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Article

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Sexual signal conspicuity is correlated with tail autotomy in an anoline lizard

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Sexual selection favors conspicuous signals that animals can use to communicate with conspecifics and/or to attract mates. However, natural and sexual selection are often in opposition, as conspicuous sexual signals can also be detected by eavesdropping predators, forcing these signals to also evolve in light of natural selection (Andersson 1994). Although individuals bearing conspicuous sexual traits may be more attractive to potential mates, they also risk their own survival, leading to potentially extreme costs to seemingly advantageous traits. Sexual signals often convey honest information about the sender and so, theoretically, the more conspicuous the signal, the more resources the sender was able to allocate to the trait. A unifying assumption of many hypotheses related to the evolution of costly signals is that intrasexual variability in signal cost is directly related to reproductive fitness (reviewed by Jennions et al. 2001). Whereas many studies reveal that more attacks are seen in the presence (vs. absence) of a sexual ornament, very few have explored how intraspecific variation in a sexual ornament affects predation risk (e.g., Kotiaho 2001). Of these few, many have used artificial models to quantify how risk increases with signal conspicuity: clay models with more conspicuous signals are attacked more than their duller or nonexistent sexual ornamented counterparts (e.g., Swierk et al. 2020). A gap in the literature remains regarding how intrasexual variability is affected by predation risk in real individuals and, in particular, with respect to the visual systems of their predators. This question is vital to address, as variation is the raw material of evolution and, particularly in intrasexual variation of sexual ornaments, forms the basis for models of sexual selection. To explore this question, we studied adult male water anoles (*Anolis aquaticus*). Adult males of most *Anolis* species have a dewlap, a colorful, and extendable flap of skin under their chin that enables them to signal to conspecifics, secure a mate, and defend territory (Losos 2009). Dewlap size and/or color are often found to be positively correlated with body size and bite force and are therefore an honest signal of male quality. High intraspecific and intrapopulation diversity of dewlap color chroma (saturation) are evident in multiple *Anolis* species, making this a useful taxon with which to observe the costs of intrasexual variation of ornaments. In addition, anoles are capable of tail autotomy, the voluntary loss of the distal portion of a tail to escape a predator. Autotomized tails may regrow, though the regrown tails do not have vertebrae, leaving a clear and permanent scar between the original and regrown tail portions. Tail autotomy can therefore be used as a proxy for past predatory attacks (Bateman and Fleming 2011). *Anolis aquaticus* is a small lizard native to the premontane and wet forests of Costa Rica and Panama and inhabits riparian edges of streams. Male water anoles have a large orange-red dewlap, which is extended frequently in order to signal to conspecifics. Water anole dewlaps have positive allometry with body size (Petelo and Swierk 2017), and individuals with larger dewlaps are also bolder and have better body condition (Putman et al. 2018). Evidence also suggests that more conspicuous, redder dewlaps (Figure 1A, C) are associated with greater head size and predicted bite-force (Petelo and Swierk 2017) than duller dewlaps (Figure 1B, D). Using *A. aquaticus* clay models with differently colored dewlaps ("dull" or "bright"), a recent study also provided empirical evidence for increased attack rates of predators on those clay models with brighter (more conspicuous) dewlaps (Swierk et al. 2020). However,

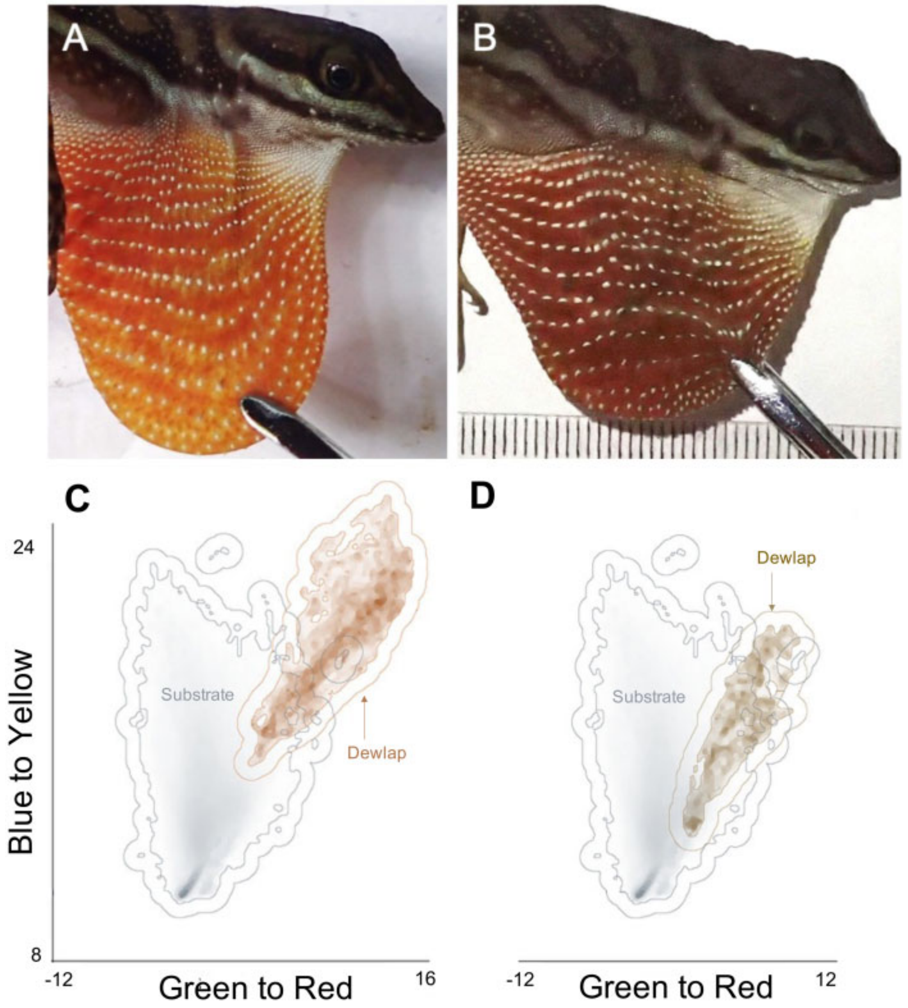

Figure 1. Representative photos of the variation in conspicuity of *A. aquaticus* dewlaps as viewed by humans, including (**A**) a conspicuous ("redder") dewlap and (**B**) a less conspicuous dewlap, both photos standardized using an 18% gray card. Color clouds (see Supplementary Methods) show the amount of overlap of the colors of a riverbank wall substrate, that is, the signaling background, with a (**C**) conspicuous "redder" dewlap, and (**D**) less conspicuous dewlap, following calibration for avian visual spectral sensitivities and acuity. *X*-axes represent a green (medium wavelength) to red (long wavelength) progression of colors, and *Y*-axes represent blue (short wavelength) to yellow (long and medium wavelength), all quantified within Receptor Noise Limited model chromaticity space. The less conspicuous dewlap (**D**) has 17 times greater overlap with the signaling background than the "redder" dewlap (**C**), as perceived through avian eyes.

this study did not consider the range of intrasexual dewlap color variation between the two extremes, leaving an open question of whether males that invest incrementally more into signal conspicuity also bear an incrementally greater predation risk. We used *A. aquaticus* to test how intrasexual variation in a sexual trait (the dewlap) corresponds to costs (history of attacks, as recorded by previous tail autotomy). We hypothesized that there would be a tradeoff between more conspicuous dewlaps and risk of injury: individuals with larger and more brightly colored dewlaps would more likely bear evidence of past attacks. To explore this question, we collected field data on *A. aquaticus* tail autotomy and dewlap size ($n = 170$) and color ($n = 54$), and we used digital photography and visual modeling to quantify this signal's conspicuity to avian predators. Detailed methods can be found in Supplementary Materials.

Following data collection and quantification of dewlap area and color using visual modeling, we examined if dewlap color related to fitness-relevant traits (body size and condition) in *A. aquaticus* using linear models. In each of these two linear models, either the value along the green-red axis ("redness") or the yellow-blue axis ("yellowness") (see Supplementary Materials for a description of these variables) was the response, and body size (measured as snout-vent length [SVL]) and body condition (the residuals of a regression of mass and SVL) were predictors. Year was included as a factor in each model. Dewlap color was positively correlated with male body condition and body size: larger green-red axis values (greater "redness") were related to higher body condition ($F_{1,50} = 5.10$, $P = 0.028$, $r = 0.304$) and SVL ($F_{1,50} = 21.13$, $P < 0.001$, $r = 0.545$). Yellow-blue axis values were neither related to body condition ($F_{1,50} = 1.42$, $P = 0.239$) nor SVL ($F_{1,50} = 2.69$, $P = 0.107$). Next, we used generalized linear models with a quasibinomial distribution to examine the relationship between dewlap conspicuity and tail autotomy. The presence/absence of tail autotomy was the binary response variable in each model, and the color variables (green-red and yellow-blue axis values) or size-corrected dewlap area were predictors. Each model also included year as a factor. Dewlap color associated with past tail autotomy: we found a significant relationship between the presence of tail autotomy and higher green-red axis values (greater "redness") ($\chi^2_1 = 5.59$, $P = 0.018$, $r = 0.291$;

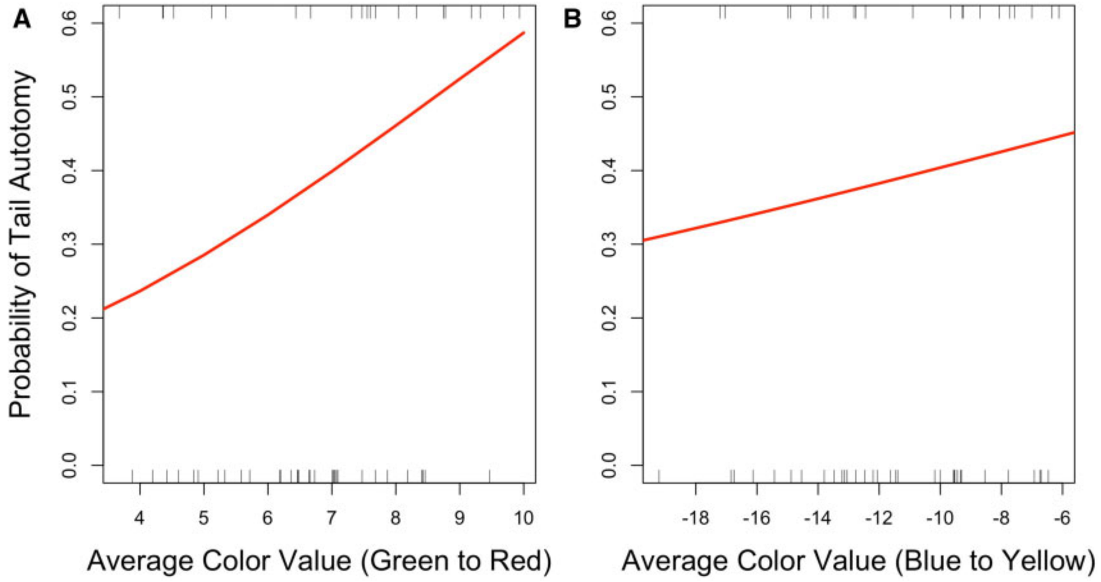

Figure 2. Probability of tail autotomy in *A. aquaticus* as predicted by dewlap (**A**) red-green axis value (greater values indicate greater "redness") and (**B**) yellow-blue axis value (greater values indicate greater "yellowness").

Figure 2A) and yellow-blue axis values (greater "yellowness") ($\chi^2_1 = 4.27$, $P = 0.039$, $r = 0.259$: Figure 2B) values. Dewlap area was not related to tail autotomy (area: $\chi^2_1 < 0.01$, $P = 0.991$). For full model results, please see Supplementary Materials.

Animals often face a tradeoff between sexual signals and antipredator adaptations. Previous work has shown that individuals with a sexual ornament are at a higher risk of predation than those without an ornament (e.g., Swierk et al. 2020), highlighting a tradeoff between survival and reproduction. However, there is little knowledge of how intrasexual variation in the conspicuity of a sexual ornament may translate to intrasexual variation in predation risk. Our study demonstrates a relationship between sexual signal conspicuity, as viewed through the lens of an avian predator, and increased attack rate in *A. aquaticus*. We found that lizard dewlaps that more strongly stimulated the red photoreceptors of avian predators (more positive green-red values) were an honest signal of male condition and size, but that they also correlated with evidence of past tail autotomy. Our study is one of the few to reveal that intrasexual variation of a sexual trait (color) is correlated with increased predation but also honestly signals male quality, supporting the underlying assumptions of multiple models of sexual selection (Andersson 1994). Dewlap color is observed by both predators and conspecifics in conjunction with other traits (e.g., personality and body color; Boyer and Swierk 2017). An individual's age, for example, may additionally influence observed rates of tail autotomy (Barr et al. 2019), as older individuals likely have accrued more damage from attempted predation and male combat. These together may provide a more comprehensive picture of patterns of tail autotomy. In *A. aquaticus*, bolder males have larger dewlaps, and tail autotomy is also more likely to be observed in individuals that are bolder (Putman et al. 2018). Therefore, boldness may increase the likelihood that males engage in male combat, which is another potential cause of tail autotomy in some lizards. That said, a recent study found that the rate of conspecific attack on *A. aquaticus* clay models did not differ between models with bright and dull dewlaps (Swierk et al. 2020). Whereas individual behavior correlated with dewlap coloration may additionally contribute to patterns of tail autotomy, these data and those of Swierk et al. (2020) suggest that predators are also more likely to find brighter dewlaps a more conspicuous target, regardless. Overall, our study demonstrates that lizards with dewlaps that are more conspicuous to avian predators also have an increased likelihood of bearing autotomized tails. These findings expand our knowledge from previous studies that considered the effect of the presence or absence of a sexual signal on predation risk. We additionally broaden the literature by addressing this question in light of predator vision modeling. Further studies can deepen our understanding of the relationships between sexual signals and their costs by examining the interactive relationships of behavioral flexibility and microhabitat choice with signal conspicuity.

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Supplementary Material

"Supplementary material can be found at https://academic.oup.com/cz."

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Conflict of interest

The authors declare no conflict of interest.

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