. Sexually selected traits provide some of the clearest examples of elaboration, yet natural selection can also be a powerful driver. The matador bug, *Anisoscelis alipes* (Hemiptera: Coreidae), has large, colorful flags on its hindlegs that, unlike many other coreid species, are not used in reproductive competition. We hypothesized that these flags either 1) warn predators of chemical defense or 2) deflect predatory attack to the removable hindlegs. We pitted matador bugs with or without flags and crickets (*Acheta domesticus*) with or without bug flags experimentally attached to their legs, against live motmot bird predators (*Momotus subrufescens* and *Electron platyrhynchum*). Contrary to the deflection hypothesis, almost none of the predatory strikes were directed at hindleg flags. Instead, we found support for the aposematism hypothesis: matador bug flags reduced attacks on palatable crickets but were unnecessary to prevent predator attacks against matador bugs. Palatability studies with naïve chicks (*Gallus gallus*) further supported a chemical defense hypothesis. Thus, these elaborate hindleg flags serve an aposematic anti-predator function, but in their absence, birds use alternative cues. These findings add to our understanding of the role of predation in driving the evolution of elaborate morphological structures.

Los rasgos con coloración brillante y contrastante con frecuencia evolucionan a pesar de ser más llamativos para los depredadores, pero en algunos casos, evolucionan específicamente para atraerlos. Los rasgos sexualmente seleccionados constituyen algunos de los ejemplos más claros de rasgos elaborados, pero la selección natural también puede ser un fuerte impulsor de evolución. El insecto matador, *Anisoscelis alipes* (Hemiptera: Coreidae), tiene estructuras en sus tibias que se asemejan a banderas grandes y coloridas que no se usan en la competencia reproductiva. Planteamos las hipótesis de que estas banderas a) advierten a los depredadores de la defensa química, o b) redirigen el ataque del depredador a las patas con autotomía. Insectos matadores con o sin banderas traseras y grillos (*Acheta domesticus*) con o sin banderas de insectos matadores adjuntadas experimentalmente a sus patas, fueron expuestos a aves depredadoras del grupo de los momotos (*Momotus subrufescens* y *Electron platyrhynchum*). Contrario a la predicción de la hipótesis de la re-dirección, casi ninguno de los ataques de depredadores se dirigió a las banderas traseras. En cambio, encontramos apoyo para la hipótesis del aposematismo: las banderas de insectos matadores redujeron los ataques a grillos que no son tóxicos, pero fueron innecesarias para evitar el ataque de depredadores contra insectos matadores. Experimentos de palatabilidad con pollos (*Gallus gallus*) apoyaron aún más una hipótesis de defensa química. Por lo tanto, estas elaboradas banderas en las patas traseras cumplen una función aposemática antidepredador, pero en su ausencia, las aves usan señales alternativas del insecto. Estos hallazgos se suman a nuestra comprensión del papel de la depredación en la evolución de estructuras morfológicas elaboradas.

Key words: anti-predator defense, aposematism, deflection, Coreidae, chemical defense.

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INTRODUCTION

Elaborate traits (complex, conspicuous traits that are derivations of pre-existing characters and that perform a novel function) are often used as signals, aimed either at communicating with conspecifics or potential predators. To conspecifics, these elaborate traits can be used to convey information about the individual's competitive quality (Bradbury and Vehrencamp 2011). To predators, elaborate traits often communicate information that would dissuade or redirect attack. For example, some animals use contrasting coloring to advertise physical defense in the form of spines and quills that could damage the predator during handling (Crofts and Stankowich 2021), or chemical defense that could harm the predator after ingestion (Eisner 1970; Edmunds 1974; Caro and Ruxton 2019) (or bluffing the latter (Stoddard 2012)). Bright, contrasting colors can also attract predator attention but divert attack to non-essential appendages, as has been demonstrated with lizard tails (Bateman et al. 2014; Fresnillo et al. 2015).

Multiple conspicuous signals can function to make the complete signal more effective at eliciting an advantageous response from a given receiver or to play different roles for different receivers (Hebets and Papaj 2005). Signals in the same sensory system can be beneficial to a chemically defended animal by promoting faster learning or more lasting memory in predators, leading to decreased damage or mortality for the defended prey (Rowe 1999;

Hebets and Papaj 2005; Skelhorn et al. 2016; Leavell et al. 2018). They can also create signal redundancy, where the multiple signals serve as “back-ups” for each other, increasing the likelihood that a receiver will perceive and integrate the signal (Roper and Cook 1989; Pegram and Rutowski 2014). Alternatively, multiple conspicuous traits may be driven by differing predator sensory systems to elicit similar or divergent responses from various predators. Birds and some arthropod predators, for instance, respond differently to the orange and iridescent green stinkbug (*Tectocoris diopthalmus*), with birds quickly learning to associate its coloration with bad taste (aposematism) (Fabricant and Smith 2014) and mantids often failing to detect the orange prey entirely (crypsis) (Fabricant and Herberstein 2015). Understanding the function and evolution of apparently conspicuous traits therefore requires detailed testing with natural predators.

Here, we provide such a test of an elaborate trait in the matador bug, *Anisoscelis alipes* (Coreidae; “leaf-footed bugs”), and sympatric bird predators, motmots (Momotidae) (Figure 1). Leaf-footed bugs are named for the cuticular tissue that protrudes off the hindlegs of many species, sometimes in a leaf-like shape. Previous work in the family has focused on the sexually dimorphic enlarged femora of many species, which are used in intrasexual competition (Miyatake 1997; Eberhard 1998; Miller and Emlen 2010). As has been found with other exaggerated weapons, these thickened femora are metabolically costly (Somjee et al. 2018) and in males typically scale

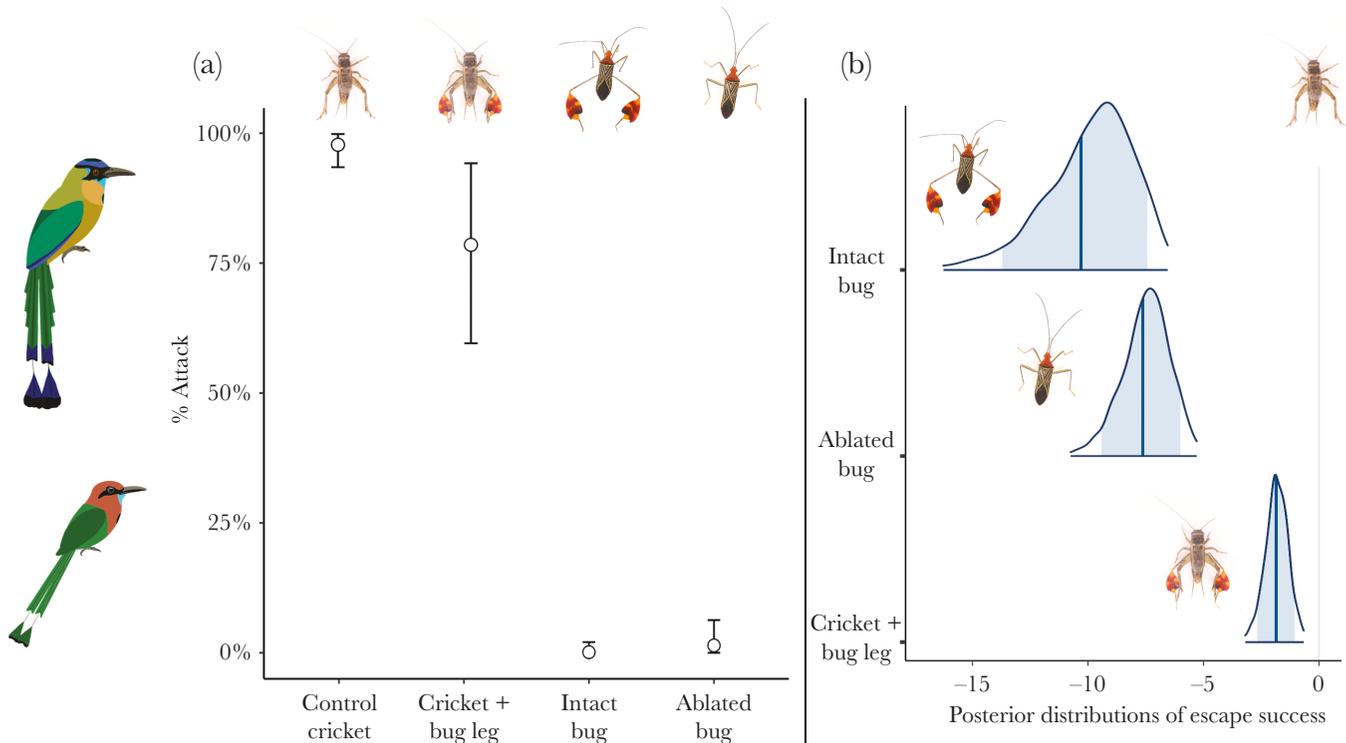


Figure 1 Tibial flags are a component of an aposematic signal suite in matador bugs. We pit differing treatments of bug (intact and flag legs ablated) and cricket (unmodified controls and modified hindlegs with bug flag legs attached) against two species of motmot (*Momotus subrufescens* (top) and *Electrola platyrhynchum* (bottom)). We found that (a) Motmots attacked control crickets almost 100% of the time, bugs—either intact or with flag legs ablated—approximately 0% of the time, and crickets with bug legs attached nearly 75% of the time. Points and error bars represent the marginal estimate means and highest posterior density interval, respectively, extracted from our Bayesian model. (b) Posterior distributions of the experimental treatments. Distribution distance from the 0-line represents the probability of a hindleg treatment reducing motmot attacks below the attack rate on control crickets. Central lines are means, blue shading represents 80% credible intervals, and distribution tails in white are 95% credible intervals. There is a 0.99 probability that experimentally adding a flag leg to a cricket decreases avian attack, compared with the unmodified control cricket. All bird illustrations are original designs by Ummat Somjee and insect images are photographs taken by Ummat Somjee.

with positive allometry (slope of trait size:body size > 1) (Mitchell 1980; Miyatake 1993; Eberhard 1998; Somjee et al. 2018). In contrast, the matador bug and multiple other members of its subfamily (Anisoscelini) possess much thinner and longer femora compared to many other coreids (Longbottom et al. 2022). The tibiae, however, are modified and expanded to more than double the dorsal surface area of the bug and are often patterned in long-wavelength colors (red, orange, etc.) in both matador sexes (see image in Figure 1). Unlike the sexually selected weapons of other coreids, neither the femur size nor the flag surface area of matador bugs scale with positive allometry relative to body size (Longbottom et al. 2022). In addition to these bright flags, the matador bug has an orange head, pronotum, and ventral surface, as well as a black and yellow-lined dorsal surface. As with many other hemipterans, adults also produce diet-derived alarm pheromone, which likely functions as a conspecific signal rather than a predator deterrent (Prudic et al. 2008; Czaplewski et al. 2018; Inoue et al. 2019). Diet studies have shown that Passiflora plants are a major host for many species within the Anisoscelini group (Rodrigues et al. 2008), and the matador bug can often be found on passion fruit plants in exposed areas (Longbottom et al. 2022). Along with other insect groups that feed on Passiflora (famously, *Heliconius* butterflies (Hay-Roe and Nation 2007)), many coreids, including the matador bug genus, *Anisoscelis*, are hypothesized to use Passiflora cyanogenic glycosides and anthocyanins for their own defense (Aldrich 1988). While this has been suggested from chemical analysis, palatability trials using live predators had not been previously performed with *Anisoscelis*.

These biological attributes could easily lead to the hypothesis that flags function as an aposematic signal. However, other aspects of the matador bug's biology indicate a different potential role of these flags. Both male and female matador bugs perform a stereotyped waving behavior with their red and orange flags, and this behavior is unrelated to the sex or behavior of nearby conspecifics, suggesting it is unlikely to be linked to sexual competition (Longbottom et al. 2022). In addition, similarly to lizard tails, some coreids, including *Anisoscelis*, engage in fast autotomy (limb loss) when their legs are grasped or damaged (although adults do not regrow the leg after it has been severed). This action is derived from a slower autotomizing ancestor, lending support to the notion that these hindlegs may have evolved to redirect predator attack to these conspicuous and non-essential appendages and then to break away when grasped (Emberts et al. 2016, 2020). The matador bug exhibits some of the most rapid autotomy among coreids (Emberts et al. 2020), and observational evidence from the field found that ~16% of individuals are missing at least one hindleg by the adult stage (Longbottom et al. 2022). This could indicate that these elaborate hindlegs have evolved as a predator deflection strategy.

We therefore propose two hypotheses for the matador bug's flags: 1) *aposematism*: colorful flags warn visual predators of noxiousness; 2) *deflection*: flags divert predatory attack to these removable appendages. To test these hypotheses, we pit matador bugs with and without flag legs and crickets with and without bug flag legs added against avian predators in large, outdoor flight cages in Gamboa, Panamá. Insectivorous birds are known to consume Heteroptera (true bugs) (Exnerová et al. 2003), including coreids found in this region, although so far only drab-colored genera that feed on non-Passiflora plants have been identified in bird diets (*Acanthocephala*, *Anasa*, *Leptoglossus*) (Beal 1918; Cottam and Knappen 1939; Orejuela 1980; Silva et al. 2021). We used adults from two species of motmot (Coraciiformes) that are sympatric with the matador bug, and thus likely had previous experience with these and other local coreids,

as predators: the whooping motmot (*Momotus subrufescens*) and the broadbill motmot (*Electron platyrhynchum*). Although they differ in size (avg mass whooping: 110 g, broadbill: 60 g) and somewhat in hunting style (whooping often glean insects from the ground while broadbill forages higher in the canopy), they primarily eat arthropods (Remsen et al. 1993). These species therefore provide two different and biologically relevant predator perspectives on the matador bug. We predicted that if this trait functions as an aposematic signal, motmots will avoid prey items with brightly colored elaborate flags. That is, matador bugs with flag legs intact and crickets with flag legs added would experience the greatest survival benefit, while matador bugs with flag legs ablated and crickets without flag legs added (control crickets) would suffer greater predation. If the flags serve a deflective function, however, we predicted that motmot strike would be directed toward appendages outfitted with these elaborate flags. To further support our findings, we also conducted palatability trials with naïve chicks and predicted that if matador bugs were chemically defended, they would be rejected more often than crickets, another novel prey animal. We tested for flags eliciting an enhanced innate avoidance response by offering half of the chicks intact matador bugs and half of the chicks bugs with flag legs removed. This study represents a critical and novel test of the role of predation in shaping the evolution of an elaborate trait in coreids. Results from this work will further elucidate the often under-appreciated role of natural selection in shaping elaborate morphological structures.

METHODS

Experimental motmot trials

We conducted our study between November–December of 2021 and January–February, and December of 2022 in Gamboa, Panamá. These periods primarily encapsulate the dry season, before nesting begins. We captured birds individually from the surrounding Soberanía National Park using mist nets and conspecific playback calls. After capture, we immediately transferred the individual to an outdoor aviary with ambient conditions on the Smithsonian Tropical Research Institute (STRI) campus (hexagon: floor area = 33.64 m², height = 5.5 m). The aviary was shaded by nearby trees and shade cloth and came equipped with a metal portion of the roof that maintains a dry area in the cage during rainstorms. We provided multiple branches for perching opportunities and water ad libitum. We allowed each bird the rest of the day and night after capture to acclimate to the cage environment and began trials the following morning. During the acclimation period, we sat in the cage with the bird and intermittently fed it a limited number of prey items (mealworms, cockroaches) off an experimental feeding platform that was attached to a large horizontal branch running along the middle of the cage (see Supplementary Videos S1–S4 for cage setup). This served to train the bird to expect food on the platform and to become more comfortable with our presence in the cage, while maintaining motivation for trials the following day. We tethered all control and experimental prey items to a nail affixed to the center of the wooden platform using fishing line (Araty, 0.25 mm superflex) that we glued onto the pronotum of the insect with UV-activated glue (Bondic, Aurora, ON). Experimental prey animals included crickets (*Acheta domesticus*) that were reared in the STRI amphibian center and the matador bug, *Anisoscelis alipes*, which were reared in an outdoor cage from wild stock (original population captured by sweep-netting at a farm in Sona, Panamá by Ummat Somjee see (Longbottom et al. 2022)

for detailed rearing information). After trials were completed each day, birds were fed an additional 4–6 mealworms before dark. All birds were released in the area of initial capture, as per IACUC SI-21028. Birds and arthropods were captured under MiAmbiente permit #: ARB-075-2021 to J.J.R. and SC/A-33-19 to U.S.

To maximize our data collection during their short captivity and maintain bird motivation during experimentation, we tested each bird with multiple trial sets over the course of 2 days (no more than three sets per day, separated by at least two hours). In each trial set, we individually offered at least two unmodified (control) crickets and one of each experimental treatment on the platform: intact bug = matador bug without modification, ablated bug = matador bug with hindlegs (flag legs) removed, cricket with bug legs = cricket with matador flag leg glued to the hindleg of a cricket (see Supplementary Videos S1–S5). To test for the natural avoidance of matador bugs, we limited the first introduction of experimental treatments to either an intact bug or ablated bug. We began and ended each trial set with an unmodified cricket to assess motivation and randomized the presentation of other experimental prey (intact bug, ablated bug, cricket with bug legs) using a random number generator, making sure they were presented in equal numbers. To maintain motivation, we offered birds one unmodified cricket every four or fewer experimental animals. We used trials with unmodified crickets as a mark of predator motivation. If a bird did not attack the cricket, we considered this the end of the trial set and removed this trial from our analyzed data set and all trials preceding it up until the last control cricket was consumed. For the most realistic responses, we would manually tap the prey animal if it stopped moving for longer than 30 s. This was a relatively uncommon occurrence, and we would only do so if the bird was not near the prey animal. The birds did not appear disturbed by our movements. We gave each bird 10 min to complete a trial and recorded all interactions with a GoPro Hero 7 Black (2.7K, 30fps), in addition to hand-coding in real time from within the cage.

Chick palatability trials

To test for bug chemical defense, we conducted palatability trials with naïve chicks (*Gallus gallus domesticus*). We kept chicks in a large, outdoor flight cage (hexagon: floor area = 97.5 m², height = 5.55 m) in Gamboa, Panamá. We ensured naivety by purchasing these chicks from a local factory where they are reared in an indoor environment on chicken feed and transporting them immediately to this outdoor flight cage upon purchase. The flight cage was sealed with fine mesh fencing that goes underground to prevent the incursion of outside animals. We can therefore be quite certain that the chicks did not have access to wild bugs before experimentation. We fed chicks on chicken feed (Pollo de Patio; 12% protein, 2% fat, 6% fiber), supplemented with a vitamin mix (ProBiolyte) and fresh vegetables daily. Chicks were 3 weeks old at the time of experimentation.

We tested a total of 15 chicks. During trials, we placed one chick inside a large pup tent (60 cm × 60 cm × 90 cm). To reduce stress and help the chick focus on the experimental trial, we paired it with a buddy chick that was kept in a smaller tent within the larger one. Buddy chicks never participated in trials (Skelhorn and Rowe 2009). We gave each chick 5 min of acclimation time after introducing it to the experimental enclosure. We presented all prey items for 3 min on a wooden platform outfitted with a screw in the middle, to which we attached fishing line (Araty, 0.25 mm superflex). All trials began with one mealworm, to train the chick to the platform

and make sure it would hunt desirable prey items in this context. After the mealworm, our trial order proceeded with a matador bug, followed by a control cricket. We then gave the chick a 15-min break inside the experimental enclosure and then conducted another set of trials, beginning with a matador bug and followed by a control cricket. If the chick never attacked a bug, or if it attacked a bug during its first experimental set, we concluded the trials after these two rounds. If the chick attacked a bug on its second round of trials, we gave it a third round to assess how it would respond after this experience. In the event that a chick discontinued eating crickets (which sometimes occurred after the chick tried a matador bug), we gave it a mealworm as an alternative palatable prey item. Any chicks that did not initially eat crickets were excluded from this dataset (one chick). To test the effect of flags against a naïve predator experiencing these bugs for the first time, we presented half of the chicks with intact bugs and half of the chicks with ablated bugs (flag legs removed). We recorded all interactions with two GoPro Hero 7 Black (2.7K, 30fps). Chicks were kept according to IACUC SI-21028.

Data analysis

We reviewed all videos using VLC media player and QuickTime Player. For the motmot trials, we coded “attack” as the bird flying toward the prey animal and attempting to capture it with its beak. We also noted the location of attack on the prey item (main body or leg) and whether the bird removed hindlegs prior to consumption. To assess the role of flags in the context of the matador bug aposematic suite, we used binomial exact tests to compare the number of times a motmot closely inspected a bug (i.e., landed on the platform or branch to which the platform was affixed) with and without flags. For the chick palatability trials, we coded “avoid” as the chick never contacting the prey animal, “peck” as a chick making contact with the prey animal, but not consuming it, and “eat” as the chick consuming the prey animal. We again identified the location of attack (main body or leg).

We performed statistical analyses of the motmot-matador bug data set in a Bayesian framework, using a binomial distribution family and logit link function. We used the “rstanarm” package (Muth et al. 2018) to run all models and “bayesplot” to visualize posterior distributions in R studio. We ran a set of hierarchical models, which all included treatment as the fixed effect and Bird ID as a random intercept to control for inter-bird individual differences. To account for the effect of potential bird learning in our trials, we included treatment sequence (within a day) as an additional fixed effect in our second model and added trial day as a random slope in our third model. These models allow for an estimation of the effect of treatment order on attack rate and a change in the strength of the outcome based on experimental day, respectively, while also permitting the intercept of the model to vary by bird individual. For individual species models, we did not have the power to estimate random slopes and therefore included both treatment sequence and day as fixed effects. We note that while our number of bird individuals in the species models did not fit the common five-level suggested minimum (Harrison et al. 2018) (we had four individuals per species), recent simulation work indicates that parameter estimates are unlikely to be negatively affected by including a random effect with fewer levels (Gomes 2022). We checked traceplots and r-hat values for all models to ensure that each model converged satisfactorily and compared model fit using a leave-one-out approach. To assess the results of our palatability

trials, we conducted exact binomial tests (see [Supplementary Material](#) and [Rubin et al. 2024](#)).

RESULTS

Motmot trials

We tested the response of four individuals each of two different motmot species (*Momotus subrufescens* and *Electron platyrhynchum*) to matador bug flags. We gathered over 200 data points (n trials *M. subrufescens* = 122, n trials *E. platyrhynchum* = 102; n trials per individual range: 12 - 43). Results from the two species were highly consistent, despite the difference in their ecology (i.e., foraging habits and size). We therefore present the pooled results primarily and discuss the results broken out by species subsequently (see [Supplementary Materials](#) for individual species results and figures). Results from our leave-one-out model comparison indicate that the best-fit model for the full data set included treatment and treatment sequence as fixed effects and bird ID as a random intercept. The best-fit model for the broadbill motmot had the same structure, while the best-fit model for the whooping motmot excluded the trial sequence and day (see [Supplementary Material](#)).

In total, motmots attacked unmodified control crickets almost 100% of the time (mean: 0.98, highest posterior density interval [HPD]: 0.94–0.99). They attacked matador bugs, both intact and ablated, ~0% of the time (intact mean: 0.00, HPD: 0.00–0.02; ablated mean: 0.01, HPD: 0.00–0.07). Motmots attacked crickets with bug legs ~20% less than unmodified crickets (cricket with bug leg mean: 0.79, HPD: 0.60–0.94) ([Figure 1a](#)). Moreover, the probability that having bug flag legs decreased a cricket's chance of being attacked was 0.99 (3997 posterior draws out of 4000) ([Figure 1b](#)). We found that trial day (1 or 2) did not affect the probability of bird attack on the prey item presented (see [Supplementary Material](#) for model outputs and plots). Trial sequence was included in the best full model, however, indicating that bird response to a given treatment was influenced to a certain degree by its experience within the experimental paradigm. When we divided the data set into the two bird species, we found that the Bayesian estimates for each of the treatments overlapped (see [Supplementary Materials](#)). We did find a difference in the number of times each species of motmot closely inspected a bug, however. The whooping motmot got close to a bug without its hindleg flags more frequently than a bug with its flag legs intact (n intact = 18, n ablated = 26, $P = 0.02$). The broadbill motmot overall approached bugs less than the whooping and did not display a difference in their inspection of intact or ablated bugs (n intact = 12, n ablated = 8, $P = 0.11$). When motmots attacked crickets (unmodified or with flags added), they almost always killed and ate the prey item, and they most commonly attacked the body rather than the hindlegs (>90% strikes). Thus, the ~20% survival benefit is a result of birds being more reticent to attack crickets with flags added, rather than mis-striking these prey. In only 1/32 (3%) trials where a motmot attacked a cricket with flags added, did it aim for the hindleg region in its initial strike. Motmots that attacked crickets with flags added frequently manipulated the prey with their beak to remove these modified hindlegs (25/27 = 93%), while this behavior was uncommon among the unmodified crickets (6/54 = 11%).

Chick palatability trials

We tested 15 chicks and were able to collect data from 14 that willingly ate a control cricket during the first experimental trial.

We offered half of the chicks ($n = 7$) intact matador bugs in all of their trials and half of the chicks ($n = 7$) matador bugs with their flag legs ablated. Chicks presented with intact matador bugs avoided these prey in 57% of trials (8/14). They pecked at (tasted ([Schuler and Hesse 1985](#))) bugs in 36% of trials (5/14) and consumed bugs in 21% of trials (3/14). Chicks presented with ablated bugs showed similar results—they avoided the bug in 40% of trials (6/15), pecked at the bug in 47% of trials (7/15) and ate the bug in 13% of trials (2/15) ([Figure 2](#)). The latency to attack bugs with and without their hindleg flags did not statistically differ, although this may be due to low sample size, as the average latency to attack intact bugs was ~35 (SE = 14.51) seconds, while the average latency to attack ablated bugs was ~18 (SE = 11.80) seconds (see [Supplementary Material](#) for raw latency times). This nonsignificant trend could indicate greater hesitancy when the chick had access to the full aposematic suite of the intact bug, but more trials are needed to increase statistical power. Three chicks performed head-shaking behavior after tasting a matador bug, which has been well described as a response to a distasteful prey object ([Supplementary Video S5](#)) ([Schuler and Hesse 1985](#)).

When we pooled the data across treatments, we found that chicks avoided matador bugs 48% of the time (14/29 trials), tasted matador bugs 41% of the time (12/29), and ate matador bugs 10% of the time (3/29 trials). This is in stark contrast to their reaction to the cricket controls, which were also novel prey. Chicks avoided crickets 14% of the time (4/29), tasted but did not eat crickets 10% of the time (3/29), and consumed crickets 76% of the time (22/29) ([Figure 2](#)). These proportions are statistically different across prey types ($P < 0.05$ for all comparisons; See [Supplementary Materials](#) for binomial test outputs). All four trials where chicks avoided a cricket took place after the chick had tasted an ablated matador bug. Chicks only aimed 2/11 strikes at matador bug flags ([Supplementary Video S6](#)).

DISCUSSION

The brightly colored flags of the matador bug appear to function as an aposematic signal to birds. Our results also offer strong evidence that flags do not act as deflective targets. Despite their deterring effect, flags are not the sole signal that avian predators use to assess prey. In direct contrast to control crickets, which were attacked nearly 100% of the time, motmots avoided intact bugs 100% of the time ([Supplementary Videos S1 and S2](#)). Bugs with flag legs ablated experienced a similar survival benefit, with only one bird attacking and eating an ablated bug in its first trial with a coreid (that is, all previous prey items were crickets). Thus, this strike may have been prompted by an assumption that prey items on the platform would be palatable. Motmots attacked crickets with flag legs ~20% less than unmodified crickets, but more often than either intact or ablated bugs ([Figure 1](#)). Flags therefore informed bird foraging decisions, but not to the exclusion of other prey attributes.

The eight motmots used in this study (four of each species) were adults and thus may have been experienced with matador bugs and other coreids commonly found in the area. We therefore used palatability trials with 14 naive chicks to investigate whether motmot avoidance of matador bugs and crickets with flags was predicated by chemical defense in these bugs. Chicks ate only 10% of matador bugs, in comparison to their behavior toward another novel prey animal, crickets, which they consumed ~75% of the time. This is indicative of an innate avoidance response to matador bugs. Previous work using naive chicks has demonstrated an unlearned

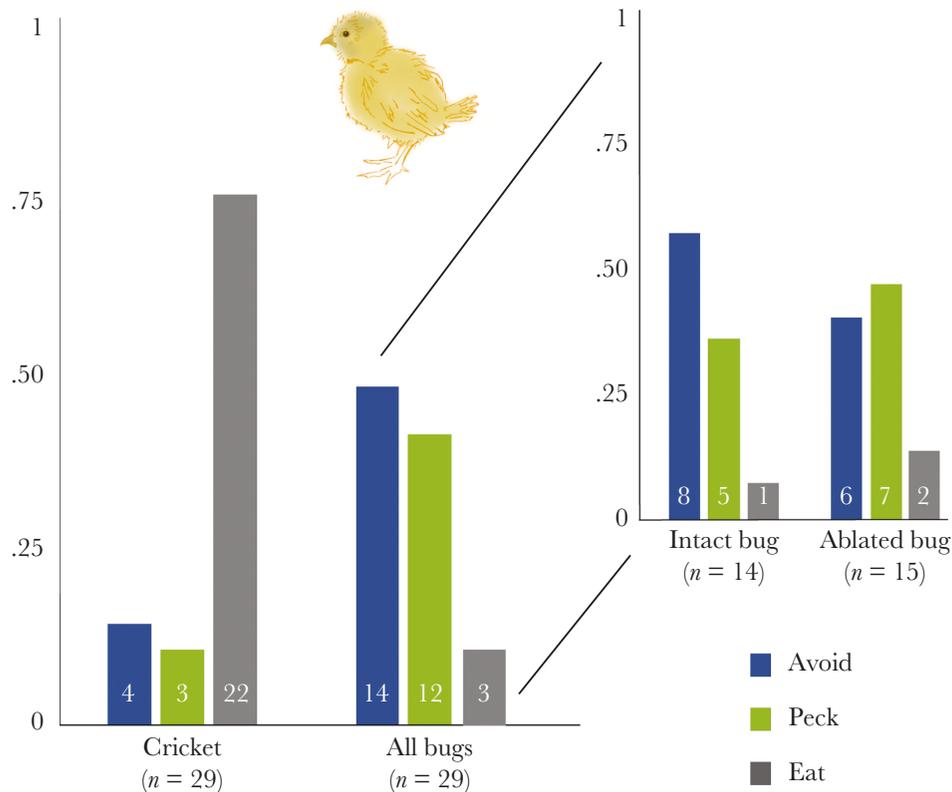


Figure 2 Trials with naïve chicks show that matador bugs are relatively unpalatable and elicit greater innate avoidance behaviors than another novel prey item, crickets. Chick behavioral responses to crickets and matador bugs were significantly different across all behavioral categories. Inset shows the pooled matador data broken down by intact bugs (with flag legs), which were offered to half of chicks (7) and ablated bugs (flag legs removed), which were offered to the other half of chicks (7). The number of trials in which a given behavior was performed by naïve chicks is written within each bar and the total number of trials with each prey treatment category is listed below the category name. Avoid is no interaction with the prey, peck is tasting (pecking) prey without consumption, and eat is full ingestion of prey animal.

aversion to classic aposematic coloration (Roper and Cook 1989), and naïve motmots have shown similar innate avoidance of potentially dangerous, conspicuously colored prey (Smith 1975). Only two chicks that tasted matador bugs (i.e., contacted with their beak or consumed some portion of the bug) then ate the next bug that was presented to them. Seven others tasted a matador bug and then either refused the next one or pecked at it, and three chicks displayed classic aversion behaviors after tasting a bug (Supplementary Video S5). Matador bugs therefore seem to be relatively unpalatable in addition to being visually unappetizing.

To determine the role of flags in the matador bug's overall aposematic appearance, we offered half of the chicks bugs with their flags intact and the other half bugs with flags removed. Chicks presented with intact matador bugs entirely avoided these prey ~60% of the time, and chicks presented with matador bugs without flags avoided these prey ~40% of the time. This could indicate a stronger innate avoidance response when the flag legs are included in the aposematic signaling suite. In concert with this notion, chicks tasted bugs with flags ~36% of the time and bugs with flags removed ~47% of the time. While these differences are not significant, they indicate a trend toward flags + body coloration eliciting a more reliable anti-predator effect than bug body color alone. We found similar evidence of an aposematic function of flags from whooping motmots, where these predators were more likely to closely approach and inspect bugs without their flag legs versus bugs with their flag legs. Broadbill motmots did not show the same pattern. Due to their differing foraging

strategies, it is possible that broadbill motmots were able to visually assess the prey and make their foraging decision from farther away, while the whooping motmot required more close-range visual confirmation when the flags were absent from the aposematic profile.

We did not find evidence for a defective effect of this elaborate trait against avian predators, as motmots and chicks almost never aimed their strikes at these colorful appendages (Supplementary Video S6). Interestingly, after capturing a cricket with bug flag legs added, both species of motmot commonly manipulated it with their bill for several seconds (2–15) and sheared off one or both bug legs before consuming the cricket (see Supplementary Video S4). This behavior was more common when handling modified crickets versus unmodified control crickets. Due to the experimental design, we cannot know whether birds were reacting to the flag itself or the UV glue. However, we did not note any subsequent aversion to prey after a motmot incidentally consumed the glue. It is therefore more likely that motmots either identified flag legs as an unrewarding component of the prey animal (Kaspari 1991), or that they detected toxins sequestered in the flag's cuticular tissue. Previous work with chemically defended butterflies has revealed that some species localize toxins in their wings, possibly to educate predators who grab this brightly colored, less essential material (compared with the head or thorax) (Mason and Deane Bowers 2017). It is possible that the conspicuous, detachable flags of the matador bug act as a last line of defense—providing a noxious reminder to predators that the bug is chemically protected.

Although flags did not divert bird attacks to the legs, they may serve a deflection purpose in other anti-predator contexts. Twitching hindwing extensions of lycaenid butterflies have been shown to divert attack by jumping spiders (Sourakov 2013) but do not elicit the same response in mantids (López-Palafox and Cordero 2017; Hendrick et al. 2022). Thus, while we did not see a redirecting effect of flags in this study, the matador bug's previously described waving behavior, coupled with fast autotomy under stress (Embets et al. 2020) provides intriguing initial evidence that they may be deflective against other predators. An in-depth analysis of the waving behavior during predatory encounters is needed, perhaps against smaller predators with visual systems that are more likely to be fooled by this lure (Bartos and Minias 2016; Vickers and Taylor 2018). Flags may also be more likely to act as deflective targets in flight, as has been shown with the trailing hindwing tails of moths fleeing bats (Barber et al. 2015; Rubin et al. 2018). Future studies testing the role of flags during aerial escape will be elucidating.

Here, we have tested for the first time the role of large, brightly colored coreid flags against predators. These flags appear to be a redundant signal (Hebets and Papaj 2005), acting as “back-up” to other aspects of the bug's aposematic profile, such as the black, yellow, and orange body and head colors (Schuler and Hesse 1985; Miller and Hollander 2010), its movements (Dowdy and Conner 2019), and possibly its alarm pheromone, although preliminary results show that olfactory emissions do not independently play a strong role in deterrence, that is, an anecdotal two-bird trial revealed that motmots did not avoid eating mealworms coated in matador bug alarm pheromone (see discussion in Supplementary Material). Olfaction has been shown to influence learning in chicks, but only in the presence of other aposematic cues (Marples and Roper 1996; Winters et al. 2021). It is therefore possible that motmots and chicks were using the bug's alarm pheromone, in concert with bug coloration, to identify the prey animal (in the cases where a bug produced this chemical). If this were the case, it would provide further support for the flag as a protective signal, as this would be another component of the aposematic suite that crickets with flag legs did not convey to the predator. Instead, the reduction of attacks on modified crickets seems to be explained solely by the addition of flag legs (Figure 1). Our study therefore demonstrates that coreid flags act as an aposematic signal on their own, but that birds can use alternative cues in the absence of flags to identify that the prey is chemically defended. According to the redundant signal hypothesis, this could have evolved to increase the reliability of the signal (that is, to make it harder for Batesian mimics to dilute the signal (Lindström et al. 1997)) or to increase the reliable reception, processing, and behavioral response of a receiver (Johnstone 1996; Hebets and Papaj 2005; Hristov and Conner 2005). Multiple signals could also have evolved to override environmental noise, if, for instance, flags are more effective at conveying this signal against convoluted backgrounds or across longer distances (Hebets and Papaj 2005). We found an intriguing suggestion that this may be the case from whooping motmots more closely inspecting bugs without flags compared to bugs with flags intact. We do not treat this as strong evidence, however, as the visual acuity of these two species is not known, and we therefore cannot assess how intensively motmots were inspecting prey from other positions in the cage. Future work in more visually complex environments where the bird is forced to make a foraging choice from a greater distance away and under increased time constraints could reveal more detail about the aposematic role of flags.

We note a few other aspects of our experiment that may not entirely reflect predator-prey interactions in the wild. Due to the nature of our experimental paradigm, birds were trained to expect prey items on the platform, and all prey were clearly easy for the bird to distinguish from the background. Thus, any element of camouflage that these traits might generate in other settings was not at play here. This was also experimentally beneficial, however, as the discrepancy in movement patterns between individual prey animals likely did not contribute to their survival success—motmots were clearly aware when we introduced a new prey item and could see it from nearly every perch in the cage (aside from rare occasions when they were on ground). Additionally, our presentation rate of chemically defended prey compared to palatable prey probably does not directly align with the true proportion in the natural world (Kikuchi et al. 2021). Thus, birds may have been on higher alert for chemically defended prey with bug gestalt than they would be in the wild. Motmots may also have shown a reduced predatory response to modified crickets simply because these prey looked “odd.” However, studies into the oddity effect have mostly shown that predators are attracted to odd prey, possibly because they are easier to track or are expected to be easier to capture (Mueller 1971; Almany et al. 2007). We also did not find any evidence that motmots were more hesitant to attack modified crickets upon initially encountering this treatment (in fact, we found a slight trend to the contrary (see Supplementary Material), thus indicating that they were not put off by these prey seeming unnatural. Finally, it is possible that the flag legs deflect the avian attack when the bug takes flight. The matador bugs in our study could fly short distances on their tether but could not achieve a full evasive flight posture or behavior.

Predation is only one natural selection force, and we note the need for studies testing the effect of these flags on flight kinematics (Berthé and Lehmann 2015) or potentially thermoregulation (Wasserthal 1975). While these other factors may have helped shape this trait, flags are clearly also a visual signal. Together with previous work that did not find an obvious function of flags in reproductive competition (Longbottom et al. 2022), the results from this study indicate that predation by birds has likely been one of multiple pressures driving the evolution of this elaborate trait. Future research with diverse predators and phylogenetic comparisons will reveal more about its evolutionary tempo and mode. Large, brightly colored flags seem to be constrained to the Anisoscellini tribe; however, small, dull-colored flags are widespread across Coreidae (Forthman et al. 2020). We suggest the need for more nuanced investigation of the flag trait—including tests of flags of differing sizes and shapes—to better understand the potential adaptive role of intermediate forms and the evolutionary route by which this elaboration would have arisen. An integrated analysis, mapping host switches to chemically defended plants and possible associated transitions in coreid hindleg morphology, could also be informative for inferring the evolutionary history of leg modifications (Loeffler-Henry et al. 2023). Recent phylogenetic analysis indicates that hindleg shape is labile across Coreidae (from enlarged femurs to expanded tibiae) (Miller et al. 2023). This diverse and speciose family therefore offers a unique opportunity to study the evolution of elaborate traits shaped by disparate selective forces.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

FUNDING

This work was supported by the Florida Museum of Natural History Travel Award, the Journal of Experimental Biology Travelling Fellowship, the UF Matthew Smith Memorial Fellowship in Animal Behavior, and STRI Anthony Coates Postdoctoral Fellowship to J.J.R., the National Science Foundation Postdoctoral Research Fellowship in Biology Grant #2209192 to J.J.F., and the Earl S. Tupper Fellowship to U.S. and the Stengl-Wyer Scholars program to U.S.

We greatly appreciate the help of Rachel Page and Gregg Cohen in facilitating this work. We thank Lovisa Dück & Christian Ramos for their invaluable assistance in the field and collecting insects. We thank Mario Santamaria for access to his farm and maracuyá plants. Sabrina Amador edited the Spanish version of the abstract. Insects were reared in 'La Chinchieria' The Bug Hut, a greenhouse facility hosted by the Smithsonian Tropical Research Institute. We would also like to acknowledge the support of MiAmbiente (Ministerio de Ambiente, Panamá) for permitting collection and research (permit #SC/A-33-19 and ARG-0120-2022).

CONFLICT OF INTEREST STATEMENT

The authors declare they have no competing interests.

AUTHOR CONTRIBUTIONS

Juliette Rubin (Conceptualization [Equal], Data curation [Equal], Formal analysis [Equal], Funding acquisition [Equal], Investigation [Equal], Methodology [Equal], Project administration [Equal], Resources [Equal], Supervision [Equal], Visualization [Equal], Writing—original draft [Equal]), Jorge Medina-Madrid (Investigation [Equal], Methodology [Equal], Project administration [Equal], Writing—review & editing [Equal]), Jay Falk (Conceptualization [Equal], Investigation [Equal], Methodology [Equal], Writing—review & editing [Equal]), and Ummat Somjee (Conceptualization [Equal], Funding acquisition [Equal], Investigation [Equal], Methodology [Equal], Project administration [Equal], Resources [Equal], Supervision [Equal], Visualization [Equal], Writing—review & editing [Equal])

DATA AVAILABILITY

Supplementary material and videos can be found in the electronic supplementary material. Analyses reported for this study can be reproduced using the data and R code in Rubin et al. (2024).

Handling Editor: Emilie Snell-Rood

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