

## PHENOTYPIC CORRELATES OF MALE SURVIVORSHIP AND REPRODUCTIVE SUCCESS IN THE STRIPED PLATEAU LIZARD, *SCELOPORUS VIRGATUS*

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Variation in sexual selection among populations and species has been suggested as an explanation for patterns of sexual size dimorphism. The strength of sexual selection on body size and other male traits was studied in a population of *Sceloporus virgatus*, a lizard in which females have a larger average size than males. Sexual selection on male size was found to be weak, with only the very smallest males having a mating disadvantage. This study provides tentative support for a sexual selection-fecundity selection tradeoff as an explanation for sexual size dimorphism in the genus *Sceloporus*, though further studies of the relationship between body size and reproductive success are needed.

### INTRODUCTION

The evolution of sexual size dimorphism (SSD) has been the subject of much recent research (Stamps, 1983; Shine, 1994; Fairbairn & Preziosi, 1996; Stamps, Losos & Andrews, 1997). Several hypotheses (not mutually exclusive) have been proposed for the evolution of SSD, including sexual selection favouring large males, fecundity selection favouring large females, and intersexual niche divergence (reviews in Hedrick & Temeles, 1989; Anderson & Vitt, 1990; Madsen & Shine, 1994; Bull & Pamula, 1996; Perry, 1996).

All three hypotheses have been supported by some evidence (Hedrick & Temeles, 1989). The sexual selection hypothesis appears especially promising for lizards, with positive correlations between male body size and some measure of male mating success reported for many species in which males are larger than females (*Anolis garmani*, Trivers, 1976; *Sceloporus jarrovi*, Ruby, 1981; *Anolis carolinensis*, Ruby, 1984; *Uta palmeri*, Hews, 1990; *Ameiva plei*, Censky, 1995; *Crotaphytus collaris*, Baird, Acree & Sloan, 1996). However, studies of lizards and other taxa have shown that the strength of the relationship between male body size and mating success can vary across populations of the same species (the water strider *Gerris odontogaster*, Arnqvist, 1992; Yarrow's spiny lizard *Sceloporus jarrovi*, Dixon, 1993; the soapberry bug *Jadera haematoloma*, Carroll & Salamon, 1995) or among closely related species (*Drosophila*, Markow, Bustoz & Pitnick, 1996). Furthermore, sexual selection for larger male size can occur even in species where females are larger than males (the water strider *Aquarius remigis*, Fairbairn & Preziosi, 1996; the sand lizard *Lacerta agilis*, Olsson & Shine, 1996). The sexual selection hypothesis, then, cannot be a sufficient explanation for SSD in lizards. As in other reptiles (Madsen & Shine, 1994), larger size would be expected to enhance reproductive success of both male and female lizards. Selective pressures might be greater for females in some conditions and for males under other circumstances.

Selective forces on size in both sexes have been examined in species from a variety of taxa (Price, 1984; Howard & Kluge, 1985; Ward, 1988; Harvey, 1990; Olsson & Shine, 1996; Arnqvist, Thornhill & Rowe, 1997). Spiny lizards (*Sceloporus*) present an excellent opportunity to estimate the action of sexual selection and fecundity selection in the evolution of SSD. Species within the genus, and even populations of the same species, vary in the extent and direction of SSD (Fitch, 1978). A positive relationship between female size and clutch size has been documented in many *Sceloporus* species (for example, papers cited in Dunham, Miles & Reznick, 1988). Sexual selection on body size in males has been examined closely only in *S. jarrovi* (Ruby, 1981; Dixon, 1993), a species in which males are larger than females. I studied selection on male size in *S. virgatus*, a species in which females are larger than males. I also considered selection on head dimensions and ventral colouration, as there is evidence that these traits may be associated with male mating success of other lizards (Sigmund, 1983; Hews, 1990; Bull & Pamula, 1996).

### METHODS

#### STUDY POPULATION AND AREA

From 1991 to 1994, I studied a population of the striped plateau lizard (*Sceloporus virgatus*) in the Chiricahua Mountains of south-eastern Arizona, near the Southwestern Research Station of the American Museum of Natural History. Detailed information about this habitat is available in Vinegar (1975). The study area (elevation 1646 m) was situated within North Fork, an ephemeral tributary of Cave Creek. The preferred habitat of *S. virgatus* in this area was small- to medium-sized rocks in and near the creek bed. *S. virgatus* densities dropped sharply as one moved away from the creek; marked individuals were rarely sighted in the grassy woodland on one side of the creek or in the steep rocky area across a road on the other side of the creek. I captured lizards along an approximately 150 m stretch of creek in 1992, and a 300 m length of creek in

1993. The width of the study area varied along the creek according to suitable habitat, but in general the width was 30-60 m.

In both 1992 and 1993, the study area was mapped so that lizard locations could be recorded. I used scan sampling (Altmann, 1974) during daily censuses to record the map location of every lizard I saw. These observations allowed me to determine the home range of each individual. I marked each lizard captured with three small (approximately 0.01 g), coloured seed beads attached at the tail base with plastic monofilament, using a modification of the technique described by Fisher & Muth (1989). This method was usually permanent and allowed for visual identification without having to recapture the animal more often than necessary for morphological measurements. The beads did not appear to interfere with movement or mating. Marked lizards were observed copulating, and some females that had been marked soon after emergence were known to lay fertilised eggs (pers. obs.). The bead marking procedures did not seem to cause infection or tail loss. In other studies of lizards, colour markings did not influence survival (Jones & Ferguson, 1980; Simon & Bissinger, 1983) or mating success (Ruby, 1981). I also clipped three or four toes from each lizard to confirm identity in the rare instance when an individual lost its beads.

I examined selection on male traits in 1992 and 1993, and I considered viability selection in 1992-93 and 1993-94. Age was not known for all individuals in the study, but lizards that were sufficiently small at the time of first capture were known to be in their first spring. Because I started marking animals in 1991, there were known one- and two-year olds in 1992 and known one-, two- and three-year olds in 1993.

#### MORPHOLOGICAL TRAITS

I measured the body length, body mass, head size, and colour pattern of each lizard caught. I measured snout-vent length (SVL) to the nearest mm with a transparent ruler and body mass to the nearest 0.1 g with Pesola spring scales. I measured head length, head width, and head depth to the nearest 0.1 mm with dial calipers. Head length was the distance from the snout to the posterior margin of the ear opening. Head width was measured as the straight-line distance from ear to ear. Head depth was measured from the top of the head above the eyes to the chin below. I also measured the length and width of the ventral throat patch on the right side with dial calipers, and I counted the number of blue scales in that patch. I calculated the approximate area of the blue throat patch as the area of an ellipse (area =  $\frac{1}{2}\pi \times \text{length} \times \text{width}$ ). I assessed the brightness of blue colouration by matching the colour of the patch against a set of colour standards (Smith, 1975) under field lighting conditions. I converted the blue brightness measurements to numerical scores ranging from 0 (no blue) to 9 (bright blue).

Individual males were captured on different days. For most characters (SVL, mass, head length, head width, head depth, blue throat patch length, and blue throat patch width), I used data from individuals captured more than once to estimate size-specific growth rates. Based on the trait values at first and last capture, I calculated growth rates for each trait for each individual. For each trait, I calculated a regression equation for the relationship between growth rate and body size (SVL). Growth rates of most traits were lower for larger individuals. Blue patch length and width changed little between first and last capture. For each individual, I then calculated the estimated values of all traits on the same day (31 May), using the actual growth rates of the individual (when available) or size-specific growth rates obtained from the regression equations. The number of blue patch scales and the intensity of blue colouration did not differ significantly between the first capture (April or early May) and the second capture (early June) (Abell, 1998), so I used the unmodified values of these traits on the second or only capture.

#### MALE SURVIVORSHIP AND MATING SUCCESS ESTIMATES

I calculated survivorship using mark-recapture data, and used survivorship from one year to the next as an estimate of male viability. If an individual present in one year was seen in the following year, that lizard was considered a survivor. If the individual was not sighted in the following year, that lizard was assumed to be dead. Most lizards had highly overlapping home ranges from one year to the next. I regularly searched areas adjoining the study site for lizards that had shifted home range. My searches of adjacent areas, along with the fact that the study area was bordered on two sides by less suitable habitat, make it likely that most individuals not seen had died rather than dispersed.

A previous study in the same area found that females that reached sexual maturity in their first spring averaged about 50 mm SVL from 31 May to 14 June (Vinegar, 1975). Reproductive females as small as 46 mm SVL have been collected (Smith, Ballinger & Rose, 1995). For most analyses, I considered a female as potentially sexually mature if her estimated SVL on 31 May was at least 45 mm. The proportion of first-year females that reproduces varies from year to year (Vinegar, 1975; Smith *et al.*, 1995), so it is likely that some of the females between about 45-50 mm SVL did not actually reproduce in the years of the study. I therefore repeated some analyses using only females that were at least 52 mm SVL. Females of this size nearly always reproduce (Smith *et al.*, 1995). I determined the most likely mate or mates of each potentially reproductive female according to the spatial criteria described below. If more than one male was a likely mate, I divided the eggs of that female among the males. Multiple paternity has been documented in clutches of *S. virgatus* (Abell, 1997).

A DNA fingerprinting study in an area adjoining the selection study area suggested that spatial proximity between males and females usually accurately predicts the mate of a particular female (Abell, 1997). Because spatial estimates of paternity were significantly correlated with actual paternity in the sample of lizards used in the fingerprinting study, I used spatial proximity to estimate male mating success.

I used the proximity criterion described in Abell (1997) to estimate mating partners of females. Male-female spatial relationships were divided into three categories on the basis of how often the male and female were sighted within 10 m of each other and the actual distance between the male and female. If a female was observed to have a spatial relationship of higher rank with one male than with any other male, I assumed she mated with that male. If a female had more than one male of equally high spatial rank, I divided her clutch among these males. If a female was never observed within 10 m of a male, I assigned her likely mating partner(s) on the basis of home range overlap alone. In such cases, the clutch was divided among all males with home ranges overlapping that of the female. In the rare cases where a female neither interacted nor overlapped with any male, I assigned that female to the male or males with the closest home range.

#### MATE FERTILITY ESTIMATES

I estimated mate fertility (Arnold & Duvall, 1994) as well as mating success for all males in my main study population. First, I used longitudinal growth data to estimate the size of all females on a particular day near the end of the breeding season. I then used a regression of clutch size with maternal SVL (Vinegar, 1975) to estimate clutch size of each female. Estimated clutch size was regarded as female fertility. The average mate fertility for a given male was calculated as the average predicted clutch size of his possible mates. When defined this way, the product of a male's mating success (total fractional number of mates) and average mate fertility is equal to the number of eggs likely to be fertilized by that male.

#### EVALUATION OF SELECTION

The eight morphological measurements included in this analysis were snout-vent length, mass, head length, head width, head depth, blue throat patch area, number of blue scales in patch, and patch colour intensity. I performed principal components analysis (Flury & Riedwyl, 1988) to describe variation among individuals with a smaller number of variables (principal components). Principal components are statistically uncorrelated with each other, so I evaluated the relationship between principal components, and components of fitness by using univariate statistical tests for each principal component.

I performed spatial autocorrelation (Sokal & Oden, 1978a, b) on the principal component scores to test for a

possible association between phenotype and the spatial distribution of males. A lack of significant autocorrelation would suggest that it is reasonable to assume that each lizard was exposed to a similar range of male phenotypes.

Selection on traits can be measured quantitatively with regression techniques, using fitness (survivorship or mating success, for example) as the dependent variable and the character values as independent variables (Lande & Arnold, 1983). Logistic regression (Hosmer & Lemeshow, 1989) is a form of regression suitable for dichotomous outcomes. Survivorship has a dichotomous outcome (live or die), so I performed univariate logistic regression to estimate the strength of viability selection on blue colouration and other characters. Mating success and mate fertility are distinct episodes of selection, so I used established methods for multi-episodic selection (Arnold & Wade, 1984a, b; Wade & Kalisz, 1989; Koenig, Albano & Dickinson, 1991) to estimate the strength of selection on blue colouration and other characters. I used a Fortran program (Koenig *et al.*, 1991) to calculate independent selection gradients.

To examine possible independent effects of age and size, I calculated Kendall's partial correlation coefficient (Siegel & Castellan, 1988) between these variables and each estimate of male reproductive fitness (number of mates and average mate fertility), holding either age or size constant.

## RESULTS

#### MALE MORPHOLOGICAL TRAITS

Including only females that were potentially mature ( $\geq 45$  mm SVL) and observed in the study area for more than a single day, there were 27 females in 1992 and 53 in 1993. Considering only males present for more than one day, there were 33 in 1992 and 57 in 1993, all large

TABLE 1. Principal components analysis, PCI-PCIII for all males, 1993,  $n=55$  (14 survived to 1994). \* indicates principal component scores higher than 0.7. Results were similar for 1992 ( $n=30$ ).

Character	PCI Body size	PCII Patch size	PCIII Blue colour intensity
Head Depth	0.96*	0.15	0.14
Head Length	0.96*	0.24	0.09
Snout-Vent	0.95*	0.23	0.15
Mass	0.95*	0.25	0.14
Head Width	0.94*	0.24	0.17
Blue Scales	0.14	0.94*	0.15
Blue Area	0.43	0.79*	0.21
Blue Intensity	0.19	0.24	0.95*
Cumulative variance	59.4%	82.2%	95.5%

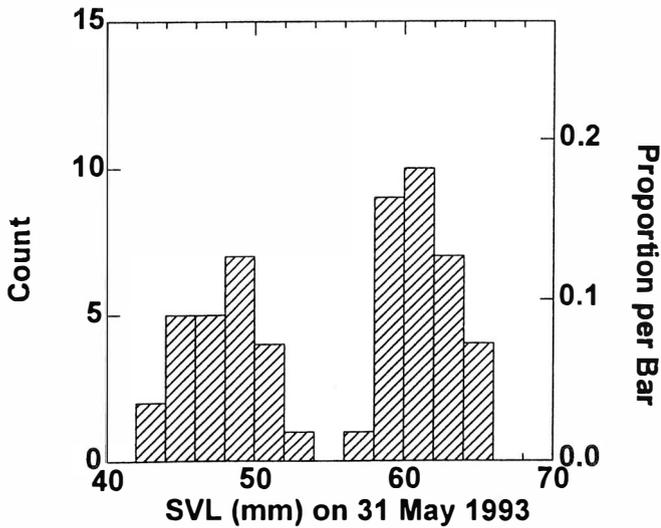


FIG. 1. Frequency distribution of male snout-vent length in 1993.

enough to be sexually mature (Ballinger & Ketels, 1982). Excluding individuals missing some morphological measurements, my sample sizes for the selection analyses were 30 males in 1992 and 55 in 1993.

Males were generally smaller than females (males: mean  $\pm$  SE 55.3  $\pm$  1.0 mm in 1993; range 42.7 mm to 65.1 mm in 1993; maximum 65.1 mm from 1991-94; potentially reproductive females: mean  $\pm$  SE 58.6 mm  $\pm$  1.4 mm in 1993; range 45.2 mm to 73.9 mm in 1993, maximum 74.3 mm from 1991-94). The distribution of male size was bimodal in both years (Fig. 1). Based on a discontinuity in the size distribution, males at least 56 mm SVL were regarded as large and males less than 54 mm as small. Of the 55 males included in the 1993 selection study, 31 were large and 24 were small. I

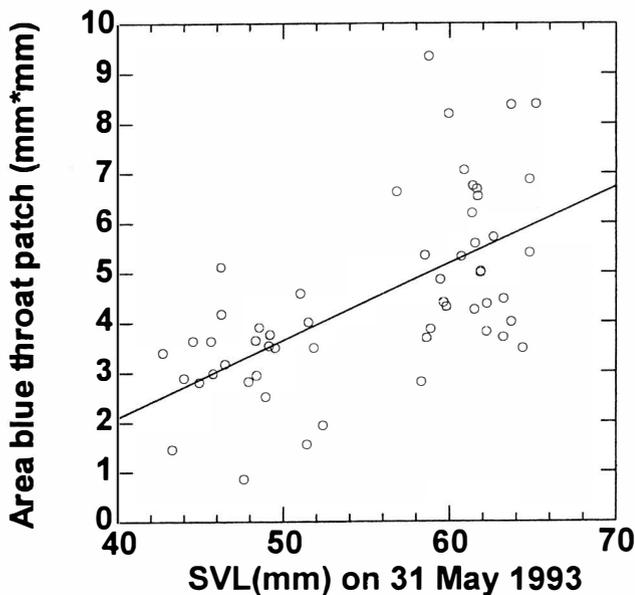


FIG. 2. Area of the blue throat patch relative to snout-vent length in males of *Sceloporus virgatus* in 1993. The regression line is  $y = 0.15x - 4.08$ ,  $r^2 = 0.38$ ,  $n = 55$ ,  $P < 0.0001$ .

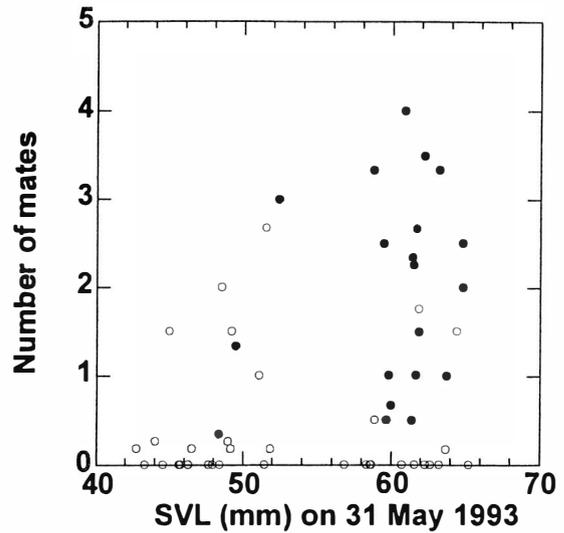


FIG. 3. Male mating success relative to snout-vent length in 1993. Females at least 45 mm SVL were regarded as reproductive. Males with at least one basking partner are shown with closed symbols.

analysed the 1993 data separately for the large and small classes of males. The 1992 data were not analysed separately for two separate size classes because the sample size was smaller and the bimodality less pronounced than in 1993.

Although the blue ventral patch of *S. virgatus* is much smaller than that of most congeners (Smith, 1939), the amount and intensity of blue colouration was highly variable in this population. The brightness of the colour spanned the entire range of the colour standards (cobalt blue dilutions, No. 168 in Smithe, 1975), with a few individuals lighter than the lightest standard. The number of blue scales in a patch ranged from 1 to 19 (mean 8.5, median 8, standard deviation 3.7). The area of the blue throat patch ranged from 0.9 mm<sup>2</sup> to 9.4 mm<sup>2</sup> (mean = 4.5 mm<sup>2</sup>; median = 4.0 mm<sup>2</sup>; SD = 1.8).

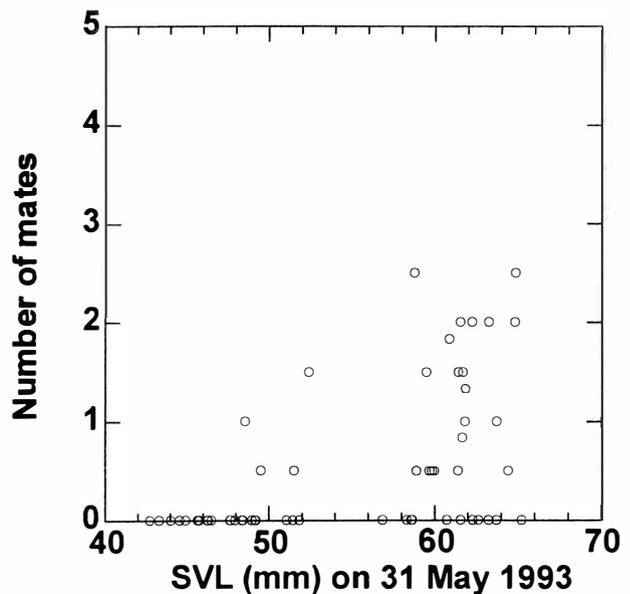


FIG. 4. Male mating success relative to snout-vent length in 1993. Females at least 52 mm SVL were regarded as reproductive.

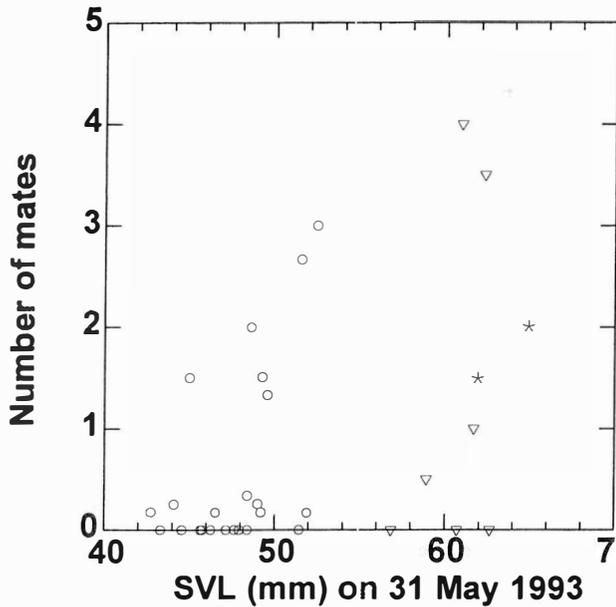


FIG. 5. Mating success relative to snout-vent length for males of known age in 1993. One-year-olds are shown with circles, two-year-olds with triangles, and three-year-olds with asterisks. Females at least 4.5 mm SVL were regarded as reproductive.

The size of the blue throat patch was significantly correlated with body size (Fig. 2), but only 38% of the variation in patch size could be explained by variation in SVL.

In both 1992 and 1993, three principal components (PCs) accounted for more than 90% of character variance (Table 1). These three PCs were readily interpretable as overall body size, blue patch size and intensity of blue colouration. Similar principal components were found when small and large 1993 males were analysed separately.

No significant autocorrelation was found between male home range overlap and any of the principal components (size PC: Moran statistic  $I=0.05$ , NS; patch size PC:  $I=-0.07$ , NS; colour intensity PC:  $I=0.04$ , NS). That is, there was no tendency for males with overlapping home ranges to be unusually similar or dissimilar in body size, patch size or blue colour intensity.

#### VIABILITY SELECTION

Of the males for which all morphological data were available, 36.7% (11 out of 30) survived from 1992 to 1993 and 25.5% (14 out of 55) survived from 1993 to 1994. I did not compare survivorship rates between the years statistically because I did not search the study area as frequently in 1994 as in 1993.

For 1992-93, I found no significant association between survivorship (viability) and any principal component. The range of body sizes was similar for males that survived to the following year and for males that did not survive. However, most survivors had a body size PC score greater than 0. For 1993-94, patch size and colour intensity were not significantly associ-

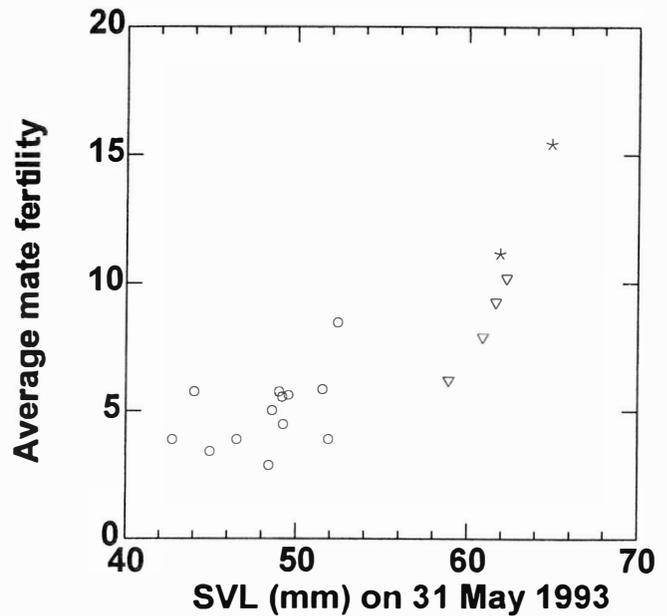


FIG. 6. Average mate fertility relative to snout-vent length for males of known age in 1993. One-year-olds are shown with circles, two-year-olds with triangles, and three-year-olds with asterisks. Only males with at least one mate are included. Females at least 4.5 mm SVL were regarded as reproductive.

ated with survivorship. Within the group of large males, there was a highly significant tendency for the largest males to have higher survivorship (logistic regression coefficient =  $1.33 \pm 0.45$  SE,  $G=6.889$ ,  $P < 0.01$ ; 10 of 31 large males survived to 1994). No relationship between size and survivorship was found in the group of small males (4 of 24 small males survived to 1994).

#### SEXUAL SELECTION AND MATE FERTILITY SELECTION

There were no significant or nearly significant sexual selection or mate fertility selection gradients on the size of the blue patch or the intensity of the colouration. Thus, there was no evidence for directional selection on blue colouration in *S. virgatus*, in either year or within either size class.

The estimates of mating success had a skewed distribution, with most males having low success and a few males having much greater success. When all males were considered together, larger body size was significantly associated with greater mating success in both years (1992:  $\beta' = 0.45 \pm 0.16$  SE;  $0.005 < P < 0.01$ ; 1993:  $\beta' = 0.37 \pm 0.13$  SE;  $0.005 < P < 0.01$ ), but there was no significant association between male size and mate fertility. A scatterplot of the 1993 data suggested a size beyond which greater size was not associated with enhanced mating success (Fig. 3). When large and small males were considered separately, no significant sexual selection or mate fertility gradients were found on the body size principal component calculated from large males alone. In the data set of small males, there was a highly significant tendency for larger males to have more mates ( $\beta' = 0.73 \pm 0.26$  SE;  $0.005 < P < 0.01$ ), but

TABLE 2. Kendall's partial correlation coefficient (T) between male reproductive fitness (mating success or mate fertility) and SVL (controlling for age) or age (controlling for SVL). All potentially reproductive females (45 mm SVL) were included. \*  $P < 0.05$ .

Fitness component	n	SVL (controlling for age)	Age (controlling for size)
		T	T
Mating success			
1992	19	0.0871	0.0700
1993	33	0.2545*	0.0208
Mate fertility			
1992	13	-0.0184	0.3521
1993	19	0.3927*	0.4028*

there was no significant relationship between size and mate fertility.

I repeated the 1993 selection analysis using only females that were almost certainly reproductive ( $\geq 52$  mm SVL on 31 May). Results were similar to those described above based on all potentially reproductive females ( $\geq 45$  mm SVL). There was no significant sexual selection or mate fertility selection on blue colouration. There was also no significant relationship between male body size and mate fertility. When all males were considered together, there was very strong sexual selection for larger males (Fig. 4;  $\beta^1 = 0.64 \pm 0.15$  SE,  $P < 0.001$ ). Within the group of large males, there was no significant selection on male body size. Within the group of small males, larger males had higher mating success ( $\beta^1 = 1.20 \pm 0.51$  SE,  $0.01 < P < 0.02$ ). The yearling females (approximately 45-52 mm SVL) had been assigned as mates of males of all sizes, so the selection results were essentially the same whether these females were included or not.

When the effects of age were controlled for with partial correlation analysis, body size was significantly positively correlated with male mating success and mate fertility in 1993 (Figs. 5, 6), but not in 1992 (Table 2). When the effects of size were controlled for with partial correlation analysis, age was not significantly correlated with male mating success in either 1992 or 1993 (Table 2, Fig. 5). In 1993 there was a significant positive correlation of age with average mate fertility (Fig. 6), and there was a corresponding non-significant trend in 1992 (Table 2).

#### DISCUSSION

Larger males tended to have more mates, but this does not necessarily imply continual directional selection for indefinitely larger males. Only the very smallest males were at a mating disadvantage. This relationship between male size and mating success is similar to that reported for *Crotaphytus collaris* (Baird *et al.*, 1996).

Traits other than the morphological characters considered in this study are probably most important in determining male fitness. The closest category of male-female spatial proximity was termed a basking partnership (Abell, 1997). Males that maintained at least one basking partnership usually had relatively high values of mating success (Fig. 2) and average mate fertility. The relationship between basking partnerships and mating success was not due simply to the fact that males in the analysis were assigned as mates of their female basking partners. Males with basking partners apparently were successful at obtaining additional mates.

Larger (and hence older) males were most successful at maintaining basking partnerships (Fig. 3; Abell, 1997). Small males were seldom observed to engage in such relationships. Males sometimes maintained basking partnerships in more than one year, but I do not have enough data to estimate the frequency of long-term partnerships. Of the five males known to have basking partnerships in 1992, three survived to 1993. One of them re-established a basking partnership with the same female. The partners of the other two males did not survive to 1993. One of these males established basking partnerships with two different females in 1993 and the other male was apparently a roving, non-territorial individual in 1993. These data indicate high variability in male-female interactions within and between years.

Age was not associated with the number of mates in either year. This result is similar to that of Olsson & Shine (1996) for the sand lizard *Lacerta agilis*, also a species in which females average larger than males. However, older males did mate with larger, and hence more fertile, females. Mate choice experiments by Fitzgerald (1982) showed that males of *S. virgatus* choose the larger female when presented with two fertile females as potential mates.

The relationship between female size and clutch size is stronger in *S. virgatus* than in most other *Sceloporus* species (Abell, unpubl. obs.). For example, in four studies of *S. jarrovi* the slope of the regression line between female SVL and litter size ranged from 0.24 to 0.31, whereas in five studies of *S. virgatus* the slope of the regression line between female SVL and clutch size ranged from 0.27 to 0.64 ( $P < 0.05$  for all regressions; *S. jarrovi*: slope 0.28 in Goldberg, 1971; 0.24 in Tinkle & Hadley, 1973; 0.31 and 0.29 in Ballinger, 1979; 0.26 in Ruby & Dunham, 1984; *S. virgatus*: 0.64 for data extracted from Cole, 1963; 0.44, 0.46 and 0.53 in Vinegar, 1975; 0.64, 0.43 and 0.53 for data extracted from Smith, 1977; 0.40 in Smith *et al.*, 1995; 0.27 and 0.59 in Abell, in press). The sharp increase in clutch size for a relatively small increase in maternal size suggests strong fecundity selection for large females in *S. virgatus*. The present study shows that sexual selection on male size is weak in *S. virgatus*, a species with females larger than males. In contrast, male reproductive success was closely associated with body size in one study of *S. jarrovi*, a species with males larger than fe-

males (Ruby, 1981). Another study of *S. jarrovi* found significant sexual selection for larger males in the higher elevation, higher density population but not in the lower elevation, lower density population (Dixon, 1993). These results provide tentative support for a sexual selection-fecundity selection trade-off as an explanation of sexual size dimorphism in *Sceloporus* lizards. Additional studies of the relationship between body size and fitness are needed for a rigorous comparative analysis.

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#### REFERENCES

- Abell, A. J. (1997). Estimating paternity with spatial behaviour and DNA fingerprinting in the striped plateau lizard, *Sceloporus virgatus* (Phrynosomatidae). *Behav. Ecol. Sociobiol.* **41**, 217-226.
- Abell, A. J. (1998). Reproductive and post-reproductive hormone levels in the lizard *Sceloporus virgatus*. *Acta Zool. Mex.* **74**, 43-57.
- Abell, A. J. (in press). Variation in clutch size and offspring size relative to environmental conditions in the lizard, *Sceloporus virgatus*. *J. Herpetol.*
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227-267.
- Anderson, R. A. & Vitt, L. J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* **84**, 145-157.
- Arnold, S. J. & Duvall, D. (1994). Animal mating systems: a synthesis based on selection theory. *Am. Nat.* **143**, 317-348.
- Arnold, S. J. & Wade, M. J. (1984a). On the measurement of natural and sexual selection: theory. *Evolution* **38**, 709-719.
- Arnold, S. J. & Wade, M. J. (1984b). On the measurement of natural and sexual selection: applications. *Evolution* **38**, 720-734.
- Arnqvist, G. (1992). Spatial variation in selective regimes: sexual selection in the water strider, *Gerris odontogaster*. *Evolution* **46**, 914-929.
- Arnqvist, G., Thornhill, R. & Rowe, L. (1997). Evolution of animal genitalia: morphological correlates of fitness components in a water strider. *J. Evol. Biol.* **10**, 613-640.
- Baird, T. A., Acree, M. A. & Sloan, C. L. (1996). Age and gender-related differences in the social behavior and mating success of free-living collared lizards, *Crotaphytus collaris*. *Copeia* **1996**, 336-347.
- Ballinger, R. E. (1979). Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* **60**, 901-909.
- Ballinger, R. E. & Ketels, D. J. (1983). Male reproductive cycle of the lizard *Sceloporus virgatus*. *J. Herpetol.* **17**, 99-102.
- Bull, C. M. & Pamula, Y. (1996). Sexually dimorphic head sizes and reproductive success in the sleepy lizard *Tiliqua rugosa*. *J. Zoology* **240**, 511-521.
- Carroll, S. P. & Salamon, M. H. (1995). Variation in sexual selection on male body size within and between populations of the soapberry bug. *Anim. Behav.* **50**, 1463-1474.
- Censky, E. J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva plei*. *Behaviour* **132**, 529-557.
- Cole, C. J. (1963). Variation, distribution, and taxonomic status of the lizard *Sceloporus undulatus virgatus* Smith. *Copeia* **1963**, 413-425.
- Dixon, K. A. (1993). *Microgeographic variation in sexual selection in the mountain spiny lizard, Sceloporus jarrovi*. PhD dissertation, University of Chicago.
- Dunham, A. E., Miles, D. B. & Reznick, D. N. (1988). Life history patterns in squamate reptiles. In *Biology of the reptilia, volume 16*, 441-522. Gans, C. and Huey, R. B. (Eds). New York: Alan Liss.
- Fairbairn, D. J. & Preziosi, R. F. (1996). Sexual selection and the evolution of sexual size dimorphism in the water strider, *Aquarius remigis*. *Evolution* **50**, 1549-1559.
- Fisher, M. & Muth, A. (1989). A technique for permanently marking lizards. *Herpetol. Rev.* **20**, 45-46.
- Fitch, H. S. (1978). Sexual size differences in the genus *Sceloporus*. *Univ. Kansas Sci. Bull.* **51**, 441-461.
- Fitzgerald, K. T. (1982). *Mate selection as a function of female body size and male choice in several lizard species*. PhD dissertation, University of Colorado.
- Flury, B. & Riedwyl, H. (1988). *Multivariate statistics: a practical approach*. London: Chapman and Hall.
- Goldberg, S. R. (1971). Reproductive cycle of the ovoviparous iguanid lizard *Sceloporus jarrovi* Cope. *Herpetologica* **27**, 123-131.
- Harvey, A. W. (1990). Sexual differences in contemporary selection acting on size in the hermit crab *Clibanarius digueti*. *Am. Nat.* **136**, 292-304.
- Hedrick, A. V. & Temeles, E. J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol. Evol.* **4**, 136-138.

- Hews, D. K. (1990). Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. *Evolution* **44**, 1956-1966.
- Hosmer, D. W. Jr & Lemeshow, S. (1989). *Applied logistic regression*. New York: John Wiley and Sons.
- Howard, R. D. & Kluge, A. G. (1985). Proximate mechanisms of sexual selection in wood frogs. *Evolution* **39**, 260-277.
- Jones, S. M. & Ferguson, G. W. (1980). The effect of paint marking on mortality in a Texas population of *Sceloporus undulatus*. *Copeia* **1980**, 850-854.
- Koenig, W. D., Albano, S. S. & Dickinson, J. L. (1991). A comparison of methods to partition selection acting via components of fitness: Do larger male bullfrogs have greater hatching success? *J. Evol. Biol.* **4**, 309-320.
- Lande, R. & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution* **37**, 1210-1226.
- Madsen, T. & Shine, R. (1994). Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution* **48**, 1389-1397.
- Markow, T. A., Bustoz, D. & Pitnick, S. (1996). Sexual selection and a secondary sexual character in two *Drosophila* species. *Anim. Behav.* **52**, 759-766.
- Olsson, M. & Shine, R. (1996). Does reproductive success increase with age or with size in species with indeterminate growth? A case study using sand lizards (*Lacerta agilis*). *Oecologia* **105**, 175-178.
- Perry, G. (1996). The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Can. J. Zool.* **74**, 1238-1245.
- Price, T. D. (1984). The evolution of sexual size dimorphism in Darwin's finches. *Am. Nat.* **121**, 500-518.
- Ruby, D. E. (1981). Phenotypic correlates of male reproductive success in the lizard, *Sceloporus jarrovi*. In *Natural selection and social behavior*, 96-107. Alexander, R. D. and Tinkle, D. W. (Eds). New York: Chiron.
- Ruby, D. E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* **40**, 272-280.
- Ruby, D. E. & Dunham, A. E. (1984). A population analysis of the ovoviparous lizard *Sceloporus jarrovi* in the Pinaleño mountains of southeastern Arizona. *Herpetologica* **40**, 425-436.
- Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia* **1994**, 326-346.
- Siegel, S. & Castellan, N. J. Jr. (1988). *Nonparametric statistics for the behavioral sciences*. 2nd edition. New York: McGraw-Hill.
- Sigmund, W. R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. *J. Herpetol.* **17**, 137-143.
- Simon, C. A. & Bissinger, B. E. (1983). Paint marking lizards: does the color affect survivorship? *J. Herpetol.* **17**, 184-186.
- Smith, D. C. (1977). *Interspecific competition and the demography of two lizards*. PhD dissertation, University of Michigan.
- Smith, G. R., Ballinger, R. E. & Rose, B. R. (1995). Reproduction in *Sceloporus virgatus* from the Chiricahua Mountains of southeastern Arizona with emphasis on annual variation. *Herpetologica* **51**, 342-349.
- Smith, H. M. (1939). The Mexican and Central American lizards of the genus *Sceloporus*. *Field Museum of Nat. Hist. Zool. Ser.* **26**, 1-397.
- Smithe, F. B. (1975). *Naturalist's color guide, part II*. New York: American Museum of Natural History.
- Sokal, R. R. & Oden, N. L. (1978a). Spatial autocorrelation in biology. 1. Methodology. *Biol. J. Linn. Soc.* **10**, 199-228.
- Sokal, R. R. & Oden, N. L. (1978b). Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. *Biol. J. Linn. Soc.* **10**, 229-249.
- Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. In *Lizard ecology: studies of a model organism*, 169-204. Huey, R. B., Pianka, E. R. and Schoener, T. W. (Eds). Cambridge: Harvard University Press.
- Stamps, J. A., Losos, J. B. & Andrews, R. M. (1997). A comparative study of population density and sexual size dimorphism in lizards. *Am. Nat.* **149**, 64-90.
- Tinkle, D. W. & Hadley, N. F. (1973). Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. *Copeia* **1973**, 272-277.
- Trivers, R. L. (1976). Sexual selection and resource-acquiring abilities in *Anolis garmani*. *Evolution* **30**, 253-269.
- Vinegar, M. B. (1975). Demography of the striped plateau lizard, *Sceloporus virgatus*. *Ecology* **56**, 172-182.
- Wade, M. J. & Kalisz, S. (1989). The additive partitioning of selection gradients. *Evolution* **43**, 1567-1569.
- Ward, P. I. (1988). Sexual selection, natural selection, and body size in *Gammarus pulex* (Amphipoda). *Am. Nat.* **131**, 348-359.