

Article

Dewlap size in male water anoles associates with consistent inter-individual variation in boldness

Breanna J. PUTMAN^{a,b,*}, Kylee R. AZURE^c, and Lindsey SWIERK^d

^aDepartment of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, USA, ^bSection of Herpetology, and Urban Nature Research Center, Natural History Museum of Los Angeles County, Los Angeles, CA 90007, USA, ^cEnvironmental Science Department, Aaniiih Nakoda College, Harlem, MT 59526, USA, and ^dSchool of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

*Address correspondence to Breanna J. Putman. E-mail: putman.bree@gmail.com

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Abstract

Male sexually selected signals can indicate competitive ability by honestly signaling fitness-relevant traits such as condition or performance. However, behavior can also influence contest outcomes; in particular, boldness often predicts dominance rank and mating success. Here, we sought to determine whether male ornament size is associated with consistent individual differences in boldness in water anoles *Anolis aquaticus*. We measured the relative size of the dewlap, a flap of skin under the chin that is a sexually selected ornament in *Anolis* lizards, and tested for associations with responses to a novel and potentially risky environment: time to emerge from a refuge into an arena and number of head scans post-emergence. We found that individuals consistently differed in both time to emerge and head scanning (i.e., individual responses were repeatable), and that dewlap size was negatively related to number of head scans. This suggests that ornament size could indicate male boldness if scanning represents antipredator vigilance. We found that males that had larger relative dewlaps were also in better body condition, but boldness (i.e., head scanning) was not related to condition. Lastly, we found consistent differences in behavior between trials, showing that anoles were becoming habituated or sensitized to the testing arena. Overall, our study shows that in addition to indicating condition and performance, dewlap size could also honestly indicate male boldness in *Anolis* lizards.

Key words: *Anolis aquaticus*, behavioral syndrome, mating success, personality, signal, sexual selection, temperament

Many animals possess sexually selected signals that act as reliable indicators of fitness-relevant traits (e.g., male quality). Males tend to convey information in the form of coloration, ornamentation, and/or behaviors that conspecific males use to assess potential competitors and that females use to assess potential mates (Andersson and Iwasa 1996; Berglund et al. 1996). Countless studies show a link between variation in signals and in mating success and/or survival (e.g., Møller 1988; Pryke et al. 2001; Papeschi and Dessì-Fulgheri 2003). However, signals should also inherently involve costs

because more conspicuous signals (or more time devoted to signaling) are more likely to attract predators and/or be energetically demanding (Engqvist et al. 2015). Male sexual signals often display that, in spite of these costs, the individual has survived and possesses superior fighting or competitive ability (Zahavi 1977). Often, the magnitude of male signals positively associates with physical traits that affect contest outcomes such as body size, body condition, or performance (e.g., bite force) (David et al. 1998; Vanhooydonck et al. 2005a; Byers et al. 2010).

Behavioral traits could also influence the outcomes of male–male competitions. For instance, boldness often consistently differs among individuals, forming a personality trait in which behavioral types (e.g., bold versus shy type) are relatively inflexible in their responses (Sih et al. 2004). Boldness broadly encompasses various animal behaviors that indicate an individual's response to a risky environment or situation (Réale et al. 2007). Bold individuals, those that are more risk-prone, are often more dominant and successful at acquiring mates compared to less bold individuals (Reaney and Backwell 2007; Colléter and Brown 2011; Ballew et al. 2017; Scherer et al. 2017). Because of their enhanced ability to acquire resources, males that are bolder tend to also have higher growth rates and be larger in body size (Brown and Braithwaite 2004; Adriaenssens and Johnsson 2010; Shine et al. 2016), which might also be preferred by potential female mates (Endler and Houde 1995; Rosenthal and Evans 1998). Indeed, females of some species use male boldness over male sexual coloration as their primary mate choice metric, such that females guppies prefer bolder males even if their sexual signal is weak (Godin and Dugatkin 1996). Female lizards also prefer bold males in high risk environments (Teyssier et al. 2014).

Because of the importance of animal personality in mating competition, some sexual traits may convey information about behavioral types. If male sexual traits indicate competitive ability, and if bolder males are more competitive, then sexual traits may positively associate with boldness. Furthermore, bold behavior may be related to the direct development of sexual traits if bold individuals are better at acquiring resources. Some research has examined the link between boldness and male coloration. In guppies, there is a positive association between orange coloration, courtship, and boldness in males (Režucha and Reichard 2016). In lizards, boldness and aggressiveness associate with distinct color morphs that also represent different reproductive strategies (Healey and Olsson 2008; Yewers et al. 2016; Pellitteri-Rosa et al. 2017). Fewer studies have examined the link between boldness and other male sexual traits, like ornament size. One study found no link between boldness and tail length, a sexually-selected trait, in barn swallows, *Hirundo rustica* (Saino et al. 2014), while another found an association between cephalic crest development and boldness in the river blenny fish *Salaria fluviatilis* (Fabre et al. 2014).

Here, we sought to determine whether variation in a male sexually selected signal, the dewlap, associates with boldness in an *Anolis* lizard. *Anolis* lizards (commonly called anoles) have been models of adaptive radiation and ecomorphological specialization, and the relationship of various morphological traits to fitness is well known (Losos 2009). The dewlap is an extensible fold of skin below the chin more commonly found in males than females. Research on variation in dewlap presence, size, and coloration within and among species has been crucial in understanding signal function, evolution, and associations with speciation (Nicholson et al. 2007; Ingram et al. 2016). Dewlap size can be an honest indicator of male bite force, jumping ability, and body size or condition (Vanhooydonck et al. 2005a, 2005b, Irschick et al. 2006; Henningsen and Irschick 2012; Curlis et al. 2017) and hence functions as an honest signal of a male's competitive ability. No work to date has yet determined whether the dewlap can also honestly signal male boldness, another trait that has the potential to influence male–male contests and female choice.

For our study, we looked at whether relative dewlap size in male water anoles *Anolis aquaticus* associates with boldness. Boldness can include behaviors such as risk-taking, response to predators (e.g., antipredator behaviors), response to threats (e.g., a trap), and

resistance to being handled (Réale et al. 2007). Thus, multiple behaviors that serve different functions or are dictated by different processes (and that are not necessarily correlated—see Watanabe et al. 2012; Beckmann and Biro 2013) can be combined into the single personality trait of boldness. For our study, boldness might be associated with dewlap size because these traits may share underlying physiological components—testosterone has been linked to dewlap size in anoles (Husak et al. 2007; Cox et al. 2009) and to boldness in other species (Pellis and McKenna 1992; Raynaud and Schradin 2014). Behavioral traits related to boldness are also often heritable (Brown et al. 2007; Carrete et al. 2016; Ballew et al. 2017), so can be subject to evolution following natural selection in subsequent generations. We measured boldness in water anoles as two distinct behaviors that may represent different processes: (1) latency to enter a novel arena from within a refuge, a common approach used to measure boldness in various taxa (see: Seda et al. 2012; Michelangeli et al. 2016a; Shine et al. 2016; Lapiedra et al. 2017), and (2) number of head scans during the first minute within the novel arena. Latency to emerge from refuge might represent a latent response to handling as an observer has to place the lizard into the arena, while head scans are typically assumed to represent antipredator vigilance (i.e., scanning for danger), increasing with risk (Baldellou and Henzi 1992; Mathot et al. 2009; Monclús et al. 2015). We predicted that bold individuals would have low latencies to emerge and exhibit fewer head scans. We also predicted that these measures of boldness would positively associate with relative dewlap size in male water anoles.

Materials and Methods

Study site and species

We performed our study on water anoles *Anolis aquaticus* at Las Cruces Biological Station in San Vito, Costa Rica. *Anolis aquaticus* is a medium-sized lizard (adult size: 52–77 mm, snout–vent length; Márquez and Márquez 2009) with a range throughout southwestern Costa Rica and northwestern Panama (Savage 2005). The water anole's habitat is defined by small streams on lowland and premontane slopes, and its ecology is strongly linked to water: predator avoidance and foraging almost entirely occurs streamside. Male water anoles have large orange–red dewlaps, which are used as sexual signals. Little is known about water anole social structure, though populations appear to be dense in patches of preferred habitat, and streamside refugia and display sites are actively contested among males (L.S., personal observation).

The study took place over a 5-week period starting in late June 2016. We captured anoles either by hand or by noosing from a section of the Rio Java within the biological reserve. We only captured adult and near-adult (> 50 mm snout–vent length, SVL) male anoles for our study. Although certain trapping methods might target a non-random portion of the population, a previous study examining different capture techniques of lizards found no effect of trapping method on selecting certain behavioral types (Michelangeli et al. 2016b). After capture, we transported anoles to the field station to measure morphological traits and perform behavioral trials. Each anole was kept in captivity for no more than 72 h and their behaviors were tested over the course of 2 days. We housed them individually in enclosures (12 × 19 × 13.5 cm) within a temperature-controlled room (20–23°C) that had a 12: 12 light/dark cycle typical for this species. The walls of each enclosure were covered so that the anoles were not able to see each other or the testing arena. After transporting them back to the station, we allowed the anoles to

acclimate to their environment for at least 12 h before we began the behavioral experiment (see ‘Behavioral experiment’ section). All anoles were returned to their place of capture at the Rio Java once they completed the behavioral experiment.

Morphological measurements

Once anoles were brought back to the station, we recorded SVL and mass. When we were finished doing these measurements for each anole, we used forceps to extend the dewlap to its greatest extent and placed the anole on a white sheet of paper next to a ruler. We then took a photo of the dewlap extended and later calculated the area of the dewlap using the computer software Image J. We took photos using an Olympus Tough TG4 (Olympus America Inc., Center Valley, Pennsylvania, USA).

Behavioral experiment

We measured boldness by examining how anoles responded to being placed into a refuge within a novel arena (i.e., a risky environment). These trials were conducted in the same light- and temperature-controlled room (20–23°C) in which the anoles were housed. Each behavioral test was performed in the morning and twice over 2 days with ~24 h in between the two tests, and the order in which anoles were tested was randomized each day. One person (K.R.A.) orchestrated the behavioral trials. For a trial, an anole was taken from its housing enclosure and placed in a 11.5 × 7 × 5 cm (L × W × H) cardboard refuge (a new one was used each trial), which was then placed into the novel testing arena that was roughly 33.5 × 20 × 21 cm (L × W × H). The testing arena was made of clear plastic, but the sides were covered with paper on the outside so that anoles could not see beyond the arena walls. The floor of the arena was covered with white paper that was changed between each trial. Trials were video recorded using an iPhone 5C (Apple Inc., Cupertino, CA, USA) affixed directly above the arena, and behaviors were quantified from video recordings after the study. The observer started video recording prior to placing the refuge (which housed the anole) into the arena. Once the refuge was in position, the observer left the room for the 30 min duration of the trial. The testing arena was cleaned thoroughly with dishwashing soap between trials to prevent any olfactory cues left behind by the previous anoles that may interfere with future tests.

At the end of our study, video recordings of the trials were assigned a random number and one person (B.J.P.), blind to anole identity, trial number, and date of trial, quantified the anoles’ behavioral responses. Two behavioral responses were measured: (1) how long it took the anole to fully emerge into the arena (time to emerge, TTE), and (2) number of head scanning events during the first minute after emerging. We defined a head scan as a lateral movement of the head from an initial motionless position. We assumed that each of these measures negatively associated with boldness (i.e., bold individuals should have lower latencies to respond and exhibit fewer head scans). If an anole never emerged from refuge during the trial, we assigned it the maximum value of 30 min.

Statistical analyses

To get relative values of morphological measurements (to account for allometric scaling), we calculated the residuals from linear regressions of log SVL on log of square-root dewlap size and log SVL on log of cube-root body mass (to obtain body condition, which also has the potential to associate with boldness; Brown and

Braithwaite 2004; Adriaenssens and Johnsson 2010). Prior to analyses, we looked for correlations among relative dewlap size, body condition, and SVL, and found that relative dewlap size was significantly positively correlated with body condition (Pearson’s $r = 0.332$, $P = 0.019$), consistent with results from past studies on anoles (Henningsen and Irschick 2012; Curlis et al. 2017). However, because the strength of the correlation was relatively low (Figure S1, Supplementary Material), we elected to include all morphological traits into our models as predictor variables and assessed collinearity between these variables by calculating the variance inflation factor (VIF), which measures how much of the variance of an estimated coefficient increases if predictors are correlated. VIFs > 10 generally indicate high multicollinearity, and values < 3 are ideal (i.e., multicollinearity is not an issue). Thus, for all analyses, we looked at the effects of relative dewlap size, body condition, and SVL on boldness (TTE and no. of scans). Because TTE and no. of scans were not correlated (Pearson’s $r = 0.217$, $P = 0.162$), they may be part of separate personality axes, and so we analyzed them separately. In Supplementary Material, we provide results from models in which we tested for the effects of dewlap size and body condition separately to demonstrate that the inclusion of these two correlated variables into a single model did not alter our overall results.

We ran linear mixed models (LMMs; *lme4* package in R—Bates et al. 2015) with relative dewlap size, body condition, and SVL as fixed effects, and anole identity and trial number as random effects, to explain variation in head scanning and TTE. Even though TTE contained time-to-event data, we were able to meet LMM assumptions through a log transformation of the data. Number of scans was square-root transformed to meet model assumptions. We also performed a Cox-proportional hazards regression analysis (*survival* package in R—Therneau 2015) with paired data (i.e., individuals were tested twice) to examine the TTE data in order to verify that the LMM on TTE produced qualitatively similar results to a model that accounts for right-censored data. We included relative dewlap size, body condition, and SVL as independent variables and anole identity and trial number as clustered variables in the survival analysis.

Repeatability (also known as the intraclass correlation coefficient) provides insights into the components contributing to variability in the data, and at the level of individual, it provides support that among-individual variation is caused by intrinsic factors (Réale et al. 2007; Nakagawa and Schielzeth 2010). To measure the repeatability of behaviors, we used the *rptR* package in R, which calculates repeatability as the group-level variance over the sum of group-level and residual variance (Stoffel et al. 2017). The statistical significance of repeatability is tested through likelihood ratio tests (LRT) by comparing a model including the grouping factor of interest to one excluding it. We calculated the adjusted repeatability, which controls for the addition of fixed effects (in our case, relative dewlap size, body condition, and SVL) identified from linear mixed models (LMM) fitted in the *rptR* package and based on 1000 bootstrapping runs (which estimates uncertainty around repeatability). We used the same LMM structures as above to estimate repeatability of TTE and head scanning at the level of anole identity to determine whether behaviors were repeatable across time within individuals, the definition of personality (Réale et al. 2007). We also examined repeatability at the level of trial number, which might arise due to habituation or sensitization to the testing arena. Significant repeatability at the level of trial would signify that anoles consistently behaved differently between trials; for instance, behavioral responses might decline with time, indicating some level of phenotypic plasticity (e.g., habituation), but individuals can still maintain their relative differences in rank

order (e.g., “bold” individuals still have relatively lower values than “shy” individuals even if there is some overlap). All tests were done in R (v. 3.2.1) and alpha was set to 0.05.

Results

In total, we tested 26 adult male water anoles, 24 of which were tested twice in the behavioral experiment, and 15 of which emerged from the refuge during both trials (i.e., we could examine repeatability of head scanning post-emergence for these individuals).

We looked at whether male dewlap size, body condition, and/or SVL associated with two behavioral responses within a novel environment, head scanning and time to emerge from refuge (TTE). We found that as relative dewlap size increased, the number of head scans performed by anoles decreased ($P = 0.044$, Table 1, Figure 1). There was no effect of body condition ($P = 0.678$, Figure 1) or SVL ($P = 0.866$) on head scanning (Table 1), which was also the case for models in which each of these predictor variables were tested separately (Table S1, S2; Supplementary Material). Another linear mixed model found that none of the predictor variables influenced TTE, although SVL had a marginally non-significant effect ($P = 0.078$, Table 1). Results were qualitatively similar from the survival analysis: TTE was not affected by relative dewlap size (hazard ratio = 0.426, $Z = -0.206$, $P = 0.837$) or body condition (hazard ratio = 0.089, $Z = -0.205$, $P = 0.838$), and SVL had a marginally non-significant effect (hazard ratio = 0.962, $Z = -1.658$, $P = 0.097$). All predictor variables in the LMMs had VIFs < 2, indicating that multicollinearity between variables had little influence on the variance of the model coefficients.

We found that both TTE and number of head scans were repeatable within individual anoles (TTE: $R = 0.464 \pm 0.151$ SE, $LRT = 6.20$, $df = 1$, $P = 0.006$, Figure 2A; no. of scans: $R = 0.563 \pm 0.174$, $LRT = 6.95$, $df = 1$, $P = 0.004$, Figure 2B), indicating that these behaviors represent personality with significant consistent differences among individuals. We also found no. of scans was repeatable at the level of trial, albeit low ($R = 0.146 \pm 0.159$, $LRT = 3.84$, $df = 1$, $P = 0.025$), such that anoles scanned more during the second trial compared to the first (Figure 2). Repeatability of TTE at the level of trial was low and not statistically significant ($R = 0.062 \pm 0.091$ SE, $LRT = 1.60$, $df = 1$, $P = 0.103$).

Discussion

In our study, male water anoles with larger relative dewlaps scanned a novel environment less than males with smaller dewlaps,

Table 1. Results of the linear mixed models predicting head scanning behavior and time to emerge from refuge (TTE) in male water anoles

Response variable	Predictor variable	$\beta \pm SE$	t	P
Head scans	(Intercept)	1.511 ± 1.358	1.113	0.266
	Relative dewlap size	-7.140 ± 3.546	-2.014	0.044
	Body condition	5.102 ± 12.295	0.415	0.678
	SVL	0.003 ± 0.020	0.169	0.886
TTE	(Intercept)	-0.014 ± 1.309	-0.011	0.991
	Relative dewlap size	1.191 ± 3.398	0.351	0.726
	Body condition	4.507 ± 11.321	0.398	0.691
	SVL	0.035 ± 0.020	1.756	0.079

Predictor variables that met statistical significance are in bold.

indicating that they could be less wary of novel or dangerous situations. Head scanning was repeatable within individuals, indicating that it could be representative of the personality trait of boldness, or response to a risky environment/situation. Previous work in various

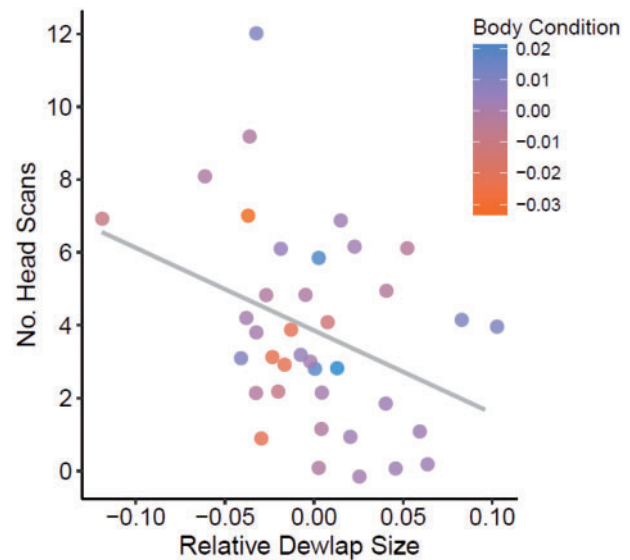


Figure 1. Relationship of relative dewlap size, body condition, and number of head scans in a novel environment for adult male water anoles. Body condition was positively correlated with dewlap size, but not with head scanning. Points on plot are slightly jittered to reduce overlap.

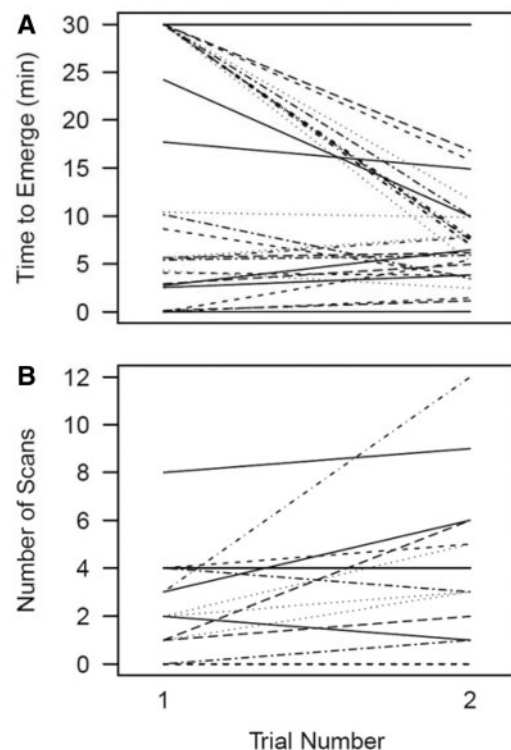


Figure 2. Spaghetti plots showing individual anole differences in (A) time to emerge (TTE) from a refuge into the novel environment between trial 1 and trial 2, and (B) number of head scans in the novel environment between trial 1 and trial 2. Each line represents an individual anole.

lizard species have found male coloration to reliably indicate personality differences (Healey and Olsson 2008; Yewers et al. 2016; Pellitteri-Rosa et al. 2017). This is the first study, to our knowledge, to show that a non-color sexual trait, dewlap size, could be an honest indicator of male personality in *Anolis* lizards.

Dewlap size in various species of anole is known to reliably indicate male size, condition, and performance (Vanhooydonck et al. 2005a, 2005b; Irschick et al. 2006; Henningsen and Irschick 2012; Curlis et al. 2017; Petelo and Swierk 2017). Here, we show that even with a relatively small number of individuals tested, dewlap size also indicated consistent differences in scanning a novel and potentially risky environment. Head scans are a measure of antipredator vigilance behavior in other animals (Baldellou and Henzi 1992; Mathot et al. 2009; Monclús et al. 2015). Vigilance helps animals assess risk and detect potential predators, but reduces time spent on foraging or other fitness-related activities (Lima and Bednekoff 1999; Putman and Clark 2015; Clermont et al. 2016). Our results demonstrate that males with larger dewlaps perform less surveillance behavior when entering a new environment. Although scanning could also be used to detect things other than predators or danger, e.g., mates, it is unlikely that the context in which they were tested (in a novel arena and without mate cues), anoles were performing mate-searching in our study. If anoles with larger dewlaps spend less time being vigilant, this could increase their available time to defend territory and/or forage. However, this type of boldness might also increase their risk of predation (Smith and Blumstein 2010). Future work could assess these trade-offs in free-ranging individuals.

We did not find a relationship between dewlap size and latency to emerge from a refuge into the novel environment, and this, in part, could be due to our relatively low sample size of individuals tested. Latency to emerge was repeatable within individual anoles, suggesting it can be part of a personality trait, but it appears to be distinct from head scanning since these behaviors were not correlated or similarly affected by dewlap size. Time to emerge from a refuge is a common measure of boldness in studies on various species, including lizards (Seda et al. 2012; Michelangeli et al. 2016a; Shine et al. 2016; Lapiedra et al. 2017). This suggests that head scanning might not be a measure of boldness, but some other personality trait, but it seems more likely that head scanning might represent a different type of boldness. Even though these behaviors, to us, may represent animals responding to risk (i.e., boldness), they may result from different perceptions of risk by the animals and have different functions. For instance, latency to emerge from refuge could represent a response to a recent predator encounter (i.e., human handling the lizard) while scanning could represent predator detection (i.e., vigilance). This is supported by a study done on hermit crabs, which found responses after a predator attack loaded on a separate axis than behaviors related to predator detection, even though all behaviors measured fell under the umbrella of boldness (Watanabe et al. 2012). Regardless, male water anoles with larger sexual signals scan their environment less, and this could be a risky strategy if scanning allows individuals to detect danger.

We also found that head scanning was repeatable at the level of trial, indicating that anoles consistently behaved differently in the second trial compared to the first. This type of change in behavioral responses to a testing arena could represent habituation, or a reduced fear of the situation. Indeed, we found that the number of anoles that failed to emerge from refuge decreased from 10 in the first trial to 1 in the second trial indicating a reduced wariness of entering the novel environment (however, these differences failed to

reach statistical significance). We found that anoles consistently scanned more during the second trial compared to the first, which, if scanning represents vigilance, would suggest a more risk-averse response, and suggests that anoles were becoming sensitized, and not habituated, to the testing arena. Either way, we show that anoles exhibited phenotypically plastic responses to change over time, but still maintained consistent individual differences in behavior, apparent in the significant repeatability in TTE and head scanning at the level of individual.

Finally, relative dewlap size was positively correlated with body condition, but not with body size (SVL) in our study. In other species of anole, dewlap size is also condition-dependent (Henningsen and Irschick 2012; Curlis et al. 2017). A separate study also found that larger male water anoles have disproportionately larger dewlaps and weaponry compared to smaller males (Petelo and Swierk 2017). Alternatively, these traits could all share a proximate mechanism, such as a common neuroendocrine mechanism (Kralj-Fišer et al. 2010). However, even though males in better condition had larger relative dewlaps, and those with larger dewlaps exhibited fewer head scans, body condition was not related to head scanning or time to emerge in a novel environment. The correlation between body condition and dewlap size was relatively weak and this likely is why we failed to detect condition-dependent boldness. Whether these traits associate with greater reproductive success remains to be tested. For instance, females might prefer males with larger dewlaps merely due to its relationship with body condition and not necessarily boldness. Bold behavior could be the mechanism that produces larger dewlaps (if bold individuals spend more time foraging and gaining energy to put toward ornament size). Further studies (with larger sample sizes) on the interplay between these three traits and on female preferences will advance our knowledge on the relative importance of sexual selection on boldness in anoles.

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Supplementary Material

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

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