Sexual dimorphism in the lizard *Sceloporus siniferus*: support for the intraspecific niche divergence and sexual selection hypotheses

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Abstract. Two hypotheses that attempt to explain the evolution of sexual size dimorphism in vertebrates are those of: (1) sexual selection and (2) intraspecific niche divergence. Sexual selection is most often attributed to female mate selection or male/male competition for females and results in variation in morphological characteristics (e.g., body size, secondary sex traits). Intraspecific niche divergence may occur when the sexes differ in dietary or habitat requirements and can lead to dietary and trophic morphological differences (e.g., internal organs etc.). In this study, we examined diet composition, trophic morphology and sexual dimorphism in the lizard *Sceloporus siniferus* from Huatulco, Mexico. Results support the conclusion that the biased size dimorphism in favour of males (male mean body mass 6.72 g vs. female mean body mass 5.67 g) is a result of sexual selection; however, trophic morphological differences, such as the larger gastrointestinal system of females and differences in diet composition between the sexes may be the result of intraspecific niche divergence and appear to be adaptations for increased nutritional acquisition associated with the elevated reproductive energy requirements of females. These results support the conclusion that both sexual selection and intraspecific niche divergence selective processes occur in *S. siniferus*.

Key words. Squamata, Phrynosomatidae, sexual dimorphism, intraspecific divergence, sexual selection, foraging strategies.

Introduction

Sexual dimorphism is widespread throughout the animal kingdom and has been described for many taxa (Darwin 1871, Alexander et al. 1978, Anderson & Vitt 1990). Two competing hypotheses have been proposed; (1) that sexual size dimorphism (SSD) in the form of anatomical differences between the sexes has evolved due to sexual selection, and (2) that such differences have evolved due to intraspecific niche divergence (Slatkin 1984, Shine 1989). To date, most researchers have concluded that SSD has arisen primarily through the sexual selection process (Selander 1972, Trivers 1976, Clutton-Brock et al. 1977, Alexander et al. 1978, Anderson & Vitt 1990), where variance in reproductive success between competing individuals of the same gender results in selection for specific adult body sizes and morphologies (Shine 1989). Research on the degree to which males exceed females in adult body size has shown body size to be highly correlated with the intensity of male–male competition for females (Selander 1972, Trivers 1976, Clutton-Brock et al. 1977, Alexander et al. 1978).

In contrast, the niche divergence hypothesis proposes that each gender adapts to different ecological niches and therefore sexual dimorphic differences in body size and/or morphology evolve due to ecological influences (Schoener 1967, Shine 1989). Niche divergence is hypothesised to evolve when the sexes differ in nutritional requirements or select different habitats. Despite the extensive literature on causal mechanisms involved in the evolution of SSD, the niche divergence hypothesis has received little attention. Although the niche divergence hypothesis is potentially applicable to all types of animals, it has been applied primarily to birds (Selander 1972, Partridge & Green 1985), and studies on other taxa have placed heavy emphasis on sexual selection and either ignored the niche divergence hypothesis or dismissed it (Woolbright 1983, Vitt & Cooper 1986). Most studies examining dimorphism in the trophic morphology of lizards have considered gape size or head width (Carothers 1984). However, these characteristics might be misleading, as dimorphism in trophic structures thought to have evolved for ecological reasons (i.e., food type and quality) may influence reproductive behaviour (e.g., male combat) and success and

would therefore not qualify as evidence of niche divergence (Selander 1972).

Female reproductive strategies have been postulated to have an effect on sexual size dimorphism among members of the genus *Sceloporus* (Fitch 1978), and elevated dietary requirements in reproducing females are thought to be directly related to the nutrients needed for egg production (Shine 1989). It is generally known that females require more energy for gametogenesis than males, as oogenesis is more costly than spermatogenesis, although males in some cases are thought to expend more energy on reproductive effort, such as searching for mates, courtship and in some cases parental care (Ballinger & Clark 1973). In addition, it has been hypothesised that sexes living in different habitats experience different ecological conditions, including food availability and quality, which may be related to SSD (Butler et al. 2000). A number of studies on lizards have demonstrated sexual segregation in food resource utilisation (Schoener 1967, Stamps 1977, Powell & Russell 1983). If natural selection were operating primarily through dietary or habitat divergence, then in addition to divergence in body size related to sexual selection, there may be shifts in the shape or relative size of other trophic morphological apparatuses, not related to mate choice (Selander 1972). Such shifts would not be predicted by sexual selection, except in cases where the shape or size of the trophic structure influenced mate competition and selection.

The species used in the current study was the phrynosomatid lizard, *Sceloporus siniferus* (Phrynosomatidae). This species has not been extensively studied and data on its ecology are lacking. However, other insectivorous members of this lizard family that have been studied were generally found to be territorial (Stamps 1977), with males being larger than females (Fitch 1981). This sexual dimorphism has been attributed to polygyny and therefore sexual selection, even though dietary niche partitioning has been identified (Carothers 1984). As a result, the primary purpose of the current study was to analyse gender differences in diet composition and trophic morphology to test whether the niche divergence hypothesis was the primary causal factor influencing trophic SSD in *S. siniferus*.

Materials and methods

All specimens were collected from El Parque Nacional Huatulco in Oaxaca, Mexico (15°39'12" N, 96°06'30" W) (Chavez et al. 2001). Collection occurred annually in the wet season between May 2000 and June 2005 using "noosing" or "stunning with rubber elastic bands". "Noosing" involved attaching a noose of thread to the end of a small fishing pole and slipping it over the neck of the lizard. Rubber elastic bands were shot at lizards to briefly stun them so that they could be captured by hand. Once captured, the lizards were sexed and weighed using a Pesola spring scale to the nearest 0.01 g and snout–vent length (SVL) was measured with vernier callipers (± 0.1 mm). Lizards were euthanised by placing them in a freezer, subsequently injected with formalin and preserved in 70% ethanol.

Lizards were dissected and the entire digestive system from oesophagus to anus was removed. Stomach contents were placed in Petri dishes and examined under a microscope (Jena-10X). Prey items were classified to the lowest taxonomic level possible (typically family), except in the case of lepidopteran, hemipteran and coleopteran larvae, which were classified to order (Borror & White 1970, Arnett & Jacques 1981, Vazquez 1987). Plant material was not classified. The numbers of individuals in each order or family were recorded and the wet weight of each taxonomic group was measured to the nearest 0.0001 g, as was non-identifiable organic matter. Intestinal contents were then discarded and the wet weight of the entire empty gastrointestinal system (oesophagus, stomach, intestines) was measured to the nearest 0.0001 g.

The weight of each order or family of prey, the number of individuals in each group, and the frequency of occurrence of each group were used to calculate the Alimentary Importance Value (AIV). The AIV calculation included: (1) the weight of each order or family of prey divided by the total weight of all prey items found over the study period, (2) the number of individuals in each order or family of prey divided by the total number of all prey items found over the study period, and (3) the number of stomachs containing a particular order or family divided by the total number of lizards collected. These three values were subsequently summed to provide an AIV for each prey group over the entire period of data collection (Acosta 1982). AIV was calculated separately for each sex and a Simpson's Diversity Index ($1/p_i^2$) was subsequently calculated to compare the diets of each sex and to examine diet breadth (Krebs 1972).

Student's t-tests were performed on body mass and SVL to assess differences in sexual size dimorphism (SSD). An analysis of covariance was then used to compare the masses of the sexes, while controlling for SVL. The weights of the gastrointestinal system for both sexes were compared using an analysis of covariance to control for body mass. The mean number of prey consumed by each sex was calculated as was the mean weight of stomach contents. Data were tested for normality, numbers of prey in each stomach were compared using a Mann-Whitney test, and the weights of stomach contents were compared using a Student's t-test.

Results

Male and female *S. siniferus* had mean body masses of 6.72 ± 0.29 g (± SE, n = 55) and 5.67 ± 0.24 g (± SE, n = 39), respectively, and male lizards were significantly heavier than females (t = 2.74, df = 74, p = 0.008). Similarly, male and female lizards had SVLs of 56.55 ± 0.96 mm (± SE) and 54.78 ± 0.61 mm (± SE), respectively, and male lizards were significantly longer than females (t = 2.81, df = 85, p = 0.006). However, there was no difference in SVL adjusted body mass between the sexes (Table 1, Fig. 1). Analysis of covariance showed that female lizards had significantly heavier
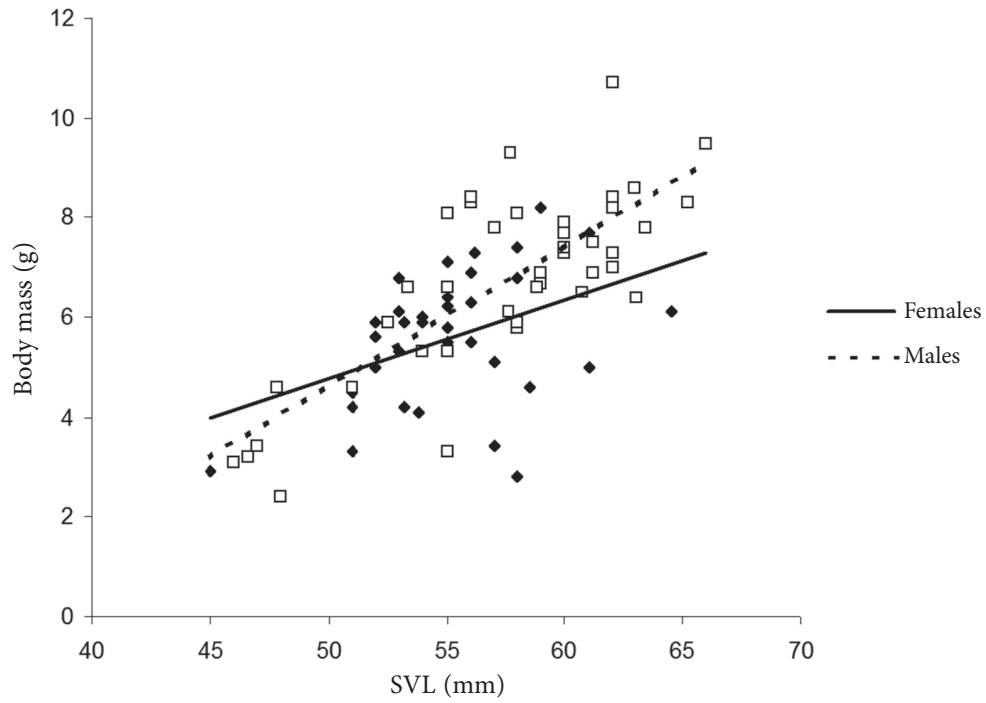
Figure 1. Sexual dimorphism in body mass relative to body length in *S. siniferus* lizards. Males are the heavier sex, but when controlling for body length, there was no difference in the relative body mass of the two sexes.
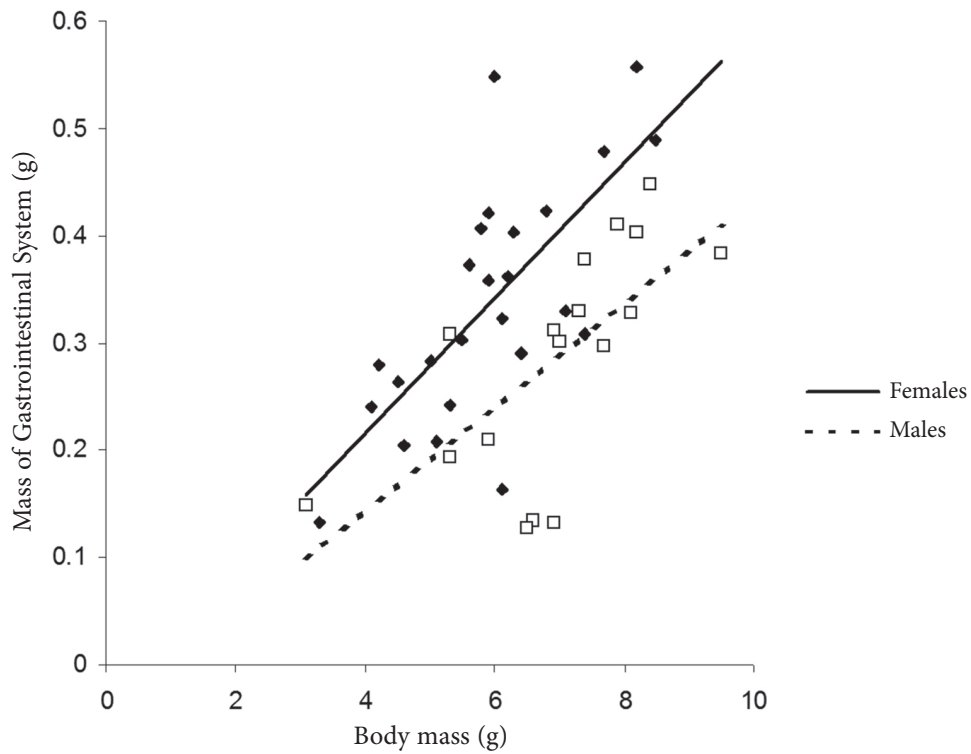
Figure 2. Sexual dimorphism in the mass of trophic morphologies relative to body mass in *S. siniferus* lizards. Controlling for body mass, females had the greater gastrointestinal system weights.

Table 1. Means of body mass and gastrointestinal system weights for male and female *Sceloporus siniferus* lizards and the results of analyses of covariance on sexual size dimorphism using snout–vent length as the covariate for body mass and body mass as the covariate for gastrointestinal system weight.

Mass	Male	Female	df	SS	F	P
Body (g)	6.72	5.67	1	5.354	3.54	0.06
Gastrointestinal system (g)	0.28	0.33	1	0.105	16.43	0.0002

Table 2. Stomach content details for invertebrate prey of male (n = 55) and female (n = 39) *Sceloporus siniferus* lizards from Hautulco, Mexico. Weight (g), abundance, frequency of occurrence, and importance value for each prey type observed in the stomachs of both sexes over the course of the study period.

Prey group	Weight (g)		Abundance		Frequency of occurrence		Importance value	
	Males	Females	Males	Females	Males	Females	Males	Females
Formicidae	0.14	0.01	69	24	9	4	0.23	0.12
Plant matter	0.32	0.04	7	5	7	5	0.19	0.13
Kalotermatidae	1.43	1.78	874	1022	17	8	1.13	1.34
Gryllidae	0.42	0.12	3	3	2	3	0.12	0.09
Lepidoptera larva	2.41	5.61	38	72	20	16	0.83	1.19
Coleoptera larva	0.09	0.04	4	1	1	1	0.04	0.03
Carabidae	0.003	0.04	1	1	1	1	0.02	0.03
Protentomidae	n/a	0.06	n/a	1	n/a	1	n/a	0.03
Termitidae	0.31	n/a	549	n/a	5	n/a	0.50	n/a
Vespidae	0.20	n/a	2	n/a	1	n/a	0.06	n/a
Hemiptera	0.10	n/a	5	n/a	3	n/a	0.07	n/a
Apidae	0.03	n/a	3	n/a	1	n/a	0.03	n/a

gastrointestinal systems than males (Table 1, Fig. 2); however, the slopes of the lines-of-best fit were not significantly different (p > 0.05).

The mean number of prey items (± SE) per stomach in male lizards was 40.16 ± 13.3, while females had a mean number of prey items of 32.34 ± 13.53 per stomach. No significant difference in the mean number of prey items per stomach was found (U = 722.5, p = 0.637, n = 79). Male and female lizards had mean stomach content weights of 0.125 ± 0.021 g (± SE) and 0.257 ± 0.047 g (± SE), respectively, and female mean stomach contents were significantly heavier than those of the males (t = 2.37, df = 66, p = 0.034). The arboreal termite family Termitidae was only present in the male diets, while Lepidoptera larvae and the terrestrial termite family Kalotermatidae had greater Alimentary Importance Values in the female diets (Table 2, Fig. 3), inferring differences in wet season habitat utilization between the sexes. In addition, male lizards generally had more diverse diets than females, with a Simpson's Diversity Index of 2.25 (n = 55) compared to 1.22 for females (n = 39).

Discussion

The data support the conclusion that intraspecific niche divergence has occurred in *S. siniferus* and is a primary factor that explains the evolution of trophic sexual size dimorphism (SSD) in this species. Differences between the sexes in diet, inferred wet season habitat utilisation, and gastrointestinal/body mass ratios are not likely explained by the sexual selection hypothesis, as each of these parameters would not be changed by mate competition. These differences between genders may have been selected for as a result of the higher nutritional requirements associated with female reproduction and/or the need to minimize food competition between the sexes. In contrast, male-biased differences in body mass and snout–vent length are likely the result of sexual selection and male–male competition for females, and the fact that male *S. siniferus* are the larger sex suggests that this species is polygynous. One indicator of a polygynous mating system is the difference in body size between the sexes, where males are larger than females, and greater degrees of polygyny are highly correlated with a greater degree of male-biased sexual dimorphism (Alexander et al. 1978, Daly & Wilson 1978). This occurs because, as competition for females increases, advantage generally shifts to larger males (Trivers 1976). Males of the lizard family Phrynosomatidae are generally territorial and their degree of polygyny has been correlated with sexual size dimorphism (Stamps 1977, 1983). Another factor that supports the polygyny hypothesis in *S. siniferus* is the fact that males have a more diverse diet than females.

Males have a Simpson's Index of 2.25 for diet, whereas the index for females is only 1.22. If males actively search for females, they may come across a wider range of prey types. However, another possible explanation for differences in dietary breadth may be differences in habitat. Habitat divergence is supported by the fact that male diets contain termites of the family Termitidae, which are generally arboreal (Creffield 1991), whereas the family Kalotermatidae found more often in the diets of females inhabit dead wood, generally found on or near the ground (Creffield 1991). This indicates that males have more elevated perching sites than females and that habitat divergence occurs in this species. However, further research on the mating behaviour of *S. siniferus* is required before this conclusion can be confirmed.

Despite the fact that males are the larger sex, females of *S. siniferus* have larger gastrointestinal systems, which is an example of trophic dimorphism. This trait in females may have evolved as an adaptation to enable the female to consume larger prey to meet higher nutrient requirements associated with female reproduction. Other studies have found that males and females differ in trophic morphological structures because of differences in diet and such divergence has been postulated to reflect the specific nutritional requirements for reproduction in females, as female parental investment is generally greater than that of the male (Shine 1989).

Although there was no significant difference in the number of prey consumed by either sex, female lizards had significantly heavier stomach contents and consumed larger prey such as lepidopteran larvae. Consuming larger prey would allow females to meet nutritional requirements and limit expending extra energy chasing numerous small prey (Skoczylas 1969, Norberg 1977). This observation may also be an adaptation to the habitat divergence, if lepidopteran larvae occur more frequently in the female habitat. Future research should focus on sampling prey species in both male and female habitats as suggested by Vitt & Zani (1998) for other insectivorous species.

Intraspecific niche divergence has not been proposed often as a cause of sexual size dimorphism (SSD), possibly due to perceived difficulties in testing for its occurrence (Shine 1989). Many researchers examining trophic dimorphism in lizards have examined structures such as head width and gape size, which are associated with sexual selection and possibly physical combat for mates (Slatkin 1984). In contrast, our data support the conclusion that the analysis of internal structures such as the gastrointestinal system, which are not influenced by sexual selection, can identify instances where intraspecific niche divergence in food and habitat specialisation has influenced the evolution of sexually dimorphic traits. The results suggest that both sexual selection and niche divergence influence the evolution of different morphologies in *S. siniferus* and that the two causal factors are not mutually exclusive.
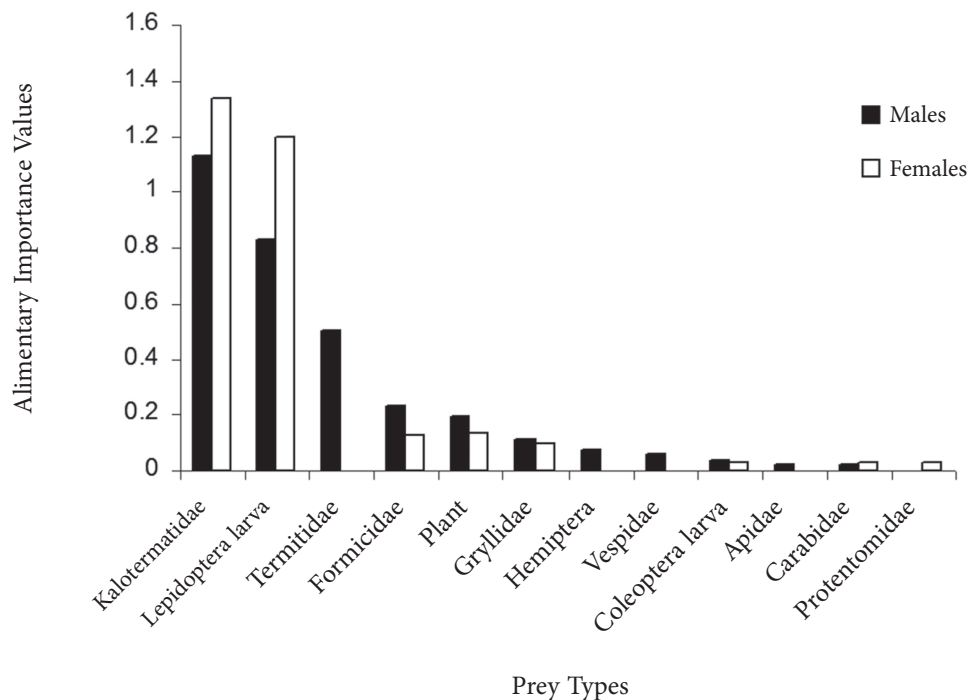

Figure 3. Alimentary importance values for prey items found in male and female *S. siniferus* stomachs between May 2000 and June 2005.

Acknowledgements

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