

# Individual (co)variation of field behavior and locomotor performance in curly tailed lizards

K. Diamond<sup>1</sup>, D. Trovillion<sup>2</sup>, K. E. Allen<sup>3</sup>, K. M. Malela<sup>4</sup>, D. A. Noble<sup>5</sup>, R. Powell<sup>6</sup>, D. A. Eifler<sup>7</sup> & M. E. Gifford<sup>8</sup>

1 Department of Biology, University of Central Florida, Orlando, FL, USA

2 Department of Fisheries and Wildlife Sciences, Oregon State University, Corvallis, OR, USA

3 Department of Biology, Truman State University, Kirksville, MO, USA

4 Department of Environmental Health, University of Botswana, Gaborone, Botswana

5 Department of Biology, Hendrix College, Conway, AR, USA

6 Department of Biology, Avila University, Kansas City, MO, USA

7 Erell Institute, Lawrence, KS, USA

8 Department of Biology, University of Central Arkansas, Conway, AR, USA

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## Correspondence

Matthew E. Gifford, Department of Biology,  
University of Central Arkansas, 201  
Donaghey Ave., Conway, AR 72035, USA.  
Email: megifford@uca.edu

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## Abstract

Animal communication among competitors often relies on honest signaling such that displays of aggression accurately reflect an individual's performance abilities. Moreover, the maintenance of honest signaling should be enhanced by the existence of consistent individual differences in behavior and performance, and individual-level correlations between them. Despite this, researchers studying honest signaling rarely measure behavioral repeatability. Here, we demonstrate that field behaviors of free-ranging lizards and a measure of locomotor performance in the laboratory are consistent among individuals (i.e. they were repeatable), although the magnitude of repeatability varies among traits. In addition, endurance appears to be correlated with display frequency in the field at the individual level, suggesting that display frequency is an honest signal of endurance. Interestingly, this correlation was strong for males, and non-existent for females. Our results extend previous studies of behavior–performance relationships by identifying a sex-specific correlation between traits and by partitioning phenotypic correlations into between- and within-individual components. This analytical approach is emerging as a powerful tool for studying individual variation in behavior and physiology.

## Introduction

Laboratory measurements of physiological performance are used frequently to understand and predict how organisms interact with their environment and to provide a functional perspective for interpreting the fitness consequences of morphological variation (Arnold, 1983; Wainwright & Reilly, 1994). Arnold's (1983) landmark paper set up a framework for measuring selection on morphological traits in two steps: the first measures the effects of morphological variation on performance and the second measures the effects of performance on fitness. Since this time, researchers have expanded and modified the morphology–performance–fitness framework to consider how behavior might be included in this framework (Garland & Losos, 1984; Irschick & Losos, 1998; Husak & Fox, 2006). The relationship between performance (e.g. locomotion, bite force) and behavior is important in the context of

honest signaling, in which certain behaviors (movements, postures, sounds) involved in agonistic and sexual interactions are thought to indicate reliable information about the signaler with regard to, for example, fighting capacity, energy reserves or fitness (Zahavi, 1975, 1977; Leal, 1999; Keyser & Hill, 2000; Akçay *et al.*, 2011; Lailvaux, Gilbert & Edwards, 2012).

Animal behavior was traditionally considered highly plastic and quickly responsive to an organism's physiological state and environmental context (Emlen, 1966; Stephens & Krebs, 1986). Contrary to this view, researchers have increasingly demonstrated that behaviors are often quite consistent among individuals, even across different contexts (both in the laboratory and in the field, reviewed in Bell, Hankison & Laskowski, 2009); observations that have led to the development of a considerable literature on behavioral syndromes and animal personalities (Koolhaas *et al.*, 1999; Gosling, 2001; Sih, Bell & Johnson, 2004; Reale *et al.*, 2007). Despite the rapid

development of the literature on behavioral consistency among individuals, few studies have integrated this new understanding into studies of honest signaling (see Akçay *et al.* 2014). This is surprising because the maintenance of honest signals should be enhanced by the existence of consistent individual differences in behaviors.

Different behaviors are utilized in different contexts; consequently, the degree of individual consistency might be expected to vary depending on the purpose of the behavior being examined and its relationship to honest signaling. For example, display behaviors are frequently used in agonistic and sexual encounters, whereas general movements are used to accomplish a wide variety of tasks (foraging, seeking a refuge, territorial defense, seeking mates). Thus, display behaviors should be more likely to represent honest signals and be more consistent within individuals (i.e. display higher repeatability) than general movements because the former is expected to signal important aspects of individual quality to conspecifics. Furthermore, because males generally engage in agonistic interactions more than females, one might expect stronger repeatability and behavior–performance correlations in the former sex. The magnitude of consistent individual differences (i.e. repeatability) in behavior and performance can provide information about the potential for a population to respond to natural selection (Falconer & Mackay, 1996; but see Dohm, 2002). Thus, the evolution of honest signaling should require both consistent individual differences in behavior and performance and correlations between these traits at the individual level. In this study, we tested the hypotheses that repeatability would differ between behaviors frequently used in different contexts (display vs. movement rates), that the magnitude of repeatability would differ between sexes and that behavior–performance correlations would be stronger in males than in females.

## Materials and methods

From 1 to 20 June 2012, we studied a population of *Leiocephalus carinatus* (Squamata: Leiocephalidae) along a 1060-m-long section of coastline at Cape Eleuthera on the island of Eleuthera, Commonwealth of the Bahamas. Our study site consisted of a sandy beach interspersed with limestone outcrops and bordered by vegetation dominated by salt-tolerant grasses, stands of sea grape *Coccoloba uvifera* and Australian pine *Casuarina equisetifolia*. The ends of the transect were bordered by an uninhabited grassy area and a largely uninhabited series of cliffs, effectively isolating this population and rendering it ideal for behavioral studies requiring repeated focal observations.

We attempted to capture all individuals with snout-vent lengths (SVLs)  $\geq 50$  mm. For a subset of animals ( $n = 21$ ), we recorded cloacal temperature ( $T_b$ ) immediately after capture using a Fluke 52 II thermometer (Fluke Corp., Everett, Washington, DC, USA) to determine appropriate temperature for measuring performance in the laboratory (see below). All  $T_b$  measurements were taken on lizards captured within 2 min of detection. We marked all capture sites with flagging so animals could be released at sites of capture.

On the day following capture, we subjected lizards to three sprint-speed trials separated by a minimum of 1 h. For sprint-speed trials, we warmed lizards under a heat source to a cloacal temperature of 33–36°C (within the range of field active  $T_b$ ) and ran them on a 1-m racetrack equipped with photocells spaced every 20 cm. Cork on the surface of the track provided traction for lizards. The same two researchers (M. E. G. and R. P.) conducted all sprint-speed trials. We measured body temperatures of each lizard prior to and immediately following each trial.

Between 09:00 and 18:00 h the next day, we measured endurance for each lizard on a custom-built motorized treadmill. We maintained the treadmill at a constant speed of 0.66 km h<sup>-1</sup>. Each lizard was slowly warmed to a cloacal temperature of 33–36°C and placed on the moving belt of the treadmill. An incandescent bulb suspended above the treadmill belt minimized loss of lizard body temperature during trials. The same researcher (K. D.) conducted all endurance tests by continuously tapping the tail and hindquarters of the lizard to encourage consistent effort. We defined endurance as the time spent on the treadmill (in seconds) until the animal was unable to right itself or was able to right itself but was unresponsive to repeated tapping (~10 taps) when placed back on the treadmill. We measured cloacal temperatures before and after endurance trials.

We measured SVL (to the nearest millimeter) and mass (to the nearest 0.5 g) for each lizard either on the day of capture or following sprint-speed testing. We determined the sex of each animal using a sexing probe inserted posteriorly into the cloaca to locate the presence of hemipenes in males, and we determined whether females were gravid by palpation. We marked each lizard with a unique code of four colored beads (two per lateral side) sewn into the base of the tail (on the dorsal side) following the protocol of Fisher & Muth (1989). Movement of the marked individuals was not affected by this marking system based on our focal observations. Beads were not removed from individuals at the end of our study so that a survivorship study could be performed the following season. We released lizards no more than 48 h after initial capture at the precise location where the animal was captured.

Corresponding to periods of greatest activity, we surveyed the entire site at 09:00–12:00 h and again at 16:00–19:00 h each day (5–18 June 2012), conducting focal observations on marked animals. We attempted to maintain a minimum distance of ~10 m during focal observations, and all observations were made with the aid of binoculars. Focal observations were taken for a maximum of 15 min; however, for our analysis, we used all data for observations of  $\geq 5$  min. We used repeated observations on a given lizard only if subsequent observations were separated by a minimum of 4 h, as this was the average time it took for a complete survey of our study site. If subsequent observations were recorded in less than 4 h, we used data for the first observation only. We recorded numbers of locomotor movements (i.e. movements greater than ~10 cm separated by a distinct pause with all four limbs at rest) and displays (e.g. head-bobs, push-ups) for the duration of each observation. We calculated display rates (displays per minute, DPM) and movement rates (moves per minute, MPM) as the number

of displays and movements per minute of observation. We used the total number of displays in analyses rather than assessing each type of display independently because our intention was to determine whether overall display frequency was correlated with performance metrics, not to assess the particular components of the display. Because field behavior can be influenced by the presence of a conspecific, for each focal observation, we also noted whether the focal lizard was in close proximity to or clearly displaying toward another lizard.

### Analysis: allometry and sex differences

We analyzed all data in R version 2.15.1 (R Development Core Team, <http://www.r-project.org/>). We tested morphological, performance and behavioral data for normality. For those traits not satisfying this assumption, we applied appropriate data transformations to improve fit and reduce skewness. We tested for differences between sexes in SVL using analysis of variance (ANOVA) and for endurance and maximal sprinting speed using analysis of covariance (ANCOVA) with SVL as a covariate.

### Analysis: repeatability

We obtained repeated observations of field behavior, providing multiple measures of DPM and MPM for each individual. Thus, we tested whether individuals differed significantly for these traits using mixed-effects models with individual identity fitted as a random effect. We standardized all dependent variables to a mean of 0 and a variance of 1 and included trial number as a categorical variable. All models concerning field behavior also included a fixed effect of ‘intraspecific interaction’ signifying whether during a given observation a lizard was in close proximity to or clearly displaying toward another lizard. ‘Sex’ was included as a fixed effect when analyzing the entire dataset for models concerning sprint speed. From these models, we calculated repeatability ( $R$ ) as the ratio of the between-individual variance ( $V_I$ ) to total phenotypic variance ( $V_P$ ).  $V_I$  is the variance represented by the random effect (individual identity), whereas  $V_P$  represents the sum of  $V_I$  and  $V_R$  (conditioned on the fixed effects). We considered repeatability estimates statistically significant if their Bayesian credibility intervals did not overlap 0. We analyzed all mixed-effects models using MCMCglmm in R (Hadfield, 2010). We explored variations in Markov chain length, prior specification, thinning interval and burn-in length to obtain final models that adequately sampled the posterior distributions, and showed limited autocorrelation among samples. Final models included 300 000 iterations, a thinning interval of 100 and a burn-in period of 3000 iterations. All models exhibited very low autocorrelation values (all values  $<0.08$ ), suggesting that the posterior distributions of parameter estimates represented independent samples.

### Analysis: among- and within-individual correlations

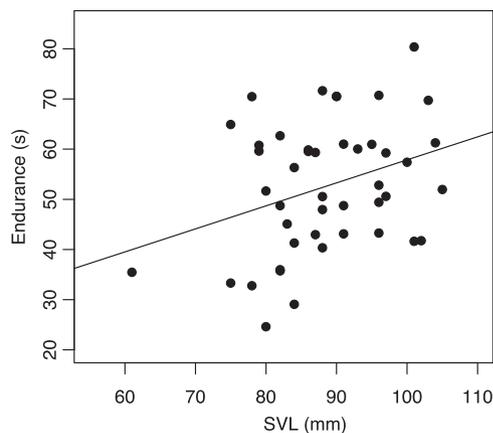
Phenotypic correlations ( $r_p$ ) are influenced by variance at two different levels, among ( $V_I$ ) and within individuals ( $V_e$ ). There-

fore, fully understanding the nature of the correlation between traits from phenotypic correlations alone can be difficult (Dingemanse & Doehtermann, 2013). The assumption that the phenotypic correlation is indicative of the between-individual correlation was recently termed the ‘individual gambit’ (Brommer, 2013). We estimated among-individual correlations ( $r_{ind}$ ) between field behavior (DPM and MPM) and performance (endurance and sprint speed) across the entire dataset and for males and females separately. Because we obtained only a single measurement of endurance for each lizard, we could not estimate  $V_e$  for this trait. Therefore, for models concerning endurance, we constrained the residual variance for endurance to be equal to 0.0001 and assumed an unstructured correlation between response variables. Thus, for these models, we estimated variance at the among-individual level for DPM and MPM, variance at the phenotypic level for endurance, residual variance for DPM and MPM, and covariance between endurance (phenotypic) and field behavior (among-individual). This allowed us to measure the correlation between the among-individual component for field behavior and endurance in a single step ( $r_{ind}$ ). This is a more conservative approach than a two-step process whereby best linear unbiased predictors are first calculated and then used to test for correlations. Because we made repeated measurements of sprint speed for each individual, we estimated both among- and within-individual correlations between field behavior and sprint speed. These models included a random effect for individual identity ( $V_I$ ) fitted to all response variables and an unstructured correlation matrix between them. This structure allowed estimation of  $r_{ind}$ . We also used an unstructured correlation matrix between the residual variances ( $V_e$ ), allowing estimation of  $r_e$  among variables. We considered among- and within-individual correlations significant if their 95% Bayesian credibility intervals did not overlap 0. See previous discussion for specifics about Bayesian MCMC runs.

## Results

### Descriptive statistics, between sex comparisons and allometry

We obtained morphological measurements, measurements of endurance and sprint speed, and behavioral observations on 45 lizards (24 males and 21 females). We sampled body temperatures ( $T_b$ ) on 21 lizards immediately upon capture to estimate activity  $T_b$  and to determine the temperature at which to perform performance tests. Lizards maintained moderate and stable  $T_b$ 's throughout the day ( $34.61 \pm 0.39^\circ\text{C}$ , mean  $\pm$  SE, 09:00–17:30 h). Lizard body temperatures during endurance trials averaged  $34.15 \pm 0.34^\circ\text{C}$ , and during sprint speed trials averaged  $34.99 \pm 0.26^\circ\text{C}$ . We made a total of 173 focal observations on lizards in the field (89 on females, 84 on males). We obtained an average of 3.4 behavioral observations on individual lizards (3.5 on males, 3.3 on females) lasting an average of 13.7 min (13.5 min for males, 13.8 min for females). SVL, body mass and endurance were all normally distributed (Shapiro–Wilk, all  $P > 0.251$ ). Sprint speed was  $\log_{10}$ -transformed to achieve normality (Shapiro–Wilk,  $P = 0.322$ ).



**Figure 1** The relationship between endurance and snout-vent length (SVL) among 45 (24 male and 21 female) wild-caught curly tailed lizards *Leiocephalus carinatus*.

As expected, males were larger than females in both SVL and body mass (SVL, males =  $94.71 \pm 1.28$  mm, females =  $81.33 \pm 1.42$  mm,  $F_{1,43} = 49.35$ ,  $P < 0.0001$ ; body mass, males =  $34.65 \pm 1.51$  g, females =  $21.55 \pm 1.15$  g,  $F_{1,43} = 45.67$ ,  $P < 0.0001$ ). Across all sampled lizards, endurance was weakly but significantly correlated with SVL ( $R^2 = 0.106$ ,  $P = 0.029$ ; Fig. 1). Males and females did not differ significantly in absolute endurance (males =  $56.01 \pm 2.57$  s, females =  $48.65 \pm 2.77$  s; ANOVA,  $F_{1,43} = 3.809$ ,  $P = 0.06$ ) or after taking SVL into account (ANCOVA,  $F_{1,42} = 0.231$ ,  $P = 0.634$ ). Endurance was not correlated with SVL within either sex (males,  $R^2 = 0.025$ ,  $P = 0.459$ ; females,  $R^2 = 0.040$ ,  $P = 0.386$ ). Across all sampled lizards, maximal sprint speed was not significantly correlated with SVL ( $R^2 = 0.079$ ,  $P = 0.395$ ), but males tended to sprint faster (maximally) than females (males =  $258.74 \pm 9.69$  cm s<sup>-1</sup>, females =  $232.49 \pm 8.94$  cm s<sup>-1</sup>;  $F_{1,43} = 4.078$ ,  $P = 0.049$ ).

### Repeatability: both sexes combined

Because field movement and display behavior could be influenced by sex or by the presence of a conspecific (rival or potential mate), we included fixed effects for 'intraspecific interaction' and for 'sex' in mixed-effects models when analyzing the entire dataset. We transformed data for DPM and MPM with an exponential transformation (i.e. we raised each value to the 0.3 power) to reduce data skew. 'Sex' had no significant effect on *average* sprint speed when all sprinting trials were analyzed together (Table 1a). The repeatability estimate for sprint speed was high and significantly different from 0 (Table 1a). When analyzing all data together, DPM did not differ significantly by sex, but was significantly influenced by the presence of a conspecific (Table 1b). Neither sex nor the presence of a conspecific had any significant influence on movement rates of lizards (Table 1c). Repeatability estimates for field behavior were significantly different from 0, although lower than the estimate for sprint speed (Table 1b,c).

Repeatability estimates for sprint speed were based on three sprint trials separated by 1 h. Repeatability estimates for field behaviors were based on observations separated by a minimum of 4 h and a maximum of 11 days (mean = 6.5 days).

### Repeatability: within sexes

Similar to analyses concerning the complete dataset, repeatabilities estimated for sprint speed were significantly different from 0 within each sex and of comparable magnitude (Table 1a). The presence of a conspecific had a significant effect on DPM in the male dataset, but not in the female dataset or in either dataset for MPM (Table 1b,c). Repeatability estimates for DPM differed substantially between the sexes. Repeatability for DPM was moderate to high for males, and very low for females with a 95% credibility interval approaching 0 (Table 1b). For MPM, repeatability estimates for both sexes were low (Table 1c).

### Among- and within-individual correlations

Using the complete dataset and analyzing each sex independently, we tested whether locomotor performance measured in the laboratory was correlated with field behaviors at the individual level. Sprint speed was not significantly correlated with either DPM or MPM in any dataset (Table 2a,b). Similarly, endurance was not significantly correlated with MPM in any dataset; however, endurance was significantly correlated with DPM in the complete dataset and for males alone (Table 2c,d; Fig. 2a,b). Endurance and DPM were not significantly correlated for females (Table 2c; Fig. 2c). No within-individual correlations were statistically significant (Table 2a,b). We conducted all analyses concerning endurance with and without SVL as a covariate because of the weak, but statistically significant, correlation between these variables at the phenotypic level (see previous discussion). Across the entire dataset, inclusion of SVL as a covariate did not alter the estimated among-individual correlations between behavior and endurance. Therefore, all analyses presented earlier did not include the covariate.

## Discussion

Because the evolution and maintenance of honest signaling would require consistency in individual behavior and in traits related to fitness, we examined repeatability of locomotor performance and two behaviors in free-ranging lizards. In addition, we tested the hypotheses that the magnitude of repeatability in field behavior and correlations between behavior and performance would be greater in males because they are more likely to engage in agonistic interactions and sexual contests for females. Our results demonstrated that locomotor performance measured in the laboratory and the behaviors of field-active lizards are repeatable, but that the magnitude of repeatability varies depending on sex and behavior type. Specifically, repeatability estimates were high for sprint speed regardless of sex, ranging from very low to high for display frequency, and were generally low for movement rate

**Table 1** Repeatability ( $R$ ) of sprint speed, exponentially transformed ( $X^{0.3}$ ) display rate (displays per minute, DPM) and movement rate (moves per minute, MPM) in field-active lizards (*Leiocephalus carinatus*) including data from all lizards ('All data') and for each sex independently ('Males' and 'Females,' respectively)

Data/Sex	Fixed effects						Random effects										
	Intraspecific interaction			Sex			Individual identity			Residual			Repeatability				
	Mean	CI <sub>low</sub>	CI <sub>high</sub>	$P$	Mean	CI <sub>low</sub>	CI <sub>high</sub>	$P$	$V_i$	CI <sub>low</sub>	CI <sub>high</sub>	$V_R$	CI <sub>low</sub>	CI <sub>high</sub>	$R$	CI <sub>low</sub>	CI <sub>high</sub>
(a) Sprint																	
All data	NA	NA	NA	NA	0.567	-2.681	3.877	0.725	29.02	18.17	42.23	12.11	8.896	15.57	0.710	0.600	0.801
Males	NA	NA	NA	NA	NA	NA	NA	NA	57.32	27.65	93.75	23.59	14.92	33.25	0.730	0.557	0.833
Females	NA	NA	NA	NA	NA	NA	NA	NA	51.08	24.49	84.55	21.35	13.40	30.19	0.696	0.552	0.837
(b) DPM																	
All data	0.552	0.124	1.005	0.017	0.327	-0.107	0.779	0.142	0.284	0.023	0.553	0.732	0.508	0.981	0.258	0.053	0.489
Males	0.656	0.137	1.173	0.017	NA	NA	NA	NA	0.556	0.109	1.09	0.523	0.299	0.790	0.560	0.219	0.758
Females	0.438	-0.250	1.154	0.212	NA	NA	NA	NA	0.093	0.003	0.286	1.018	0.641	1.431	0.016	0.003	0.247
(c) MPM																	
All data	0.364	-0.066	0.826	0.109	0.012	-0.424	0.447	0.950	0.206	0.034	0.426	0.809	0.581	1.062	0.175	0.039	0.391
Males	0.498	-0.101	1.113	0.113	NA	NA	NA	NA	0.266	0.011	0.649	0.810	0.475	1.192	0.148	0.013	0.499
Females	0.237	-0.426	0.937	0.492	NA	NA	NA	NA	0.220	0.029	0.505	0.866	0.549	1.238	0.119	0.035	0.407

Parameters from mixed-effects models with fixed effects of intraspecific interaction and sex, and a random effect for individual identity. Estimates of within- and between-individual variances ( $V_R$  and  $V_i$ , respectively) and repeatability ( $R$ ) are reported with their 95% Bayesian credibility intervals (CI). Repeatability estimates whose 95% credibility intervals did not overlap 0 were considered statistically significant.

**Table 2** Among- and within-individual correlation ( $r_{ind}$  and  $r_e$ , respectively) for all data and for each sex independently using multivariate mixed-effects models

Data	Among-individual			Within-individual		
	$r_{ind}$	CI <sub>low</sub>	CI <sub>high</sub>	$r_e$	CI <sub>low</sub>	CI <sub>high</sub>
(a) DPM versus sprint speed						
All data	0.269	-0.186	0.691	-0.093	-0.317	0.150
Males	0.308	-0.366	0.735	-0.270	-0.511	0.129
Females	-0.013	-0.563	0.595	-0.014	-0.317	0.290
(b) MPM versus sprint speed						
All data	0.171	-0.368	0.613	-0.054	-0.250	0.203
Males	0.239	-0.351	0.762	-0.068	-0.440	0.218
Females	0.077	-0.589	0.582	0.016	-0.262	0.351
(c) DPM versus endurance						
All data	<b>0.404</b>	<b>0.059</b>	<b>0.730</b>	-	-	-
Males	<b>0.559</b>	<b>0.035</b>	<b>0.837</b>	-	-	-
Females	0.102	-0.443	0.673	-	-	-
(d) MPM versus endurance						
All data	0.240	-0.288	0.581	-	-	-
Males	0.259	-0.279	0.725	-	-	-
Females	0.064	-0.525	0.622	-	-	-

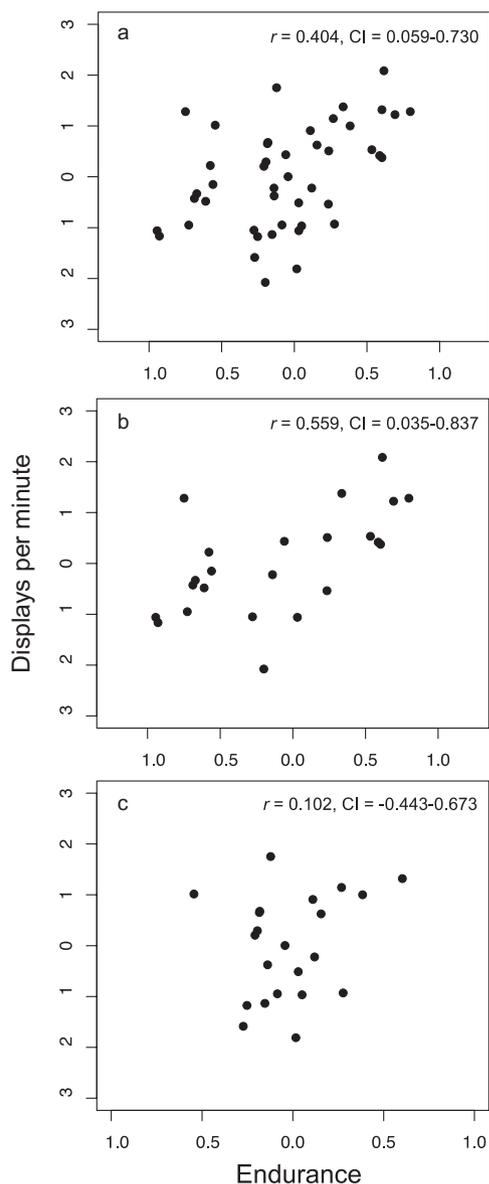
Because we obtained a single measurement of endurance for each lizard, we were able to estimate only the variance at the phenotypic level for this trait. Estimates of among- and within-individual correlations are reported with their 95% Bayesian credibility intervals (CI). Correlations whose 95% credibility intervals did not overlap 0 were considered statistically significant (shown in bold).

(Table 1). Interestingly, we found differences between sexes in the correlation between field behavior and endurance; individual males (but not females) that exhibited displays at a greater frequency (i.e. higher DPM) also tended to have greater endurance. Conversely, movement rate (MPM) of individuals

was not correlated with either locomotor performance trait in either sex or across the entire dataset.

Sexual differences in behavioral repeatability have been found previously, with estimates for males generally higher than those for females (Nakagawa *et al.*, 2007; Bell *et al.*, 2009). Andrew (1972) and Wingfield (1994) suggested that males might exhibit greater repeatability than females due to the integrating influence of testosterone, which could favor more predictable behavioral responses in males. A non-mutually exclusive alternative hypothesis is that greater repeatability in males is driven by sexual selection for behaviors indicated by a sexually selected trait, and therefore might represent an honest signal. This hypothesis requires that the display behavior be correlated with another trait on which sexual selection operates.

The lack of relationship between movement rates in the field (MPM) and locomotor performance is consistent with the results of comparative phylogenetic studies across a broad range of lizard species (Garland, 1999). The consistently low level of repeatability in movement rates is consistent with the idea that these behaviors are multipurpose and heavily influenced by the internal physiological state of the organism and external environmental pressures (Emlen, 1966; Stephens & Krebs, 1986). This low level of repeatability and the inherent variation associated with MPM likely breaks down any relationship between this behavior and locomotor performance (which is highly repeatable). The strong relationship between display rates (DPM) and endurance is consistent with the results from other studies (Clobert *et al.*, 2000; Brandt, 2003; Perry *et al.*, 2004), but we demonstrate that this relationship is sex-specific. Display rates differ consistently among individual males, but not among individual females. Males of polygynous species frequently compete with one another for access to females, and in many lizards (including *L. carinatus*),



**Figure 2** Display behavior (displays per minute, DPM) in field-active lizards (*Leiocephalus carinatus*) as a function of endurance measured in the laboratory. Bivariate plots depict predictions for the random effect of individual identity extracted from multivariate mixed-effects models from Table 2. Panel (a) includes all individuals, panel (b) includes males only and panel (c) includes females only.

these interactions involve display behaviors (Henderson & Powell, 2009). Our results agree with the notion that potentially reliable signals should be repeatable within individuals. Finally, ‘honest’ behaviors should signal some aspect of male quality, or fitness, or be strongly correlated with another trait that is associated with fitness. Husak & Fox (2006) demonstrated that sexual selection could operate on locomotor performance in lizards. Consequently, the strong relationship

between display behavior and endurance in *L. carinatus* could indicate that display behavior is an honest signal of endurance capacity.

In this study, we demonstrated that behaviors generally associated with agonistic and sexual interactions (e.g. display behaviors) are more consistent within individuals than behaviors used in a broader array of contexts (e.g. movement rates) in free-ranging lizards. In addition, we also showed that the magnitude of consistency differs between the sexes, with males exhibiting substantially higher repeatability of display behaviors than females. Although rarely explicitly tested, this result is consistent with the fact that display behaviors are used by males to signal different aspects of individual quality to females or other males; females generally do not engage in these behaviors. The maintenance of honest signals should require not only consistent within-individual variation in ‘signaling’ behaviors and performance but also individual-level correlations between behaviors and performance metrics linked to fitness. In *L. carinatus*, display behaviors are repeatable in males and strongly correlated with endurance, a performance metric frequently correlated with fitness in other lizards (Husak & Fox, 2006). In this study, we were unable to test whether endurance was significantly repeatable, so our behavior–performance correlation analysis assumes that the within-individual variance for this trait is 0. Despite this shortcoming, endurance is a highly repeatable trait in other lizards (Garland & Else, 1987; Huey & Dunham, 1987), suggesting that among-individual variance for this trait is typically high. Given this, we feel that our approach provides a reliable estimate of the underlying between-individual correlation. When testing hypotheses of honest signaling in the future, we encourage researchers to make repeated measurements of both behaviors and performance over similar time frames and use mixed-effects models to partition phenotypic correlations into within- and between-individual components (see Dingemanse & Dochtermann, 2013; Brommer, 2013).

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