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APOSEMATIC SIGNAL VARIATION PREDICTS MALE–MALE INTERACTIONS IN A POLYMORPHIC POISON FROG

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Many species use conspicuous “aposematic” signals to communicate unpalatability/unprofitability to potential predators. Although aposematic traits are generally considered to be classic examples of evolution by natural selection, they can also function in the context of sexual selection, and therefore comprise exceptional systems for understanding how conspicuous signals evolve under multifarious selection. We used males from a highly territorial poison frog species in a dichotomous choice behavioral test to conduct the first examination of how aposematic signal variation influences male–male interactions. Our results reveal two behavioral patterns: (1) male dorsal brightness influences the behaviors of male conspecifics such that males approach and call to brighter males more frequently and (2) a male’s dorsal brightness predicts his own behavior such that bright males approach stimulus frogs faster, direct more calls to bright stimulus frogs, and exhibit lower advertising call pulse rates (a fitness-related trait). These findings indicate the potential for sexual selection by male–male competition to impact aposematic signal evolution.

KEY WORDS: Aggression, brightness, *Dendrobates pumilio*, selection—sexual, warning coloration.

Many species use conspicuous “aposematic” signals to communicate unpalatability to potential predators, a strategy that is widespread throughout the animal kingdom (Ruxton et al. 2004). Although aposematic traits are generally considered to be classic examples of evolution by natural selection (Müller 1879), they can also function in the context of conspecific communication (Summers et al. 1999; Jiggins et al. 2001). Aposematic organisms therefore comprise exceptional systems for understanding how conspicuous traits evolve under multifarious selection. However, several potentially important selective forces remain unexplored in aposematic systems. For example, aposematic traits might influence the intensity and/or outcomes of aggressive interactions between male conspecifics. This is especially probable given the well-documented role that conspicuous, nonaposematic signals play in male territorial behaviors (Andersson 1994). Male brightness/coloration is one conspicuous signal that males

may attend to during territorial interactions in aposematic species. Studying the presence or absence of male selection on warning coloration will elucidate the potential for evolutionary feedbacks between intrasexual selection (e.g., male–male competition) and other forms of selection on aposematic signals.

Many frogs of the family Dendrobatidae are aposematic, exhibiting bright coloration and patterning and sequestering toxins acquired from their diet (Santos et al. 2003). The strawberry poison frog, *Dendrobates pumilio* (formerly *Oophaga pumilio*, see Santos et al. 2009), is perhaps the most polymorphic of the poison frog species. *Dendrobates pumilio* is monomorphic in coloration across most of its range from Nicaragua to Panama, but in the Bocas del Toro archipelago in western Panama the species exhibits dramatic variation in both hue and brightness across island populations and on the mainland (Daly and Myers 1967; Siddiqi et al. 2004). The selective forces that have produced this remarkable

variation remain unclear. *Dendrobates pumilio* has the potential for color vision (Siddiqi et al. 2004) and there is evidence of sexual selection by female preference on male coloration and brightness in this species (Summers et al. 1999; Reynolds and Fitzpatrick 2007; Maan and Cummings 2008, 2009). Sexual selection by female choice on ecologically important traits can result in sexual dimorphism in those traits (Lande and Arnold 1985). Coincident with theory, one population of *D. pumilio* contains males that are significantly brighter than females (Maan and Cummings 2009).

Although past studies indicate the potential for female preferences to drive color variation in *D. pumilio*, the other major component of sexual selection, male–male competition, has not yet been investigated. It has been hypothesized that male secondary sexual characteristics can originate through male–male competitive interactions (Berglund et al. 1996). This may be particularly true for highly territorial species such as *D. pumilio*. Male *D. pumilio* exhibit territory site fidelity (McVey et al. 1981) and vigorously defend their sites through vocalizations and close-range aggressive encounters (Bunnell 1973; Forester et al. 1993; Baugh and Forester 1994; Gardner and Graves 2005; Prohl 2005). Thus, the selective pressures imparted by male–male competition may conflict with or facilitate signal divergence mediated by predators or female preference across populations.

Given the evidence for female preference for brighter males in some populations of this species, we predicted that male–male interactions could also be mediated by male brightness. We examined if and how aposematic signal variation affects male–male interactions in *D. pumilio* by experimentally manipulating the brightness of stimulus males and recording the responses of focal males, and assessing whether the brightness of stimulus males and/or focal males predicted the outcomes of male interactions. Here we report that a male's brightness both robustly predicts his own behavior and influences the behavior of competitors. Together, these findings indicate that male intrasexual selection may serve as a mechanism to affect color variation in *D. pumilio*.

Methods

ANIMALS

Male *D. pumilio* ($N = 75$) were captured during daytime hours during July and August of 2009 and kept at the Bocas del Toro Field Station of the Smithsonian Tropical Research Institute, Panama. We used frogs from one population (Isla Solarte) in which females have previously been shown to prefer to interact with brighter males and in which there is sexual dimorphism, as well as intrasexual variation, in dorsal brightness (Maan and Cummings 2009). Male frogs were located in the field; if they were calling ($N = 25$), their calls were recorded for a minimum of 1 min using a Marantz PMD660 portable digital recorder (Marantz, Mahwah, NJ). Frogs were then captured and measured

for snout-vent length (SVL: to the nearest 0.1 mm), mass (to the nearest 0.01 g), body temperature at the dorsal surface (within 0.1°C), and spectral reflectance in a temperature-controlled room (approximately 23°C) within 24 h of capture. Body temperature was measured using an infrared laser thermometer (Mastercool, Randolph, NJ) immediately prior to spectral reflectance measurements for a majority of the frogs tested in behavioral assays ($N = 57$) because it can induce facultative color change in other amphibians (Tattersall et al. 2006) and is associated with fitness in ectotherms (Huey and Kingsolver 1989). Frogs were housed individually in outdoor terraria, fed a diet of termites, ants, and fruitflies, with fresh water provided twice daily.

MALE COLORATION

Spectral reflectance measurements were taken of each male at the head, dorsum, belly, and throat (2 measurements per region) using a EPP200C UV-VIS spectrometer, SL-4 Xenon lamp, and R400-7 reflectance probe (StellarNet Inc., Tampa, FL). Spectralon white standard measurements were taken between frogs to account for lamp drift.

CALL ANALYSIS

Male calls were edited for length and background noise in Audacity software and analyzed for call characteristics in Raven software. The call characteristics analyzed included mean call rate, mean call duration, duty cycle (mean call rate \times mean call duration), pulse rate (number of pulses per call segment), and dominant frequency, as described by Prohl (2003). Call characteristics were scored independently by two observers and averaged.

EXPERIMENTAL TREATMENTS AND SETUP

Rival choice experiments

Focal male responses toward brighter and duller stimulus males were evaluated in a series of two-way choice experiments modified from those used previously in our laboratory (Fig. 1A; Maan and Cummings 2009). Focal frogs were presented with two stimulus males originating from the focal frogs' native population. Stimulus male pairs were matched for size, mass, and dorsal reflectance spectra (all differences between males were within one standard deviation of the population mean). The setup was similar to previous experiments (Maan and Cummings 2009) and consisted of three boxes of UV-transparent clear acrylic, one focal male chamber (40 \times 20 \times 20 cm) and two stimulus male chambers (half circles with a radius of 10 cm and 20 cm high). The visual background of each stimulus male chamber was black to minimize differences in color contrast between the stimuli, and a visual barrier blocked the stimulus males' view of each other. Experiments were carried out in an illumination-controlled room, and both stimulus males were illuminated with light that mimics conditions on the forest floor, using one 22-inch UV 20W bulb

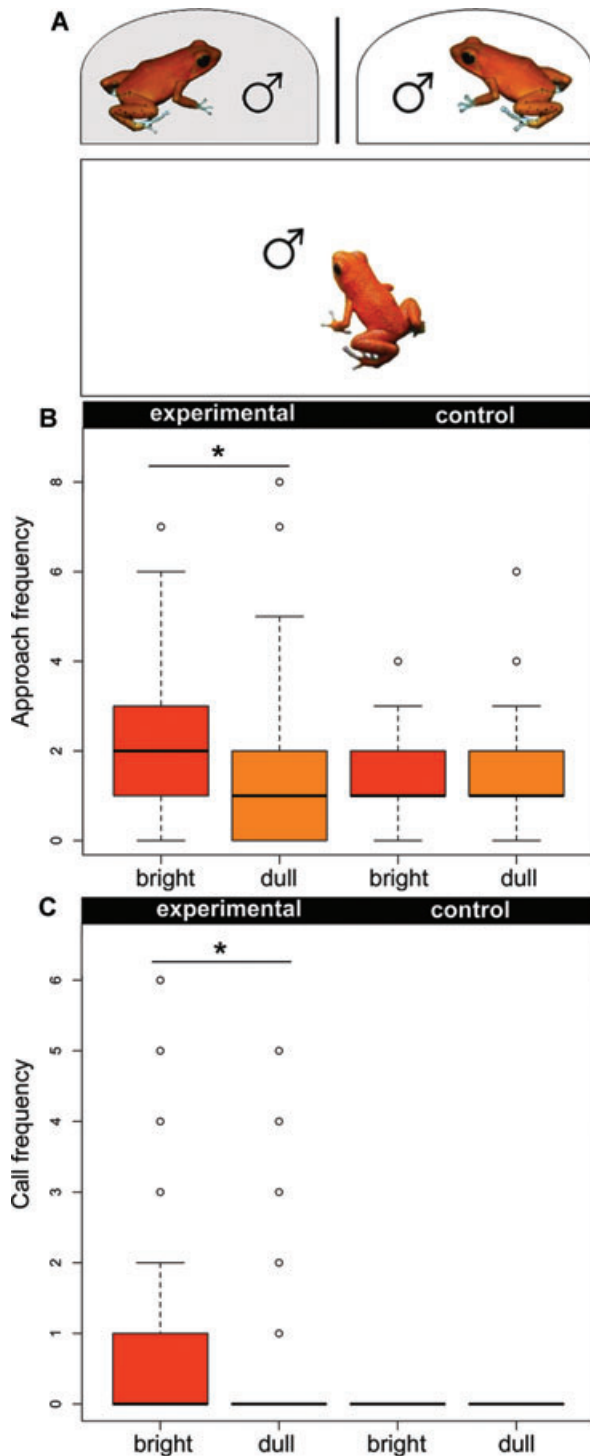


Figure 1. Behavioral responses of focal males to stimulus males. (A) Schematic of agonistic choice experimental setup showing two stimulus males (small compartments) and the focal male (large compartment). Box-and-whisker plots of (B) experimental and control trial approach frequencies of focal males to bright and dull chambers, and (C) experimental and control trial call frequencies of focal males to bright and dull chambers. Boxes span the first and third quartile of the data, and horizontal black lines represent the median. Whiskers span the range of the data, excepting outliers (open circles).

and one 100 W “Daylight Blue” incandescent bulb, filtered by two green–blue filters (Lee 728, CyanGel 4315). We manipulated focal male perception of stimulus male brightness by using neutral density filters (one Lee 298 and one GamColor 1514) above one stimulus male for the first 10 min of observation. For the next 10 min, these filters were moved to the other male’s chamber, thus reversing the brightness difference between the stimulus males. We reduced male brightness by ~65%, within 2.5 standard deviations of mean male brightness in the Solarte population. Irradiances for both the dull and bright lighting conditions fell within the upper quartile of territory irradiance flux ($\log[\sum I\{\lambda\}]$ from 300 to 700 nm] in this population (Cummings and Maan, unpubl. data). Control experiments used identical light treatments but with empty male chambers to control for a possible focal male tendency to approach darker or brighter areas.

No focal male was tested more than twice per day, and stimulus pairs were used for a maximum of eight experiments per day. All frogs were tested within one week of capture. Focal males were acclimated to the experimental chambers for at least 60 min and allowed to interact freely with a native female within their chamber to motivate territorial behavior. Stimulus males were acclimated for 30 min without visual contact. After acclimation, visual barriers were removed and the focal male was placed under a glass in the middle of his chamber to allow observation of both stimulus males for 2 min. The glass was then lifted and the focal male was observed for two 10-min periods.

Territorial interactions in *D. pumilio* involve approach by the intruder male and impingement on or near a male’s territory followed by a stereotyped series of behaviors, including calling and approaches (pers. obs., Bunnell 1973; Baugh and Forester 1994; Gardner and Graves 2005; Prohl 2005), that can either lead to escalation (physical contact involving chases and wrestling) or submission by the intruder male and subsequent exit from the male’s territory. Thus, to score male behaviors, we defined an “interaction zone” as the area within 4 cm (2 body lengths) of each stimulus male, as done previously (Maan and Cummings 2008, 2009). In each trial, we recorded the focal male’s latency to approach an interaction zone, time spent in the interaction zone with each stimulus male, the number of times that focal males approached each stimulus male, as well as the number of calls to each stimulus male. After 10 min of observation, visual barriers were inserted again, positions of neutral density filters were reversed, and the focal male was confined under a glass for 2 min. After this, the barriers were removed and observations resumed. Most males were tested in both experimental and control treatments.

Analysis of brightness

Dorsal reflectance spectra were obtained by averaging measurements of the head and dorsum (two measurements per region). To

measure “brightness” differences between males, we evaluated the log of the difference in total reflectance flux ($\log[\sum R\{\lambda\}]$ from 300 to 700 nm) and the estimated difference in brightness contrast (ΔL) of frog coloration when viewed against a natural background by a *D. pumilio* viewer using a receptor-based visual model described previously (Maan and Cummings 2009).

Data analysis

All statistical tests were performed in R software. Count data (approaches, calls) were summed across the two trials for each male, and data from all males were used in these analyses ($N = 75$ in experimental trials, $N = 71$ in control trials). Focal frog approach and call count data were analyzed using Wilcoxon signed-rank tests to accommodate for data that were not normally distributed. Latency analyses were restricted to males that entered the interaction zone in both trials (57 out of 75 males in experimental trials, 52 out of 75 in controls). Latencies were averaged across trials for each included male. Five males did not approach the interaction zone in either trial. Total focal frog approach latency and interaction time data were modeled using generalized linear models (GLM) with underlying Poisson or quasi-Poisson distributions, and proportions of focal frog approach, call and interaction time with the different stimuli using a Binomial or quasi-Binomial distribution to adjust for nonnormality and underdispersion/overdispersion of data. Individuals that did not approach the interaction zone or call were not included in proportion analyses. A Chi-square goodness-of-fit test was used to assess whether focal males exhibited a bias in the first stimulus male that they approached.

First, we tested whether focal males exhibited differential responses toward the more brightly or darkly illuminated stimulus males (experimental trials) or empty chamber (controls). Subsequently, we evaluated whether focal male behavior was predicted by a male’s own brightness. We also tested whether male brightness predicted advertisement call characteristics, body size, mass, or body temperature using linear models.

Results

FOCAL MALE PREFERENCES FOR BRIGHTER STIMULUS MALES

Focal males approached (Fig. 1B; $V = 1139$, $P = 0.011$, $N = 75$) and called to (Fig. 1C; $V = 271.5$, $P = 0.014$, $N = 75$) the more brightly illuminated stimulus male significantly more often than the dull stimulus male. Focal males did not exhibit biases in the first frog that they approached ($\chi^2 = 0.5$, $P = 0.480$), or interaction time with bright versus dull stimuli ($V = 1546$, $P = 0.076$, $N = 75$; mean = 400.9 sec for bright chambers, 308.4 sec for dull chambers). Males showed no bias in the number of approaches

(Fig. 1B; $V = 506$, $P = 0.698$, $N = 71$) or time spent ($V = 1111$, $P = 0.864$, $N = 71$; mean = 346.6 sec for bright chambers, 349.9 sec for dull chambers) in front of empty chambers with differing illumination during control trials. No males called during control trials (Fig. 1C).

BRIGHTNESS OF FOCAL MALES AND FOCAL MALE BEHAVIOR

Brighter focal males approached stimulus males faster than duller focal males ($\log[\sum R\{\lambda\}]$): $F = 5.9355$, $P = 0.018$, $N = 57$; (shown in Fig. 2A); ΔL : $F = 10.166$, $P = 0.002$). This tendency remained even when an exceptionally bright focal male was removed from the analysis ($\log[\sum R\{\lambda\}]$: $F = 4.3333$, $P = 0.042$; ΔL : $F = 8.0055$, $P = 0.007$, $N = 56$). Focal male brightness did not predict latency to approach control chambers ($\log[\sum R\{\lambda\}]$: $F = 2.1092$, $P = 0.153$; ΔL : $F = 2.1396$, $P = 0.150$, $N = 52$).

Brighter focal males directed a greater proportion of their calls to the bright stimulus frog than did duller focal males (Fig. 2B; $\log[\sum R\{\lambda\}]$: $Z = 2.140$, $P = 0.032$; ΔL : $Z = 2.182$, $P = 0.029$, $N = 29$); this tendency remained even when the brightest male was removed from the analysis ($\log[\sum R\{\lambda\}]$: $Z = 2.588$, $P = 0.010$; ΔL : $Z = 2.679$, $P = 0.007$, $N = 28$). However, focal frog brightness did not predict the proportion of approaches to ($\log[\sum R\{\lambda\}]$: $Z = 0.066$, $P = 0.948$; ΔL : $Z = 0.132$, $P = 0.895$, $N = 69$) or the proportion of time spent with the brighter stimulus frog ($\log[\sum R\{\lambda\}]$: $F = 0.4357$, $P = 0.512$; ΔL : $F = 0.6344$, $P = 0.429$, $N = 70$). No relationships were detected between focal male brightness and the total number of approaches ($\log[\sum R\{\lambda\}]$: $Z = -0.568$, $P = 0.570$; ΔL : $Z = 0.176$, $P = 0.860$, $N = 75$), calls ($\log[\sum R\{\lambda\}]$: $Z = -0.400$, $P = 0.689$; ΔL : $Z = -1.096$, $P = 0.273$, $N = 75$) or total interaction time spent with stimuli ($\log[\sum R\{\lambda\}]$: $F = 0.1006$, $P = 0.752$; ΔL : $F = 0.0038$, $P = 0.951$, $N = 75$).

A negative relationship was observed between focal male brightness and body temperature (Fig. 2C; $\log[\sum R\{\lambda\}]$: $F = 5.1423$, $P = 0.027$, $N = 60$), although this result was not significant using brightness estimates calculated with the frog visual model (ΔL : $F = 3.003$, $P = 0.088$). Brightness was not correlated with mass ($\log[\sum R\{\lambda\}]$: $F = 0.9225$, $P = 0.34$; ΔL : $F = 0.6019$, $P = 0.440$, $N = 75$), SVL ($\log[\sum R\{\lambda\}]$: $F = 1.3123$, $P = 0.256$; ΔL : $F = 1.6451$, $P = 0.204$, $N = 75$), or SVL-mass residuals, a common measure of body condition ($\log[\sum R\{\lambda\}]$: $F = 0.082$, $P = 0.776$; ΔL : $F = 0.0037$, $P = 0.952$, $N = 75$). Finally, we found that brighter males exhibited lower advertisement call pulse rates in the field than duller males (Fig. 2D; $\log[\sum R\{\lambda\}]$: $F = 5.0684$, $P = 0.034$; ΔL : $F = 5.2791$, $P = 0.031$, $N = 25$). Ambient temperature did not account for differences in call pulse rates ($F = 0.0615$, $P = 0.807$, $N = 20$). Brightness was not predictive of mean call rate, mean call duration, duty cycle, or dominant frequency (data not shown).

Discussion

Our agonistic choice experiments demonstrate that males of at least one of the polymorphic *D. pumilio* populations attend to the brightness of potential rivals during male–male interactions. Brighter stimulus males elicited significantly more calls and approaches from focal males than did their dull counterparts (Figs. 1B,C). Both of these behaviors are central components of aggressive interactions between males in the field (Crothers, pers. obs., Bunnell 1973; Gardner and Graves 2005; Prohl 2005), and the finding that both bright and dull males respond to a potential rival's brightness suggests a population-wide response to this cue. It is possible that brighter males were approached and called to more often in experimental trials by virtue of their enhanced conspicuousness. However, our findings are unlikely to result from simple differences in the detectabilities of bright versus dull males, as focal frogs neither approached bright males first in behavioral tests, nor spent more time interacting with them. Furthermore, no simple preferences for brightly illuminated chambers were observed, as we found no biases in male behaviors directed at empty chambers with differing illumination.

Although focal males responded significantly more towards brighter potential intruders than duller ones, the nature of the response differed depending upon the focal male's own brightness. We found that focal male brightness predicted focal male behavior, with brighter males approaching stimulus frogs faster than their dull counterparts and directing more of their calls to bright stimulus frogs (Figs. 2A,B). Other physiological attributes that correlate with brightness may underlie the behavioral differences among males of differing brightness. For instance, the correlation between male body temperature and brightness (Fig. 2C) might indicate that brighter males are in better condition (Huey and Kingsolver 1989), and therefore able to respond more aggressively. This correlation is unlikely to result from simple changes in ambient temperature during the course of our experiments, because (1) measurements were performed in a temperature controlled room, and (2) previous investigators have not found temperature effects on *D. pumilio* coloration (Summers et al. 2003). Further investigation into mechanisms underlying color variation in this species will prove especially informative.

Interestingly, brighter males exhibit a lower call pulse rate than duller males (Fig. 2D), which several lines of evidence indicate may likewise be a fitness-related trait. Vocalizations have reliably predicted outcomes of territorial disputes in *D. pumilio* and related species (Stewart and Rand 1991; Baugh and Forester 1994), and a previous study (Prohl 2003) indicates that pulse rate correlates negatively with mating success in this species. Thus, we provide indirect evidence that bright males exhibit call characteristics that may have fitness consequences in the field.

In species in which males provide some parental care, sexually selected traits (such as male brightness in this population) are predicted to be condition dependent, functioning as honest indicators of an individual's condition/quality (Andersson 1986). Advertising conspicuously with enhanced brightness may enhance mating success but only in individuals that have the energetic reserves necessary to bear the costs of the signal (Price 2006). As calling alone is energetically expensive in many anuran taxa (Navas et al. 2008) frequent territorial interactions between adjacent males could impose fitness costs, even if interactions do not escalate to full contact. Taken together, our behavioral (latency response and call pulse rate) and physiological data (correlation between brightness and body temperature) suggest that male brightness may thus function as an indicator trait in poison frogs.

There is ample evidence for bright ornamentation functioning as a badge of status in many taxa (Andersson 1994; Pärt and Qvarnström 1997; Korzan and Fernald 2007), and orange and red coloration (as exhibited by the Solarte population) is well documented as a common signal of dominance and aggression (Pryke 2009). Males in this population could thus use brightness to assess rival territorial abilities (Berglund et al. 1996). Because males vary greatly in brightness within this population (mean $\Delta L = 15.8927$; SD = 2.1580), the differences we observed in male behavior may have perceptible consequences in the field. If focal male behaviors predict defensive capabilities in the field, with brighter males having greater defense of their territories, then male–male interactions may be acting synergistically with female preference to promote male brightness in this population. Alternatively, if eliciting greater response from rivals incurs fitness costs for bright males, male–male interactions could act in opposition to female mating preferences and constrain male brightness. Our results cannot distinguish between these or alternative scenarios in which male competitive interactions may affect the direction of aposematic signal evolution, but future studies will address the fitness consequences of *D. pumilio* male response to rival brightness.

In conclusion, our behavioral results suggest that there is a third component to the evolution of aposematic signals in this species—the response of males to signal variation. Male *D. pumilio* respond to the brightness of potential rivals, preferentially approaching and calling to bright stimulus males, and brighter males approach potential rivals faster and direct proportionally more calls to brighter rivals. Previous work has shown that predators and potential mates attend to coloration (Summers et al. 1999; Jiggins et al. 2001; Ruxton et al. 2004) and brightness in aposematic species (Prudic et al. 2007; Maan and Cummings 2009), and here we demonstrate that male rivals also respond differentially to signal variation. Because territorial interactions

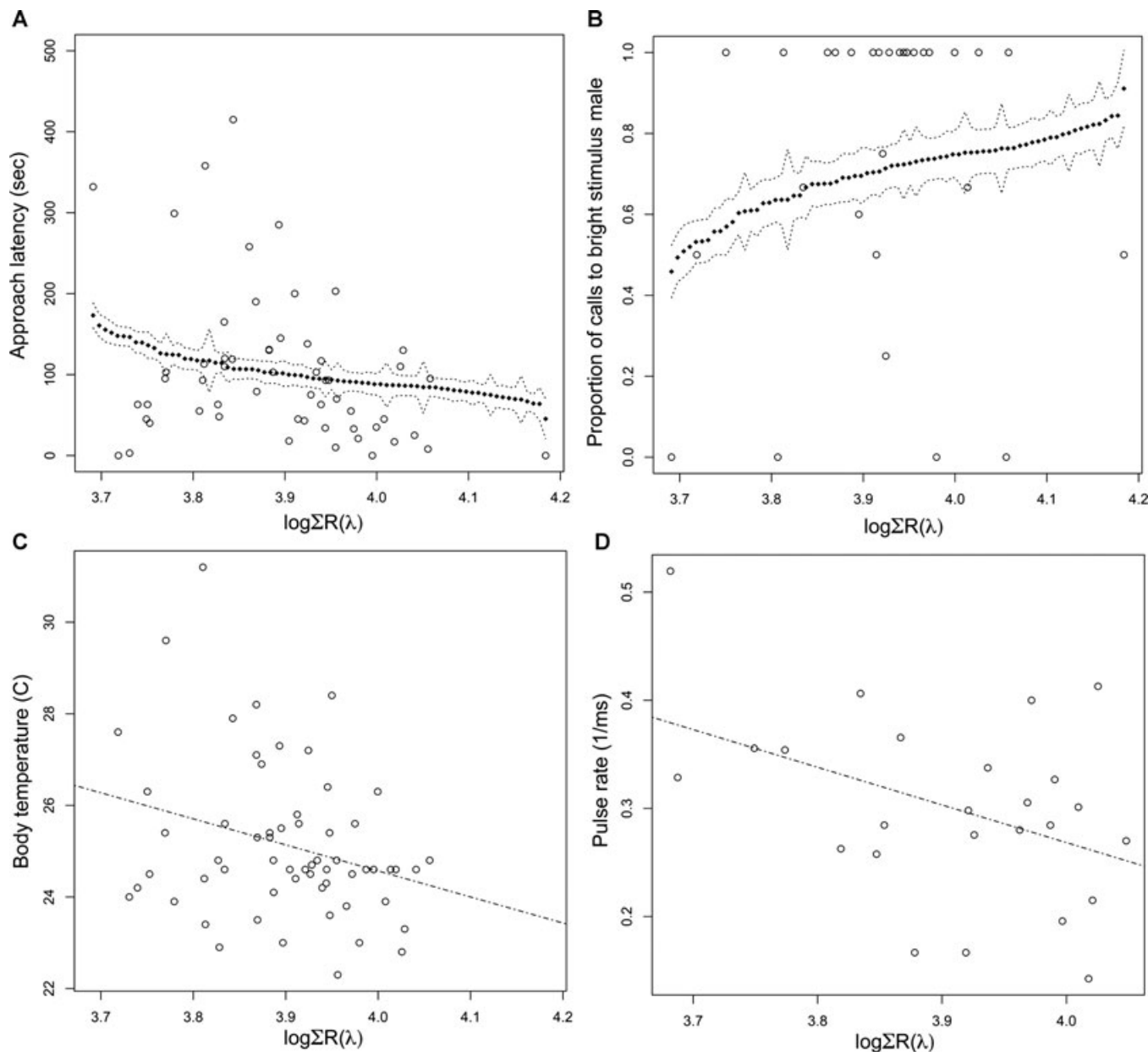


Figure 2. Relationships to focal male brightness ($\log[\Sigma R(\lambda)]$). Open circles represent datapoints for all panels. (A) Latency for focal male to approach interaction zone. Solid diamonds represent predicted probability values of the quasi-Poisson GLM. Dotted lines flanking the predicted values represent the standard error. (B) Proportion of calls directed to bright stimulus male by focal male. Solid diamonds represent predicted probability values of the binomial GLM. Dotted lines flanking the predicted values represent the standard error. (C) Body temperature at dorsal surface for males at time of reflectance measurements. Dotted line represents best-fit line predicted by linear model (Multiple R^2 : 0.08144, Adjusted R^2 : 0.0656). (D) Call pulse rate of males in the field. Dotted line represents best-fit line predicted by linear model (Multiple R^2 : 0.1806, Adjusted R^2 : 0.1449).

between males within the Solarte population are common (Crothers, pers. obs.), differential territorial responses based on rival brightness may be a significant component of signal selection. Females in this population prefer to interact with bright males and males are significantly brighter than females (Maan and Cummings 2009); whether differential responses of males toward brighter potential rivals acts in parallel or in conflict with

female-mediated color divergence depends on the outcomes of these interactions in the field. Together, our data provide the first evidence of males using an aposematic signal (brightness) as a cue during territorial behaviors and tantalizing evidence that brightness may be a conditional signal in these populations. Ongoing studies in the field will further elucidate the roles that male–male competition plays in the evolution of aposematic signals within

these populations, and clarify how multiple agents of selection contribute to signal evolution within this species.

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