

RESEARCH ARTICLE

Sex-specific multivariate morphology/performance relationships in *Anolis carolinensis*

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ABSTRACT

Animals rely on their ability to perform certain tasks sufficiently well to survive, secure mates and reproduce. Performance traits depend on morphology, and so morphological traits should predict performance, yet this relationship is often confounded by multiple competing performance demands. Males and females experience different selection pressures on performance, and the consequent sexual conflict over performance expression can either constrain performance evolution or drive sexual dimorphism in both size and shape. Furthermore, change in a single morphological trait may benefit some performance traits at the expense of others, resulting in functional trade-offs. Identifying general or sex-specific relationships between morphology and performance at the organismal level thus requires a multivariate approach, as individuals are products of both an integrated phenotype and the ecological environment in which they have developed and evolved. We estimated the multivariate morphology→performance gradient in wild-caught, green anoles (*Anolis carolinensis*) by measuring external morphology and forelimb and hindlimb musculature, and mapping these morphological traits to seven measured performance traits that cover the broad range of ecological challenges faced by these animals (sprint speed, endurance, exertion distance, climbing power, jump power, cling force and bite force). We demonstrate that males and females differ in their multivariate mapping of traits on performance, indicating that sex-specific ecological demands likely shape these relationships, but do not differ in performance integration.

KEY WORDS: Phenotypic integration, Sexual dimorphism, Functional performance, Performance trade-off

INTRODUCTION

Animals in nature are required to conduct a variety of ecological tasks in their day-to-day existence, ranging from foraging and predator escape to reproduction, that can have important effects on individual fitness. Many of these tasks are bolstered, if not entirely enabled, by dynamic whole-organism performance abilities, such as running, jumping, climbing or biting (Bennett and Huey, 1990; Lailvaux and Irschick, 2006; Husak et al., 2009). These different

tasks frequently require different kinds of performance, which may place disparate and conflicting demands on the underlying individual morphology and physiology (Arnold, 1983). Consequently, an important trend throughout the animal kingdom is that excellence in a particular performance trait comes at the expense of less-than-excellent performance in others (Van Damme and Wilson, 2002; Van Damme et al., 2002; Pasi and Carrier, 2003). For example, animals that are specialized for endurance running tend to have poor maximum sprint speeds, and vice versa (Vanhooydonck et al., 2001; Vanhooydonck et al., 2014), because the morphological and physiological requirements for each are not concordant. But while investigations of bivariate functional trade-offs between pairs of performance capacities are common (e.g. Losos et al., 1993; Van Damme et al., 1996; Wilson et al., 2002; Herrel and Bonneaud, 2012), studies that test for morphology/performance relationships among entire suites of different performance traits within the same species are less common. Doing so is important for understanding the extent to which organisms may be constrained in their phenotype as a result of multiple conflicting selection pressures.

The basis of both functional trade-offs and functional integration lies in the ecomorphological paradigm, which tells us that an individual's performance is determined by its underlying morphology and physiology (Arnold, 1983). However, intraspecific variation in morphology is widespread. One of the most striking sources of such variation is sexual dimorphism, whereby males and females differ markedly in size, shape or physiology. Despite a large body of literature on sexual dimorphism in size, shape, color and behavior in animals (reviewed in Rice, 1984; Hedrick and Temeles, 1989; Shine, 1989), the functional basis of sexual dimorphism in performance remains poorly understood for the vast majority of animal species (Thomas et al., 2015). In some cases where sex differences in performance have been reported, the causes of such differences can be obviously ascribed to factors such body size, such that the larger sex exhibits greater performance than the smaller sex, or to gravidity/pregnancy, which tends to impair performance in the sex that bears the young (e.g. Veasey et al., 2001; Shine, 2003; but see Scales and Butler, 2007). However, there are also several cases where males and females of a given species differ in one or more types of performance even after scaling effects are accounted for (reviewed in Lailvaux, 2007), suggesting that those differences are rooted in either intrinsic physiological factors or variation in shape.

Empirical support for such differences has been found in select species; for instance, male alligators have more active mitochondria during the breeding season than females, which has been suggested to fuel the higher seasonal demand for male locomotor performance (Seebacher et al., 2003; but see Koch et al., 2021). Indeed, sex-specific selection on either a given performance trait or other phenotypes linked to that trait can drive divergent expression of performance in various ecological contexts (Husak and Lailvaux,

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2014; Tarka et al., 2014; Husak et al., 2021). From a multivariate perspective, males and females may even show sex-specific relationships between morphology and performance, as is the case for jumping in the frog *Xenopus tropicalis* (Herrel et al., 2014). If physiological differences between males and females affect the patterns of integration between traits differently in each sex, and if functional trade-offs prevent individuals from maximizing performance among suites of traits, then males and females may not only exhibit differences in performance but also show different patterns of performance integration driven by intrinsic differences in physiology (Vincent and Lailvaux, 2008).

The green anole lizard, *Anolis carolinensis*, is a model system for understanding both ecology and evolution and for testing hypotheses relating to whole-organism performance capacities. As such, there is a large body of literature investigating the relationship between morphology and performance in this and related species (e.g. Bels et al., 1992; Spezzano and Jayne, 2004; Vanhooydonck et al., 2005; Foster and Higham, 2012). Previous studies on performance in green anoles specifically have detected evidence for sex-specific effects beyond those explained by scaling (Herrel et al., 2007). For example, Irschick et al. (2005) showed that adult female green anoles are always the best performers relative to size compared with both juveniles and adult males for clinging and jumping ability, and some differences in jump performance between adult male and female green anoles are likely attributable to differences in shape rather than size (Lailvaux and Irschick, 2007). Because of the integrative nature of the overall multivariate performance phenotype (Ghalambor et al., 2003), sex differences in morphology can also have implications for the expression of other performance traits in males relative to females in ways that may not be immediately apparent. For example, Lailvaux et al. (2019) found an among-individual trade-off between sprinting and bite force in female green anoles only, most likely driven by the costs of large male heads imposed on females via intralocus sexual conflict that females do not compensate for (see also Cameron et al., 2013). However, we currently lack a proper understanding of whether patterns of integration among morphology and suites of performance traits differ between male and female green anoles.

We measured seven whole-organism performance traits in a large sample of wild-caught adult male and female *Anolis carolinensis* lizards and tested for sex-specific integration among those traits. Evidence for performance integration was seen as correlations between performance traits, similar to morphological integration (Vincent and Lailvaux, 2008; Conner et al., 2014). High correlation between performance traits indicates that the same factors affect more than one type of performance. We also measured head and limb dimensions in all individuals and muscle sizes in a subset of lizards to test for functional relationships among morphology and performance beyond allometric effects (cf. Garland, 1984). We expect *A. carolinensis* male and female lizards to be under selection pressure related to divergent ecological conditions, given that males likely suffer stronger selection on performance traits such as biting (as a result of male combat; Lailvaux et al., 2004; Henningsen and Irschick, 2012) and endurance or exertion (as a result of males patrolling larger territories; Nunez et al., 1997; Jenssen and Nunez, 1998; Jenssen et al., 2000; Miles et al., 2001). We tested the following specific hypotheses: males and females (1) are sexually dimorphic in both morphology and performance after controlling for size difference, and (2) exhibit differences in the pattern of morphology→performance relationships. Specifically, we predict that males will be more integrated in terms of performance than females, showing higher positive correlations between performance

traits that likely responded to selection, and will show larger effects of morphology on performance than females as a result of potentially stronger selection on male performance traits in nature relative to females.

MATERIALS AND METHODS

All procedures were approved by the University of New Orleans Institutional Animal Care Committee (IACUC protocol #14-005). We caught 125 adult green anoles, *Anolis carolinensis* Voigt 1832 (64 males, 61 females), from various locations in the Greater New Orleans area and measured seven different performance capacities (jumping ability, sprint speed, endurance, exertion distance, bite force, clinging ability and climbing ability). Therefore, sample sizes were determined by availability of animals and sampling effort. We measured morphology on the same day as capture, as well as bite force, clinging ability and climbing speed. All other performance measures were conducted within 3 weeks of capture. Because endurance and exertion are taxing for the animals, they were always measured on different days, and no other performance traits were measured on the same day as either. The order of performance measurements was also randomized for each individual to control for potential order effects (Lailvaux et al., 2019; Husak et al., 2021).

Lizards were housed in plastic cages (28.5 cm×17.5 cm×21 cm) with mulch substrate and a wooden dowel perch. Each shelving rack of cages was 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 h:12 h. 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.) every 2–3 days.

Morphology

We used digital calipers to measure snout–vent length (SVL); limb segments (humerus, radius, metacarpus, longest finger, femur, tibia, metatarsus, longest toe); and head dimensions (head length, width, height) to the nearest 0.01 mm. Body mass was measured with a digital balance (Mettler Toledo PR8002 DeltaRange) to the nearest 0.01 g. Toe-pad size was measured by placing the lizard inside a flatbed scanner (HP Scanjet G3110), scanning the toe-pad area at 600 dpi, and then digitally measuring toe-pad size with tpsDIG (<http://sbmorphometrics.org/soft-dataacq.html>, accessed 22 June 2019).

At the end of all performance trials (see below), lizards were euthanized with tricaine methanesulfonate (MS222; Conroy et al., 2009), fixed in formalin, and stored in 70% ethanol. Vital organs were removed (heart, liver, lungs), patted dry, and weighed on an analytical balance (Mettler Toledo XS105) to the nearest 0.001 mg. For a subset of 31 males and 31 females chosen at random from the sample pool, 10 muscles related to locomotor performance were also dissected out and weighed to the nearest 0.001 mg. The muscles and their proposed functions (Herrel et al., 2008) are found in Table 1.

Performance

Each individual was measured up to 5 times for each performance trait and the trial that showed maximum performance was retained for statistical analyses (Losos et al., 2002; Adolph and Pickering, 2008), with the exception of endurance and exertion, which were only measured once each in accordance with standard methods. All performance measures were conducted in a room set to 33°C (approximately the preferred field body temperature for both sexes; see Huey and Webster, 1976; Lailvaux and Irschick, 2007) for

Table 1. Muscles chosen for analysis in *Anolis carolinensis* and their proposed function

Forelimb	Function	Hindlimb	Function
M. biceps	Elbow flexion	M. ambiens	Knee extension
M. triceps brachii	Elbow extension	M. pubioschiotibialis	Knee flexion and femoral adduction
M. latissimus dorsi	Humeral retraction	M. iliobibularis	Knee flexion
M. trapezius	Shoulder rotation and stability	M. gastrocnemius pars fibularis	Ankle extension
M. pectoralis par superficialis	Humeral retraction	M. caudofemoralis longus	Femoral retraction

Information on function taken from Herrel et al. (2008).

biting, sprinting, exertion, endurance and jumping, or placed inside an incubator set to 33°C for 1 h prior to and in between trials for clinging and climbing.

We measured bite force using an isometric Kistler force transducer (type 9023, Kistler, Winterthur, Switzerland) connected to a type 5058a Kistler charge amplifier (for a detailed description, see Herrel et al., 1999; Herrel et al., 2001). We induced lizards to bite a bite plate by tapping their cheek until their mouth opened, then lining up the mouth with the center of the force plate until the lizard bit forcefully, as in Lailvaux et al. (2012, 2019).

To measure clinging ability, lizards were dragged backwards with both forelimbs in contact with a sheet of acetate taped to the top of a Kistler Z17097 piezoelectric force plate connected to a Kistler 9685 charge amplifier (Bloch and Irschick, 2004; Elstrott and Irschick, 2004). Digital traces were read from a Kistler 5691 DAQ-book onto a Windows computer using Bioware software version 4.1.02. Because the force plate measures forces exerted in the x , y and z planes, clinging force was measured as the force trace on the y -axis.

We measured sprint speed using a custom-made 2 m long track consisting of a 5 cm diameter dowel covered with cork substrate inside a wooden structure with fitted laser sensors placed every 25 cm (SCL Timer, Trackmate Racing, Surrey, BC, Canada) (Lailvaux et al., 2020). When the beams are interrupted by the lizard running past, the time is recorded such that consecutive beam interruptions allow accurate measurement of the time it takes for each lizard to traverse each 25 cm interval. The track was placed at a 45 deg angle to encourage lizards to run up rather than hop, as is typical behavior on level ground (Losos and Irschick, 1996; Perry et al., 2004; Lailvaux et al., 2020). Lizards were placed at the beginning of the track, and encouraged to run with a gentle tap on the tail. For each trial, the highest speed measured for a 25 cm distance was recorded.

We measured climbing using a custom-built, vertical track with a cork substrate. Acetate walls bound either side of the track to prevent escape and maintain a straight path upwards. Trials were recorded with a high-speed camera (TroubleShooter TS1000MS, Fastec Imaging Corporation 2007) at 250 frames s^{-1} . Lizards were placed near the bottom of the track and encouraged to run up with gentle tap using a wooden dowel. Once they reached the top, they were collected and placed back in the incubator. We placed a 1 cm \times 1 cm grid in view of the camera for calibration, and digitized the tip of the snout frame by frame using ProAnalyst motion-tracking software (ProAnalyst, Xcitex Inc. 2006) to calculate average climbing speed, which we measured by finding 2–3 full footsteps and taking the average speed across this distance. This was converted to a measurement of climbing power by multiplying by the acceleration due to gravity (see Irschick et al., 2003).

We measured endurance using a treadmill modified to operate at roughly 0.4 km h^{-1} . To prevent lizards from escaping the treadmill setup, plastic walls were erected and lizards were encouraged to stay within the center of the treadmill belt by hand. Endurance was measured as the length of time the lizard maintained a relatively constant speed while being lightly tapped on the tail for motivation

(Husak et al., 2021), until exhaustion. If the lizard stopped, it was inspected for signs of exhaustion by placing it on its back (as in Perry et al., 2004; Lailvaux et al., 2018). Exhaustion was determined as failure of the lizard to right itself. If the lizard was not fully exhausted, the trial continued. Timing stopped when the lizard was determined to be fully exhausted.

We measured exertion as the distance a lizard could run at maximum speed while being chased around a circular track with a wooden substrate 1 m in circumference (as in Mautz et al., 1992; Cullum, 1998; Lailvaux et al., 2003). The raceway was marked off into 10 segments at 10 cm intervals, and at the start of a trial the lizard was placed on the first numbered segment and encouraged to run using a soft paintbrush. We considered a lizard to be exhausted when it was unable to right itself after being turned onto its back (Lailvaux et al., 2003). We measured the distance run by counting how many times around the track the lizard traveled, plus the number of segments away from the starting segment the lizard was when the trial ended. Number of segments was converted to total centimeters (10 cm per segment). The room was heated to 33°C, and only one trial per lizard was conducted, consistent with previous studies (Mautz et al., 1992; Cullum, 1998; Lailvaux et al., 2003).

Finally, we measured jumping using a Fastec high-speed video camera at 500 frames s^{-1} (Toro et al., 2006; Lailvaux et al., 2010). We placed a mirror at a 45 deg angle above the jumping arena to simultaneously capture both dorsal and lateral views and used a 1 cm \times 1 cm grid placed both on the wall perpendicular to the camera view, as well as on the jumping platform, in view of the mirror for calibration of all planes. We applied six non-toxic white-out dots (Wite-Out[®] Brand Quick Dry Correction Fluid, Bic USA Inc.) to the lizards to aid in motion tracking (Toro et al., 2006). Three dots were evenly spaced on the dorsal side: one near the neck, one near the center of mass and one near the base of the tail. We also placed three corresponding dots on the lateral side of the lizard facing the camera. A perch was placed at a distance far enough away from the jumping platform to encourage the lizards to employ their maximal jump capacity. Once filming began, the lizard was placed at the edge of the platform and encouraged to jump with a loud, startling clap (Toro et al., 2003). We then calculated the maximum mass-specific jumping power as our measure of jumping capacity. The morphological and performance raw data are shown in Table S1.

Sexual dimorphism

To test for sexual dimorphism between morphology and performance variables, we performed a MANCOVA for each group of multivariate dependent variables: head dimensions; limb segment factors; muscle (all 10 muscle mass measurements); and finally all seven performance variables. We partitioned morphology and muscle into separate datasets, both because the sample sizes were different, as muscles and organs were not dissected from all lizards, and to avoid issues with statistical power incurred by too many dependent variables in a single test (see Lailvaux and Irschick, 2007, for a similar approach). Sex was the fixed factor and

SVL was used as a covariate, and we included the interaction between sex and size. To determine the best-fit MANCOVA, we sequentially dropped terms from the full model and compared fits using partial *F*-tests.

Sex-specific performance integration

We first estimated a sex-specific performance correlation matrix to measure the degree of integration among performance traits as evidenced by positive and negative pairwise relationships among pairs of performance traits. To do so, we \log_{10} transformed performance to improve linearity of relationships, and calculated the pairwise correlations between all performance traits separately for males and females. Significance of those correlations was assessed using Student's *t*-distribution and a significance level of 0.05. To compare the sex-specific performance correlation matrices, we performed a principal components analysis (PCA) and compared specific PCs. To compare the overall performance integration between males and females, we calculated an integration index following Pavlicev et al. (2009), which is the ratio between the variance of the eigenvalues divided by the maximum eigenvalue variance, which is just the number of traits minus 1. The higher the eigenvalue variance, the more variation is accumulated in a single direction, and the higher the integration. These analyses are available as an R script in Supplementary Materials and Methods.

Because phenotypic correlations comprise both intra- and inter-sexual variation, which can potentially mask each other (Careau and Wilson, 2017a), trade-offs among specific sets of performance traits are best evaluated using variance partitioning approaches requiring a specialized experimental design that is both logistically challenging and potentially taxing for the organisms being measured (Careau and Wilson, 2017b; Lailvaux et al., 2019). Our intention here was not necessarily to rigorously evaluate all possible performance trade-offs in this way, but rather to connect multivariate morphology to multivariate performance and test whether this mapping underlies potential performance trade-offs. In particular, by identifying opposing and congruent effects of the same morphological traits on different performance measures (i.e. opposing effects as performance gradients of opposing signs on the same traits, and non-opposing effects as performance gradients of the same sign), we can ascertain whether the multivariate mapping of morphology on performance inferred from the *F*-matrices is compatible with the patterns of performance integration inferred by the performance correlation matrix. For instance, we expected functional trade-offs (negative correlations of higher magnitude) to be present when the same morphological traits showed opposing effects on different types of performance traits (i.e. an increase in the trait length would increase one performance but decrease another). Therefore, the more traits affecting several types of performance (more one-to-many relationships of morphology→performance), the more performance traits would show negative or positive correlations and, consequently, higher performance integration.

Sex-specific performance gradients

To map the contributions of our many morphological variables to the suite of performance traits, we used an *F*-matrix model (Ghalambor et al., 2003; Walker, 2007; Bergmann and McElroy, 2014). Arnold (1983) proposed the use of standardized partial regression coefficients to estimate performance gradients that measure the direct effect of each morphological trait on each performance type, allowing one to partition the variation in performance due to separate traits despite their being integrated

Table 2. Results from best-fit MANCOVA for each set of morphological variables

	Pillai's trace	Approximate <i>F</i>	d.f.	<i>P</i>
Head				
Sex	0.43	30.47	3, 121	<0.005
SVL	0.74	114.29		<0.005
Limb				
Sex	0.39	9.48	8, 117	<0.005
SVL	0.74	24.42		<0.005
Muscles				
Sex	0.33	2.31	10, 48	<0.005
SVL	0.74	13.72		<0.05
Sex×SVL	0.38	2.91		<0.05

'Head' includes head width, length and height. 'Limb' includes all forelimb and hindlimb segments. 'Muscles' includes all 10 muscle masses.

into a single phenotype. Placing these performance gradients into a matrix allows the mapping of many morphological traits to many performance traits, although the correlation between different types of performance is not taken into account. By creating sex-specific *F*-matrices, we were able to identify differences in morphology→performance relationships as well as compare between sexes the amount of functional constraint each phenotypic or performance trait is under (Bergmann and McElroy, 2014).

We first tested traits for normality using the Lilliefors test. Then, for traits that conformed to normality, we estimated the sex-specific performance gradients of the multiple performance traits (i.e. the *F*-matrices) by running multiple linear regressions of each performance trait on the morphological (external morphology *F*-matrices) or muscle measures (muscle *F*-matrices). The performance values were mean-standardized (relative performance) and the traits were scaled to have zero mean and unit standard deviation. The traits were not size adjusted because we included SVL or mass in the analysis, given that we expected these traits to show significant performance gradients. We conducted separate models for external and musculature traits because despite our large sample size we lacked the statistical power to reliably run a regression with 22 traits. The *F*-matrix comprises the performance gradients (i.e. partial regression coefficients of morphology on performance) in columns associated with each performance trait. We assessed significance of the performance gradients using a resampling procedure in which individual performance was shuffled across individuals 1000 times, separate for males and females, and the multiple regressions were re-run with the 1000 random data sets. By doing this, we were able to construct null distributions of performance gradients for each trait and calculate the *P*-value associated with the empirical gradient. These analyses are available as an R script in Supplementary Materials and Methods.

RESULTS

Sexual dimorphism in morphology and performance

Sexual dimorphism was apparent in all morphological traits. Separate MANCOVAs revealed significant differences in trait

Table 3. Results from best-fit MANCOVA for all seven performance variables

Performance	Pillai's trace	Approximate <i>F</i>	d.f.	<i>P</i>
Sex	0.231	3.989	7, 93	<0.005
SVL	0.66	25.82		<0.005
Sex×SVL	0.314	6.095		<0.005

SVL, snout–vent length.

Table 4. Performance correlation matrices for female and male *A. carolinensis*

	Sprint	Endurance	Exertion	Bite force	Cling	Jump
Females						
Endurance	0.111					
Exertion	-0.068	0.259				
Bite force	-0.186	0.249	0.071			
Cling	0.120	-0.298	-0.316	0.094		
Jump	-0.011	-0.086	0.019	-0.010	-0.078	
Climb	0.029	-0.047	0.027	0.026	-0.021	-0.012
Males						
Endurance	0.078					
Exertion	-0.111	0.104				
Bite force	-0.003	0.116	0.293			
Cling	-0.020	0.066	0.003	0.063		
Jump	0.132	0.096	-0.078	0.125	-0.330	
Climb	0.274	-0.061	0.123	-0.056	-0.035	0.115

Values are pairwise correlations using individual performance. Values in bold are significant at $P < 0.05$.

means between the sexes. In Table 2, results are presented for the best-fit MANCOVA models (significant results from model comparison tests). Morphology significantly differed between sexes, with males having both larger heads and longer limbs for their size than females (consistent with Irschick et al., 2005) although size also significantly contributed to this variation. Sex and size were similarly significant in terms of muscle mass variation; however, there was also a significant interaction between sex and size.

Performance data also significantly differed between the sexes (Table 3). Terms for sex, size and the interaction between them were all significant. This indicates that the sexes differ in size-adjusted variation among the suite of performance traits expressed.

Sexual dimorphism in performance integration

Males and females showed different patterns of performance integration, with evidence for just one absolute performance

Table 5. F-matrices of performance gradients of external morphology on all performance traits in female and male *A. carolinensis*

	Sprint	Endurance	Exertion	Bite force	Cling	Jump	Climb
R²							
Female	0.131	0.228	0.035	0.656	0.227	0.123	0.187
Male	0.193	0.408	0.461	0.861	0.240	0.258	0.195
F-matrix							
Female							
HL	-0.002	-0.016	0.016	-0.036	-0.281	-0.004	0.012
HH	0.000	-0.015	-0.010	0.054	0.150	0.001	-0.025
HW	-0.026	0.039	-0.012	0.179	0.115	0.003	0.014
Femur	0.000	-0.013	0.015	0.024	-0.214	0.004	-0.026
Tibia	0.013	0.003	-0.008	-0.003	0.247	-0.006	0.051
Metatarsus	0.004	-0.012	0.006	-0.034	-0.209	-0.001	-0.006
Long toe	-0.002	0.009	0.007	0.007	-0.051	-0.005	-0.009
Humerus	0.019	-0.028	0.006	-0.031	-0.281	0.001	-0.015
Radius	0.004	0.006	-0.005	-0.028	0.152	0.001	-0.013
Metacarpus	0.007	0.007	0.008	0.004	-0.054	0.001	-0.014
Long finger	-0.005	0.008	-0.006	0.039	0.152	-0.001	0.021
SVL	0.015	-0.002	-0.015	0.012	-0.153	0.000	0.000
Toepad area	-0.017	0.031	0.007	-0.014	0.403	0.001	0.015
Male							
HL	0.002	0.078	0.000	0.046	0.295	-0.003	-0.043
HH	-0.011	0.000	0.011	0.051	-0.222	0.008	-0.023
HW	-0.009	-0.028	-0.018	0.026	0.109	-0.007	-0.014
Femur	0.009	0.007	0.013	0.005	-0.030	0.003	-0.040
Tibia	0.018	-0.008	-0.059	-0.010	-0.048	0.000	0.005
Metatarsus	-0.021	0.001	0.070	0.012	0.079	-0.008	0.003
Long toe	-0.005	-0.003	-0.004	0.010	0.012	0.003	0.012
Humerus	0.005	-0.002	-0.027	-0.008	0.048	-0.005	-0.010
Radius	-0.007	0.025	0.020	-0.023	0.018	0.000	0.013
Metacarpus	-0.008	0.006	0.023	-0.003	-0.065	0.001	-0.003
Long finger	0.002	0.004	-0.023	-0.004	-0.007	0.007	0.004
SVL	0.016	-0.035	0.006	0.032	-0.148	-0.001	0.026
Toepad area	-0.001	-0.015	0.049	0.024	-0.077	0.005	0.057

The table shows both R^2 values associated with each performance and the performance gradients of each trait on each performance. Significance was tested with Monte Carlo resampling (see Materials and Methods) and is indicated in bold. All morphological traits (HL, head length; HH, head height; HW, head width; femur, tibia, metatarsus, longest toe, humerus, radius, metacarpus and longest finger length; SVL, snout-vent length) were measured in mm; bite force and clinging were measured in N; sprinting and climbing were measured in cm s^{-1} ; exertion was measured in m; endurance was measured in min; toepad area was measured in mm^2 ; and jumping was measured in W kg^{-1} .

trade-off for each sex: in females, a negative correlation between endurance and clinging, and in males, a negative correlation between jumping and clinging (Table 4). Males also showed significant performance facilitation (positive correlations between performance traits) of bite force with endurance and exertion. The PCA analysis of these performance correlation matrices indicates that the axes of most variation in females always incorporate performance trade-offs (performances with higher loadings have opposing signs), whereas one of the axes in males describes changes in the same direction for endurance, exertion and bite force (Table S2). Despite these differences, the overall performance integration was very similar between the sexes: 0.0074 for females and 0.0065 for males.

Sex-specific direct effects on performance

Males and females also showed different patterns of direct effects of external morphology (Table 5) and muscle size (Table 6) on performance (see Fig. 1 for a schematic representation of only the significant effects). In females, we found more one-to-many effects of traits on performance: head width positively affected bite force and endurance; toepad area positively affected endurance and clinging; *m. triceps* positively affected endurance and exertion, but negatively affected clinging force; and *m. ambiens* negatively affected exertion and but positively affected climbing. Mass in females only influenced bite force (Table 6). In contrast, in males, most significant effects were one-to-one effects (one trait influencing only one performance), except for metatarsus and head length for external morphology (Table 5) and mass and *m. ambiens* for muscle traits (Table 6).

If the same traits affect different performance traits in opposite ways, such that a longer trait would increase one performance but

decrease the other, a trade-off can be a consequence of such a pattern. By inspecting Tables 5 and 6 for opposing effects of the same traits on different performance traits, we expected to find a trade-off of exertion with sprinting and jumping in males, because of opposing effects of the metatarsus on these performance traits (Table 5), and a trade-off between exertion and endurance, because of opposing effects of *m. ambiens* on these traits (Table 6). In females, we expected trade-offs of clinging force with endurance and exertion because of the opposing effects of *m. triceps* on these performance types, and between climbing and exertion because of the contrasting effects of *m. ambiens* on these performance traits (Table 6). However, these expectations were not met by the results of the performance correlations.

DISCUSSION

Organisms are required to conduct a variety of ecologically relevant performance tasks in nature, resulting in potentially conflicting selection pressures on the underlying morphology that could result in either suboptimal performance expression for particular traits, or trade-offs among multiple traits, or both. In species with significant sexual dimorphism, sex-based differences in the morphological apparatus enabling performance can also drive different patterns of performance integration and multivariate morphology→performance relationships which might be further exacerbated by sex-specific selection on performance. We tested for sex differences in performance integration and in the multivariate performance gradient using a large sample of green anole lizards.

Our hypothesis of sexual dimorphism in multivariate performance was supported, with our results clearly showing differences in both morphology and performance between the sexes after controlling for size effects, as well as differences in how

Table 6. F-matrices of performance gradients of muscle size on all performance traits in female and male *A. carolinensis*

	Sprint	Endurance	Exertion	Bite force	Cling	Jump	Climb
R²							
Female	0.303	0.354	0.759	0.722	0.577	0.161	0.687
Male	0.594	0.503	0.402	0.929	0.340	0.515	0.375
F-matrix							
Female							
Mass	-0.011	0.003	0.011	0.137	0.030	-0.001	-0.035
<i>M. ambiens</i>	0.002	-0.001	-0.075	0.059	0.250	-0.009	0.060
<i>M. pubioschiotibialis</i>	0.007	0.030	-0.030	0.102	0.281	-0.003	-0.031
<i>M. iliofibularis</i>	-0.006	-0.025	-0.133	-0.102	-0.171	0.011	-0.011
<i>M. gastrocnemius</i>	-0.057	-0.011	0.050	0.104	0.125	0.006	0.009
<i>M. caudofemoralis</i>	0.026	-0.003	-0.011	0.050	-0.155	-0.008	0.033
<i>M. biceps</i>	0.001	-0.013	-0.107	0.051	-0.004	-0.002	0.037
<i>M. triceps brachii</i>	0.030	0.047	0.151	0.001	-0.564	-0.003	0.034
<i>M. latissimus dorsi</i>	0.000	0.016	0.151	-0.083	-0.283	-0.001	-0.040
<i>M. trapezius</i>	-0.001	0.018	0.055	-0.019	0.294	-0.003	0.015
<i>M. pectoralis</i>	0.004	-0.017	-0.062	0.029	0.374	0.010	-0.003
Male							
Mass	-0.002	0.073	-0.038	0.143	0.115	0.015	0.024
<i>M. ambiens</i>	-0.025	-0.039	0.086	-0.012	0.042	-0.013	0.044
<i>M. pubioschiotibialis</i>	0.020	0.003	-0.067	0.000	-0.085	-0.004	-0.030
<i>M. iliofibularis</i>	-0.044	-0.049	-0.043	-0.013	-0.209	-0.017	0.071
<i>M. gastrocnemius</i>	0.021	0.018	0.012	-0.014	0.064	0.003	0.015
<i>M. caudofemoralis</i>	0.010	-0.040	0.047	0.079	0.127	0.002	-0.038
<i>M. biceps</i>	0.019	0.022	0.027	-0.002	-0.321	-0.006	0.021
<i>M. triceps brachii</i>	0.015	0.004	-0.017	0.005	0.085	0.006	-0.077
<i>M. latissimus dorsi</i>	-0.022	-0.024	0.014	-0.027	0.138	-0.009	-0.024
<i>M. trapezius</i>	0.022	0.007	0.037	0.009	0.116	0.006	-0.034
<i>M. pectoralis</i>	-0.002	0.045	-0.004	-0.018	0.035	0.011	-0.007

The table shows both R^2 values associated with each performance and the performance gradients of each trait on each performance. Significance was tested with Monte Carlo resampling (see Materials and Methods) and is indicated in bold. Body mass and muscle traits were measured in g; bite force and clinging were measured in N; sprinting and climbing were measured in cm s^{-1} ; exertion was measured in m; endurance was measured in min; and jumping was measured in W kg^{-1} .

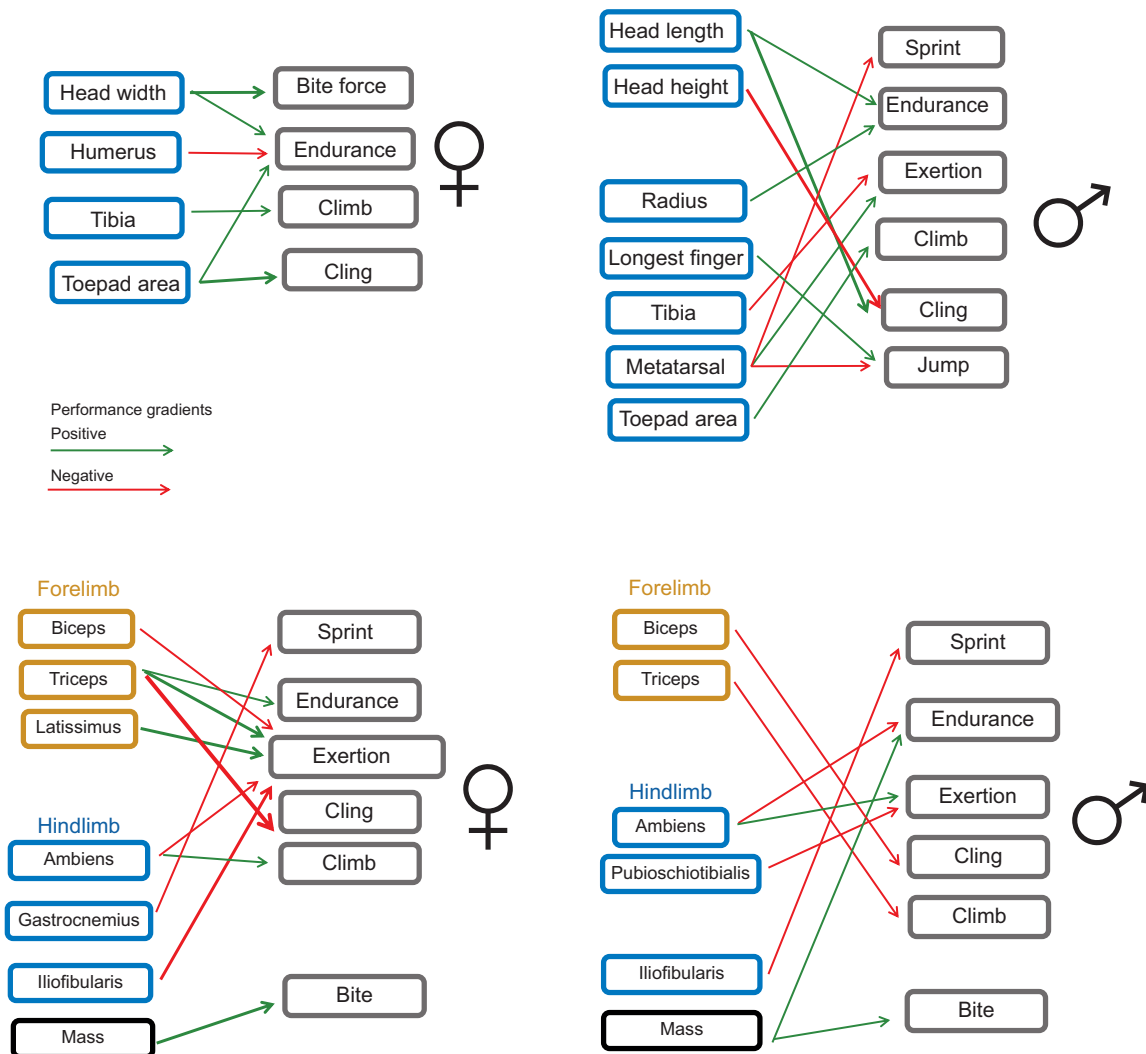


Fig. 1. Mapping of external morphology (upper panel) and of muscle size (lower panel) on performance in female and male *Anolis carolinensis*. The setae represent partial regression coefficients for each trait on each performance that were analyzed separately. Only the significant performance gradients from Tables 5 and 6 are shown by using Monte Carlo resampling. Animals were wild caught and sample sizes were $n=61$ for females and $n=64$ for males.

morphological traits map to performance traits. Differences in male and female muscle morphology revealed by MANCOVA coupled with sex-specific differences in direct performance imply differences in functional and performance demands as well. However, we did not find support for our prediction that males would have stronger performance integration than females, even though males had more significant pairwise performance correlations than females. Performance integration is similar between sexes because most performance correlations are low in both males and females, and the stronger correlations are of the same magnitude (Table 4). This pattern indicates that few performance traits must influence each other in both sexes. Yet, as already mentioned in Materials and Methods, performance correlations are best estimated using variance partitioning methods. Therefore, the performance correlations we found may be imprecise.

With regard to the performance gradients, many of the relationships between morphology and performance we observed are both intuitive and reflect common morphology→performance relationships; for example, larger head width correlates with higher bite forces; larger toepads correlate with stronger clinging forces in females; and longer limb segments and larger limb

muscles correlate with several locomotor performance traits in both sexes. However, it is also important to note that some phenotypic correlations with performance may not indicate a causal relationship, but rather a correlation between the trait and other, unmeasured, morphological or physiological traits. Similarly, the lack of significance of the direct effects of head traits on bite force in males does not exclude a causal relationship between them, as found in other studies (e.g. Herrel et al., 2001; Huyghe et al., 2005), but may indicate that the effects were not strong enough in the specific sample we worked with, given that the magnitude of the bite force gradient in males was lower than the significant effect of head width on bite force in females (Table 5). Performing a path analysis to calculate the performance gradients may aid in interpreting causal relationships between morphology and fitness.

Inspection of the F-matrices reveals apparent trade-offs whenever the signs of the effect of a morphological trait on two different performance traits oppose each other (i.e. different signs for effects in the same row). Our prediction that both performance and morphology→performance relationships should be stronger in males compared with females was supported only for external

morphology, in which performance gradients were of higher magnitude in males than in females (Table 5). By contrast, we found several effects of limb muscles on locomotor performance in females, and most of these effects pertained to exertion (Table 6). This may indicate that green anole females suffer stronger selection on exertion than males, although the ecological relevance of exertion is understudied and poorly understood in anoles (but see Leal, 1999). It also suggests that selection on muscle contractile properties (especially considering oxidative fibers that enhance stamina; Bonine et al., 2005) is stronger or more effective on females than on males. Selection could be more effective on females if they harbor more genetic variance in muscle traits than males. Also, empirical evidence favoring longer limbs is mostly seen in male lizards (e.g. Kaliontzopoulou et al., 2013), perhaps indicating that females do not respond as well as males to selection on external morphology. However, this explanation is at odds with Lowie et al. (2019), who found effects of muscle size only in male anoles and not in females.

We did not find a match between expected performance trade-offs inferred by the F-matrices and negative correlations in the performance correlation matrix. Therefore, despite the opposing influence of some external traits and some muscles on different performance traits, these effects do not manifest as trade-offs in performance expression within females. The reason for this discrepancy is unclear, and could reflect differences in the behavioral compensation during the execution of different performance tasks, or an effect of integrating the muscle and the external morphology on realized performance that masks or alters the effect on performance of the muscle itself. Indeed, we also do not see any trade-offs between bite force and any other performance trait, as has been reported previously in female green anoles between sprinting and biting (Lailvaux et al., 2019). This difference is likely the result of differences in methodology, with our approach here being to concentrate on maximal multivariate performance, whereas Lailvaux et al. (2019) used all of the available data within a specialized (and logistically challenging) repeated experimental design to test for individual-level trade-offs among a handful of traits. These differences in approach and findings highlight the importance of considering the type of performance data that one wishes to collect, and while the larger and more traditional approach that we have used here is appropriate for estimating the multivariate performance gradient, it is clearly less than ideal for focusing specifically on performance trade-offs (Careau and Wilson, 2017a).

Further investigation of the F-matrix also yields insight into redundancies in phenotypes (Bergmann and McElroy, 2014). While some traits have negative effects on performance, there may be other traits that can ‘rescue’ the performance trait, as evidenced by the myriad of effects of limb muscles on exertion in females. Besides redundancy, trade-offs themselves can shield a phenotype from being adversely affected by a single trait as that trait may positively influence another ecologically relevant trait, as in one-to-many mapping that we found in both males and females (Fig. 1). Thus, approaching functional trade-offs from a multivariate perspective gives us much more insight than investigating only two traits, as complexity and redundancy in the phenotype could mask phenotypic correlations.

Despite the utility of laboratory measures of maximum performance for understanding the performance gradient, an important caveat with regard to our current results is that selection in nature does not act on performance in isolation, but in concert with habitat use. For example, Wheatley et al. (2018) showed that ecological context strongly influences the level of performance

exhibited by wild *Antechinus mystichus*, which likely balance the costs of performance against the selective consequences of making mistakes when moving and maneuvering. This may be particularly true for anoles which typically use a variety of different habitat types. Indeed, Calsbeek and Irschick (2007) found evidence of correlational selection on morphology, performance and habitat type in *Anolis sagrei* lizards, showing that selection on performance is intimately tied to the habitat and context in which it is expressed. Given this, it could be that the patterns of integration we document here, as well as the amount of variance explained by the traits on performance, would be different if one were also to consider habitat type in addition to morphology and performance. Such a study that also considers sex-specific variation in a multivariate performance context would be an extremely demanding, albeit useful avenue for understanding how the performance environments affect patterns of performance integration.

In conclusion, our investigation of the multivariate morphological and performance phenotype in a common lizard species revealed distinct differences between males and females. Indeed, sexual differences go beyond scaling effects, and likely reflect sex-specific ecological and functional contexts. Furthermore, we have uncovered these differences only because of the complexity and range of the traits measured, and these differences in traits and inter-trait relationships would not have been recognized without preserving the broader phenotypic context.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.M.C., S.P.L.; Methodology: M.N.S., A.M.C., S.P.L.; Formal analysis: M.N.S.; Investigation: A.M.C.; Writing - original draft: M.N.S.; Writing - review & editing: S.P.L.; Supervision: S.P.L.

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