

FASTER LIZARDS SIRE MORE OFFSPRING: SEXUAL SELECTION ON WHOLE-ANIMAL PERFORMANCE

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Abstract.—Sexual selection operates by acting on variation in mating success. However, since selection acts on whole-organism manifestations (i.e., performance) of underlying morphological traits, tests for phenotypic effects of sexual selection should consider whole-animal performance as a substrate for sexual selection. Previous studies have revealed positive relationships between performance and survival, that is, natural selection, but none have explicitly tested whether performance may influence reproductive success (through more matings), that is, sexual selection. Performance predicts dominance in some species, implying the effects of sexual selection, but how it does so has not been established, nor is it certain whether performance might be a by-product of selection for something else, for example, elevated circulating testosterone levels. We investigated the potential for sexual selection on sprint speed performance in collared lizards (*Crotaphytus collaris*), considering the potential mediating effects of circulating hormone levels. Among territorial, adult male collared lizards, only sprint speed significantly predicted territory area and number of offspring sired as determined by genetic paternity analysis. Body size, head size, and hind limb length had no effect. Neither plasma testosterone levels nor corticosterone levels correlated with sprint speed, territory area, or number of offspring sired. Thus, our results provide a direct link between whole-animal performance and reproductive success, suggesting that intrasexual selection can act directly on sprint speed performance and drive the evolution of underlying morphological traits.

Key words.—Fitness, natural selection, sprint speed, territoriality, testosterone.

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Sexual selection often is invoked to explain the evolution of phenotypic traits, but empirical confirmation of intra- and intersexual selection has focused mainly on morphological and behavioral traits (Andersson 1994; Berglund et al. 1996; Hill et al. 1999). Such sexually selected traits may also be under the influence of natural selection (e.g., differential survival), leading to simultaneous selection pressures that may be parallel or opposing (Ryan et al. 1982; Endler 1983; Grether and Grey 1996). A complete test for selection should include the phenotypic trait directly affected by selection, and many authors have emphasized the importance of whole-animal performance traits, the manifestations of underlying variation in morphology and physiology (Bartholomew 1958; Huey and Stevenson 1979; Arnold 1983). In this performance-outward scheme, variation in morphology constrains variation in whole-animal performance, which in turn determines variation in fitness (Arnold 1983). This framework has often been applied to examine aspects of natural selection related to differential survival (Jayne and Bennett 1990; Kingsolver 1999; Le Galliard et al. 2004; Miles 2004), but, as shown in this paper, it may also be applied in studies of sexual selection. The possibility of whole-animal performance traits being a target of sexual selection is appealing, because whole-animal performance traits represent aspects of the phenotype that that may be a quantifiable indicator of male “quality” (Kokko 1998; Kokko et al. 2002, 2003) conveyable via sexual signals (e.g., Vanhooydonck et al. 2005, 2006) or display (e.g., Leal 1999; Lappin et al. 2006).

There has been a recent interest in sexual selection as an evolutionary force operating on whole-animal performance traits. In particular, locomotor performance of lizards has

been suggested to be under the influence of sexual selection, as it has been shown to predict dominance in lizards in experimental arenas (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004). However, the link between locomotor performance and dominance is unclear. First, these studies lacked any explanation of how locomotor performance might be functionally connected to dominance (and presumably fitness) through variation in behavior (Garland and Losos 1994; Irschick and Garland 2001). For example, did individuals actually use maximal performance capacity during the male-male contests? Second, alternative hypotheses, such as a spurious correlation between locomotion and dominance due to other phenotypic correlations, were equally as plausible as the hypothesis that sexual selection acts directly on locomotor performance. Specifically, locomotor capacity may be a physiological “carry-along” with testosterone, which may be selected for other reasons. If higher circulating testosterone levels provide a fitness advantage (e.g., Raouf et al. 1997; Sinervo et al. 2000; Reed et al. 2006) by mediating some behavioral trait (e.g., aggression) or sexual signal (e.g., dewlap size) important to fitness, and testosterone levels also enhance locomotor performance, then dominant males may have high locomotor performance simply because of that physiological connection and not because performance provides an advantage per se in establishing dominance. Several studies with squamate reptiles, by far the most studied taxa with regard to locomotor performance, have either observationally (Garland and Else 1987) or experimentally (John-Alder et al. 1996, 1997; Klukowski et al. 1998; Sinervo et al. 2000) found a positive correlation between locomotor performance and testosterone levels. Similarly, experimentally elevated levels of the stress hormone corticosterone have been shown to reduce sprint speed in lizards (Meylan and Clobert 2004). Therefore, performance may be correlated with fitness merely as a by-product of

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intercorrelation with circulating hormone levels, which affect other aspects of fitness more explicative of reproductive success. However, because circulating hormone levels are a proximate mechanism of regulating male traits, and likely not the phenotypic trait under direct selection, it must be made clear what traits are under hormonal influence and how selection might “see” those traits in an ecological context. Thus, studies seeking to evaluate a phenotypic trait as a target of selection should investigate how circulating testosterone levels, or levels of other relevant hormones, mediate performance as well as influence fitness via correlations with other phenotypic traits.

Studies of performance relevant to fighting have more completely addressed how those performance traits functionally link to dominance. Shore crabs with stronger claws (Sneddon et al. 2000) and lizards that bit harder (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006) were more likely to dominate worse performers during staged interactions. Similarly, *Euoniticellus intermedius* beetles with greater maximal exertion capabilities had greater fighting ability than those with less exertion capabilities (Lailvaux et al. 2005). Key to these latter studies is that the performance trait under investigation had an intuitive and empirically based connection to behavior involved in male competition (e.g., intrasexual selection).

The link between locomotor performance and dominance may be indirect and unclear, but the link between locomotor performance and territory defense in nature may be direct and intuitive. Peterson and Husak (2006) found that maximal sprint speed predicted territory size better than body size did in collared lizards (*Crotaphytus collaris*), suggesting that faster-sprinting individuals were able to translate their higher speeds into a greater share of the limited, suitable habitat. Subsequent studies revealed that territorial male collared lizards used near-maximal sprint speed capacity only when responding to a rival territorial male tethered at their territory boundary (Husak 2005; Husak and Fox 2006), further indicating that sexual selection may act directly on maximal sprint speed.

Our objective was to test the hypothesis that sexual selection can operate on maximal sprint speed in male collared lizards (*Crotaphytus collaris*), taking into account previous research on the use of sprint speed in nature and how sprint speed influences survival (Husak 2006), while simultaneously testing an alternative mechanistic hypothesis (e.g., correlation with circulating testosterone or corticosterone levels). Collared lizards display sexual dimorphism in body size and head and limb size, with males being larger than females (Fitch 1956; McCoy et al. 1994; Lappin 1999). Males and females typically become sexually mature during their first year (hereafter “yearlings”; Baird et al. 1996; Baird and Timanus 1998), but males typically do not acquire and defend an exclusive territory until their second year (Baird et al. 1996). We measured maximal sprint speed and circulating testosterone and corticosterone levels to determine how well those traits explained variation in annual reproductive success relative to morphological traits. Specifically, we predicted that maximal sprint speed would positively relate to annual reproductive success. If sexual selection is operating on performance, then maximal sprint speed should explain a

significant amount of variation in annual reproductive success. That is not to say, however, that circulating testosterone and/or corticosterone levels may not mediate sprinting capacity nor explain further variation in reproductive success. In contrast, if reproductive success is predicted by circulating hormone levels alone, then sexual selection is operating on some other trait mediated by those hormones (such as an unmeasured behavioral or morphological trait), and not on maximal sprint speed. Further, since selection is presumed to act on performance rather than the underlying morphological traits, we predicted that sprint speed would predict reproductive success better than would morphological traits.

METHODS AND MATERIALS

General Methods

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma, on a substrate consisting of concrete-covered riprap boulders. In 2003 and 2004 we captured adult (\geq two years of age) and yearling (\sim one year of age) male and female lizards by noosing. Each lizard was permanently marked by toe clipping, and each was given a unique pattern of colored paint spots for visual identification at a distance (after Baird et al. 1996). In most cases, toes were saved in lysis buffer for genetic analysis (see below). Individuals that were captured and marked the previous year as hatchlings were considered yearlings, whereas those that were marked the previous year before hatchlings emerged were considered \geq two years of age. Hatchlings emerge in late summer to early fall in this part of Oklahoma (Husak et al. 2004). We captured hatchling lizards as they emerged and processed them as above. We used surveying equipment to generate coordinates for scale maps of the site and determine home range sizes (see Husak and Fox 2003a,b). The maps were scale representations of the study area with points on the maps designating numbered flags on the actual site. The flags were spaced (approximately 11 m) such that several could be seen from any given location, and accurate locations could be determined for each lizard sighting by visual triangulation. We walked the site daily during the entire breeding season (late April to late June), observed lizards with binoculars, and mapped their locations so that territories could be defined by the minimum convex polygon procedure, using at least 31 (mean \pm 1 SEM = 37.4 ± 1.4 ; range = 31–48) sightings per lizard. Although many of the territorial males were present in 2003 and 2004, we used each male only once in analyses in the first year for which we had complete data for that male in order to avoid pseudoreplication.

Maximal Sprint Speed

At the peak of the breeding season (late May; Baird et al. 2001) we transported lizards to Oklahoma State University and held them for one day to encourage the passage of gut contents. Snout-vent length (SVL), total hind limb length (HL), and head width (HW; following Lappin and Husak 2005) of lizards were measured with vernier calipers to the nearest 0.1 mm. On the mornings of their second and third days of captivity, we placed lizards individually in mesh bags

inside a lighted incubator set at 37°C. Three times a day (trials being separated by at least two hours), each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag. The racetrack had a high-friction sandpaper substrate. We video recorded runs on Hi8 tape, and later viewed the tapes and counted number of frames it took a lizard to traverse 1-m intervals (following Braña 2003; Husak 2006). Speeds obtained with this method were comparable to those found by Peterson and Husak (2006), who used a racetrack with infrared beams. We classified the quality of each run as "good" or "poor" (van Berkum and Tsuji 1987), and data from poor runs (pauses, reversals) were discarded. Only the single fastest 1-m split for each run was analyzed. Immediately following a run, we confirmed the lizard's body temperature with a quick-read cloacal thermometer. After all trials were completed, we released lizards at their exact point of capture. The fastest and second-fastest performances of each individual, regardless of the day on which they occurred, were significantly correlated indicating high repeatability ($r = 0.94$, $P < 0.001$).

Hormone Assays

The collection of blood samples was concurrent with a study of seasonal variation in circulating steroid hormone levels (J. F. Husak and M. B. Lovern, unpubl. data), so to avoid the potential influence of prior handling on hormone levels, we sampled males only once a season. This limited the number of lizards available for sampling during the peak of the breeding season ($N = 14$), and how hormone levels were included in statistical analyses (see below). We collected approximately 100 μ l of whole blood by puncturing the suborbital sinus with a hematocrit capillary tube. Blood was collected from lizards over a four-day period in late May one week before sprint speed was determined (taken between 1000 and 1300 h). If a lizard moved more than 1 m while we attempted to capture it, we did not capture the lizard that day for blood collection. Blood was collected in less than 1.5 min after capture so as not to alter circulating hormone levels. Once a sample was collected it was transferred to a 0.75-ml microcentrifuge tube and placed on ice until it was returned ≤ 5 h later to the laboratory, where the plasma fraction was separated by centrifugation and stored at -70°C until assays were conducted.

Plasma samples were thawed and mixed with 0.5 ml dH_2O to provide sufficient volume for steroid extraction. Plasma levels of testosterone and corticosterone were measured by standard radioimmunoassay (RIA) techniques following extraction and chromatographic separation (Wingfield and Farner 1975). We equilibrated samples overnight at 4°C with 1000 cpm of $^3\text{H-T}$ (NET-370, 70 Ci/mmol) and 1000 cpm of $^3\text{H-CORT}$ (NET-399, 71 Ci/mmol) from Perkin-Elmer Life Sciences (Wellesley, MA) for individual recovery determinations. Plasma samples were then extracted twice with diethyl ether, dried in a 37°C water bath under nitrogen gas, and reconstituted in 10% ethyl acetate in isooctane. To remove neutral lipids and to isolate testosterone and corticosterone, all samples were transferred to diatomaceous earth (Celite, Sigma, St. Louis, MO) columns for chromatographic separation. Neutral lipids and dihydrotestosterone were elut-

ed with 2 ml of isooctane and 1.5 ml of 10% ethyl acetate in isooctane, respectively, and discarded. Testosterone and corticosterone were eluted with 2 ml of 20% and 2.5 ml of 52% ethyl acetate in isooctane, respectively, and saved. After this, samples were dried in a 37°C water bath under nitrogen gas, resuspended in phosphate buffered saline, and maintained overnight at 4°C. Competitive binding RIAs were performed using the respective tritiated steroid tracer (for testosterone or corticosterone) and antisera from Wien Laboratories (Succasunna, NJ) for testosterone (T-3003) and Sigma for corticosterone (C8784). Prior to conducting assays on samples for this study, parallelism between serially diluted plasma samples from collared lizards and serially diluted standards was confirmed for both steroids using extra samples collected from lizards not involved in this study. The standard curves for both hormones ranged from 1.95 to 500 pg and were run in duplicate. Samples were run in duplicate, averaged, and adjusted for individual recovery and initial sample volume. The intra-assay coefficient of variation (CV) was 5.6 % for testosterone and 4.2 % for corticosterone.

Paternity Assignment

Blood or toes were collected from as many potentially reproducing individuals (>95%) and hatchlings as possible. Genomic DNA was extracted from approximately 50 μ l of whole blood or two phalanges following the method of Longmire et al. (1997). Before the extraction process, toes were removed from lysis buffer, smashed with the end of a sterile syringe, and returned to fresh lysis buffer. The same extraction procedure was used for toes and blood, except toes were left incubating with proteinase K at 37°C for 24 h longer. We amplified 10 microsatellite loci using the polymerase chain reaction (PCR) with previously published primers developed by Hutchison et al. (2004). Primers were redesigned to allow multiplex gel loading, and annealing temperatures were adjusted to allow optimization of PCR product (Table 1).

We conducted PCR amplifications in 15- μ l volumes containing 1.2 μ l genomic DNA, 0.5 μ l of each primer, 3.8 μ l double distilled H_2O , and 9 μ l True Allele Premix (Perkin-Elmer Applied Biosystems, Foster City, CA). The thermal profile consisted of a denaturation and enzyme activation cycle at 95°C (12 min); and 30 cycles of 95°C (30 sec) denaturation, 46–58°C (30 sec) annealing (temperature depended on locus, Table 1), and a 72°C (30 sec) elongation. We used a final 72°C (2 min) incubation to ensure that all reactions had gone to completion. We used an automated DNA sequencer (model 377, Perkin-Elmer Applied Biosystems) to visualize variation at individual microsatellite loci. Amplicons for each locus (never more than four loci per lane) from a single individual were mixed (1.5 μ l PCR product) and 1.5 μ l of this mixture was combined with 3.5 μ l of loading mixture (2.5 μ l formamide, 0.5 μ l ROX size standard, 0.5 μ l loading dye). The PCR-loading dye mixture was denatured at 95°C for 5 min and 1.5 μ l was loaded into a single lane of a 5% polyacrylamide gel. Genotypes were visualized using Genescan and Genotyper software (Perkin-Elmer Applied Biosystems).

We first examined genotypic data for the presence of null

TABLE 1. Locus names, polymerase chain reaction primers, and annealing temperatures used for analysis of collared lizard (*Crotaphytus collaris*) paternity analysis. The name of each locus was originally described by Hutchison et al. (2004), but all primer sequences were modified to allow multiplex gel loading, and annealing temperatures were modified for product optimization.

Locus	Forward primer	Reverse primer	Temperature (°C)
Orig6	6FAM-AGGACACAAACATTCTTATC	TCTGAGTATTCCCTGCTT	46
Orig7	6FAM-AGGTTGTGGTCTGTAGCA	GGATCTGTCCCAATAATG	51
Orig11	6FAM-CACTATAAGATGTAGCACTTGC	GGTAAGCACCAGATTGAGC	54
Orig24	HEX-AGTTGAACTCGATGCTCT	ATTGAACCCATGGTAAAG	50
Orig25	HEX-AGCCTTTACTGTGAGACCCA	TCATGAAATGAAGCAAAATTAATAATA	49
Orig26	6FAM-TATACATTCTTGAGTTCCCG	CAATGAGGGATATAAGGTGG	52
Enr3	HEX-CCTCAGCAGAAGCACCAGC	TATTGAGCAGGACAGGGAAG	58
Enr21	6FAM-AGGAAGGCTCAAAGGTTAC	ATTTCCACACAGGAGGAGGAGG	58
Enr48	HEX-TTGTTTCTTATTTTACTTGCCT	AGGTATGTGCTGTCTGAGG	48
N5	HEX-CTGCCATATCATGAAGGGTG	AATCAGCACACTGGGAAAG	52

alleles using Micro-Checker (University of Hull, Hull, U.K.). We then used Cervus 2.0 (Marshall et al. 1998) to assign parents to hatchling lizards at 80% confidence (Coltman et al. 1998; Marshall et al. 1998). Three loci showed relatively high frequencies of null alleles. One locus (Orig11; null allele frequency = 0.101) was not very polymorphic, so it was removed from analysis. The other two (Orig7, N5; null allele frequencies = 0.142 and 0.098) were highly polymorphic, making them desirable to include in the analyses. To prevent false exclusion, all offspring that were found to be homozygotes at either of these two loci were entered as typed at only one allele (following LeBas 2001). This prevents offspring that are carrying their parent's null allele from being mismatched from their true parent. Only males were included as potential parents.

Statistical Analysis

Hormone levels did not significantly differ between 2003 and 2004 (testosterone: $t_{12} = 0.64$, $P = 0.48$; corticosterone: $t_{9,8} = 1.24$, $P = 0.25$), so these two years were pooled for analyses. Because the number of individuals obtained for hormone assays was limited (14 of the 19 lizards used in the analyses described below), we first looked for correlations between circulating testosterone or corticosterone levels and sprint speed and annual reproductive success. If any of the correlations were significant, we included hormone levels in subsequent analyses.

To evaluate the power of body size and morphology versus sprint speed in predicting territory area and number of offspring sired, we performed two sets of ordinary least squares regression analyses. First, we regressed the two estimates of annual fitness against absolute morphological and sprint speed measures in separate analyses. Second, we regressed the two estimates of fitness against residuals from (log-transformed) morphology and performance measurements regressed on (log-transformed) body size in separate analyses to examine the relationship of size-adjusted morphology and performance on fitness. We then used multiple regression to determine what best predicted either territory size or number of offspring sired, including body size (SVL), head width, maximal sprint speed, hind limb length, and hormone levels (if necessary) as independent variables. Morphological and performance data were log-transformed before analysis. The two dependent variables (territory area and number of off-

spring sired) were analyzed with separate multiple regressions. We determined the degree of multicollinearity among independent variables included in the multiple regression models by examining the correlation matrix of independent variables and variance inflation factors (VIFs) for each variable in the regression models (Neter et al. 1996). Large correlation coefficients among variables ($r > 0.7$) and VIFs greater than 10 are indicative that multicollinearity may be influencing model estimates (Neter et al. 1996).

RESULTS

Adult males were on average 104.3 (± 0.65 SEM) mm SVL and had heads 26.1 (± 0.53) mm wide, hind limbs 83.1 (± 1.24) mm long, and ran 3.55 (± 0.11) m/s. Territory areas (mean = 1727.8 m² ± 201.4) spanned a large range of values (431–2587 m²). Of 154 offspring in the two years, 146 were assigned a sire with at least 80% confidence. Of those, 68 (47%) were assigned to territorial males for which we had data on sprint speed and territory area. The remaining offspring were assigned to the same male in a different year (44, 30%), other territorial males for which we did not have a complete dataset (9, 6%), and yearling males (25, 17%). Of the males for which we had a complete dataset, the number of offspring sired ranged from one to 10 (mean = 3.6 ± 0.6). The number of offspring sired was significantly and positively correlated with territory area ($r = 0.55$, $P = 0.02$).

Testosterone levels did not correlate with sprint speed ($r = 0.004$, $P = 0.85$), territory area ($r = -0.49$, $P = 0.13$), or number of offspring sired ($r = 0.045$, $P = 0.90$). Corticosterone levels also did not correlate with sprint speed ($r = 0.19$, $P = 0.13$), territory area ($r = 0.033$, $P = 0.92$), or number of offspring sired ($r = 0.35$, $P = 0.29$). Thus, circulating hormone levels were not included in multiple regressions.

Sprint speed significantly and positively predicted territory area ($F_{1,16} = 13.53$, $r^2 = 0.46$, $P = 0.002$) and number of offspring sired ($F_{1,17} = 15.70$, $r^2 = 0.48$, $P = 0.001$; Fig. 1A). Body size (SVL) did not predict territory area ($F_{1,16} = 4.02$, $r^2 = 0.20$, $P = 0.06$) or number of offspring sired ($F_{1,17} = 0.02$, $r^2 = 0.001$, $P = 0.88$; Fig. 1B). Hind limb length did not significantly predict territory area ($F_{1,16} = 2.98$, $r^2 = 0.16$, $P = 0.10$), but it did positively predict number of offspring sired ($F_{1,17} = 4.89$, $r^2 = 0.22$, $P = 0.04$; Fig. 2A). Head width did not predict territory area ($F_{1,16} = 3.23$, $r^2 =$

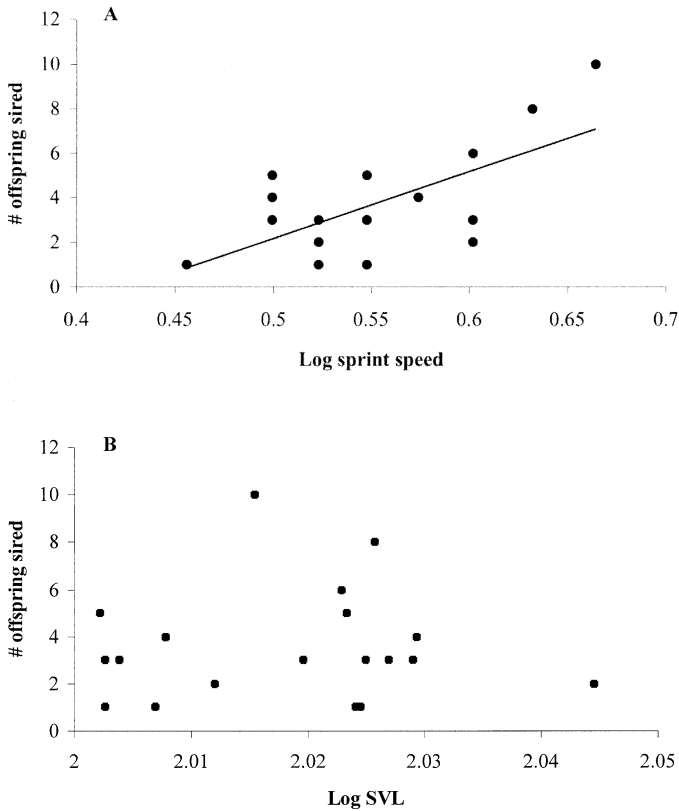


FIG. 1. Relationships between (A) number of offspring sired and sprint speed, and (B) number of offspring sired and body size (snout-vent length; SVL) in territorial male collared lizards at Sooner Lake, Oklahoma. Sprint speed was the only statistically significant predictor of annual fitness (see text for details).

0.16, $P = 0.09$) or number of offspring sired ($F_{1,17} = 2.05$, $r^2 = 0.11$, $P = 0.17$). Size-corrected sprint speed significantly and positively predicted territory area and number of offspring sired ($F_{1,16} = 6.88$, $r^2 = 0.30$, $P = 0.02$; $F_{1,17} = 20.11$, $r^2 = 0.54$, $P < 0.001$, respectively). Size-corrected hind limb length did not predict territory area ($F_{1,16} = 0.30$, $r^2 = 0.02$, $P = 0.59$), but did positively predict number of offspring sired ($F_{1,17} = 9.55$, $r^2 = 0.36$, $P = 0.007$). Size-corrected head width did not predict territory area ($F_{1,16} = 0.25$, $r^2 = 0.02$, $P = 0.63$) or number of offspring sired ($F_{1,17} = 4.22$, $r^2 = 0.20$, $P = 0.06$).

Multiple regression with territory area as the dependent variable and with independent variables of SVL, head width, hind limb length, and maximal sprint speed produced a significant model ($F_{4,13} = 4.35$, $P = 0.019$). A significant model also was generated with the same independent variables and number of offspring sired as the dependent variable ($F_{4,14} = 5.00$, $P = 0.010$). All independent variables included in the model had pairwise Pearson correlation coefficients < 0.70 except for correlations between SVL and head width ($r = 0.74$) and head width and hind limb length ($r = 0.78$). However, VIFs were < 4.0 for all variables. Taken together, these diagnostics suggest that multicollinearity was not problematic in our model estimates. In the multiple regression models, sprint speed was the only significant predictor of territory area ($\beta = 0.83$, $P = 0.006$) and number of offspring sired

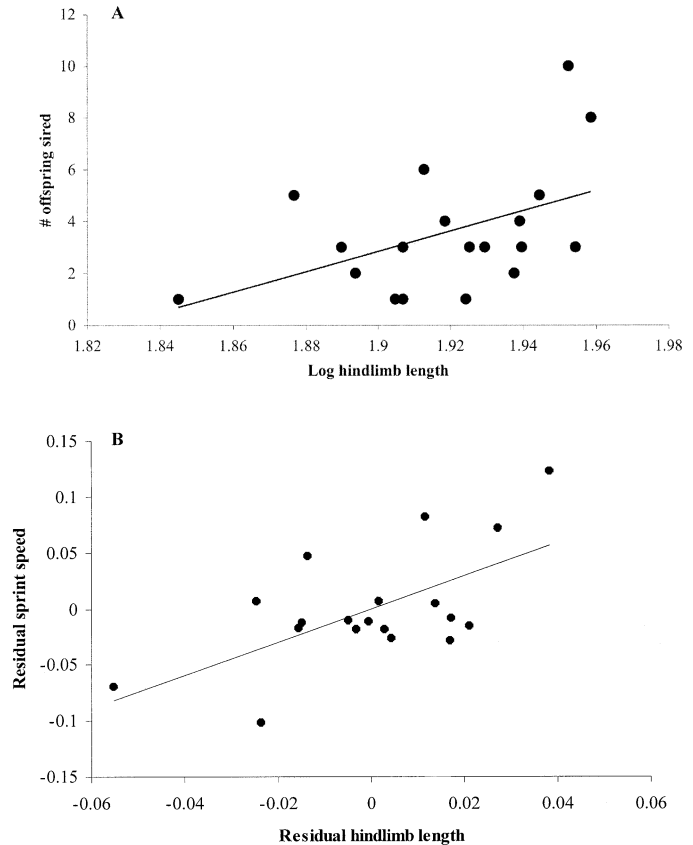


FIG. 2. Relationships between (A) number of offspring sired and hind limb length, and (B) residual sprint speed and residual hind limb length in territorial male collared lizards.

($\beta = 0.64$, $P = 0.018$). Using residual sprint speed and residual hind limb length values (calculated by regressing each of the log-transformed variables on log-SVL) in the model instead of absolute values resulted in qualitatively similar results. With the removal of sprint speed as an independent variable, the multiple-regression model with territory area as the dependent variable lost statistical significance ($P = 0.30$), whereas the multiple-regression model with number of offspring sired as the dependent variable was marginally non-significant ($P = 0.064$). In the latter model only hind limb length approached statistical significance ($P = 0.058$; all other variables $P > 0.08$).

DISCUSSION

Our results directly link variation in maximal sprint speed performance to genetically determined annual male reproductive success, demonstrating the importance of sexual selection as a factor involved in the evolution of whole-animal performance in polygynous species. Our results are strengthened by the lack of a relationship between sprint speed and circulating testosterone and corticosterone levels. We found that only sprint speed predicted territory size and annual reproductive success in territorial male collared lizards, whereas measures of body size, head size, limb size, and circulating testosterone and corticosterone levels did not. Faster territorial males had higher reproductive success than slower ter-

ritorial males, most likely because faster males mated with more females that were overlapped by their territories (see also Peterson and Husak 2006). Previous studies have focused on linking performance with estimates of survival (see introduction), leaving unexplored the possibility of sexual selection as an important factor in the evolution of whole-animal performance.

Whole-animal performance traits are integrated manifestations of underlying morphological and physiological traits, leading to the prediction that variation in the latter traits should predict variation in performance. Residual sprint speed was significantly predicted by residual hind limb length in territorial males ($r = 0.63$, $P = 0.004$; Fig. 2B), suggesting that selection on sprint speed may be an important influence on the evolution of hind limb length in collared lizards. This is consistent with the observed sexual dimorphism in hind limb length in collared lizards, where males have relatively longer limbs than females (McCoy et al. 1994). Body size was not a significant predictor of annual reproductive success, and it was not significantly correlated with sprint speed ($r = 0.39$, $P = 0.10$), suggesting that, for similarly sized territorial males, sprint speed is more important than body size in determining reproductive success (see also Lappin and Husak 2005). The lack of a body size effect on reproductive success agrees with results for another population of collared lizards (Baird et al. 2003) and with results found in another lizard species, *Sceloporus virgatus* (Abell 1997).

Annual reproductive success may be related to sprint speed indirectly via confounding phenotypic or genetic correlations between sprint speed and overall health and vigor or behavioral motivation (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004). In this situation, maximal sprint speed capacity of collared lizards would be a condition-dependent trait (Schluter et al. 1991; Clobert et al. 2000; Jennions et al. 2001), and selection on sprinting would not necessarily result in an evolutionary (genetic) response (Arnold 1983; Lande and Arnold 1983; Garland and Losos 1994). However, maximal sprint speed has been found to be heritable in the broad sense in several lizard species (Garland 1988; Tsuji et al. 1989; Bennett and Huey 1990; Warner and Andrews 2002; but see Sorci et al. 1995). Additionally, we found that sprint speed of territorial males during the peak of the breeding season did not differ from that after the breeding season (paired t -test: $t_{18} = 0.02$, $P = 0.98$) in concordance with body condition decline, suggesting that this trait is not completely condition dependent.

Alternatively, sprint speed may be correlated with circulating testosterone levels (e.g., Garland et al. 1990; Robson and Miles 2000), which may be under selection for other reasons (see below). Previous studies showing a positive correlation between locomotor performance and laboratory-determined dominance have suggested that the link may be due to correlational selection on other sexually selected traits influenced by circulating testosterone levels. In turn, higher circulating testosterone levels enhance sprint speed performance (Klukowski et al. 1998). We found no correlation between circulating levels of testosterone and either maximal sprint speed or annual reproductive success, despite observations that experimentally elevated levels of testosterone cause increased aggression (Moore 1986; Sinervo et al.

2000), sprint speed (relative to sham-implanted individuals, Klukowski et al. 1998), territory size (Fox 1983; DeNardo and Sinervo 1994), and mating success (Sinervo et al. 2000). Similarly, we found no effect of corticosterone, experimentally elevated levels of which have been shown to reduce sprint speed (Meylan and Clobert 2004). The lack of a significant correlation between hormone levels and performance in the lizards of our study may be due to a small sample size, but it may also be interpreted as supporting the hypothesis that above (or below) some threshold level, variation in hormone levels has no biologically significant effect on sprint speed. However, the relationship between natural variation in circulating hormone levels and performance traits remains unclear (Perry et al. 2004; Lappin and Husak 2005). It is important to note that, despite the lack of a relationship between circulating testosterone and corticosterone levels and sprint speed in adult lizards, there is still the possibility of steroidal effects resulting from individual differences in exposure earlier in ontogeny, and as a result not detectable by measuring adult hormone levels (e.g., Meylan and Clobert 2004). Future research will help to clarify this possibility.

Sexual selection could operate on maximal sprint speed if speed contributes directly to effective defense of a territory with the result of excluding other males and reducing their relative fitness (Snell et al. 1988; Pough 1989). Supporting this hypothesis, we found a strong positive correlation between sprint speed and territory size, which translates to spatial overlap with more mates (Peterson and Husak 2006). Since the inception of the morphology-performance-fitness paradigm (Arnold 1983), many have proposed that behavior acts as a filter between performance and fitness, such that examination of how and when organisms use a performance trait can lead to powerful conclusions concerning what selective pressures are operating (Garland and Losos 1994; Irschick and Garland 2001; Irschick 2003). We propose that territorial defense is the behavioral filter through which adult male collared lizards use their maximal sprint capacity and gain fitness via intrasexual selection.

Territorial male collared lizards often sprint toward rivals during intrasexual encounters (Yedlin and Ferguson 1973; Baird et al. 2003; Peterson and Husak 2006), and concurrent research on the population of collared lizards studied here (Husak 2005; Husak and Fox 2006) revealed that territorial male collared lizards used speeds closer to maximal sprint speed capacity (90% of maximal capacity) when responding to rival territorial males that were tethered at the boundary of their territories than when escaping predators (68%) or when foraging (31%). Further, despite large variation in maximal sprint speed capacity among territorial males (e.g., Fig. 1), all (even the inherently better performers) used near-maximal capacity when responding to a rival, whereas better performers used less of their near-maximal capacity than poorer performers in the other two contexts (Husak 2005; Husak and Fox 2006). The use of sprint speed during intrasexual encounters, combined with the results that sprint speed significantly predicted territory size and annual reproductive success, suggests that sprint speed is under the direct influence of intrasexual selection.

If sexual selection favors faster sprint speed, how might natural selection via differential survival influence it? It is

likely that natural selection pressures parallel those of sexual selection in territorial males. Territorial males use a greater proportion of their maximal capacity when responding to rivals compared to when escaping predators and foraging (Husak 2005; Husak and Fox 2006), but the proportion of maximal capacity used when escaping predators is still high relative to values found in other species (Irschick 2000a,b, 2003). However, a study testing for a link between sprint speed and survival failed to find such a relationship in adult collared lizards (Husak 2006), suggesting that selection on sprint speed for predator avoidance is not strong for this age class, or that there is selection for a threshold speed at escaping predators, one that most adult lizards can attain. However, a performance-survival link was found for hatchling collared lizards (Husak 2006), revealing that selection for effective predator escape may be intense early in life.

We found that sprint speed was the only significant predictor of annual reproductive success of the traits that we measured, but it is unlikely that sprint speed alone explains variation in mating success. Probably multiple factors are under the influence of sexual selection in collared lizards, but via different specific mechanisms (e.g., Lande and Arnold 1983; Andersson 1994). Lappin and Husak (2005) suggested that biting and bite-force performance are important during male fights and for early spatial sorting, whereas we argue that sprint speed is important for territory defense after territories are already established. Collared lizard males in central Oklahoma typically maintain the same territories for repeated years (Baird et al. 2001), suggesting that there is strong selective pressure to be able to effectively patrol an area in a territorial neighborhood where space is very limited and the opportunities to acquire a different territory are infrequent (Baird et al. 2003). The important similarity emerging from Lappin and Husak (2005) and our study is that, in both, selection was operating at the level of whole-animal performance.

Baird et al. (2003) argued that male display attributes, and not body size or other morphological traits (i.e., static; Hill et al. 1999), were the best predictors of mating success in collared lizards. Display rate and patrol rate (important attributes found by Baird et al. 2003) may be under correlated selection with sprint speed if there is the same underlying physiological basis. However, further research is necessary to determine to what extent easily modifiable behavioral traits, such as display traits, that have been shown to predict mating success (Holmberg et al. 1989; Hill et al. 1999; Topping and Millar 1999; Kodric-Brown and Nicoletto 2001) interact with and/or are constrained by whole-animal performance traits and variation in its underlying morphological and physiological traits. We predict that in other polygynous taxa where easily modifiable, nonmaximal behavioral traits significantly predict mating success, there is an underlying whole-animal performance trait that is under the direct influence of sexual selection.

In summary, our results have shown a direct link between whole-animal performance and reproductive success, suggesting that sexual selection may have farther-reaching effects on the phenotype than previously considered. We found maximal sprint speed capacity to be a strong predictor of reproductive success in collared lizards, but other species

may have different performance traits that are more relevant to their life histories and are important in determining mating success. Performance capacities of crushing structures (such as claws, jaws, and mandibles) or other integrated whole-organism traits (such as endurance capacity, jumping capacity, or maximal acceleration) may be most important during male combat, depending on the nature of male competition for mates. We encourage future investigators to consider the role of whole-animal performance in the biology of their study taxa.

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