Ethology

No Evidence for Female Association with High-Performance males in the Green Anole Lizard, *Anolis carolinensis*

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Abstract

Sexual selection theory suggests that females may gain significant indirect fitness benefits from mating with males expressing good genes, particularly in animal species where the males provide no parental care. Whole-organism performance abilities have previously been shown to enhance both survival and reproductive success in a range of taxa, and females who mate with high-performance males might therefore gain significant indirect performance benefits. We tested the hypothesis that females associate preferentially with high-performance males in the green anole lizard *Anolis carolinensis* in laboratory trials using multivariate statistical techniques. Our results indicate that male performance abilities do not influence female mating preferences, either in isolation or as a combined suite of traits. Thus, any indirect performance benefits that a female might gain for her offspring are likely not a result of a female choice process.

Introduction

A controversial question in sexual selection is whether female mating preferences have evolved to favour genetically superior males (Andersson 1994; Rowe & Houle 1996; Kokko et al. 2003). ‘Good genes’ are thought to be signalled in many cases by elaborate or showy secondary sexual male characters (Andersson 1994; Kokko et al. 2003). Consequently, researchers interested in understanding female mating preferences have typically focused on the role of these characters in sexual advertisement (e.g. Candolin 2003), and on the relationship between male ornaments and fitness components such as survival (Møller & Alatalo 1999; Brooks 2000; Jennions et al. 2001). However, male genetic quality might also be manifest in several other ways that impact on fitness besides survival (Hunt et al. 2004). For example, Arnold’s (1983) influential ecomorphological paradigm posits a link between whole-organism performance ability and fitness (see also Irschick & Garland 2001; Miles 2004; Le Galliard et al. 2004), and performance abilities are increasingly being implicated in ecological tasks associated with mate acquisition and reproductive success (e.g. Lailvaux et al. 2004, 2005; Lappin & Husak 2005). Good males might therefore be expected to exhibit superior whole-organism performance abilities or other physiological capacities (S. P. Lailvaux & D. J. Irschick, unpubl. data), and females may mate preferentially with such males.

A handful of studies have presented evidence that male performance ability is a criterion for female choice (but see Sullivan & Walsberg 1985). For example, females express a preference for male ornaments correlated with swimming endurance in the guppy *Poecilia reticulata* (Nicoletto 1993). Furthermore, a recent study on *P. reticulata* using artificial insemination showed a positive association between paternal colouration and the ability of newborn offspring to evade capture (Evans et al. 2004). These findings suggest that females who mate with high performance males could gain considerable indirect benefits in the form of high performance offspring (Alatalo et al. 1998; Welch et al. 1998; but see Zeh 2004), particularly given the documented heritability of locomotor performance (van Berkum & Tsuji 1987; Tsuji et al. 1989; Bennett & Huey 1990; Jayne & Bennett 1990; Brodie & Garland 1993; Garland 1994; Vanhooydonck et al. 2001). Such benefits may be particularly important in animals such as lizards, where males contribute little to reproduction other than sperm (Hews 1990).

Performance abilities, in general, and locomotor capacities, in particular, have been well studied in lizards relative to other taxa (Garland & Losos 1994; Irschick & Garland 2001). Lizards might therefore be expected to be ideal study organisms for investigating the role of performance in female choice. However, female choice has seldom been noted in lizards, despite numerous investigations into lizard mating systems (Tokarz 1995; Olsson & Madsen 1995; Olsson 2001; but see Censky 1997; Kwiatkowski & Sullivan 2002; López et al. 2003). In a recent study, Hamilton & Sullivan (2005) suggested that female choice in lizards is likely a multivariate process, and showed that female *Urosaurus ornatus* select males based on several cues or aspects of secondary sexual signals. Given this finding, and the potential importance of lizard performance abilities to both survival (Irschick & Garland 2001; Le Galliard et al. 2004) and male combat (Lailvaux et al. 2004; Lappin & Husak 2005), one could predict that male performance may be one of a suite of targets for female mating preferences in lizards, along with, for example, secondary sexual ornaments and olfactory cues (López et al. 2003). Head size is an especially likely candidate for a male trait affecting female choice, as head size is typically correlated with bite force in lizards (e.g. Herrel et al. 2001a,b), and may therefore act as an easily assessed 'proxy' for bite force.

We carried out behavioural trials in the green anole lizard *Anolis carolinensis* to determine if females associate with males exhibiting high performance capacities. The green anole's documented mating system is one of female defence polygyny, in which males establish and defend territories based on female location (Jenssen et al. 2001). However, recent studies have shown that females may sneak matings with satellite males that do not hold territories of their own (Orrell & Jenssen 2003). In addition, females have also been observed to overlap more than one male's territory in the field during reproductive periods (Ruby 1984), and are known to reject mating attempts from certain individuals, particularly sub-adult males (T.A. Jenssen, personal communication). Several other studies have also provided intriguing hints for the existence of female mating preferences in *A. carolinensis* (reviewed in Tokarz 1995). For example, Andrews (1985) showed that females associated preferentially with certain males rather than others in a laboratory setting, but was unable to identify the criteria on which females were basing their choices. Here, we test the hypothesis that female preference for male anoles is based on a suite of male traits, including performance ability. We measured two types of male performance, jumping and biting, both of which have been shown to affect the outcome of male fights in *A. carolinensis* (Lailvaux et al. 2004). We also measured several other male traits that could potentially affect female choice: dewlap size (a sexually dimorphic male character in anoles), head size, body condition and limb morphology. Dewlap size is thought to be an important component of male sexual advertisement signalling in anoles (Sigmund 1983; but see Tokarz et al. 2005), and likely plays a role in male combat in some Caribbean species (Vanhooydonck et al. 2005; S. P. Lailvaux & D. J. Irschick, unpubl. data). Finally, we calculated from limb measurements an index of fluctuating asymmetry (FA), which has previously been shown to affect locomotor performance in other lizard species (e.g. López & Martín 2002), and may also be relevant for female choice (Swaddle 2003).

Materials and Methods

Adult male and female anoles were captured on the Tulane University campus in June 2003, during the *A. carolinensis* breeding season. We palpated all females for eggs upon capture. We then maintained females in the laboratory for up to 2 wk prior to each trial, as female anoles ovulate single eggs at approximately 2 wk periods (Crews 1973; Licht 1973). Thus, we ensured that only non-gravid, sexually receptive females were used in choice trials. Each lizard was maintained in a separate 37.8-l enclosure with fluorescent lighting, fed live crickets three times a week, and watered ad libitum. To facilitate reproductive condition, the experimental room was kept on a 12L:12D photocycle (Licht 1971). The laboratory was maintained at a constant 25°C.

Performance

Bite force

We followed the protocol of Herrel et al. (2001a,b) to measure bite force by using an isometric Kistler force transducer (type 9023, Kistler Inc. Winterthur, Switzerland) mounted on a retort stand and connected to a Kistler charge amplifier (type 5058a, Kistler Inc.). We placed the free ends of the plates between the jaws of the animal, and induced the lizard to bite forcefully. We repeated bite measurements five times for each animal, with a 30-min rest period between measures. The largest bite force obtained from such a session was taken as maximum bite force for that individual. We placed all individuals inside an incubator at 32°C for 1 h prior to bite force measurement, and between measures.

Jumping

Following the protocol of Toro et al. (2003, 2004), we placed anoles on a force platform and induced them to jump onto a horizontal branch positioned at the level of the platform and placed just out of reach. Use of the force platform enabled us to estimate the three-dimensional ground forces during jumping, and to calculate several key variables, including peak velocity during take-off, peak acceleration and distance jumped (see Toro et al. 2003 for a detailed explanation). We motivated the lizards to jump by startling the animals with a hand clap. Only jumps that began with all four feet square on the platform were included in the analyses. Each individual was jumped three times, and the best overall jump based on velocity, acceleration and distance was used as the estimate of that individual's maximal jumping distance (Toro et al. 2003; Lailvaux et al. 2004). We placed all lizards in an incubator at 32°C for 1 h prior to jumping measurements and between jumps.

Morphology

For each individual, we took the following morphological measurements using Mitutoyo digital calipers (± 0.01 mm): snout–vent length (SVL), head length, head width, head height and hindlimb length (length of the entire, fully extended hindlimb, from insertion on the trunk to the tip of the longest toe, excluding the claw). We also measured the mass of each male using a Denver Instruments M-220 electronic balance (± 0.01 mg). We calculated condition as the residuals of a linear regression of ln(mass) against ln(SVL) (Anderholm et al. 2004).

We calculated individual hindlimb FA values as the unsigned right-minus-left hindlimb lengths divided by the mean left and right character values [$(|R - L|)/0.5(R + L)$; Palmer & Strobeck 1986; López & Martín 2002]. To estimate the reliability of our limb measures, we measured the limbs of 10 males six times and calculated repeatability (Lessels & Boag 1987). Repeatability for both limbs was very high (left hindlimb $r = 0.97$, $F_{5,9} = 90.723$, $p < 0.001$; right hindlimb $r = 0.97$, $F_{5,9} = 94.528$, $p < 0.001$).

Dewlap Area

To determine male dewlap area, we positioned the lizard sideways and gently pulled the ceratobranchial forward using a pair of forceps, fully extending the dewlap (this method is highly repeatable, see Vanhooydonck et al. 2005). Extended dewlaps were photographed using a Nikon Coolpix 995 digital camera, and the resulting images digitized using TPSDIG v. 1.3.1.

Male Association Trials

We conducted male association trials using a protocol similar to those of Andrews (1985) and LeBas & Marshall (2001). Two size-matched males (within 3 mm SVL of each other, Lailvaux et al. 2004; Perry et al. 2004) and one female were placed in marked, partitioned areas of equal size in a 1 × 0.3 × 0.3 m terrarium overnight to habituate (Fig. 1). We size-matched males because body size is frequently correlated with performance capacities (e.g. Toro et al. 2003; Lailvaux et al. 2005), and we were interested in male performance independent of size effects (see also Lailvaux et al. 2004). Previous anole performance studies using similarly size-matched male pairs have shown that sufficient variance in jumping ability, bite force and morphology (including dewlap size and head size) exists for important performance differences between size-matched males to be detectable (Lailvaux et al. 2004; S. P. Lailvaux & D. J. Irschick, unpubl. data; see also Perry et al. 2004). Thus, we argue that the opportunity for females to assess performance and morphology differences between male pairs was not excluded by our size-matched design.

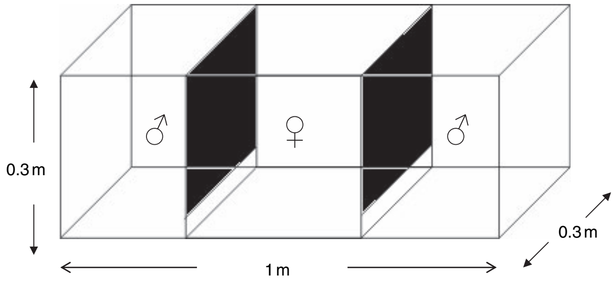

Fig. 1: Cage layout for female association trials. Dark areas indicate semi-opaque panels demarcating the cage areas. Females were able to move between areas through the gaps below the panels. The bigger males were unable to pass through the gaps, and each male was therefore confined to his own area

The female was placed in the centre area, with one male in each of the side areas, as in Andrews (1985). Each male had a 4-cm diameter perch in his section of the cage. The centre area was separated from the two side areas by two plastic screens. Gaps between the screens and the bottom of the cage were large enough to allow the females to move freely between the three areas, but small enough to prevent the larger males from leaving their section of the cage (Fig. 1). As a further precaution, the males were lightly tethered to their perches with cotton thread. However, the males were not immobilized by the threads, and were able to move off the perch (but not to leave their cage areas), thus allowing females the opportunity to assess male locomotor abilities. The screens were partially opaque, which allowed the females to see the males on either side of her central compartment through the screen, but prevented the males from seeing each other at opposite ends of the cages. Indeed, through all the trials no males were ever observed to display at each other, and we found no evidence that any male was aware of the other's presence. During the habituation period, the two screens were covered by black cardboard, preventing the female from leaving the central area or seeing the males. After 24 h, the partitions were removed, and the lizards videotaped for 2 h with a video camera aligned orthogonally to the test arena.

Each male was given a 'score' that measured the amount of time the female spent in his cage area. Thus, if a female spent 5 min with the male in the left compartment, that male earned a score of 5. Scores were rounded to the nearest minute. If a trial ended with both males earning identical scores (time spent equally with both males), then those data were not analysed. Only trials in which the female visited each male at least once were included in the analysis (LeBas & Marshall 2001). Overall, 23 association trials were included in the final analysis. We also examined the cages 3 h after the end of each trial, and noted the position of the female in the cage. In 21 out of 23 trials, the female was observed to be in the same compartment as at the end of the trial.

Statistical Analyses

Following Hamilton & Sullivan (2005), we analysed all association trials using logistic regression. All data were tested for normality prior to analysis using Lillifors test. No variables differed significantly from a normal distribution, except for condition and FA, which typically follows a half-normal distribution (Palmer & Strobeck 1986). No data transformations were made; however, logistic regression is fairly robust to such departures from normality (SPSS manual 12.0). Initial data exploration also showed that multicollinearity was within acceptable levels (tolerance $\gg 0.1$ for all variables), and therefore not substantial enough to distort the results of the logistic regression (Quinn & Keogh 2002). Consistent with Hamilton & Sullivan (2005), we also performed two-tailed pairwise comparisons for each variable in addition to the logistic regression analysis (see also Brandt 1999; Neat & Huntingford 1999). All pairwise comparisons were paired t-tests, except for condition and FA, which were analysed using Wilcoxon signed-rank tests.

Results

Females visited each male's demarcated area in all but three of the trials. A typical trial involved the female tentatively entering a male's area and head-bobbing. Males appeared to court females, frequently jumping off the perches and approaching the females as far as their tethers allowed. Displays from at least one male (i.e. headbobs and dewlap extensions) were observed in only 11 of 23 interactions (48%), and were typically brief, unlike male displays observed in male combat trials (S.P. Lailvaux personal observation). For this reason, male display behaviour was not analysed. By the end of the trial, the female had typically taken up a position on one of the male's perches. No copulations were observed.

The logistic regression model with the combined phenotypic variables correctly predicted the outcome of the female association trials in only 12 out of 23 trials (52%), a result that was not significantly different from chance (model Nagelkerke $R^2 = 0.152$, $p = 0.518$). Results from the logistic regression were, in this case, concordant with the individual pairwise comparisons – selected and unselected males did not differ significantly among any of the measured traits (Table 1). Thus, although our experimental design had the same power (0.82, LeBas & Marshall 2001) to detect differences similar in magnitude to those reported previously for other lizard species (e.g. LeBas & Marshall 2000), females appear not to be choosing males on the basis of any of the measured traits (Fig. 2). More explicitly, our results suggest that neither male performance (which females were given the opportunity to assess directly), nor any morphological traits associated with performance (which might act as morphological 'proxies' for

Table 1: Male performance and morphological traits evaluated in female association trials, and p-values associated with statistical comparisons between chosen and unchosen males. All pairwise comparisons were paired t-tests except where noted

Male trait	Pairwise score	p	p (logistic)
Head length	−0.691	0.497	0.69
Head width	0.232	0.819	0.855
Head height	0.915	0.37	0.472
Dewlap	1.016	0.321	0.421
Bite force	0.626	0.538	0.718
Velocity	0.288	0.776	0.77
Acceleration	−0.299	0.768	0.763
Condition	0.745[a]	0.456	0.232
FA	0.13[a]	0.737	0.662

[a] Wilcoxon signed-rank score.

performance) have any effect on female mating preferences in *A. carolinensis*.

Discussion

Hamilton & Sullivan (2005) showed that whereas pairwise comparisons of individual male traits did not reveal differences between chosen and unchosen males in the tree lizard *U. ornatus*, multivariate statistical analysis implicated several male morphological features as predictors of female choice. Given the importance of whole-organism performance capacities to male combat (and likely survival) in several lizard species including *A. carolinensis*, (Garland et al. 1990; Robson & Miles 2000; Miles 2004; Lailvaux et al. 2004; Perry et al. 2004), we predicted that, if presented with the opportunity, females might associate and mate preferentially with high-performance males in order to gain indirect genetic reproductive benefits. Contrary to this prediction, however, we found no relationship between performance and female choice for either maximum male jump velocity and acceleration, or for maximum male bite force in *A. carolinensis*. Thus, if females are indeed choosing particular males (Andrews 1985), performance ability is unlikely to be a choice criterion.

On the rare occasions when female mating preferences have been documented in female lizards, female choice has typically been associated with male body size. For example, Censky (1997) showed

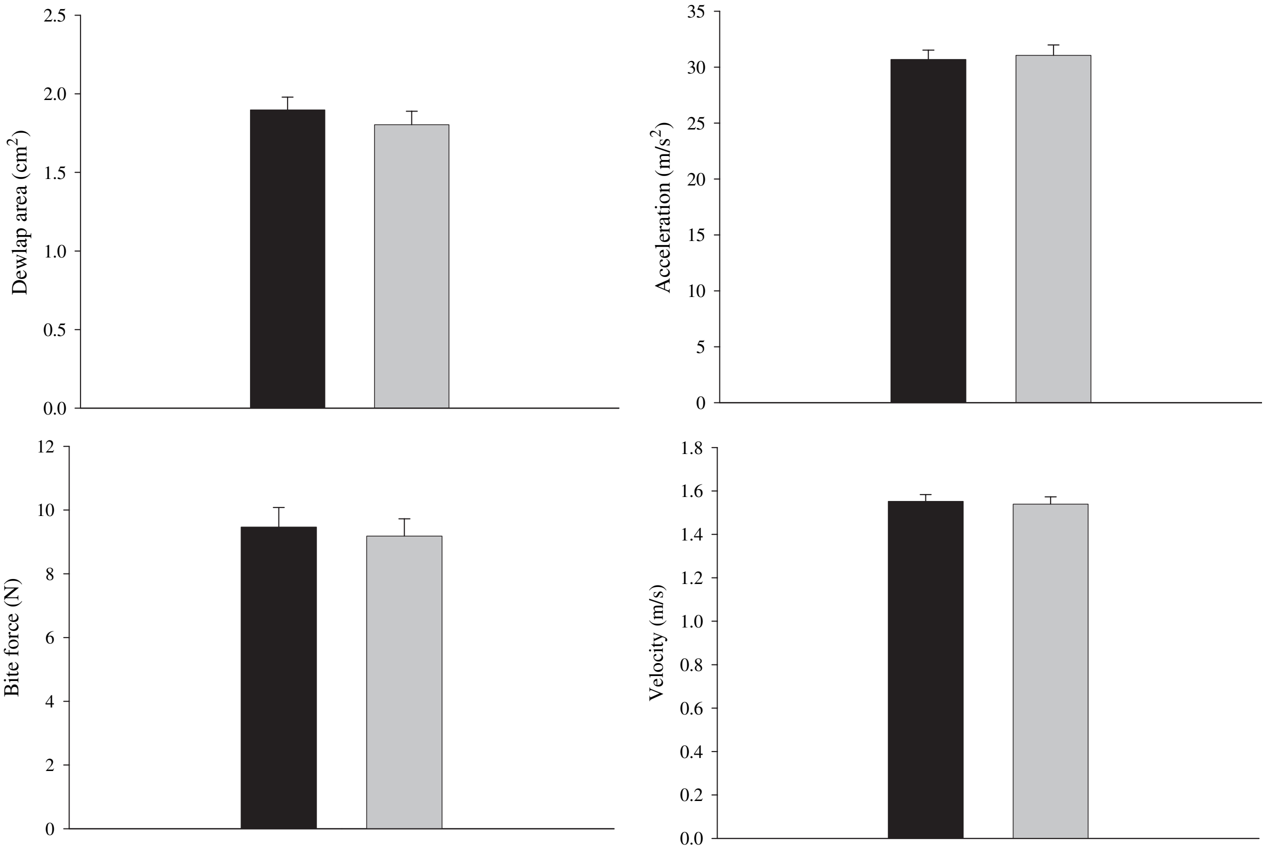

Fig. 2: Selected male morphological and performance variables for chosen (black) and unchosen (grey) males. All values are means ± SE

that female *Ameiva plei* lizards reject small males, and appear to choose only large males as mates, and Cooper & Vitt (1993) reported a similar result for the broad-headed skink *Eumeces laticeps*. Lailvaux et al. (2004) presented evidence for the existence of two different age-dependent male *A. carolinensis* morphs, lightweight and heavyweight males, that differ in size (SVL), head shape, and residual bite performance, raising the possibility that females might choose older and larger heavyweights preferentially over younger, smaller lightweight males. Such a preference would not have been revealed by our size-matched experimental design. However, Andrews (1985) previously postulated, and found no evidence for male size-based female mating preferences in *A. carolinensis* (see also MacDonald & Echternacht 1991). Furthermore, a companion study allowing *A. carolinensis* females to choose between lightweight and heavyweight males was unable to reject the null hypothesis of no female preference for male body size (Lailvaux, unpublished data). Finally, females in our study showed no significant preferences either for males with larger heads, a key diagnostic character separating lightweight and heavyweight males, or for males in better condition. Taken together, these findings suggest that overall male size is not a criterion for female choice in *A. carolinensis*, and our size-matched design is likely appropriate for this species. Indeed, given that our experimental design replicated several important features of previous studies on female choice in anoles and other lizards, including cage layout (Andrews 1985), trial duration (LeBas & Marshall 2001) and statistical power (LeBas & Marshall 2000), we argue that our failure to reject the null hypothesis of no relationship between male performance and female choice is not because of any methodological problems.

In addition to lacking preferences for male performance or head size, *A. carolinensis* females also appear to show no preferences for male dewlap size. Dewlaps have been cited as a key factor driving speciation and diversification in Caribbean and Central and South American anoles (Losos & Chu 1998). Males of various *Anolis* species vary markedly in the relative size of their dewlaps, and previous studies have suggested that female choice may have been an important causal factor in dewlap evolution (e.g. Sigmund 1983). However, our laboratory data indicate otherwise, as male green anoles rarely displayed their dewlaps at females, and females did not choose males on the basis of their dewlap size. In this respect, our results are consistent with those of previous researchers who have found no role for anole dewlap size or display in male sexual advertisement (Greenberg & Noble 1944). For example, the mating success of *Anolis sagrei* males that were surgically prevented from extending their dewlaps has been shown to be similar to that of control males in both laboratory (Tokarz 2002) and field-based studies (Tokarz et al. 2005). Orrell & Jenssen (2003) also suggested that female choice is unlikely to exert a strong selection pressure on dewlap size or displays in *A. carolinensis*, given the lower male display rates and limited male display patterns observed during heterosexual interactions in this species. While our current dataset provides no support for dewlap size as a target for female mating preferences in *A. carolinensis*, future studies of female choice in a male performance context might consider examining dewlap colour as well as size (see Tokarz 1995 for a summary and discussion of the role of dewlap colour in anole female choice).

Finally, we found no evidence to suggest that male FA affects female association preferences in green anoles. In the lacertid lizard *Lacerta monticola*, limb FA was positively associated with head height (a predictor of male dominance), but negatively associated with escape speed, suggesting that the relationship between FA and male whole-organism performance is complex, and likely mediated by resource allocation trade-offs (López & Martín 2002). Although comparable studies evaluating the relationship between performance and FA are lacking, such a relationship was not evident from our data in the context of female choice; neither FA nor any measure of male performance emerged as significant predictors of female association, either individually or in conjunction with each other. Thus, although the role of secondary sexual character FA in sexual advertisement is still hotly debated (e.g. Bjorksten et al. 2000; Polak & Starmer 2005), our findings indicate that FA in morphological traits associated with function is unlikely to be of importance to female choice in *A. carolinensis*.

In conclusion, we were unable to reject the null hypothesis of no relationship between male performance abilities and female choice in *A. carolinensis*. Our findings are not altered by the use of multivariate analysis, as recommended by Hamilton & Sullivan (2005). Thus, female mating preferences do not appear to be based on any of our measured variables in the Tulane anole population, and we are unable to provide support for the notion of female choice as an integrated, multivariate process in green anoles.

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