

Locomotor Performance and Sexual Selection: Individual Variation in Sprint Speed of Collared Lizards (*Crotaphytus collaris*)

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Whole-animal performance traits, such as locomotor performance, are central to current concepts of phenotypic adaptation, yet the possible evolution of such traits via sexual selection is an underexplored hypothesis. We studied a cursorial, polygynous, territorial lizard to test two predictions of sexual selection theory applied to whole-animal performance: a secondary sexual performance characteristic may be sexually dimorphic, and variation in performance among males should be correlated to mating success. Maximal sprinting performance was measured in a series of wild-caught adult collared lizards (*Crotaphytus collaris*) from a single Oklahoma population. Sprint speed varied repeatably among individuals, but did not scale to body size among adults. Contrary to our first prediction, sprint speed did not differ between sexes. However, among 11 adult males sprint speed was strongly correlated to territory size and a spatial index of potential mating success (independent of body size), which indicates phenotypic intrasexual selection, whether direct or indirect, for whole-animal locomotor performance. The lack of sexual dimorphism in sprint speed may reflect trade-offs with other sexually selected traits (e.g., head size) and/or condition-dependence of running capability. Sexual selection of social behavior may underlie more generally the evolution of physiological performance, and therefore of suborganismal physiology and morphology.

THE adaptive evolution of physiological and morphological traits is mediated by selection on ecologically realized whole-organism performance (Bartholomew, 1958; Huey and Stevenson, 1979). Arnold (1983a) described an operational framework for the measurement of current selection on suborganismal (e.g., physiological) traits in natural populations; key to the scheme was the inclusion of whole-organism performance as a mechanistic link between phenotypic design traits and their ecological and evolutionary consequences. This “performance-outward” approach, in which the larger question of the adaptive significance of suborganismal characteristics is partitioned into two subsidiary questions (how, proximately, does design affect performance and how, ultimately, does performance affect fitness?), has stimulated both empirical application and theoretical refinement (Pough, 1989; Reilly and Wainwright, 1994; Kingsolver and Huey, 2003). Yet the latter question—how performance influences fitness—has seldom been addressed empirically, despite publication of an explicit prescriptive methodology (Arnold, 1986; Bennett and Huey, 1990).

Among the best studied of integrative organismal performance traits is sprint speed in lizards (reviewed by Garland and Losos, 1994; Irschick and Garland, 2001; Van Damme and Vanhooydonck, 2001). Sprinting ability is highly variable among conspecifics (Bennett and Huey, 1990), and individual variation is generally both repeat-

able (at least over short time periods; Huey and Dunham, 1987; van Berkum et al., 1989; Bonine and Garland, 1999) and heritable (at least in the broad sense; Garland, 1988; Tsuji et al., 1989; Warner and Andrews, 2002). Thus, the prerequisites for its evolution by natural or sexual selection are characteristic of lizard sprint speed.

Sprint speed is plausibly and empirically associated with fitness components such as foraging proficiency (particularly for sit-and-wait ambush foragers, e.g., most iguanian lizards) and predator escape (Webb, 1986; Hertz et al., 1988; Irschick, 2003). Yet the few studies designed to measure natural selection (as differential survival) on sprint speed have yielded mixed results: for *Urosaurus* lizards (Miles, 2004), garter snakes (Jayne and Bennett, 1990), and *Sceloporus undulatus* (Warner and Andrews, 2002), sprint speed was significantly related to subsequent survival (in at least some years, cohorts, or analyses) but preliminary analyses indicated no such relationship in *Sceloporus occidentalis* and *S. merriami* (Bennett and Huey, 1990; Garland and Losos, 1994).

The evolution of physiological performance traits such as sprint speed may also be influenced by sexual selection (differential reproductive success due to competition for mates). Empirical demonstrations of intra- and inter-sexual selection have typically focused on a limited number of phenotypic traits (e.g., body size, weapon size, coloration, displays; see Table 6.A of Andersson,

1994), yet *any* trait that is correlated with lifetime reproductive success through its effect on mating success (exclusive of survival and fecundity; Arnold, 1983b) can be, and indeed will be, subject to sexual selection. Such traits may also be affected by natural selection (differential survival and/or fecundity), and such simultaneous selection pressures may exert parallel or opposing influences (Darwin, 1871; Arnold, 1983b; Kodric-Brown and Brown, 1984). Sexual selection pressures can be very strong (Kingsolver et al., 2001), particularly in polygynous populations (Andersson, 1994), and there seems no reason for physiological and performance traits to be exempt from their effects.

Sexual selection pressures have been invoked in discussions of the evolution of maximal aerobic capacity and locomotor endurance (e.g., Bennett and Ruben, 1979; Sinervo et al., 2000; Miles et al., 2001). Similarly, sprint speed is plausibly subject to direct intrasexual selection in some mating systems, and territorial polygyny in cursorial lizards seems a likely context. In staged encounters between size-matched pairs of male fence (*Sceloporus occidentalis*) and tree (*Urosaurus ornatus*) lizards, the dominant “winner” was usually the faster of the two (Garland et al., 1990; Robson and Miles, 2000; but see Perry et al., 2004), suggesting that sprint speed could be subject to sexual selection (if social dominance is correlated to mating success).

From the general hypothesis that whole-animal physiological performance could evolve via intrasexual selection, we derived two testable predictions for lizard sprint speed. First, because sexual selection is characterized by differences in the selection pressures operating on the two sexes (Darwin, 1871; Andersson, 1994), we predicted that sprinting performance would be sexually dimorphic, with adult males faster than adult females. Such sexual differences in sprint speed have been documented in many lizard species (e.g., Snell et al., 1988; Cullum, 1998; Lailvaux et al., 2003), but not in all (e.g., Bennett, 1980; Garland, 1984; Vanhooydonck et al., 2001). Second, we predicted a positive relationship between variation in sprint speed and annual mating success for territorial males, but not for females. In other words, we predicted sexual dimorphism in phenotypic performance (sprint speed) and a sexual difference in a specific component of fitness (the influence of sprint speed on annual mating success). The first prediction concerns the results of sexual selection in the past, and the second pertains to current selection pressures.

We tested these predictions with measurements of sprint speed and spatial behavior for

adult collared lizards active in the summer of 2000. *Crotaphytus collaris* is an archetypical polygynous, territorial, iguanian lizard, and the details of its social organization and behavior are well known (Baird et al., 2003). Collared lizards are highly cursorial, often running bipedally, and we have frequently observed males to sprint during social encounters (see Discussion). Males live three to four years on average and first breed at the age of two (Baird et al., 2001), so annual mating success is a substantial component of lifetime success. As adults, collared lizards are notably sexually dimorphic in body size, relative head size, and relative leg length, as well as coloration and behavior (McCoy et al., 1994, 1997; Baird et al., 1996). Taken together, these patterns suggest that strong sexual selection has operated on male collared lizards (Baird et al., 1997, 2003). Furthermore, the degree and pattern of sexual dimorphism varies among microgeographically isolated populations (Baird et al., 1997; McCoy et al., 2003), suggesting continued responsiveness to local selection pressures. Does sexual selection also affect sprinting performance?

MATERIALS AND METHODS

We studied adult collared lizards from a single population inhabiting Sooner Lake Dam, 24 km south of Ponca City, Oklahoma. The dam comprises a homogeneous substrate of boulders stabilized with poured concrete. Social and spatial behavior was quantified in the field during the breeding season of 2000. In May and June, lizards were captured and permanently marked with colored beads for individual recognition at a distance (Fisher and Muth, 1989). The site was walked daily. Lizards were observed with binoculars, and their locations were precisely mapped relative to a grid so that minimum-convex-polygon territories could be delineated (Rose, 1982; Stone and Baird, 2002), using a minimum of 20 sightings per lizard. Territory and home range sizes were calculated using ArcView GIS (Environmental Systems Research Institute, Redlands, CA). We counted the number of adult female home ranges overlapped by the territory of each adult male as an index of potential mating success (Lappin and Husak, 2005).

Near the end of the breeding season, in July 2000, a subset of marked (and previously observed) lizards were recaptured, transported to Oklahoma State University, and held in terrariums for one day to encourage the passage of gut contents. On the mornings of their second and third days of captivity, lizards were placed

TABLE 1. ALLOMETRY STATISTICS FOR SPRINT SPEED OF COLLARED LIZARDS FROM SOONER LAKE, OKLAHOMA. Regression coefficients shown (with standard errors in parentheses) correspond to the form:

$$\log_{10}(\text{sprint speed}) = [\text{slope} \cdot \log_{10}(\text{snout} - \text{vent length})] + \text{intercept}$$

with sprint speed in m/s and snout-vent length (SVL) in mm. "Ontogenetic series" equation includes unpublished data for hatchling and yearling lizards from the same population (see text).

Regression parameter	Ontogenetic series	All adults	Adult males
<i>slope</i> :	0.52 (0.07)	0.35 (0.37)	-0.29 (0.96)
<i>intercept</i> :	-0.50 (0.14)	-0.17 (0.74)	1.12 (1.95)
<i>r</i> ² :	0.39	0.03	0.01
<i>n</i> :	81	31	15

inside a 37 C incubator (field-active body temperature). 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, and was equipped with vertically paired infrared photocells at 25-cm intervals; a running lizard broke the beams sequentially and the elapsed time (msec) for each interval was recorded by computer. Immediately following a run, the lizard's body temperature was measured with a digital thermocouple thermometer. In some cases, when equipment failed or a lizard was especially uncooperative, we re-ran an individual immediately. Thus, each lizard ran three to six times on each of two days. Sprint speeds of 50 hatchling and yearling lizards were measured by the same protocol in September–October 1999 and May 2000, respectively; these unpublished data were used to calculate an ontogenetic scaling regression. All lizards were released at their exact point of capture.

Although many runs were smooth, bipedal sprints down the entire track, others included quadrupedal running, brief pauses and hesitations, or even occasional reversals. The quality of each run was classified subjectively (van Berkum and Tsuji, 1987; Losos et al., 2002). Data from "poor" runs with long pauses or reversals were discarded (Losos et al., 2002), and only the single fastest 0.25-m split for each run was analyzed. Analyses of the fastest 0.5-m split yielded similar results and are not reported here.

All data (except body temperature and the number of overlapped females) were \log_{10} -transformed for analysis. We calculated four indices of the short-term repeatability of individual variation in sprint speed (Pearson's *r*; Hayes and Jenkins, 1998). First, day-to-day repeatability was quantified by the correlation of each individual's fastest 0.25-m speed (log m/s) for each day. The two daily best performances of

some lizards differed markedly, presumably because induced sprinting performance integrates motivation and responses to immediate environmental stimuli (van Berkum and Tsuji, 1987; Garland and Losos, 1994; Losos et al., 2002). We therefore also correlated the best and second-best performances of each individual, regardless of the day on which each occurred, as a more meaningful estimate of the repeatability of morphologically and physiologically constrained maximal capacity for sprint speed. Further, because sprint speed typically scales with body size (Garland and Losos, 1994), we recalculated both day-to-day and maximum repeatabilities using body-size-independent residuals derived from a linear regression of log-transformed maximum sprint speed on log snout-vent length for an entire ontogenetic series of *C. collaris* from our population (Table 1; unpublished data for 50 lizards with SVL = 45–86 mm).

RESULTS

Maximal sprint performance was variable among adult collared lizards, with a nearly 2-fold range in absolute speed (2.35 to 4.54 m/s), a coefficient of variation (CV) of 5.9%, and a standard deviation of log-log SVL residuals of 6.3 (an approximate CV of body size-adjusted speeds; Garland, 1984; Tsuji et al., 1989; Sorci et al., 1995). Individual variation in sprint speed was significantly repeatable by all four indices calculated (all $P < 0.005$). Day-to-day repeatability of sprint speed was 0.50 (Pearson's *r*) after statistical removal of the effect of body size, well within the range of estimates for a variety of other species (Bonine and Garland, 1999). The correlation between each individual's best and second-best speeds—even if they occurred in different runs on the same day, and whether or not they were adjusted for body size—was even higher ($r = 0.84$).

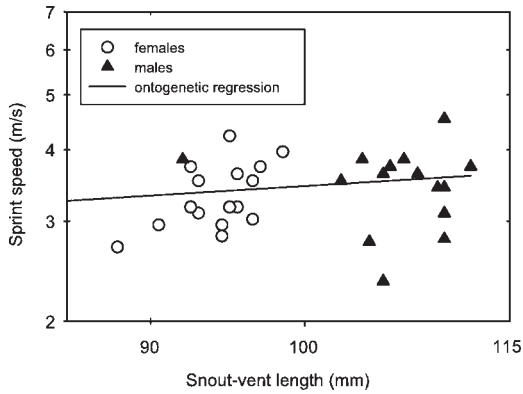


Fig. 1. Allometry of maximal sprint speed in adult collared lizards. Axes are logarithmic. Least-squares regression line is for an entire ontogenetic series (including unpublished data not shown; see text).

Body size (log snout-vent length) accounted for only 3% of total variation in log sprint speed among adults (Table 1; Fig. 1). Body temperature measured immediately after maximal performances varied from 32.8 to 41.6 C (mean = 37.4 C), but was not a significant covariate of sprint speed (multiple regression of log speed on log snout-vent length and body temperature: $P = 0.848$) and did not differ between sexes (ANOVA: $F_{1,29} = 0.079, P = 0.781$). Sexes did not differ in sprint speed (Fig. 1; ANOVA of log sprint speed: $F_{1,29} = 0.484, P = 0.492$; ANCOVA with log SVL covariate: $F_{1,28} = 0.038, P = 0.847$).

We had data on both sprint speed and territory size for 11 adult males. For them, body size was a weak correlate, and therefore a poor predictor, of sprint speed (SVL: $r = 0.162, P = 0.634$; mass: $r = 0.437, P = 0.178$). However, log sprint speed was strongly and positively correlated to log territory size (Fig. 2A; $r = 0.803, P = 0.003$), and this correlation was much stronger than those of log territory size with log SVL and log mass ($r = 0.236$ and $0.490, P = 0.484$ and 0.126 , respectively). Further, because territory size was a strong correlate of the number of adult female home ranges overlapped ($r = 0.732, P = 0.010$), sprint speed was positively related to potential mating success (Fig. 2B). Territories of different males did not overlap detectably, and the home ranges of all females overlapped only one ($n = 13$) or two ($n = 2$) male territories. Among females ($n = 15$ with data for sprint speed and home range size), sprint speed did not correlate with home-range size (Fig. 2A; $r = 0.006$), nor with the number of potential mates (male territories overlapped; $r = 0.048$).

DISCUSSION

We discuss our results in the context of Arnold's (1983a) performance-outward paradigm. Our data link variation in sprinting performance to a component of fitness (potential mates within defended territories) and demonstrate the potential importance of intra-sexual selection, an underexplored path of the fitness gradient, for the evolution of organismal

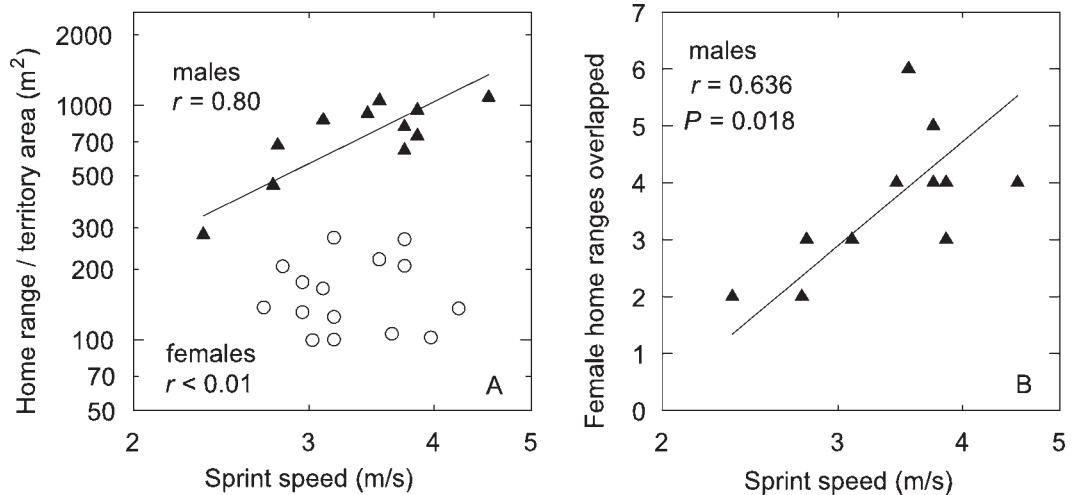


Fig. 2. Relationships between maximal sprint speed and (A) home range or territory size and (B) number of adult female home ranges overlapped by adult male territories, for collared lizards on Sooner Lake Dam, Oklahoma, during the breeding season of 2000. Axes are logarithmic except for number of females (B). Lines shown are reduced major axis regressions (for males only), r values are Pearson correlation coefficients, and the P value in (B) is for a one-tailed test.

performance. Surprisingly, however, our results do not substantiate a predicted population-level consequence of sexual selection, i.e., sexual dimorphism in performance.

Performance.—Territorial polygyny induces intrasexual selection favoring male traits that enhance effective territory defense, and because females are less affected by these selection pressures, sexual dimorphism often evolves. Sprint speed is sexually dimorphic in many lizards. In at least one case (van Berkum et al., 1989), it is dimorphic in adults but not in hatchlings. By analogy to morphological traits, this pattern is indicative of a secondary sexual characteristic resulting from hypertrophic growth (Cooper and Vitt, 1989; Brooks, 1991; Emerson, 2000). Indirect effects of sexual selection were invoked to explain the parallel sexual dimorphism in hindlimb length and sprint speed of lava lizards (*Microlophus albemarlensis*; Snell et al., 1988). The authors argued that sexual selection for effective territory defense has favored males that are more likely than females to stand their ground when approached by a predator and that this decreased wariness led to predator-mediated natural selection for longer legs and concomitant greater speed in males. Male collared lizards are probably also subject to higher predation rates than females (Baird et al., 1997; Stuart-Fox et al., 2003). Yet, despite sexual dimorphism in limb lengths (McCoy et al., 1994), we detected no corresponding sexual dimorphism in sprint speed.

Absence of sexual dimorphism is not necessarily evidence for absence of sexual selection pressures, for two reasons. First, sprint speed may trade off against other traits subject to sexual selection. For example, male collared lizards have much larger heads than females (both absolutely and relative to SVL; McCoy et al., 1994); bite-force performance is positively associated with estimated mating and reproductive success among males (Lappin and Husak, 2005). All else equal, a heavier head should slow a lizard running either bipedally or quadrupedally. Head size and sprint speed are negatively correlated among adult males of the lizard *Lacerta monticola* (López and Martín, 2002). Second, there could be seasonal variation in male sprinting capacity (perhaps testosterone dependent) and, concomitantly, sexual dimorphism. Our measurements were made in early July, whereas rates of territory patrol by male collared lizards elsewhere in Oklahoma peak in June (Baird et al., 2001), and the body condition of male lizards often deteriorates over the breeding season (Abell, 2000). We therefore consider our test for performance dimorphism to be conservative.

Fitness.—Though indirect, our use of spatial overlap data as a proxy for the number of mates acquired by males is well precedented (references in Stamps, 1983; Abell, 1999; Haenel et al., 2003) and, in this case, likely to be robust: all available ecological, behavioral, and morphological data are consistent with classical territorial polygyny, with concomitant intrasexual selection, in *C. collaris* (Lappin and Husak, 2005). The use of home-range overlap for potential mating success requires only one reasonable assumption: that each male mated with all females within his territory. In our sprint-speed sample of females, 13 occupied home ranges within only one adult male's territory, and two females had home ranges overlapped by the territories of two males each. Even in situations of higher lizard density, increased overlap, and competing alternative male strategies, the number of females spatially overlapped should remain a robust index of annual mating success for territorial males (Stamps, 1983; Baird et al., 1996; Haenel et al., 2003).

Ideally, the quantification of sexual selection requires data on the realized mating success of all adult males in a population (Lande and Arnold, 1983; Andersson, 1994), which in turn calls for a population-wide genetic analysis of paternity. In two populations of *Sceloporus* lizards (each much less territorial than *Crotaphytus*), multiple paternity was uncommon and indices derived from home range overlap were correlated with reproductive success determined from DNA fingerprinting (Abell, 1997; Haenel et al., 2003; but see LeBas, 2001). Preliminary microsatellite data for Oklahoma collared lizards corroborates their textbook territorial polygyny: territorial males achieved much higher reproductive success than nonterritorial yearlings, and females were rarely inseminated by males that did not overlap their home ranges (J. Hranitz and T. Baird, pers. comm.).

Fitness gradient.—In male collared lizards, maximal sprinting performance was strongly correlated with both territory size and the number of potential mates (Fig. 2). Indeed, sprint speed was a much better predictor of territory size and potential mating success than was body size (Olsson and Madsen, 1998). These patterns are consistent with our second prediction—that variation in sprint speed would be related to annual mating success for territorial males but not females—and we infer that sprint speed is subject to contemporary phenotypic sexual selection in male collared lizards.

A phenotypic correlation between sprinting capacity and mating success is, by definition,

sexual selection for sprinting capacity, but the causal selection pressures may be direct or indirect (Lande and Arnold, 1983; Arnold, 1987; Mitchell-Olds and Shaw, 1987). Sexual selection on sprint speed could be direct, if speed contributes directly to effective territory defense (Snell et al., 1988; Pough, 1989). Male lizards are often observed to sprint during territorial interactions (Huey and Dunham, 1987), and a male defending his territory against neighbors on two or more fronts could, conceivably, parlay quickness into a larger share of the limited rocky habitat. In a field study of our population (Husak and Fox, 2003), resident adult male collared lizards were experimentally exposed to an unfamiliar male at a territorial boundary. In 22 such staged encounters, 13 males sprinted to the vicinity of the intruder before displaying, six displayed then sprinted, and only three displayed without sprinting (unpubl. data). This behavior has been described previously as “charging” (Yedlin and Ferguson, 1973); the speed of approach could even function as an informative part of an aggressive territorial display. Male collared lizards also sprint during territorial chases (Baird et al., 2003).

One powerful means of inferring the most important selection pressures for maximal performance capacity is to compare the proportion of their maximal capacity that lizards actually use in alternative behavioral contexts (Irschick and Garland, 2001; Irschick, 2003). For example, wall lizards (*Podarcis muralis*) attain high speeds while escaping predators and while involved in intraspecific pursuits (Braña, 2003). In a follow-up to the present study, field-realized speeds of collared lizards were measured when foraging, escaping predators, and responding to a tethered rival male within their territory, and these speeds were compared to the maximal capacity measured in the laboratory (Husak, 2003). Unlike females and juveniles, adult males sprinted at speeds closer to their maximal capacities while responding to rivals than while escaping “predators” (91% vs. 72%, respectively). This further suggests that intrasexual selection is operating directly on sprint speed in this population of collared lizards.

Alternatively, territory size and mating success may be related to sprint speed indirectly, reflecting confounding phenotypic or genetic correlations of both sprint speed and social dominance with overall health and vigor, behavioral motivation, and/or testosterone levels (Garland et al., 1990; Robson and Miles, 2000; Losos et al., 2002). If so, variation in maximal sprinting capacity of collared lizards could be primarily

condition-dependent (Schluter et al., 1991; Clobert et al., 2000; Jennions et al., 2001), in which case phenotypic selection on sprinting performance need not entail an evolutionary (genetic) response (Arnold, 1987; Lande and Arnold, 1983; Garland and Losos, 1994). However, sprinting capacity is heritable in other iguanian species (see Introduction).

In male lizards with seasonal activity periods, circulating testosterone (T) levels peak during (or just before) the breeding season, concomitant with increased territorial behavior (e.g., Moore, 1986; John-Alder et al., 1997; Klukowski and Nelson, 1998). Supplemental-T studies have demonstrated a suite of correlated effects, including increases in sprint speed (Klukowski et al., 1998), territory size (Fox, 1983; DeNardo and Sinervo, 1994), and access to females (Sinervo et al., 2000). Thus, sprint speed and territory size could be related solely through mutual intercorrelation with circulating T.

Sprint speed could also be affected indirectly by sexual selection on genetically correlated traits (Arnold, 1987; Hayes and Garland, 1995). For example, bite force also predicts territory size and potential mating success (Lappin and Husak, 2005), and both bite force and sprint speed could respond similarly to general muscular hypertrophy. Alternatively, both sprinting (Bennett, 1989) and aspects of territory defense (Bennett et al., 1981; Pough and Andrews, 1985; Wilson et al., 1990) are fueled anaerobically. Perhaps variation in sprinting capacity reflects variation in the capacity for anaerobic exercise, which could be favored for its support of frequent and vigorous display behavior rather than sprinting. Similarly, sprint speed is positively correlated with locomotor endurance capacity in some lizards (Garland and Losos, 1994), which implies that sprint speed could evolve indirectly as one component of a general capacity for locomotor performance. In terms of the performance-outward paradigm, territory size is a manifestation of behavior, yet territory size itself likely depends on such behavior as display frequency and patrol rate (Baird et al., 2003), which may be more direct functions of physiological performance capacity. All of these ideas are testable hypotheses of alternative mechanisms underlying our principle conclusion: sprinting capacity is subject to phenotypic sexual selection in collared lizards.

Interpretation of studies of survival selection on performance is often hampered by poor understanding of the causal mechanisms involved (Endler, 1986; Pough, 1989; Garland and Carter, 1994), whereas social behavior is directly observable in many lizards, and its

consequences for mating success are readily inferred (e.g., Baird et al., 1996, 2001). Territorial iguanian lizards such as *C. collaris* thus offer attractive systems for further exploration of the evolution of physiological performance capacity by sexual selection. Because organismal performance capacity integrates lower-level variation in morphology, physiology, endocrinology, biochemistry, and neuromuscular organization, sexual selection may have evolutionary effects at suborganismal levels of organization that are more widespread than heretofore suspected.

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