

Conflict, compensation, and plasticity: Sex-specific, individual-level trade-offs in green anole (*Anolis carolinensis*) performance

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Abstract

Trade-offs in performance expression occur because animals must perform multiple whole-organism performance tasks that place conflicting demands on shared underlying morphology. Although not always detectable within populations, such trade-offs may be apparent when analyzed at the level of the individual, particularly when all of the available data are taken into account as opposed to only maximum values. Detection of performance trade-offs is further complicated in species where sexual dimorphism drives performance differences between males and females, leading potentially to differing patterns of trade-offs within each sex. We tested for within- and between-individual trade-offs among three whole-organism performance traits (sprint speed, endurance, and bite force) in adult male and female *Anolis carolinensis* lizards using all of the measured performance data. Sprinting and endurance did not trade-off among individuals in either sex, but we found a significant negative among-individual relationship between sprint speed and bite force in females only, likely driven by the mechanical burden of larger than optimal heads imposed on females through intralocus sexual conflict. We also found evidence for marked within-individual plasticity in male bite force, but no within-individual trade-offs between any traits in either sex. These data offer new insight into the sex-specific nature of performance trade-offs and plasticity and, ultimately, into the constraints on multivariate performance evolution.

KEYWORDS

mixed-models, performance, sexual conflict, trade-offs

1 | INTRODUCTION

Animals that are specialized to conduct certain ecological tasks may also be required to conduct several different such tasks on a regular basis. These requirements frequently place conflicting demands on the organisms' underlying morphology and physiology that cannot be met simultaneously. Specialization in certain characteristics, therefore, comes at the cost of less-than-optimal expression in others (Dudley & Gans, 1991; Stearns, 1989) leading to trade-offs in trait expression, particularly for traits associated with whole-organism

performance (Clemente & Wilson, 2015; Nasir, Clemente, Wynn, & Wilson, 2017; Pasi & Carrier, 2003). Although the mechanical bases of these trade-offs are well-understood at lower levels of organization, evidence of trade-offs at the organismal level is inconsistent (Wilson & James, 2004). For example, sprinting and endurance running have incompatible morphological and physiological requirements, namely the short-term generation of anaerobic power (T. M. Williams et al., 1997; Williams, Wilson, Rhodes, Andrews, & Payne, 2008) versus long-term, efficient oxygen delivery, respectively (Lindstedt et al., 1991; McKean & Walker, 1974; Myers & Studel,

1985; Steudel, 1990). Despite this incompatibility, studies have variously found strong (Herrel & Bonneaud, 2012), mixed (Vanhooydonck et al., 2014), or no support (de Albuquerque, Bonine, & Garland, 2015; Huey, Dunham, Overall, & Newman, 1990; Sorci, Swallow, Garland, & Clobert, 1995; Wilson, James, & Van Damme, 2002) for such a trade-off at both the intra- and interspecific levels, and sometimes conflicting results from the same taxa (e.g., lacertid lizards; Vanhooydonck et al., 2014; Vanhooydonck, Van Damme, & Aerts, 2001).

Performance trade-offs can be difficult to detect because researchers overwhelmingly employ performance measurement protocols that focus on obtaining single “personal best” measures of maximum performance (Adolph & Pickering, 2008; Head, Hardin, & Adolph, 2012; Losos, Creer, & Schulte, 2002) and consequently do not allow for the rigorous statistical estimation of both within- and among-individual (co)variation (Brommer, 2013; Dingemans & Dochtermann, 2013; Houslay & Wilson, 2017). Careau and Wilson (2017a) used simulations to show that although within-individual performance variation can mask performance trade-offs among different individuals, these among-individual trade-offs are recovered by the use of multivariate mixed-models (MMM) that partition variation in performance both among and within individuals. For example, trade-offs among suites of performance traits in decathletes and heptathletes only become apparent at the within- and among-individual level once the performance variation is partitioned appropriately (Careau & Wilson, 2017b). Doing so requires repeated measurement of the performance traits of interest at different periods of time, a procedure that historically has not been standard in the field of performance biology (but see Newar & Careau, 2018 for another recent example).

Detection of performance trade-offs is further complicated by the inherently multivariate nature of the integrated performance phenotype (Ghalambor, Reznick, & Walker, 2004; Ghalambor, Walker, & Reznick, 2003). Studies that consider functional trade-offs often test for bivariate relationships between specific pairs of performance traits, such as sprinting and endurance, that rely on similar morphological apparatus and thus are expected to covary. However, performance traits are integral characteristics of the entire organism and are seldom expressed in isolation. As such, a given pair of performance traits might be linked not only to each other but also to other performance/life-history traits via shared (or conflicting) functional or energetic pathways (Husak & Lailvaux, 2017; Lailvaux & Husak, 2014). For instance, in addition to the potential relationship between sprinting and endurance, sprinting has also been found to trade-off against bite force in *Hemidactylus frenatus* geckos because high bite forces require large heads, which impede locomotor ability (Cameron, Wynn, & Wilson, 2013). Studies that measure trade-offs among multiple performance traits repeatedly are not common, likely due to the logistical challenges involved in doing so, yet they are necessary if we are to properly understand the constraints driving functional trade-offs.

Finally, intraspecific variation poses yet another challenge to understanding performance trade-offs. Significant sexual dimorphism in morphology or physiology might influence performance capacities in sex-specific ways (reviewed in Lailvaux, 2007; Van Damme, Entin,

Vanhooydonck, & Herrel, 2008). In some cases, intralocus sexual conflict over the expression of a given trait can manifest as different (possibly suboptimal) expression of that same trait in one sex relative to the other (reviewed in Arnqvist & Rowe, 2005; Bonduriansky & Chenoweth, 2009) and thus potentially also as distinct suites of functional trade-offs in males compared with females (Husak & Lailvaux, 2014). The trade-off between bite force and sprint speed in *H. frenatus*, for example, is only evident in males because females compensate for the locomotor decrement imposed on them via selection for high male bite force by expressing longer hindlimbs, and thus higher sprint speeds (Cameron et al., 2013). Although the functional costs of intralocus conflict over a single performance trait can be ameliorated in various animal species by the evolution of similar compensatory mechanisms (Husak & Swallow, 2011; Husak, Ribak, Wilkinson, & Swallow, 2011), the consequences of sex differences in performance for the expression of the multivariate performance phenotype, as well as the various trade-offs among the constituent performance traits, remains poorly understood (Husak & Lailvaux, 2014; Lailvaux & Husak, 2014), particularly at the among- and within-individual levels.

In this paper we use multivariate mixed-models to test for both within- and among-individual trade-offs in sprinting, endurance, and bite force in male and female green anole lizard (*Anolis carolinensis*). These animals are ideal for addressing trade-offs among multiple performance traits because anoles in nature regularly employ a variety of performance abilities, relying on sprinting for predator escape, and on slower, sustained locomotion for foraging and patrolling territories (Irschick & Losos, 1998; Irschick, Carlisle et al., 2005; S. B. Jenssen, Greenberg, & Hovde, 1995). Furthermore, green anoles exhibit marked sexual dimorphism in head shape, with males having significantly larger heads for their size than females (Herrel, McBrayer, & Larson, 2007), likely a consequence of male combat-based sexual selection on bite force (Lailvaux & Irschick, 2007; Lailvaux, Herrel, Vanhooydonck, Meyers, & Irschick, 2004). Consequently, there is scope for sex-specific trade-offs between bite force and both of the measured locomotor traits, which we consider here as well. We tested the following specific hypotheses: (a) Sprinting and endurance trade-off at the among- and within-individual levels in both male and female *A. carolinensis*; (b) sprinting and bite force trade-off at both among- and within-individual levels in males only as a result of the large heads required to support high male bite forces.

2 | MATERIALS AND METHODS

All procedures were approved by the University of New Orleans Institutional Animal Care Committee (IACUC protocol #14-005). We caught 121 adult green anoles (61 males and 60 females) from New Orleans, LA in July, 2014 and brought them back to the laboratory at the University of New Orleans. Lizards were housed individually in 28.5 x 17.5 x 21 cm plastic cages with mulch substrate and identical wooden dowel perches oriented towards uniform 75 W incandescent bulbs positioned above each cage to provide opportunity for basking.

Each shelving rack of cages was also provided with Repti-Sun 5.0 UVB 310 40 W Fluorescent Lamps to mimic natural sunlight. Animal room conditions were maintained at approximately 30°C, 70% relative humidity, with a light:dark cycle of 12:12 hr (Kolbe & Losos, 2005). We covered the sides of the cages with dark paper to prevent lizards in adjacent cages from seeing each other (as in Lailvaux, Gilbert, & Edwards, 2012; Lailvaux, Leifer, Kircher, & Johnson, 2015). Lizards were misted at least twice daily and fed a diet of 1–2 crickets supplemented with calcium powder (Repti Calcium, Zoo Med Laboratories Inc., CA) every 2–3 days.

2.1 | Performance measurement timeline

We measured lizards for bite force, sprint speed, and endurance on two separate occasions using standard methods (details below). We conducted all initial performance measures for each individual within 2 weeks of capture, as is standard. As these lizards were caught towards the end of the breeding season, and because we were primarily interested in quantifying within- and among-individual variation within that same breeding season, we remeasured performance again exactly 3 weeks after the initial performance measures for each individual. Performance trials were conducted by the same investigators in both performance measurement sessions (endurance and sprinting AMC; biting SPL). Although we conducted the methods with the aim of determining maximum performance, as in previous studies, we nonetheless retained and used all of the measured performance data for the final analysis (see below). All performance measures were conducted within a room heated to 33°C (approximately the preferred body temperature for this species; Lailvaux & Irschick, 2007). To control for order effects, and to prevent exhausting the animals by forcing them to perform multiple trials in a short time, we randomized the order of the performance measures for each lizard such that individuals were measured for only two of the three trials per day, and were measured for the third the next day.

2.2 | Bite Force

As in previous studies of anole bite force (e.g., Lailvaux & Irschick, 2007; Lailvaux et al., 2012) we measured bite force using an isometric Kistler force transducer (type 9023, Kistler, Winterthur, Switzerland) connected to a type 5058a Kistler charge amplifier (see Herrel, Spithoven, van Damme, & de Vree, 1999; Herrel, Van Damme, Vanhooydonck, & de Vree, 2001 for a detailed description). Lizards were induced to bite a force plate by tapping their cheek until their mouth opened, then lining up the mouth with the center of the force plate in a standardized manner until the lizard bit forcefully. Bite trials were repeated every hour for a total of five trials per animal (Adolph & Pickering, 2008; Losos et al., 2002) with a 1-hr rest between trials.

2.3 | Sprint Speed

We measured sprint speed using a custom-made racetrack consisting of a wooden dowel cork substrate inside a wooden structure with

fitted infrared sensors placed every 25 cm (SCL Timer, Trackmate Racing, Surrey BC, Canada). When the beams are interrupted by the lizard running past, the time is recorded, such that consecutive beam interruptions allow for accurate measurement of the time it takes for each lizard to traverse each 25 cm interval. We angled the track at 45 degrees to the horizontal to encourage lizards to run along the track rather than hop, as is typical behavior on level ground (Perry, Levering, Girard, & Garland, 2004). We encouraged lizards to run from the beginning of the track with a gentle tap on the tail and recorded the highest speed measured over a 25 cm distance as maximum speed. This is a repeatable, standard measure for *Anolis* lizard sprint speed (Foster & Higham, 2012; Husak, Keith, & Wittry, 2015). Lizards were sprinted up to five times per individual with an hour rest between trials. Trials wherein a lizard stopped, reversed directions, or failed to sprint consistently across any of the 25-cm intervals between sensors were not included.

2.4 | Endurance

We measured endurance using a custom treadmill with a belt speed of 0.3 km/hr (Cox, Stenquist, Henningsen, & Calsbeek, 2009; Husak et al., 2015; Perry et al., 2004). To prevent lizards from escaping, we erected plastic walls around the treadmill set up and encouraged the lizards to stay within the center of the treadmill belt by hand. We considered endurance to be the time the lizard maintained a relatively constant speed while being lightly tapped on the tail for motivation (Husak, Ferguson, & Lovern, 2016; Le Galliard, Clobert, & Ferrière, 2004). If a lizard stopped, it was inspected for signs of exhaustion by placing it on its back, with exhaustion indicated by a lizard's failure to right itself. If a lizard was not fully exhausted and did right itself, the trial continued. We stopped timing when the lizard was fully exhausted. Because endurance is taxing for the animals, only one trial per lizard was conducted per performance measurement session; in other words, endurance was measured on two separate occasions, but not repeatedly to determine the maximum, as was done for sprinting and biting.

2.5 | Statistical analysis

For all analyses, we fitted mixed-effects models using the R package ASREML-R (Butler, Cullis, Gilmour, & Gogel, 2009) in R version 3.5.1 (R Core Team, 2018). We first used univariate mixed-models separately for each trait to check that the data conformed to model assumptions (using visual diagnostics), determine the fixed effects structure, and to test for significance of among-individual variation. We log-transformed sprint speed and endurance and used raw values of bite force. The fixed effects specification in each case included sex, snout-vent length (measured in mm using Mitutoyo digital calipers and standardized to a mean of 0 and variance of 1), and measurement session. For bite force and sprint speed we also included a fixed effect of trial number (as each individual was measured multiple times within each session). The random effects specification for bite force and sprint speed included random effects of individual ID

(among-individual variance, V_{ind}) and session nested within individual (within-individual among-session variance, $V_{session}$), as well as residual (within-individual within-session, V_e) variance. As endurance was measured only once per session, this model included a random effect of individual ID only, with residual variance also estimated.

We then used MMMs to estimate both trait repeatabilities and correlations among traits for sprint speed, endurance, and bite force separately for male and female green anoles. Although we use best linear unbiased predictors (BLUPs) for illustrative purposes to plot correlations between traits (as in Newar & Careau, 2018), we used a multivariate mixed model for our analysis because BLUPs are inappropriate for hypothesis testing (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010; Houslay & Wilson, 2017; Postma, 2006). We standardized all response traits (bite force, log-transformed sprint speed, log-transformed endurance) to a variance of 1 by dividing by the overall standard deviation before analysis. Note that we used the overall standard deviation (i.e., including both sexes) such that (co)variances are comparable across sex-specific models. The MMM contained all three performance traits as dependent variables and fixed effects as determined in the univariate modeling

process. We fit the full model using a 3×3 unstructured covariance matrix at the among- and within-individual levels and included a further diagonal matrix that enabled estimation of within-assay variances for bite force and log-transformed sprint speed. These matrices enabled us to partition correlations into their among-individual (r_{ind}) and within-individual among-session ($r_{session}$) components for each sex. Note that for hypothesis testing of single covariance terms we used bivariate models, testing a model with an unstructured covariance matrix to a diagonal matrix (i.e., where the covariance is constrained to 0). We calculated repeatability and its standard error from the MMM using the R package "nadiv" (Wolak, 2012). For endurance, repeatability was estimated simply as $R = V_{ind} / (V_{ind} + V_e)$. For bite force and sprint speed, we calculated both short-term and long-term repeatability, where $R_{short-term} = (V_{ind} + V_{session}) / (V_{ind} + V_{session} + V_e)$ and $R_{long-term} = V_{ind} / (V_{ind} + V_{session} + V_e)$.

We tested the significance of variance components using likelihood ratio tests of nested models, in which we estimated χ^2_{nDF} as twice the difference in model log likelihoods. The number of degrees of freedom (n) is the number of additional parameters in the more complex model, although note that when testing a single random effect we assume the

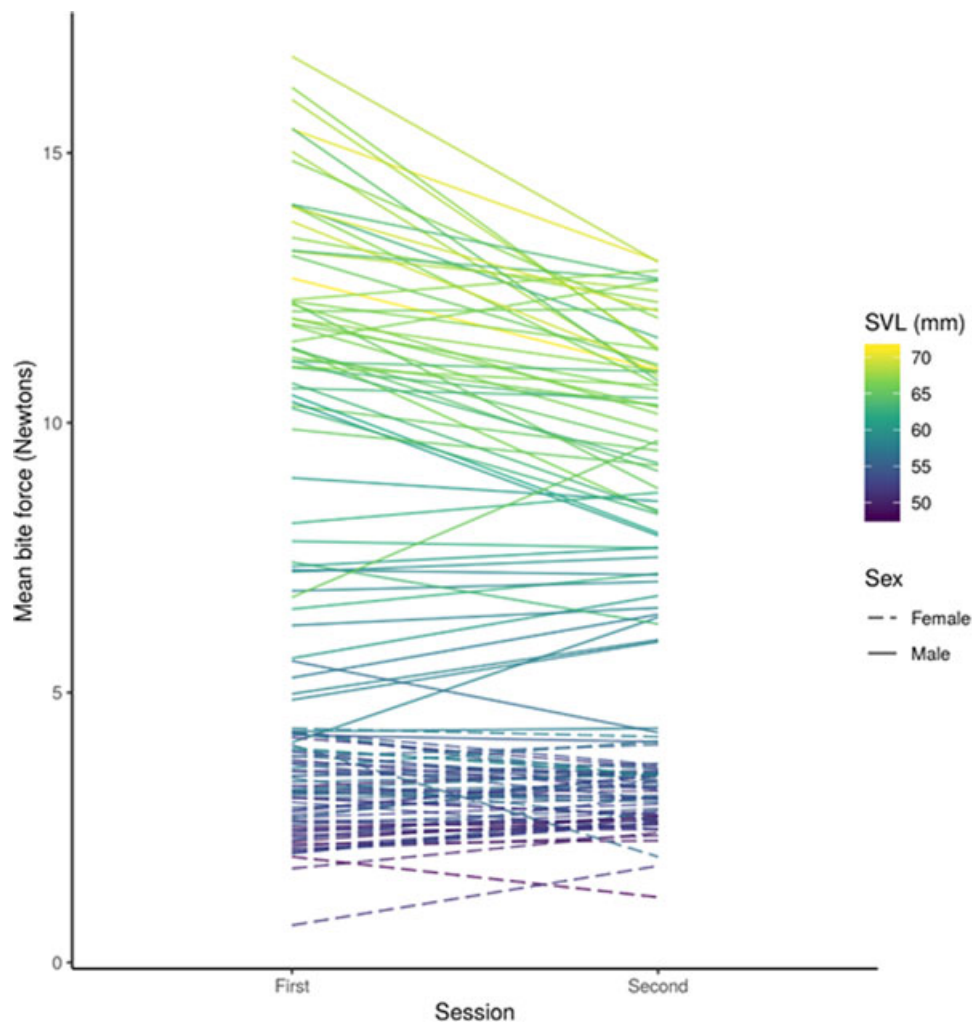


FIGURE 1 Mean bite force in Newton for each male (solid lines) and female (dashed lines) green anole lizard recorded in both the first and second measurement sessions. Larger males show marked plasticity in bite performance between sessions [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Relationships among bite force, log (sprint speed) and log (endurance capacity) for male *A. carolinensis* lizards

A. Among-individual	Bite	Log (sprint)	Log (endurance)
Bite	0.071 (0.019)	-0.062 (0.241)	-
Log (Sprint)	-0.011 (0.028)	0.183 (0.080)	-
Log (Endurance)	-	-	~0
B. Within-individual	Bite	Log (sprint)	Log (endurance)
Bite	0.042 (0.011)	-0.090 (0.199)	0.14 (0.14)
Log (Sprint)	-0.009 (0.020)	0.244 (0.08)	-0.110 (0.134)
Log (Endurance)	0.029 (0.029)	-0.055 (0.068)	1.007 (0.131)
C. Within-session	Bite	Log (sprint)	Log (endurance)
Bite	0.090 (0.006)	-	-
Log (Sprint)	-	0.505 (0.040)	-
Log (Endurance)	-	-	~0

Note. SE: standard error. Bolded values on the diagonals represent variances \pm SE, whereas values below and above the diagonals represent covariances \pm SE and correlations \pm SE respectively.

test statistic to be asymptotically distributed as an equal mix of χ^2_0 and χ^2_1 (denoted as $\chi^2_{0,1}$; Self & Liang, 1987; Visscher, 2006).

($V_{ind} = 0.019 \pm 0.006$, $\chi^2_{0,1} = 11.2$, $p < 0.001$), with moderate short-term and lower long-term repeatability ($R_{short-term} = 0.46 \pm 0.04$, $R_{long-term} = 0.19 \pm 0.06$).

3 | RESULTS

3.1 | Among-individual variation

3.1.1 | Bite force

Males produced higher bite forces than did females, consistent with the findings of earlier studies (e.g., Herrel et al., 2007). Our initial models produced distinct patterns in the residuals, and further exploratory plotting of the data indicated plasticity in bite force across sessions and related to both sex and size, requiring the addition of all interactions between these fixed effects terms. Larger males tended to bite more forcefully, although this effect decreased from the first measurement session to the second (sex \times SVL \times session: Wald $F = 8.97$, $df = 1,96.7$; $p = 0.003$; Figure 1). We found significant differences between males and females in bite force variance at all levels ($\chi^2_3 = 821.8$, $p < 0.001$) and we, therefore, used sex-specific models to test for significance of among-individual variation.

We found significant among-individual variation in bite force for both males ($V_{ind} = 1.25 \pm 0.34$, $\chi^2_{0,1} = 20.6$, $p < 0.001$) and females ($V_{ind} = 0.14 \pm 0.04$, $\chi^2_{0,1} = 16.7$, $p < 0.001$). Short-term repeatability was higher among females relative to males ($R_{short-term,f} = 0.72 \pm 0.03$, $R_{short-term,m} = 0.56 \pm 0.04$; Figure S1), although long-term repeatability was similar across the sexes ($R_{long-term,f} = 0.39 \pm 0.08$, $R_{long-term,m} = 0.35 \pm 0.07$).

3.2 | Sprint speed

We found no differences across sex on average sprint speed (raw mean and standard error: females = 0.57 ± 0.01 , males = 0.63 ± 0.01 ; Wald $F = 0.77$, $df = 1,114.5$; $p = 0.38$), nor were there differences between males and females in sprint speed variance at all levels ($\chi^2_3 = 0.1$, $p > 0.99$). There was significant among-individual variance

3.3 | Endurance

Males showed lower levels of endurance relative to females (Wald $F = 9.56$, $df = 1,116.7$; $p = 0.002$). We found no evidence of significant among-individual variation in this trait ($V_{ind} = 0.005 \pm 0.009$, $\chi^2_{0,1} = 0.35$, $p = 0.28$).

4 | TRAIT COVARIANCES

Tables 1(a-c) and 2(a-c) provide variances (on the diagonal), covariances (below-diagonals) and correlations (above-diagonals) at the among-individual (a), within-individual (b), and within-session (c) levels for bite force, log-transformed sprint speed and log-transformed endurance for males (Table 1) and females (Table 2). Given the lack of significant among-individual variance in (log-transformed) endurance, we were unable to estimate among-individual covariances involving this trait. At the within-individual level, we found no significant covariance between endurance and sprinting in male ($\chi^2_1 = 0.90$, $p = 0.34$; Table 1b) or female ($\chi^2_1 = 1.62$, $p = 0.20$; Table 2b) lizards.

Contrary to our hypotheses, we found that bite force and (log-transformed) sprint speed do not trade off among male lizards ($\chi^2_1 = 0.15$, $p = 0.70$; Table 1a, Figure 2a); however, they do among females ($\chi^2_1 = 4.29$, $p = 0.04$; Table 2a, Figure 2b). These traits do not trade off at the within-individual level in either sex (Tables 1b and 2b).

5 | DISCUSSION

Despite long-standing interest in trade-offs involving functional traits, few studies have applied variance partitioning approaches to

TABLE 2 Relationships among bite force, log (sprint speed) and log (endurance capacity) for female *A. carolinensis* lizards

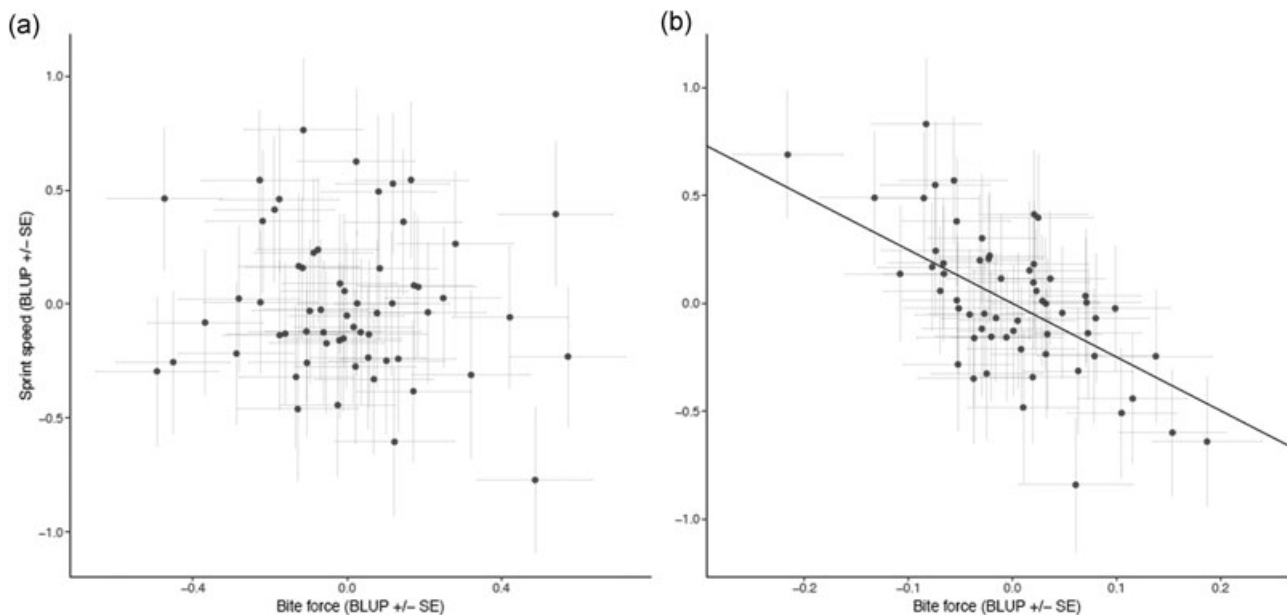
A. Among-individual	Bite	Log (sprint)	Log (endurance)
Bite	0.008 (0.002)	-0.463 (0.238)	-
Log(Sprint)	-0.019 (0.010)	0.173 (0.078)	-
Log(Endurance)	-	-	~0
B. Within-individual	Bite	Log (sprint)	Log (endurance)
Bite	0.007 (0.001)	-0.067 (0.184)	0.225 (0.117)
Log(Sprint)	-0.003 (0.007)	0.222 (0.074)	-0.194 (0.135)
Log(Endurance)	0.017 (0.009)	-0.083 (0.061)	0.829 (0.109)
C. Within-session	Bite	Log (sprint)	Log (endurance)
Bite	0.006 (0.000)	-	-
Log(Sprint)	-	0.507 (0.042)	-
Log(Endurance)	-	-	~0

Note. SE: standard error. Bolded values on the diagonals represent variances \pm SE, whereas values below and above the diagonals represent covariances \pm SE and correlations \pm SE respectively.

tease apart the influence of among- and within-individual variation and covariation on phenotypic relationships among different performance abilities (Careau & Wilson, 2017a; 2017b). We adopted this approach here and tested for such correlations among sprinting, biting, and endurance in both male and female green anole lizards. We show not only that males and females exhibit different patterns of among-individual trade-offs, but we also present evidence for significant sex- and size-specific plasticity in bite force.

Our first hypothesis, that sprint speed and endurance capacity trade-off at both the among- and within-individual levels in both sexes, was not supported. Endurance capacity showed no significant among-individual variation, meaning that the endurance measures for each lizard were as variable as the whole sample. Consequently,

endurance did not covary with any other trait at this level. Because all of the phenotypic variation in endurance was necessarily of the residual (i.e. within-individual variation) type given that there was no significant among-individual variation, this variance did not translate into shared covariance, and thus any significant relationship with either bite force or sprint speed in either male (Table 1) or female (Table 2) *A. carolinensis*. This lack of among-individual variation in endurance capacity is perhaps not surprising; despite interspecific variation in endurance that appears to be broadly correlated with activity levels (Garland, 1999), lizards generally possess poor endurance capacities due to both their ectothermic physiology and to locomotor gaits that are unsuited to breathing while in motion (Carrier, 1987). Furthermore, evidence suggests that lizard

**FIGURE 2** Best linear unbiased predictors (BLUPs) extracted from the covariance matrix of a multivariate mixed model representing the random effect of individual identity for each male (a) and female (b) green anole lizard measured for both bite force and sprint speed. Gray lines represent BLUP standard errors

endurance capacity can be enhanced either through increased use via the exercise response in green anoles (Husak et al., 2015) or through social modulation in species, such as *Sceloporus undulatus* (John-Alder, McMann, Katz, Gross, & Barton, 1996). Consequently, it could be that trade-offs between sprinting and endurance would become evident should individuals invest more in endurance, although this possibility remains to be demonstrated in nature (but see Husak & Lailvaux (in press)).

Our second hypothesis, that sprinting and biting would trade-off only in male green anoles, was not supported at the among-individual level. Although we did indeed find a significant negative among-individual correlation between sprinting and biting—such that individuals that were fast runners were consistently also poor biters over the time span of performance measures, and vice-versa—that relationship existed in female lizards, not in males (Figure 2). This correlation is influenced primarily by genetic and permanent environmental effects (Dingemanse & Dochtermann, 2013), both of which are likely to exist in these data. This negative bite-sprint relationship differs from that found in *H. frenatus* geckos by Cameron et al. (2013) in that it occurs in females rather than in males in green anoles, although it is still driven by the same mechanisms via selection for larger bite force in males (Herrel et al., 2007; Lailvaux et al., 2004). Irschick, Vanhooydonck, Herrel, and Meyers (2005) found that male green anoles have significantly longer hindlimbs for their size than females, which would allow males to compensate for their larger heads, whereas the females may not be able to do so and pay the locomotor cost of enhanced male bite capacity thrust upon them through intralocus sexual conflict (Husak & Lailvaux, 2014; Husak & Swallow, 2011). If this is the case, then it suggests either that sprint speed is likely to be of more importance to males than it is to females (see Husak, Fox, Lovern, & Van Den Bussche, 2006); or that sexual conflict over head size is unresolved due to some other constraint that is not apparent from our current data set. Future work in this area might involve measuring the sign and magnitude of the genetic correlation between the male and female morphological apparatus that supports green anole whole-organism performance, similar to work showing that sexual conflict over wing length and flight performance in the great reed warbler *Acrocephalus arundinaceus* currently appears to favor males (Tarka, Akesson, Hasselquist, & Hansson, 2014).

Although not involved in any within-individual trade-offs with other performance traits, bite force exhibited significant within-individual variation in male green anoles. This bite plasticity manifested as a decrease in bite force between the first and second performance assays in larger males only (Figure 1). Even accounting for this plasticity, females also showed higher short-term repeatability than males: this was driven by females being more consistent across sessions, whereas males were more variable within sessions. The within-session variability could simply be a function of larger variation in the size of males relative to females, but the among-session variation does appear to be size-specific. Lailvaux et al. (2012) previously reported evidence for plasticity in male *A. carolinensis* bite force, but that study used lizards that were raised

to sexual maturity from juveniles over several months and induced plasticity experimentally via a dietary manipulation. Our finding here of size- and sex-specific plasticity for bite force in mature animals that were maintained within a common environment over a very short time frame is thus highly novel. Previous studies have reported an intraspecific dimorphism in male head size and bite force within populations of green anoles in southeast Louisiana, such that there is a clear distinction between smaller (but sexually mature) “lightweight” males, and older and larger “heavyweight” males (Lailvaux et al., 2004; Vanhooydonck, Herrel, Van Damme, Meyers, & Irschick, 2005), probably maintained by size-dependent disruptive selection (Irschick & Lailvaux, 2006) at the lightweight–heavyweight transition. Although it is tempting to suggest that the apparent onset of size-dependent bite force plasticity might coincide with this transition (~64 mm svl), we found no evidence for such concurrence in this data set. However, previous studies of the endocrine factors possibly affecting bite force in lizards from these same populations showed different scaling patterns of circulating testosterone and corticosterone in lightweights and heavyweights, and in particular different relationships between testosterone and corticosterone in the different male morphs (Husak, Irschick, Meyers, Lailvaux, & Moore, 2007). That change in the male hormonal milieu as size increases could affect bite force plasticity, although we are not aware of any experimental studies that have tested this possibility.

Given this size-dependent plasticity in bite force, one can also ask why this form of plasticity was not evident in either sprint speed or endurance in our study, particularly given the known training effect on endurance in this same species. One possibility is that bite force is generally more plastic than either; indeed, Husak et al. (2015) observed no effect on sprint performance when training *A. carolinensis* for sprinting ability (although they did note changes in muscle fiber composition and cross-sectional area in response to a sprint training regimen). This explanation is not entirely consistent with the existing data on bite force variation in other lizard species; for example, bite force has been shown to be exempt from thermal dependence in some species of agamids ostensibly on the grounds that biting ability is crucial as a defense mechanism and thus maintained under low temperatures even when other performance abilities are compromised (Herrel, James, & Van Damme, 2007; Hertz, Huey, & Nevo, 1983). If it is the case that bite force is “protected” against environmental variation, then one might expect canalized bite force expression, which is not what we find. The fact that bite plasticity appears to have both age- and sex-dependent components, having been previously induced in juveniles (Lailvaux et al., 2012) and observed here only in larger (and, most likely, older) males suggests a possible role for life-history trade-offs in affecting bite ability in green anoles as well (Lailvaux & Husak, 2014). The existence of this size- and sex-specific plasticity is a cautionary note for performance studies that house individual lizards under laboratory conditions for long periods of time.

In conclusion, we present evidence for an among-individual trade-off between sprinting and bite force in female green anole lizards only, likely driven by unresolved intralocus sexual conflict over head

size due to sexual selection on male bite force through male combat. The lack of such a relationship among males points to the existence of male compensation for the effects of high bite force on other performance traits. We also show for the first time significant sex-specific and size-dependent plasticity in bite force. Future studies that estimate the between-sex genetic covariances (i.e., *B* matrix) for green anole morphology and performance would be useful for understanding the extent to which such conflict might be compensated for in males (Gosden, Shastri, Innocenti, & Chenoweth, 2012). Taken together, these results illustrate the value and importance of expanding our performance measurement methodology to consider multivariate variation beyond maximum performance (Careau & Wilson, 2017a; Head et al., 2012).

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REFERENCES

- Adolph, S. C., & Pickering, T. (2008). Estimating maximum performance: Effects of intraindividual variation. *Journal of Experimental Biology*, *211*, 1336–1343.
- de Albuquerque, R. L., Bonine, K. E., & Garland, T. (2015). Speed and endurance do not trade off in Phrynosomatid lizards. *Physiological and Biochemical Zoology*, *88*, 634–647.
- Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton: Princeton University Press.
- Bonduriansky, R., & Chenoweth, S. F. (2009). Intra-locus sexual conflict. *Trends in Ecology & Evolution*, *24*, 280–288.
- Brommer, J. E. (2013). On between-individual and residual (co)variances in the study of animal personality: Are you willing to take the "individual gambit"? *Behavioral Ecology and Sociobiology*, *67*, 1027–1032.
- Butler, D., Cullis, B. R., Gilmour, A. R., & Gogel, D. J. (2009). *ASREML-R reference manual, release 3.0*. Hemel Hempstead, UK: VSN International Ltd.
- Cameron, S. F., Wynn, M. L., & Wilson, R. S. (2013). Sex-specific trade-offs and compensatory mechanisms: Bite force and sprint speed pose conflicting demands on the design of geckos (*Hemidactylus frenatus*). *Journal of Experimental Biology*, *216*, 3781–3789.
- Careau, V., & Wilson, R. S. (2017a). Of uberfleas and krakens: Detecting trade-offs using mixed models. *Integrative and comparative biology*, *57*, 362–371.
- Careau, V., & Wilson, R. S. (2017b). Performance trade-offs and ageing in the 'world's greatest athletes'. *Proceedings of the Royal Society B-Biological Sciences*, *284*, 9.
- Carrier, D. R. (1987). Lung ventilation during walking and running in 4 species of lizards. *Experimental Biology*, *47*, 33–42.
- Clemente, C. J., & Wilson, R. S. (2015). Balancing biomechanical constraints: Optimal escape speeds when there is a trade-off between speed and maneuverability. *Integrative and comparative biology*, *55*, 1142–1154.
- Cox, R. M., Stenquist, D. S., Henningsen, J. P., & Calsbeek, R. (2009). Manipulating testosterone to assess links between behavior, morphology, and performance in the Brown Anole *Anolis sagrei*. *Physiological and Biochemical Zoology*, *82*, 686–698.
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*, 39–54.
- Dudley, R., & Gans, C. (1991). A critique of symmorphosis and optimality models in physiology. *Physiological Zoology*, *64*, 627–637.
- Foster, K. L., & Higham, T. E. (2012). How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis*. *Journal of Experimental Biology*, *215*, 2288–2300.
- Garland, T. J. (1999). Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour*, *58*, 77–83.
- Ghalambor, C. K., Walker, J. A., & Reznick, D. N. (2003). Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integrative and comparative biology*, *43*, 431–438.
- Ghalambor, C. K., Reznick, D. N., & Walker, J. A. (2004). Constraints on adaptive evolution: The functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *The American Naturalist*, *164*, 38–50.
- Gosden, T. P., Shastri, K. L., Innocenti, P., & Chenoweth, S. F. (2012). The B-matrix harbors significant and sex-specific constraints on the evolution of multicharacter sexual dimorphism. *Evolution*, *66*, 2106–2116.
- Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. B. (2010). The Misuse of BLUP in ecology and evolution. *American Naturalist*, *175*, 116–125.
- Head, A. W., Hardin, J. S., & Adolph, S. C. (2012). Methods for estimating peak physiological performance and correlating performance measures. *Environmental and Ecological Statistics*, *19*, 127–137.
- Herrel, A., & Bonneaud, C. (2012). Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *Journal of Experimental Biology*, *215*, 3106–3111.
- Herrel, A., McBrayer, L. D., & Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society*, *91*, 111–119.
- Herrel, A., James, R. S., & Van Damme, R. (2007). Fight versus flight: Physiological basis for temperature-dependent behavioral shifts in lizards. *Journal of Experimental Biology*, *210*, 1762–1767.
- Herrel, A., Spithoven, L., van Damme, R., & de Vree, F. (1999). Sexual dimorphism of head size in *Gallotia galloti*: Testing the niche divergence hypothesis by functional analyses. *Functional Ecology*, *13*, 289–297.
- Herrel, A., Van Damme, R., Vanhooydonck, B., & de Vree, F. (2001). The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology*, *79*, 662–670.
- Hertz, P. E., Huey, R. B., & Nevo, E. (1983). Homage to Santa Anita: Thermal sensitivity of sprint speed in Agamid lizards. *Evolution*, *37*, 1075–1084.
- Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, *28*, 948–952.
- Huey, R. B., Dunham, A. E., Overall, K. L., & Newman, R. A. (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological Zoology*, *63*, 845–872.
- Husak, J. F., & Swallow, J. G. (2011). Compensatory traits and the evolution of male ornaments. *Behaviour*, *148*, 1–29.
- Husak, J. F., & Lailvaux, S. P. (2014). An evolutionary perspective on conflict and compensation in physiological and functional traits. *Current Zoology*, *60*, 755–767.
- Husak, J. F., & Lailvaux, S. P. (2017). How do we measure the cost of whole-organism performance traits? *Integrative and comparative biology*, *57*, 333–343.

- Husak, J. F., Keith, A. R., & Wittry, B. N. (2015). Making Olympic lizards: The effects of specialised exercise training on performance. *Journal of Experimental Biology*, 218, 899–906.
- Husak, J. F., Ferguson, H. A., & Lovern, M. B. (2016). Trade-offs among locomotor performance, reproduction, and immunity in lizards. *Functional Ecology*, 30, 1665–1674.
- Husak, J. F., Fox, S. F., Lovern, M. B., & Van Den Bussche, R. A. (2006). Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution*, 60, 2122–2130.
- Husak, J. F., Ribak, G., Wilkinson, G. S., & Swallow, J. G. (2011). Compensation for exaggerated eye stalks in stalk-eyed flies (Diptera: Diopsidae). *Functional Ecology*, 25, 608–616.
- Husak, J. F., Irschick, D. J., Meyers, J. J., Lailvaux, S. P., & Moore, I. T. (2007). Hormones, sexual signals, and the performance of green anole lizards. *Hormones and Behavior*, 52, 360–367.
- Husak, J.F. & Lailvaux, S.P. (in press). Experimentally enhanced performance decreases survival in nature. *Biology Letters*.
- Irschick, D. J., & Losos, J. B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, 52, 219–226.
- Irschick, D. J., & Lailvaux, S. P. (2006). Age-specific forced polymorphism: Implications of ontogenetic changes in morphology for male mating tactics. *Physiological and Biochemical Zoology*, 79, 73–82.
- Irschick, D. J., Vanhooydonck, B., Herrel, A., & Meyers, J. J. (2005). Intraspecific correlations among morphology, performance, and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biological Journal of the Linnean Society*, 85, 211–221.
- Irschick, D. J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C. R., Vanhooydonck, B., ... Herrel, A. (2005). A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society*, 85, 223–234.
- Jenssen, T. A., Greenberg, N., & Hovde, K. A. (1995). Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs*, 9, 41–62.
- John-Alder, H., McMann, S., Katz, S. L., Gross, A., & Barton, D. S. (1996). Social modulation of exercise endurance in a lizard (*Sceloporus undulatus*). *Physiological Zoology*, 69, 547–567.
- Kolbe, J. J., & Losos, J. B. (2005). Hind-limb length plasticity in *Anolis carolinensis*. *Journal of Herpetology*, 39, 674–678.
- Lailvaux, S. P. (2007). Interactive effects of sex and temperature on locomotion in reptiles. *Integrative and comparative biology*, 47, 189–199.
- Lailvaux, S. P., & Irschick, D. J. (2007). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist*, 170, 573–586.
- Lailvaux, S. P., & Husak, J. F. (2014). The life-history of whole-organism performance. *Quarterly Review of Biology*, 89, 285–318.
- Lailvaux, S. P., Gilbert, R. L., & Edwards, J. R. (2012). A performance-based cost to honest signalling in male green anole lizards (*Anolis carolinensis*). *Proceedings of the Royal Society B-Biological Sciences*, 279, 2841–2848.
- Lailvaux, S. P., Leifer, J., Kircher, B. K., & Johnson, M. A. (2015). The incredible shrinking dewlap: Signal size, skin elasticity, and mechanical design in the green anole lizard (*Anolis carolinensis*). *Ecology and Evolution*, 5, 4400–4409.
- Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J., & Irschick, D. J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London B: Biological Sciences*, 271, 2501–2508.
- Le Galliard, J., Clobert, J., & Ferrière, R. (2004). Physical performance and darwinian fitness in lizards. *Nature*, 432, 502–505.
- Lindstedt, S. L., Hokanson, J. F., Wells, D. J., Swain, S. D., Hoppeler, H., & Navarro, V. (1991). Running energetics in the pronghorn antelope. *Nature*, 353, 748–750.
- Losos, J. B., Creer, D. A., & Schulte, J. A. (2002). Cautionary comments on the measurement of maximum locomotor capabilities. *Journal of Zoology*, 258, 57–61.
- McKean, T., & Walker, B. (1974). Comparison of selected cardiopulmonary parameters between the pronghorn and the goat. *Respiratory Physiology*, 21, 365–370.
- Myers, M. J., & Steudel, K. (1985). Effect of limb mass and its distribution on the energetic cost of running. *Journal of Experimental Biology*, 116, 363–373.
- Nasir, A., Clemente, C. J., Wynn, M. L., & Wilson, R. S. (2017). Optimal running speeds when there is a trade-off between speed and the probability of mistakes. *Functional Ecology*, 31, 1941–1949.
- Newar, S. L., & Careau, V. (2018). The fast and the curious: Locomotor performance and exploratory behaviour in eastern chipmunks. *Behavioral Ecology and Sociobiology*, 72, 12.
- Pasi, B. M., & Carrier, D. R. (2003). Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. *Journal of Evolutionary Biology*, 16, 324–332.
- Perry, G., Levering, K., Girard, I., & Garland, T. J. (2004). Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour*, 67, 37–47.
- Postma, E. (2006). Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *Journal of Evolutionary Biology*, 19, 309–320.
- Self, S. G., & Liang, K. Y. (1987). Asymptotic properties of maximum-likelihood estimators and likelihood ratio tests under nonstandard conditions. *Journal of the American Statistical Association*, 82, 605–610.
- Sorci, G., Swallow, J. G., Garland, T., & Clobert, J. (1995). Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipera*. *Physiological Zoology*, 68, 698–720.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268.
- Steudel, K. (1990). The work and energetic cost of locomotion .1. The effects of limb mass-distribution in quadrupeds. *Journal of Experimental Biology*, 154, 273–285.
- Tarka, M., Akesson, M., Hasselquist, D., & Hansson, B. (2014). Intralocus sexual conflict over wing length in a wild migratory bird. *American Naturalist*, 183, 62–73.
- Van Damme, R., Entin, P., Vanhooydonck, B., & Herrel, A. (2008). Causes of sexual dimorphism in performance traits: A comparative approach. *Evolutionary Ecology Research*, 10, 229–250.
- Vanhooydonck, B., Van Damme, R., & Aerts, P. (2001). Speed and stamina trade-off in lacertid lizards. *Evolution*, 55, 1040–1048.
- Vanhooydonck, B., Herrel, A., Van Damme, R., Meyers, J. J., & Irschick, D. J. (2005). The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis*) lizard population. *Behavioral Ecology and Sociobiology*, 59, 157–165.
- Vanhooydonck, B., James, R. S., Tallis, J., Aerts, P., Tadic, Z., Tolley, K. A., ... Herrel, A. (2014). Is the whole more than the sum of its parts? Evolutionary trade-offs between burst and sustained locomotion in lacertid lizards. *Proceedings of the Royal Society B-Biological Sciences*, 281, 10–20132677.
- Visscher, P. M. (2006). A note on the asymptotic distribution of likelihood ratio tests to test variance components. *Twin Research and Human Genetics*, 9, 490–495.
- Williams, S. B., Wilson, A. M., Rhodes, L., Andrews, J., & Payne, R. C. (2008). Functional anatomy and muscle moment arms of the pelvic limb of an elite sprinting athlete: The racing greyhound (*Canis familiaris*). *Journal of Anatomy*, 213, 361–372.
- Williams, T. M., Dobson, G. P., Mathieu Costello, O., Morsbach, D., Worley, M. B., & Phillips, J. A. (1997). Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 167, 527–535.

- Wilson, R. S., & James, R. S. (2004). Constraints on muscular performance: Trade-offs between power output and fatigue resistance. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, S222–S225.
- Wilson, R. S., James, R. S., & Van Damme, R. (2002). Trade-offs between speed and endurance in the frog *Xenopus laevis*: A multi-level approach. *Journal of Experimental Biology*, 205, 1145–1152.
- Wolak, M. E. (2012). nadv: An R package to create relatedness matrices for estimating non-additive genetic variances in animal models. *Methods in Ecology and Evolution*, 3, 792–796.

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