



Faster male lizards are better defenders not sneakers

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Locomotion is an important trait to individual fitness in numerous animal taxa for predator escape and prey acquisition. However, the role of locomotion in mating success has been largely unexplored. Even studies linking sprint speed with proxies of fitness (e.g. dominance) and actual measures of mating success (e.g. genetic reproductive success) have struggled to test explicit hypotheses as to how high-performance individuals attain higher fitness. We studied a free-ranging population of male collared lizards, *Crotaphytus collaris*, to determine why faster males sire more offspring. Specifically, we tested the alternative hypotheses that faster males are 'fast defenders' versus 'fast sneakers' by using molecular genetic techniques to examine patterns of maternity and paternity in the population. We found that females that were defended by faster males had a lower proportion of offspring sired by males that did not defend them (support for a fast defender hypothesis). In contrast, we found no relation between males' sprint speed and the proportion of their offspring that were produced by females other than those they defended (no support for a fast sneaker hypothesis). In species in which locomotor performance is important to male competition, these alternative hypotheses should be simultaneously tested and complemented with behavioural data to discriminate them from female choice.

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Locomotion contributes importantly to the fitness of individuals, as fast speeds are often used while escaping predators, capturing prey and interacting with conspecifics (reviewed in Irschick & Garland 2001; Lailvaux & Irschick 2006). While the importance of locomotion to the first two ecological tasks has been studied extensively in recent years (reviewed in Irschick & Garland 2001; Husak & Fox 2006), the third context has been explored only recently (Crompton et al. 2003; Husak et al. 2006; Lailvaux & Irschick 2006). Performance-based approaches to the study of adaptation are appealing because selection, be it natural or sexual selection, typically operates on the functional output of complex morphological systems, with evolutionary change occurring secondarily on the morphological traits that underlie performance (Bartholomew 1958; Huey & Stevenson 1979; Arnold 1983). Thus,

individuals with a faster maximal sprint speed capacity (as measured in the laboratory) have an increased probability of survival (Jayne & Bennett 1990; Miles 2004; Husak 2006a and references therein), most likely due to better success at escaping predators (Irschick & Losos 1998; Husak & Fox 2006). Nevertheless, the role of locomotion in the context of mating success remains ambiguous. Previous studies on lizards revealed that faster sprint speeds lead to increased dominance (Garland et al. 1990; Robson & Miles 2000; Perry et al. 2004), but the means by which being faster aided in the acquisition of a dominant status remains unknown. Hence, studies are needed that address the question of how better locomotion may lead to increased fitness via enhanced mating success.

Intrasexual selection in a territorial species may favour faster males by two very different means. First, faster males may be better able to defend a larger territory and/or more females by better excluding rival males from usurping mates (Husak et al. 2006; Peterson & Husak 2006). A territory defence advantage for better locomotor performers has been suggested for a variety of vertebrate taxa, including birds (e.g. Blomqvist et al. 1997; but see Kruger 2005), gliding lizards (Mori & Hikida 1992; Shine et al. 1998) and

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seals (Alexander et al. 1979) among others (Andersson 1994). Second, faster males may be better able to 'sneak' copulations from females other than those that they defend. In this scenario, males with higher sprint speed capacities would be able to enter and leave another male's territory without detection and/or retribution before or after sneaking a copulation. Such a scenario has been suggested in some ungulate species (e.g. Hogg & Forbes 1997). These two hypotheses make very different predictions about patterns of parentage in a population, but both may be operating simultaneously. That is, fast males may be better defenders and better sneakers. An advantage of our approach is that, because the predictions and data necessary to test each hypothesis are mutually exclusive, a simultaneous test of both hypotheses is possible. The 'fast defender' hypothesis predicts that females defended by faster males should produce a smaller proportion of offspring sired by other males. The 'fast sneaker' hypothesis predicts that faster males should have a higher proportion of offspring with females that they are not defending. If one knows the patterns of both maternity and paternity of a set of offspring, it is possible to determine whether faster males have an advantage in mating success through one or the other mechanism or both.

We tested these alternative hypotheses by determining parents of offspring in a free-ranging population of collared lizards, *Crotaphytus collaris*. Previously we showed in this population that faster males sire more offspring (Husak et al. 2006) and that territorial males use near-maximal sprint speed capacity while responding to rival males in their territory (Husak & Fox 2006). These findings led us to hypothesize that the fitness advantage gained by males was due to being better defenders, but we did not distinguish between this hypothesis and the alternative that faster males may also be better at sneaking copulations with the females of rival males in nearby territories. We combined field studies with molecular genetic techniques to determine how faster male collared lizards sire more offspring than slower males.

METHODS

General Methods

The study site was an approximately 2 ha area at Sooner Lake dam in Pawnee County, Oklahoma, U.S.A. on a substrate consisting of concrete-covered boulders. In 2003 and 2004 we captured adult (≥ 2 years old) and yearling (~ 1 -year-old) male and female lizards by noosing and permanently marked them with toe-clips and a unique pattern of coloured paint spots for visual identification at a distance (Husak & Fox 2003a, b). Individuals that were captured and marked the previous year as hatchlings were considered yearlings, whereas those that were captured the previous year before hatchlings emerged were considered at least 2 years old. In most cases, toes were saved in lysis buffer for genetic analysis (see below). Hatchlings emerge in late summer–early autumn in this part of Oklahoma (see Husak et al. 2006). Many of the same individual territorial male lizards were present in

2003 and 2004, but we used each male only once in analyses in the first year for which we had complete data for that male. The sample of males used in our analyses represents most of the territorial males in the population.

Details of the study area and how we determined territories and home ranges are reported elsewhere (Husak & Fox 2003a, b; Husak et al. 2006; Peterson & Husak 2006). Briefly, scale maps of the site and daily sightings (made during the entire breeding season, late April–late June) were used to determine territory and home range sizes. Territories of adult males and home ranges of females were defined by the minimum convex polygon procedure, using more than 30 sightings per territorial male lizard and more than 20 sightings per female. Using the spatial locations of territories and home ranges, we determined which females were overlapped by which territorial males. The most common situation at our study site is for females to be overlapped by only one male's territory (Husak & Fox 2003a, b; Lappin & Husak 2005). Nevertheless, six females (11%) were overlapped by two males' territories, two for which we had adequate spatial and genetic data (contributing a total of three offspring). Because multiple male overlaps were rare, we did not include these females in our analyses or in the determination of male mating success.

Maximal Sprint Speed

Methods for determining maximal sprint speed follow Husak (2006a) and are highly repeatable (Husak et al. 2006; Husak 2006a). At the peak of the breeding season we transported lizards to Oklahoma State University and held them for 1 day to encourage the passage of gut contents. Three times a day (trials being separated by at least 2 h) for 2 days, each lizard was removed from a lighted incubator set at 37°C and immediately chased down a 3 m racetrack into a black bag. We used Hi8 video (30 frames/s) to record runs and determine the number of frames (i.e. time) that it took each lizard to traverse 1 m intervals (Husak 2006a). We classified the quality of each run as 'good' or 'poor' (van Berkum & Tsuji 1987), discarding 'poor' runs (pauses, reversals). Immediately following a run, we measured the lizard's body temperature with a quick-read cloacal thermometer. After all trials were completed, we released all lizards at their exact point of capture. The single fastest 1 m sprint for each lizard was used for analyses.

Ethical note

Because *C. collaris* lack natural markings that reliably distinguish individuals, we toe-clipped subjects prior to release to allow individual identification. Toe clipping was the minimal required to identify the large number of lizards in our study population and was performed according to the guidelines jointly published by the three North American herpetological societies (*Guidelines for Use of Live Amphibians and Reptiles in Field Research: Applied Ecology Research Group* 1987). We did not observe any adverse effects of toe clipping on the survival of lizards, in agreement with the majority of other studies that have

addressed this issue (see Husak & Fox 2003b). In addition, male behaviour was not noticeably affected because resighted males were found patrolling their territory and displaying to conspecifics.

Parentage Assignment

Methods for parentage analysis are detailed in Husak et al. (2006). Briefly, blood or toes were collected from as many sexually mature individuals and hatchlings as possible during each breeding season. Genomic DNA was extracted from approximately 50 μ l of whole blood or two phalanges (Longmire et al. 1997). We amplified microsatellite loci using polymerase chain reaction with previously published primers (Hutchison et al. 2004; Husak et al. 2006) and following the protocols of Husak et al. (2006). Genotypes were visualized using Genescan and Genotyper softwares (Perkin–Elmer Biosystems, Foster City, CA, U.S.A.). We examined genotypic data for the presence of null 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) was removed from analysis because it was not highly polymorphic, whereas the other two (Orig7, N5) were highly polymorphic, making them desirable to include in the analyses (see Husak et al. 2006 for details). To prevent false exclusion, all offspring that were homozygotes at either of these two loci were entered as typed at only one allele (LeBas 2001), preventing offspring that were carrying their parent's null allele from being mismatched from their true parent. We first included only males as potential candidate parents in the analyses but then included 'known' fathers in subsequent analysis to determine mothers.

Analysis

For each female we determined both the number of offspring attributed to the male whose territory overlapped hers and the number of offspring for that female sired by other males whose territories did not overlap hers. We divided the number of offspring attributed to other males by the total number of offspring produced by that female to calculate the proportion of offspring sired by other males. To avoid pseudoreplication, we averaged the proportions for all females overlapped by a given male to produce a single value that represented the average proportion of his females' offspring that were sired by other males (FO_{other}). For each male we determined the number of offspring sired with females that his territory overlapped and the number of offspring sired with females that his territory did not overlap. We divided the number of offspring sired with nonoverlapped females by the total number of offspring sired by the male to determine the proportion of offspring sired with nondefended females (MO_{other}). We assigned only one offspring to each of four males. Each of these males' one offspring represented the only offspring attributable to each of four females

whose home ranges the males overlapped. Because we were interested in patterns of paternity within males and their females, males with only one offspring were irrelevant to our analyses and were excluded. However, there was the potential that other females overlapped by these males had offspring sired by nonoverlapping males. Hence, females other than those that produced the males' single offspring were included in calculations of FO_{other} if they produced offspring. We used general least-squares regression to test the fast defender and fast sneaker hypotheses. The fast defender hypothesis predicts a negative relationship between FO_{other} and male sprint speed. The fast sneaker hypothesis predicts a positive relationship between MO_{other} and male sprint speed. Because proportion data are often not normally distributed, we first tested for normality of FO_{other} and MO_{other} variables with a Kolmogorov–Smirnov test. Both the MO_{other} ($P = 0.74$) and the FO_{other} ($P = 0.49$) variables were normally distributed, so we used untransformed data in analyses.

RESULTS

Of 154 offspring in the 2 years, 146 were assigned a sire with at least 80% confidence. Of those 146, 68 (47%) were assigned to territorial males ($N = 15$) for which we had data on sprint speed and territory area. Most of the remaining offspring (44, 30%) were attributable to the same males but in the second year (see Husak et al. 2006 for details on the remaining offspring). We were able to assign a mother ($N = 25$) to all 68 genotyped offspring.

Male territories averaged (mean \pm SE) 1814.6 ± 216.2 m² and overlapped each other on average $11.6 \pm 1.3\%$. Female home ranges averaged 175.8 ± 15.3 m². On average, $97.6 \pm 1.3\%$ of a female's home range was overlapped by their defending male.

Fast Defender Hypothesis

On average, $39 \pm 0.04\%$ of offspring produced by females were from males other than those they overlapped, but FO_{other} ranged 0–67%. There was a significant negative relationship between FO_{other} and sprint speed ($F_{1,13} = 9.06$, $r^2 = 0.41$, $P = 0.01$; Fig. 1a), supporting the fast defender hypothesis.

Fast Sneaker Hypothesis

On average, $34 \pm 0.06\%$ of offspring sired by males were from females that they did not defend in their territories, but MO_{other} ranged 0–67%. Sprint speed was not a significant predictor of FO_{other} ($F_{1,13} = 0.022$, $r^2 = 0.002$, $P = 0.88$; Fig. 1b). Thus, we found no support for the fast sneaker hypothesis.

DISCUSSION

A growing number of studies have linked locomotor capacity to an individual's probability of survival (e.g. Jayne & Bennett 1990; Miles 2004; Husak 2006a, b and

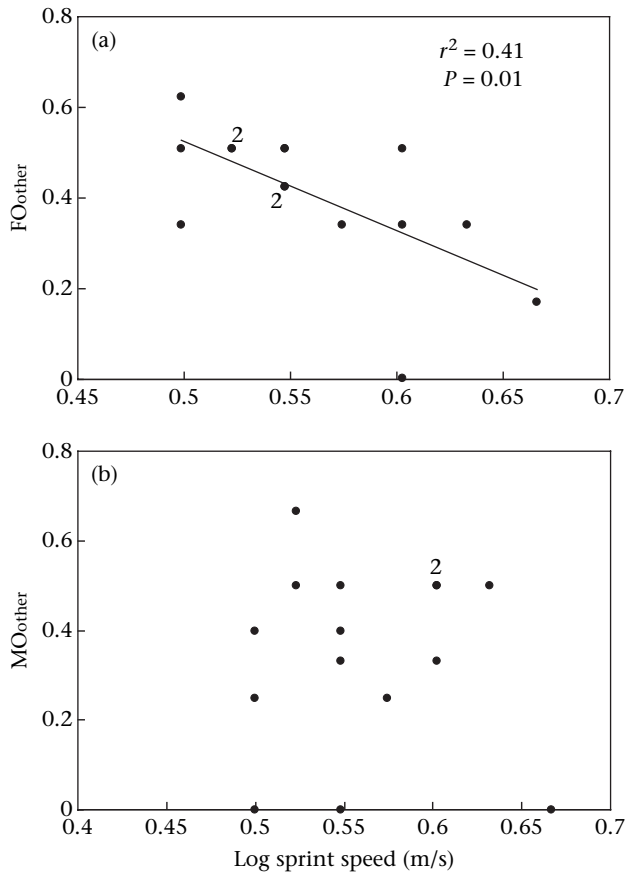


Figure 1. Relationship between maximal male sprint speed (log transformed) and (a) the proportion of offspring produced by females (averaged for each male; see text) that were sired by males other than those they overlapped (FO_{other}) and (b) the proportion of offspring sired by males with females that they did not defend in their territories (MO_{other}). Numbers next to data points represent the number of overlapping points.

references therein) via an advantage given during prey capture and/or predator escape, but few studies have explored the role of locomotion in male–male competition (Crompton et al. 2003; Husak et al. 2006). Our test of two alternative hypotheses clarifies how a fast territorial male lizard can increase its mating success relative to that of its slower rivals. We found that faster males sired more offspring by being better defenders and ensuring that the females that they defended produced more of their offspring. We did not find any evidence that being faster gives a male an advantage in sneaking copulations from rivals. Thus, being a faster male results in holding a larger territory that overlaps more females (Peterson & Husak 2006) and being able to better defend those females and sire more offspring than slower rivals (Husak et al. 2006).

Agreeing with previous studies of genetic mating systems (Hughes 1998), we found that most individuals produced some offspring with mates other than those involved in the male–harem grouping. However, the mechanism for this in our study species remains unknown. We do not know whether females and males obtain matings with non-overlapping individuals by female movement off male territories, male movement into other males' territories or sperm

stored from a previous year's matings. Both males and females tend to remain in the same territories and home ranges for multiple breeding seasons (i.e. years) after they are established (Baird et al. 2001; Husak & Fox 2003a, b). It is unknown whether female collared lizards are capable of sperm storage, so we cannot comment on the latter hypothesis. However, personal observations (J. Husak & S. Fox, unpublished data) reveal that both males and females occasionally make forays into surrounding areas, either going undetected or eliciting a response from the resident male. Most likely the resulting patterns of parentage are due to a combination of male movement into surrounding territories and female movement into areas other than those overlapped by the male defending her. In a similar population of collared lizards in Oklahoma, Baird et al. (1997) suggested that the habitat structure in areas like our study site (a boulder field with high visibility due to sparse vegetation) results in the potential for females to assess multiple males, thus increasing the potential for sexual selection on male traits and the possible benefits of multiple matings by females (Arnqvist & Nilsson 2000; Jennions & Petrie 2000; Hosken & Stockley 2003). We found high variation in the proportion of offspring attributed to females other than those a male defended (MO_{other} ; Fig. 1b). At this time we cannot explain what traits predict male success at extrapair matings because body size was not correlated with MO_{other} (Pearson correlation: $r_{13} = 0.29$, $P = 0.29$). We also do not know exactly how males 'sneak' in and out of rival male territories. Given our findings (i.e. no relationship between sprint speed and MO_{other}), they may not use high speeds. However, it is possible that males do use high speeds but not necessarily maximal capacity. Future work will help to clarify these issues.

The fast sneaker hypothesis predicted a positive relationship between sprint speed and male extrapair matings, but female choice for faster males may also predict such a relationship. In this scenario, females would be overlapped and defended by one male but choose to mate with a nonoverlapping, faster male. The fitness advantage of this strategy for females is unknown, but it is possible that the spatial availability of suitable food or refuges could force a female to be defended by one male but seek matings with another. While female choice is thought to be rare in lizards (Olsson & Madsen 1995), it has been documented (e.g. Censky 1997; Hamilton & Sullivan 2005 and references therein), even in this species (Baird et al. 1997), and high-performance males may provide 'indirect benefits' (Kirkpatrick & Ryan 1991; Andersson 1994; Kokko 1998; Kokko et al. 2003; Kotiaho & Puurtinen 2007) to females by siring high-performance offspring with high fitness. However, this hypothesis remains controversial (reviewed in Kotiaho & Puurtinen 2007). At any rate, we did not find a positive relationship between sprint speed and MO_{other} , but we raise this point for future investigators. To determine which of the two hypotheses is correct, parentage data should be complemented by quantitative behavioural data of male and female movement out of defended space.

Our general approach is applicable to numerous taxa and their associated sexually selected traits. Studies seeking to determine how individuals acquire a reproductive advantage may find our methods useful. We can gain

a better understanding of the mechanisms of selection by taking an integrative and multifaceted approach to hypothesis testing as in our study. Numerous investigators have proposed for a variety of taxa that being a better locomotor performer may provide an advantage during male–male contests (Andersson 1994; see also Introduction). In our study species we found that faster adult males have larger territories, overlap more females and sire more offspring (Husak et al. 2006; Peterson & Husak 2006). While this finding alone is interesting, it does not provide a mechanism for how these relationships come about. Our finding that only adult males use near-maximal capacity while responding to rivals in their territories adds to our confidence that speed is important during male competition for exclusive access to mates. Importantly, we found no survival advantage for faster adult males (Husak 2006a), ruling out the hypothesis that faster males have more offspring simply because they survive better to reproduce more than slower males. Even with all these data there was still no explanation for how faster males sired more offspring. Examining patterns of parentage allowed us to examine whether being faster made males better defenders or more successful at sneaking copulations from rivals' females. We suggest that future studies seeking to determine the adaptive significance of morphological and/or performance traits should look not only for higher fitness in 'better' individuals but also at how having 'better' traits translates to increased fitness. This is best achieved by studying the behaviour of free-ranging individuals in the appropriate contexts in addition to conducting genetic studies of parentage. Our approach can be useful to test specific hypotheses about how better locomotor performers can attain higher fitness.

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