

Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles

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Synopsis Sexual dimorphism in phenotypic traits associated with the use of resources is a widespread phenomenon throughout the animal kingdom. While ecological dimorphisms are often initially generated by sexual selection operating on an animal's size, natural selection is believed to maintain, or even amplify, these dimorphisms in certain ecological settings. The trophic apparatus of snakes has proven to be a model system for testing the adaptive nature of ecological dimorphisms because head size is rarely under sexual selection and it limits the maximum ingestible size of prey in these gape-limited predators. Significantly less attention has been paid to the evolution of ecological dimorphisms in lizards, however, which may be due to the fact that lizards' feeding apparatus can be under both sexual and natural selection simultaneously, making it difficult to formulate clear-cut hypotheses to distinguish between the influences of natural and sexual selection. In order to tease apart the respective influences of natural selection and sexual selection on the feeding apparatus of squamates, we take an integrative approach to formulate two hypotheses for snakes and lizards, respectively: (1) For gape-limited snakes, we predict that natural selection will act to generate differences in maximum gape, which will translate into differences in maximum ingestible prey size between the sexes. (2) For lizards which mechanically reduce their prey, we predict that the degree of dimorphism in head size should be positively correlated to the degree of dimorphism in bite force which, in turn, should be correlated to dimorphism in aspects of size or hardness of prey. Finally, we predict that functional differences in the feeding apparatus of these animals will also be linked with differences in sex-based feeding behavior and with selection of prey.

Introduction

Sexual dimorphism in phenotypic traits associated with the use of resources is a widespread phenomenon throughout the animal kingdom (Darwin 1871; Selander 1972; Ralls 1976; Slatkin 1984; Shine 1989, 1991; Cullum 1998; Myersterud 2000; Temeles et al. 2000; Lailvaux et al. 2003; Heatwole et al. 2005; Vincent 2006). As discussed in the introduction to this symposium (Lailvaux and Vincent in review), ecological dimorphisms are often generated initially by sexual selection acting on an animal's body size (either male–male combat or selection for increased fecundity leading to larger body sizes), but are typically amplified or maintained by natural selection (Slatkin 1984; Myersterud 2000). Even so, the potential role(s) of natural selection in this process is not always clear-cut. For example, Slatkin (1984) showed by taking a quantitative genetic modeling approach that sex-based divergence in phenotype and in ecological traits can evolve in

a manner similar to competitive character displacement (i.e., one or both sexes diverge in ways that reduce intersexual competition for resources) (Fig. 1). In contrast, empirical work has shown that in species exhibiting size dimorphism in size (SSD; body size in females differs from that in males), intersexual ecological divergence is more likely to evolve purely as the result of adaptation to divergent niches (i.e., the sexes have different adaptive peaks due to differences in body size) (Selander 1972; Ralls 1976; Shine 1991; Myerstud 2000; Vincent 2006). Although previous authors have formulated several sub-hypotheses (e.g., predation risk, differential energetic requirements) under the “dimorphic niche hypothesis” (reviewed by Myersterud 2000; Shine and Wall 2004), here we will largely restrict our attention to the broad implications of the hypothesis. Understanding the evolutionary origins and adaptive significance of ecological dimorphisms is still further complicated by the fact that hormones can play a pivotal role

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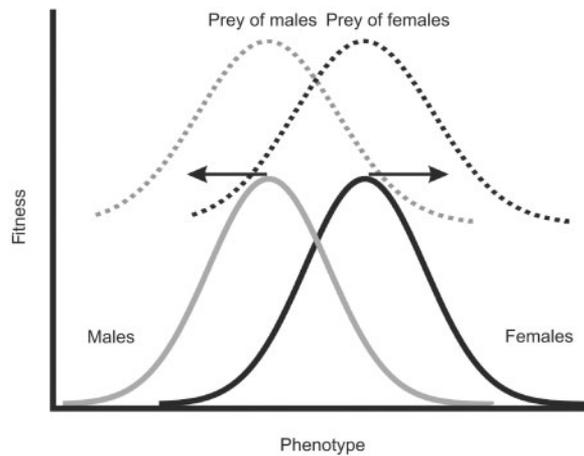


Fig. 1 Graph illustrating natural selection driving phenotypic divergence between males (grey lines) and females (black lines). The directions of selection (indicated by arrows) are predicted to track the mean dimensions of the prey. Please note that three possible scenarios exist: (1) Male phenotype remains stable through time (stabilizing selection), with females changing their mean phenotype: (2) the reverse of 1: and (3) males and females both diverge in mean phenotype as depicted in this figure. These scenarios are highly similar to the predictions based on quantitative genetic modeling of ecological character displacement (Slatkin 1984), but can also evolve as a result of adaptation to divergent ecological niches (see text for details).

in the evolution of SSD in many animal species (Lerner and Mason 2001; Cox and John-Alder 2005 and references therein; but see Taylor and DeNardo 2005 for a counterexample), which may in turn influence the ecology of the sexes.

The feeding apparatus of gape-limited snakes (that do not reduce the size of their prey before ingestion) has proven to be a model system for testing the adaptive nature of ecological dimorphisms for two reasons: (1) head size is believed to rarely be under sexual selection in snakes (e.g., Shine 1991), and (2) because head size limits the maximum size of prey that can be consumed; the sex with the larger head should thus consume larger prey (Shine 1991; Houston and Shine, 1993; Pearson et al. 2002; Shetty and Shine 2002; Shine et al. 2002; Shine and Wall 2004; Vincent et al. 2004a). In contrast, significantly less attention has been paid to the evolution of dietary dimorphisms in other types of squamates such as lizards. This lack of research is likely due to the fact that the feeding apparatus of lizards can be under both sexual and natural selection simultaneously, and these animals extensively chew their prey prior to ingestion (see Herrel et al. 1996, 1999,

2001a, b for an overview; Reilly et al. 2001). Consequently, it is significantly more difficult to generate clear-cut hypotheses to test for the presence of adaptive ecological dimorphisms in lizards compared to snakes.

Furthermore, a potentially serious confounding factor in the analysis of adaptive sex-based morphological divergence is the pervasive influence of hormones on animal growth and development. This issue is particularly relevant for both lizards and snakes because steroid hormones such as testosterone have been shown to directly influence the degree of SSD, as well as the shape of the feeding apparatus (Crews et al. 1985; Shine and Crews 1988; Lerner and Mason 2001; Cox et al. 2006), due to its inhibitory effect on male growth in some species (reviewed by Cox and John-Alder 2005). For example, red-sided garter snakes (*Thamnophis sirtalis parietalis*) exhibit significant sexual dimorphism in both body size and relative jaw length (corrected for body size), with females being larger in both aspects. The proximate cause of this dimorphism, however, was shown to be higher levels of circulating testosterone in males than in females, thus causing males to grow more slowly than females (Crews et al. 1985; Lerner and Mason 2001), and not sex-based ecological divergence (but see Krause et al. 2003; Krause and Burghardt in press for recent counterevidence). Further supporting this claim, Shine and Crews (1988) showed that the marked dimorphism in relative jaw length did not always translate into differences between the sexes in maximum size of prey consumed in natural populations. As a result, sex-based divergence in head shape—in the absence of quantitative dietary data—should not be viewed as compelling evidence for adaptive ecological divergence between the sexes.

In order to tease apart the respective influences of natural and sexual selection on the one hand, and developmental effects on the feeding apparatus of male and female squamates on the other, we formulate two straightforward testable hypotheses for snakes and lizards, respectively. Our overarching goal is to provide a quantitative framework that will enable future researchers to clearly distinguish between adaptive and nonadaptive influences on the feeding apparatus of male and female animals, and to point out areas that still need to be addressed with empirical data. We subsequently test these hypotheses by both reviewing the scientific literature on intersexual dietary divergence in lizards and snakes, and by providing empirical data to fill in critical gaps for some species.

Intersexual dietary divergence in snakes

Theoretically, there are two nonmutually exclusive mechanisms by which the sexes in gape-limited snakes may exploit different types, shapes, and/or maximum sizes of prey. (1) The sexes can differ in absolute size of head and body because larger-bodied snakes can consume larger maximum sizes of prey (Arnold 1993; Forsman and Lindell 1993), and/or (2) the sexes can differ in relative head dimensions (head shape) when they overlap in body size, enabling males and females of similar body sizes to consume different diets (Houston and Shine 1993; Vincent et al. 2004a). To invoke adaptive scenarios for the evolution of sex-based ecological divergence, however, we suggest that morphological divergence in either body size or head shape should be coupled with divergence in feeding behavior (foraging mode, prey handling method/time, sensory modalities used for prey detection), realized diet, and subsequently differential prey selection between the sexes. We suggest that multiple lines of evidence are needed to support the hypothesis of adaptation in this case because sexual selection and/or developmental effects alone can cause sex-based morphological divergence, which in turn could result in spurious correlations arising between intersexual morphology and diet in these animals. For example, Shine (1991) showed that most macrostomatan (enlarged gape) snakes exhibit female-biased dimorphism in body size, which is likely the result of selection on fecundity and offspring size in these animals (Shine 1991; Rivas and Burghardt, 2001). At the same time, however, this larger body size could result in females taking larger maximum sizes of prey than do males simply because of females' increased functional capacity to do so, not as a result of natural selection acting to reduce intersexual competition for resources or driving adaptation to divergent niches. By contrast, if natural selection is either maintaining or driving the sex-based morphological divergence, one would expect clear functional links amongst intersexual morphology, feeding behavior, realized diet, and selection of prey, given that sexual selection and developmental effects should not influence either feeding behavior or dietary selection in snakes. We thus reviewed the literature on sexual dietary dimorphisms in snakes and supplemented that review with our own unpublished data to fill in gaps whenever possible (Table 1). It should be noted that we only included species for which dietary data for both sexes had been reported (but see Shine 1991 for a large data set on intersexual morphology in snakes).

Empirical examples from snakes

Our nonexhaustive literature search resulted in data on the intersexual dietary habits of 38 species of snake, among 25 genera, and five families (Table 1), with all species belonging to a single monophyletic clade, Macrostromata (literally meaning, "large-mouthed" snakes) (Cundall and Greene 2000). Our review revealed that at least some aspects of intersexual phenotype (i.e., morphology and/or behavior) was clearly associated with sex-based dietary divergence in 73.6% of the snake species studied to date, suggesting that ecological dimorphisms are widespread amongst macrostomatans. Moreover, the gender with the relatively larger feeding structures—independent of body size—always consumed the larger prey, with some species even lacking SSD altogether but still exhibiting significant differences in head shape and diet (e.g., Colubridae: *Coronella austriaca*) (Luiselli et al. 1996). Sexual dimorphism in body size is thus not a prerequisite for the evolution of ecological dimorphisms in snakes, whereas dimorphisms in shape of the head are almost always present when the sexes differ in diet.

Interestingly, the majority of species that did not exhibit a clear link between intersexual phenotype and diet belonged to a single monophyletic clade (i.e., terrestrial elapids). Specifically, Shine et al. (in press) showed that most venomous terrestrial elapids exhibit significant SSD, with adult females having larger maximum body sizes than those of conspecific adult males, but males in this case tended to have longer heads relative to body size than did females (Table 1). Nonetheless, the relatively larger heads of males in this clade were generally not associated with males taking larger maximum prey sizes than do females (i.e., both sexes tended to consume relatively small [compared to the size of the predator] ectothermic vertebrates, except perhaps in one species, *Aspidelaps scutatus* [Shine et al. 1996c]. Given that terrestrial elapid males are known to vigorously bite each other during male–male combat in a manner similar to that of lizards (Lailvaux et al. 2004; Huyghe et al. 2005). Shine et al. (2006) suggested that this relatively longer head in males is, therefore, the result of sexual selection (i.e., male–male combat favoring males with relatively larger heads), and not adaptation to divergent niches.

Nonecological factors driving sex-based divergence in head shape, however, were not limited to venomous terrestrial elapids. Two colubrid species (*Elaphe quadrivirgata* and *Symphimus mayae*) were

Table 1 List of snake taxa in which the ecological-dimorphism hypothesis has been evaluated

Species	Larger sex	Head shape	Feeding behavior	Realized diet	Prey selection	References
Acrochordidae						
<i>Acrochordus arafurae</i>	F	Females have longer jaws and quadrates relative to skull length	Females forage in deeper water; rely more on chemical cues to detect prey; and feed less often	Females eat larger fish	Females prefer larger fish; males are nonselective piscivores	Shine and Lambeck 1985; Camilleri and Shine 1990; Houston and Shine 1993; Vincent et al. 2005
Colubridae						
<i>Boiga irregularis</i>	M	Same		Males eat larger birds, mammals; females mostly lizards		Savidge 1988; Shine 1991
<i>Coluber constrictor mormon</i>				Females eat large vertebrates; males primarily eat crickets		Shewchuk and Austin 2001
<i>Coronella austriaca</i>	Same		Females feed less frequently than do males	Females eat larger mammals; males mostly lizards		Luiselli et al. 1996
<i>Elaphe quadrigata</i>	M	Females have relatively wider heads	Sexes do not differ in maximum ingestible prey size or handling time	Both sexes primarily consume frogs	Both sexes prefer small frogs	Mori and Vincent, unpublished data; Tanaka et al. 2001
<i>E. quatuorlineata</i>	F			Females eat larger bird prey		Filippi et al. 2005
<i>Geophis nasalis</i>	F			Females eat larger worms		Seib 1981
<i>Mehelya capensis</i>	F	Females have longer and wider heads relative to skull length		Females eat larger maximum prey sizes (frogs and lizards)		Shine et al. 1996a
<i>Natrix maura</i>	F	Females have relatively longer heads	Males delay feeding and feed for a shorter period of time than do females	Females eat large frogs; males eat smaller fish	Females prefer large frogs; males prefer smaller fish	Shine 1991; Santos et al. 1998; Santos et al. 2000
<i>N. natrix</i>	F	Females have relatively longer and wider heads	No data	Females eat larger toads than do males	No data	Gregory 2004
<i>Nerodia cyclopion</i>	F	Females have relatively longer heads	Females forage in deeper water	Females eat larger fish	Females prefer larger fish; males are non-selective	Mushinsky et al. 1982; Shine 1991
<i>N. rhombifer</i>	F	Females have relatively longer heads	Females forage in deeper water	Females eat larger fish	Females prefer larger fish; males are non-selective	Mushinsky et al. 1982; Shine 1991
<i>N. sipedon</i>	F	Females have relatively longer heads		Females eat larger fish prey		King 1986, 1993; Shine 1991
<i>Opheodrys aestivus</i>	F			Females eat larger dragon flies; males mostly caterpillars		Plummer, 1981

(continued)

Table 1 Continued

Species	Larger sex	Head shape	Feeding behavior	Realized diet	Prey selection	References
<i>Pseudablabes agassizii</i>	F	Same		Both sexes consume small spider prey		Marques et al. 2006
<i>Symphimus mayae</i>	Same	Females have relatively longer heads	Same	Both sexes eat small cricket prey		Stafford 2005
<i>Thamnophis sirtalis</i>	F	Females have relatively longer heads and jaws		Females eat larger toads		Krause et al. 2003
<i>Telescopus dhara</i>	F	No data	Females are ambush foragers; males are active foragers	Females eat larger birds; males mostly lizards		Zinner 1985
<i>Thelotornis capensis</i>	Same	Females have relatively longer heads		Females eat larger maximum prey sizes (lizards)		Shine et al. 1996b
Elapidae						
<i>Aspidelaps lubricus</i>	F	Males have relatively longer heads	No data	Both sexes eat a wide range of small vertebrate prey	No data	Shine et al. in press
<i>A. scutatus</i>	F	Males have relatively wider heads		Males eat larger frogs; females eat more small mammals		Shine et al. 1996c
<i>Laticauda colubrina</i>	F	Females have relatively wider and longer heads	Males feed in deeper crevices, presumably aided by their relatively narrow heads	Females eat larger eels	Females prefer conger eels; males prefer moray eels	Radcliffe and Chiszar 1980; Shetty and Shine, 2002; Shine et al. 2002
<i>L. frontalis</i>	F	Females have relatively longer heads	Females forage in deeper water	Females eat larger eels	Larger females prefer larger eels	Shine et al. 2002
<i>Hemachatus haemachatus</i>	Same	Males have relatively longer heads	No data	Both sexes eat a wide range of small vertebrate prey	No data	Shine et al. in press
<i>Naja anchietae</i>	Same	Males have relatively longer heads	No data	Both sexes eat a wide range of small vertebrate prey	No data	Shine et al. in press
<i>N. annulifera</i>	M	Same	No data	Both sexes eat a wide range of small vertebrate prey	No data	Shine et al. in press
<i>N. melanoleuca</i>	F	Males have relatively longer heads		Both sexes eat a wide range of small vertebrate prey		Luiselli et al. 2002; Shine et al. in press
<i>N. mossambica</i>	Same	Males have relatively longer heads		Both sexes eat a wide range of small vertebrate prey		Shine et al. in press

(continued)

Table 1 Continued

Species	Larger sex	Head shape	Feeding behavior	Realized diet	Prey selection	References
<i>N. nigricincta</i>	F	Males have relatively longer heads		Both sexes eat a wide range of small vertebrate prey		Shine et al. in press
<i>N. nivea</i>	Same	Males have relatively longer heads		Both sexes eat a wide range of small vertebrate prey		Shine et al. in press
<i>Pseudechis porphyriacus</i>	M	Males have relatively longer heads		Males eat larger frogs; females more lizards		Shine 1979, 1991
Pythonidae						
<i>Moreila spilota imbricata</i>	F	Females have wider and deeper heads	Males spend more time feeding	Females eat larger mammals		Pearson et al. 2002, 2003
<i>Python regius</i>	F		Males forage in trees; females forage on or near the ground	Females eat larger mammals; males more birds		Luiselli and Angelici 1998
<i>P. reticulatus</i>	F	Same	Adult females fed more frequently than males	Females eat larger mammals		Shine et al. 1998a
Viperidae						
<i>Agkistrodon contortrix</i>	M	Same		Males eat larger mammals; females more invertebrates		Fitch 1982; Shine 1991
<i>A. piscivorus</i>	M	Males have relatively longer quadrates and deeper heads	Males handle fish better and ingest them faster than females	Males eat taller prey	Males prefer fish, females prefer snakes	Vincent et al. 2004a, b; Vincent unpublished data
<i>Bitis caudalis</i>	F			Females eat larger mammals; males mostly lizards		Shine et al. 1998b
<i>Vipera ursinii</i>	F			Females eat larger mammals		Agrimi and Luiselli 1992

also reported to exhibit significant dimorphisms in shape of the head (i.e., females had relatively larger heads in both cases) without a corresponding shift in intersexual diet (Table 1). Previous authors have suggested that the evolution of larger heads in female snakes, in the absence of a dietary dimorphism, may be the result of either hormonal effects (i.e., male growth is inhibited by higher levels of circulating testosterone) (Cox and John-Alder 2005) or possibly sexual selection (i.e., males selecting females with relatively larger heads) (Rivas and Burghardt 2001; Luiselli et al. 2002). We suggest that hormones are not likely to play a major role in producing the relatively larger heads of females in these two colubrids because the males of one species

(*E. quadrivirgata*) were both larger than conspecific females and grew faster (Mori and Hasegawa 2002), and the sexes of the other species (*S. mayae*) did not differ in maximum body size. By the simple process of elimination, then, it would appear that the males of these two colubrids may actually be choosing to breed with females with relatively larger heads, although any empirical data that would test this hypothesis are currently lacking [but see Rivas and Burghardt (2001) for a theoretical argument]. Even so, previous authors have cast serious doubt on the possibility that male snakes may choose to breed with females with relatively larger heads on the grounds that most snakes employ chemical and not visual cues during mate recognition (Shine 1991).

Hence, the female-biased dimorphisms in head shape in these two colubrids clearly warrants further investigation to resolve this apparent paradox.

Despite the fact that numerous studies have now tested the ecological hypothesis in relation to dimorphism in snakes, we were only able to find eight taxa that met all five of our criteria for rigorously testing it (Table 1). Surprisingly, six of these eight species were either highly aquatic or semi-aquatic, with most species being only distantly related to one another (i.e., acrochordid filesnakes, natricine colubrids, and laticaudid sea kraits). Furthermore, all of these aquatic species show clear functional links amongst divergence in body size, head shape, feeding behavior, realized diet, and prey selection. Within these taxa, females tend to be substantially larger in body size, have relatively longer and wider heads, consume and prefer larger prey, and forage in deeper water than do conspecific males (Table 1). For example, females of the highly aquatic Arafuræ filesnake (*Acrochordus arafuræ*) are nearly twice as large as conspecific males in body size (max female SVL = 170 cm; max male SVL = 105) (Camilleri and Shine 1990) and have significantly longer jaws and quadrates relative to skull length (Camilleri and Shine 1990). Coupled with this morphological divergence, females ambush large fishes in deep water, whereas males actively search for smaller fishes in shallow water (Shine and Lambeck 1985; Houston and Shine 1993). Laboratory-based studies further showed that this sex-based divergence in foraging mode of filesnakes is directly linked to the sensory modalities used in the detection of prey (Vincent et al. 2005). Specifically, actively foraging males respond most intensely to long-lasting chemical cues (fish scent, regardless of movement) whereas ambush females see ambush and respond most strongly to movement (Table 1). The highly similar patterns reported for other distantly related taxa strongly suggest that adaptive ecological dimorphisms have evolved in a convergent manner amongst aquatic snakes in general (Shetty and Shine 2002; Shine et al. 2002; Shine and Wall 2004).

By contrast, we only found two terrestrial snake species that met all five of our criteria, even though several terrestrial taxa do show clear functional links among divergence in head shape, feeding behavior, and realized diet (Table 1). Further, these two taxa present a mixed picture for the adaptive nature of intersexual divergence in terrestrial snakes. Specifically, Pearson et al. (2002, 2003) showed that terrestrial carpet pythons

(*Morelia spilota imbricata*) from tropical Australia exhibit marked geographic variation in intersexual divergence in body size, head shape, and realized diet, depending on local availability of prey. Overall, females tended to have larger body sizes, wider and longer heads, and consumed much larger mammalian prey whereas the smaller males primarily consumed lizards. Presumably in compensation for taking smaller prey, males in most populations subsequently spent significantly more time foraging than did females. The only other terrestrial snake species meeting all our criteria (*E. quadrivirgata*) did not support the ecological hypothesis (see earlier text). Hence, unlike aquatic snakes in which adaptive ecological dimorphisms have clearly evolved several times independently, the evidence for terrestrial snakes is less clear-cut.

In summary, our review led to three general conclusions for snakes. (1) Intersexual dietary divergence only evolves within snakes when one sex forages on a relatively large prey item (e.g., birds, mammals, large fish) compared with the size of the predator and never within species that consume relatively small prey (invertebrates, small frogs, lizards), even when SSD is already present within a species (e.g., terrestrial elapids) (Table 1). Maximum ingestible size of prey, therefore, appears to be the main axis of ecological differentiation between the sexes in snakes, and this general pattern holds across all five families examined here. (2) Dimorphisms in shape of the head are commonly linked to intersexual dietary divergence across macrostomatans, with the remaining cases being attributable primarily to sexual selection. Moreover, we did not find any clear-cut cases supporting the hypothesis that hormones alone can drive dimorphisms in head shape in snakes as was previously believed (also see Krause et al. 2003; Krause and Burghardt, in press). (3) Although numerous studies have reported dimorphisms in diet and head shape in snakes (Table 1), only a few studies have examined either sex-based foraging behavior or sex-based selection of prey in these animals. Finally, the overwhelming majority of studies that have addressed these two issues have been performed on aquatic snake taxa, making it difficult to compare patterns of sex-based ecological divergence between aquatic and terrestrial species in a robust manner.

Intersexual dietary divergence in lizards

For lizards that mechanically reduce their prey (Reilly et al. 2001), the selective drive causing dimorphisms in diet is often more difficult to

determine than it is for snakes. Not only can head size, performance and dietary dimorphisms be the result of a dimorphism in body size, which in turn is likely under both natural and sexual selection, but even in the absence of dimorphism in body size the dietary dimorphism could still be an epiphenomenon of sexual selection on bite force in males. Although differences in bite force have been shown to be correlated with differences in handling times and size and hardness of prey (Verwajen et al. 2002; Herrel et al. 2006), bite force has also been shown to be important in male dominance (e.g., Lailvaux et al. 2004; Huyghe et al. 2005). Thus, even if one of the sexes has a bigger head, shows higher bite forces and eats larger prey this does not imply *per se* that natural selection is the driving agent for the observed dimorphism. Sexual selection leading to differences in head size and bite force between the sexes because of its importance in male combat, for example, could secondarily result in differences in diet between the sexes.

Thus, for lizards that mechanically reduce their prey, we predict that the degree of dimorphism in head size should be positively correlated with the degree of dimorphism in bite force, which should in turn be correlated with the dimorphism in aspects of size or hardness of prey if natural selection for resource partitioning is to be a likely candidate for the observed dimorphism. In essence, in species with large differences in head size between the sexes males and females should differ greatly in bite force and should take greatly different sizes of prey. If sexual selection is driving the dimorphism in head size, we would also expect a correlation between the degree of dimorphism in head size and the degree of dimorphism in bite force, but not necessarily with degree of dimorphism in prey size. In essence, species with large differences in head size should also have differences in bite force and although not necessarily showing great differences in prey size between the sexes, such may occur.

Empirical examples from lizards

A nonexhaustive literature search resulted in data on size of the body and/or head for 140 species of lizards belonging to 13 families and 49 genera (Table 2). Of these, only 24 were not dimorphic in body size suggesting that body size dimorphism is a common phenomenon in lizards. Of these remaining species, only 21 showed female-biased dimorphism in body size. Data on head size were available for 99 species, only six of which were not dimorphic in head size. Interestingly, only in three species

(*Gambelia wisizenii*, *G. copei* and *Draco melanopogon*) (Lappin and Swinney 1999; Shine et al. 1998c) was a female-biased dimorphism in head size observed. Thus, not only is dimorphism in size of the head common in lizards, it is generally male-biased. Interestingly, for those species for which data were available, the dimorphism in bite-force mimicked that of head size in all cases. This is not entirely surprising as head size has been demonstrated to be a good predictor of bite force in lizards (e.g., Herrel et al. 1999, 2001a, b) and other vertebrates (Herrel et al. 2005; Herrel and Gibb, 2006). Given that dimorphism in size of the head in lizards is typically male-biased and that it appears to result in a dimorphism in bite force which is important during male–male interactions (Lailvaux et al. 2004; Huyghe et al. 2005), sexual selection is likely the main selective force driving dimorphism in head size in most cases.

Information on prey size for the two sexes was available for only 33 species. In 21 of these, males consumed larger prey than did females; in seven species both sexes consumed prey of similar size; and only in five species did females eat larger prey than did males. Although this data set is rather limited, it does suggest that head size dimorphisms are translated into differences in prey size between the sexes in lizards. Even so, the role of natural selection in maintaining or driving these prey-size dimorphisms is presently unclear due to the prominent role of sexual selection in driving the dimorphisms of head size in the first place.

In conclusion, this brief review suggests that in lizards dimorphism in head size is common and associated with dimorphism in bite force, with the larger-headed gender biting harder. Although the larger-headed gender also consumes larger prey in most cases, these data cannot address whether niche divergence drives the observed dimorphisms in head size and bite force. The most likely scenario at present is one in which sexual selection leading to larger heads in one sex resulted in a dimorphism in bite force. Secondarily, this may have resulted in differences in the size of prey eaten by both sexes in many species of lizards. Clearly, more quantitative data on head size, bite force, and dimorphism in diet are needed to test these hypotheses in a rigorous manner. Moreover, the causal relationship between bite force and diet needs to be examined in more detail for both sexes by investigating its effect on handling time and the cost of capture and transport of prey. A single study in which handling times were examined for two species of lacertid lizards suggested that the dimorphism in bite force

Table 2 Summary on sexual dimorphism in body size (SSD), head size (SHSD), prey size and bite force for a broad sample of lizards. Also indicated is whether the dimorphism is male-based or female-biased

Family	genus	species	SSD	M/F	SHSD	M/F	prey size	bite force	Reference
Phrynosomatidae	<i>Sceloporus</i>	<i>virgatus</i>	Yes	F					Abell 1998
Phrynosomatidae	<i>Sceloporus</i>	<i>aeneus</i>	No						Lemos-Espinal et al. 2002
Phrynosomatidae	<i>Sceloporus</i>	<i>palaciosi</i>	No						Lemos-Espinal et al. 2002
Phrynosomatidae	<i>Sceloporus</i>	<i>siniferus</i>	Yes	M	Yes	M			Lemos-Espinal et al. 2001
Phrynosomatidae	<i>Sceloporus</i>	<i>undulatus</i>	Yes	F	Yes	M		M > F	Cooper and Vitt 1989, Herrel and Meyers, unpublished data
Phrynosomatidae	<i>Phrynosoma</i>	<i>douglasi</i>	Yes	F			F > M		Powell and Russell 1984; Zamudio 1998;
Phrynosomatidae	<i>Phrynosoma</i>	<i>hernandesi</i>	Yes	F					Zamudio 1998
Phrynosomatidae	<i>Phrynosoma</i>	<i>ditmarsii</i>	Yes	F					Zamudio 1998
Phrynosomatidae	<i>Cophosaurus</i>	<i>texanus</i>	Yes	M					Sugg et al. 1995
Phrynosomatidae	<i>Uta</i>	<i>palmeri</i>	Yes	M	Yes	M			Hews et al. 1996
Iguanidae	<i>Amblyrhynchus</i>	<i>cristatus</i>	Yes	M					Wikelski and Trillmich 1997
Iguanidae	<i>Dipsosaurus</i>	<i>dorsalis</i>	No		No				Carothers 1984; Herrel and Meyers, unpublished data
Iguanidae	<i>Conolophus</i>	<i>pallidus</i>	Yes	M	No				Carothers 1984
Iguanidae	<i>Conolophus</i>	<i>subcristatus</i>	Yes	M	Yes	M			Carothers 1984
Iguanidae	<i>Iguana</i>	<i>iguana</i>	Yes	M	Yes	M			Carothers 1984
Iguanidae	<i>Ctenosaura</i>	<i>hemilopha</i>	Yes	M	Yes	M			Carothers 1984
Iguanidae	<i>Ctenosaura</i>	<i>similis</i>	Yes	M	Yes	M			Carothers 1984
Iguanidae	<i>Sauromalus</i>	<i>obesus</i>	Yes	M	Yes	M		M > F	Carothers 1984; Lappin et al. 2006
Iguanidae	<i>Sauromalus</i>	<i>hispidus</i>	No		No				Carothers 1984
Iguanidae	<i>Sauromalus</i>	<i>varius</i>	No		No				Carothers 1984
Crotaphytidae	<i>Crotaphytus</i>	<i>collaris</i>	Yes	M	Yes	M	M > F	M > F	McCoy et al. 1994; Best and Pfaffenberger, Lappin pers. com.
Crotaphytidae	<i>Gambelia</i>	<i>wislizenii</i>	Yes	F	Yes	F			Lappin and Swinney 1999
Crotaphytidae	<i>Gambelia</i>	<i>silva</i>	Yes	M	Yes	M			Lappin and Swinney 1999
Crotaphytidae	<i>Gambelia</i>	<i>copei</i>	Yes	F	Yes	F	F > M		Tollestrup 1983; Lappin and Swinney 1999
Polychrotidae	<i>Anolis</i>	<i>sagrei</i>	Yes	M	Yes	M	M > F	M > F	Schoener 1968; Stamps 1999; Butler and Losos 2002; Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>acutus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>aeneus</i>	Yes	M	Yes	M	M > F		Schoener and Gorman 1968; Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>angusticeps</i>	Yes	M	Yes	M	M > F	M > F	Schoener 1968; Stamps et al. 1997; Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>auratus</i>	No						Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>bimaculatus</i>	Yes	M					Stamps et al. 1997

(continued)

Table 2 Continued

Family	genus	species	SSD	M/F	SHSD	M/F	prey size	bite force	Reference
Polychrotidae	<i>Anolis</i>	<i>capito</i>	Yes	F					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>carolinensis</i>	Yes	M	Yes	M	M > F	M > F	Preest 1994; Stamps et al. 1997; Vanhooydonck et al. 2005
Polychrotidae	<i>Anolis</i>	<i>conspersus</i>	Yes	M	Yes	M	M > F		Schoener 1967
Polychrotidae	<i>Anolis</i>	<i>crisatellus</i>	Yes	M				M > F	Butler and Losos 2002, Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>cupreus</i>	Yes	M			F = M		Fleming and Hooker 1975; Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>cuvieri</i>	Yes	M	Yes	M		M > F	Butler and Losos 2002; Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>distichus</i>	Yes	M	Yes	M	M > F	M > F	Schoener 1968; Stamps et al. 1997; Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>evermanni</i>	Yes	M				M > F	Butler and Losos 2002, Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>frenatus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>garmani</i>	Yes	M	Yes	M	M > F	M > F	Stamps et al. 1997; Butler and Losos 2002; Herrel et al. 2004a
Polychrotidae	<i>Anolis</i>	<i>grahami</i>	Yes	M	Yes	M	M > F	M > F	Butler and Losos 2002; Herrel et al. 2004a
Polychrotidae	<i>Anolis</i>	<i>gundlachi</i>	Yes	M					Butler and Losos 2002
Polychrotidae	<i>Anolis</i>	<i>humilis</i>	Yes	F					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>krugi</i>	Yes	M	Yes	M		M > F	Butler and Losos 2002, Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>limifrons</i>	Yes	F			F > M		Andrews 1979; Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>lineatopus</i>	Yes	M			M > F	M > F	Stamps et al. 1997, Butler and Losos 2002; Herrel et al. 2006
Polychrotidae	<i>Anolis</i>	<i>lionotus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>nebulosus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>occultus</i>	Yes	F					Butler and Losos 2002
Polychrotidae	<i>Anolis</i>	<i>oculatus</i>	Yes	M			F > M		Andrews 1979; Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>opalinus</i>	Yes	M					Butler and Losos 2002
Polychrotidae	<i>Anolis</i>	<i>poecilopus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>poncensis</i>	Yes	M					Butler and Losos 2002
Polychrotidae	<i>Anolis</i>	<i>polylepis</i>	Yes	M	Yes	M	F > M		Andrews 1971; Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>pulchellus</i>	Yes	M	Yes	M		M > F	Butler and Losos 2002; Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>richardi</i>	Yes	M	Yes	M	M > F		Schoener and Gorman 1968
Polychrotidae	<i>Anolis</i>	<i>roquet</i>	Yes	M	Yes	M	M > F		Schoener and Gorman 1968
Polychrotidae	<i>Anolis</i>	<i>smaragdinus</i>	Yes	M				M > F	Stamps et al. 1997; Herrel, unpublished data

(continued)

Table 2 Continued

Family	genus	species	SSD	M/F	SHSD	M/F	prey size	bite force	Reference
Polychrotidae	<i>Anolis</i>	<i>stratulus</i>	Yes	M				M > F	Butler and Losos 2002, Herrel, unpublished data
Polychrotidae	<i>Anolis</i>	<i>tropidonotus</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Anolis</i>	<i>valencienni</i>	Yes	M	Yes	M	M > F	M > F	Stamps et al. 1997; Butler and Losos 2002; Herrel et al. 2004a
Polychrotidae	<i>Anolis</i>	<i>wattsii</i>	Yes	M					Stamps et al. 1997
Polychrotidae	<i>Polychrus</i>	<i>acutirostris</i>	Yes	F					Vitt and Lacher 1981
Tropiduridae	<i>Tropidurus</i>	<i>torquatus</i>	Yes	M	Yes	M			Pinto et al. 2005
Tropiduridae	<i>Tropidurus</i>	<i>melanopleurus</i>	Yes	M	Yes	M	M > F		Perez-Mellado and Riva 1993
Tropiduridae	<i>Tropidurus</i>	<i>itambere</i>	Yes	M	Yes	M	M > F		Van-Sluys 1993
Tropiduridae	<i>Microlophus</i>	<i>albemarlensis</i>	Yes	M	Yes	M			Snell et al. 1988
Tropiduridae	<i>Microlophus</i>	<i>occipitalis</i>	Yes	M	Yes	M			Watkins 1996
Tropiduridae	<i>Microlophus</i>	<i>atacamensis</i>	Yes	M	Yes	M			Vidal et al. 2002
Tropiduridae	<i>Liolaemus</i>	<i>occipitalis</i>	Yes	M	Yes	M			Verrastro 2004
Tropiduridae	<i>Leiocephalus</i>	<i>carinatus</i>	Yes	M	Yes	M		M > F	Schoener et al. 1982; Herrel, unpublished data
Tropiduridae	<i>Leiocephalus</i>	<i>inaguae</i>	Yes	M	Yes	M			Schoener et al. 1982
Tropiduridae	<i>Leiocephalus</i>	<i>loxogrammus</i>	Yes	M	Yes	M			Schoener et al. 1982
Tropiduridae	<i>Leiocephalus</i>	<i>greenwayi</i>	Yes	M	Yes	M			Schoener et al. 1982
Tropiduridae	<i>Liolaemus</i>	<i>lutzae</i>	Yes	M	Yes	M			Rocha 1996, 1999
Scincidae	<i>Niveoscincus</i>	<i>microlepidotus</i>	Yes	M	Yes	M			Olsson et al. 2002
Scincidae	<i>Eumeces</i>	<i>elegans</i>	Yes	M	Yes	M			Griffith 1991; Huang 1996
Scincidae	<i>Eumeces</i>	<i>fasciatus</i>	Yes	M	Yes	M			Griffith 1991
Scincidae	<i>Eumeces</i>	<i>inexpectatus</i>	Yes	M	Yes	M			Griffith 1991
Scincidae	<i>Eumeces</i>	<i>laticeps</i>	Yes	M	Yes	M		M > F	Griffith 1991; Herrel and Moon, unpublished data
Scincidae	<i>Eumeces</i>	<i>laticutatus</i>	Yes	M	Yes	M			Griffith 1991
Scincidae	<i>Oligosoma</i>	<i>nigriplantare</i>	Yes	F					Spencer et al. 1998
Scincidae	<i>Oligosoma</i>	<i>lineocellatum</i>	Yes	F					Spencer et al. 1998
Scincidae	<i>Egernia</i>	<i>coventryi</i>	No		Yes	M			Clemann et al. 2004
Lacertidae	<i>Lacerta</i>	<i>agilis</i>	Yes	F	Yes	M			Olsson 1994; Gvozdk and Boukal 1998
Lacertidae	<i>Podarcis</i>	<i>sicula</i>	Yes	M	Yes	M		M > F	Herrel et al. 2004b; Vogrin 2005
Lacertidae	<i>Podarcis</i>	<i>atrata</i>	Yes	M	Yes	M		M > F	Herrel et al. 1996; Herrel et al. 2004b
Lacertidae	<i>Gallotia</i>	<i>galloti</i>	Yes	M	Yes	M		M > F	Herrel et al. 1999; Herrel et al. 2004b
Lacertidae	<i>Lacerta</i>	<i>vivipara</i>	Yes	F	Yes	M	F = M	M > F	Brana 1996; Herrel et al. 2001b; Gvozdk and Van Damme 2003; Herrel et al. 2004b

(continued)

Table 2 Continued

Family	genus	species	SSD	M/F	SHSD	M/F	prey size	bite force	Reference
Lacertidae	<i>Podarcis</i>	<i>bocagei</i>	Yes	M	Yes	M	F = M		Brana 1996
Lacertidae	<i>Podarcis</i>	<i>hispanica</i>	Yes	M	Yes	M	M > F	M > F	Brana 1996; Herrel et al. 2004
Lacertidae	<i>Podarcis</i>	<i>muralis</i>	Yes	M	Yes	M	M > F	M > F	Brana 1996; Herrel et al. 2001b; Herrel et al. 2004b
Lacertidae	<i>Lacerta</i>	<i>monticola</i>	No		Yes	M	F = M		Brana 1996
Lacertidae	<i>Lacerta</i>	<i>lepida</i>	No		Yes	M	M > F		Brana 1996
Lacertidae	<i>Lacerta</i>	<i>schreiberi</i>	No		Yes	M	F = M		Brana 1996
Lacertidae	<i>Lacerta</i>	<i>bilineata</i>	No		Yes	M	F = M	M > F	Brana 1996; Herrel et al. 2004b
Cordylidae	<i>Platysaurus</i>	<i>intermedius</i>	Yes	M					Lailvaux et al. 2003
Cordylidae	<i>Cordylus</i>	<i>niger</i>	No		Yes	M			Cordes et al. 1995
Cordylidae	<i>Cordylus</i>	<i>cordylus</i>	No		Yes	M			Cordes et al. 1995
Cordylidae	<i>Pseudocordylus</i>	<i>melanotus</i>	Yes	M					Mouton and van Wyk 1993
Cordylidae	<i>Cordylus</i>	<i>giganteus</i>	Yes	F					van Wyk 1992
Cordylidae	<i>Cordylus</i>	<i>cataphractus</i>	Yes	M	Yes	M			Mouton et al. 1999
Teiidae	<i>Cnemidophorus</i>	<i>murinus</i>	Yes	M	Yes	M			Dearing and Schall 1994; Baird et al. 2003
Teiidae	<i>Cnemidophorus</i>	<i>tigris</i>	Yes	M	Yes	M			Anderson and Vitt 1990; Cullum 1998
Teiidae	<i>Cnemidophorus</i>	<i>burti</i>	Yes	M					Cullum 1998
Teiidae	<i>Cnemidophorus</i>	<i>inornatus</i>	Yes	F					Cullum 1998
Teiidae	<i>Cnemidophorus</i>	<i>septemvittatus</i>	No						Cullum 1998
Teiidae	<i>Cnemidophorus</i>	<i>ocellifer</i>	Yes	M	Yes	M			Anderson and Vitt 1990
Teiidae	<i>Cnemidophorus</i>	<i>littoralis</i>	No		Yes	M	F = M		Teixeira-Filho et al. 2003
Teiidae	<i>Ameiva</i>	<i>ameiva</i>	Yes	M	Yes	M			Anderson and Vitt 1990
Teiidae	<i>Ameiva</i>	<i>plei</i>	Yes	M	Yes	M	F = M		Censky 1996
Teiidae	<i>Crocodilurus</i>	<i>amazonicus</i>	No		Yes	M			Mesquita et al. 2006
Teiidae	<i>Dracaena</i>	<i>guianensis</i>	No	M	Yes	M			Mesquita et al. 2006
Xenosauridae	<i>Xenosaurus</i>	<i>grandis</i>	No		Yes	M		M > F	Smith et al. 1997; Herrel et al. 2001a
Xenosauridae	<i>Xenosaurus</i>	<i>newmanorum</i>	Yes	F	Yes	M		M > F	Smith et al. 1997; Herrel et al. 2001a
Xenosauridae	<i>Xenosaurus</i>	<i>platyceps</i>	Yes		Yes	M		M > F	Herrel et al. 2001a
Xenosauridae	<i>Xenosaurus</i>	<i>rectocollaris</i>	No		No				Lemos-Espinal et al. 1996
Agamidae	<i>Draco</i>	<i>melanopogon</i>	Yes	F	Yes	F			Shine et al. 1998d
Agamidae	<i>Agama</i>	<i>agama</i>	Yes	M	Yes	M			Shine et al. 1998d
Agamidae	<i>Acanthocercus</i>	<i>atricollis</i>	No		Yes	M			Reaney and Whiting 2002
Agamidae	<i>Agama</i>	<i>tuberculata</i>	Yes	M	Yes	M			Shine et al. 1998d
Agamidae	<i>Amphibolurus</i>	<i>muricatus</i>	Yes	M	Yes	M			Shine et al. 1998d
Agamidae	<i>Calotes</i>	<i>crisatellus</i>	Yes	M	Yes	M			Shine et al. 1998d
Agamidae	<i>Calotes</i>	<i>versicolor</i>	No		Yes	M			Radder et al. 2001

(continued)

Table 2 Continued

Family	genus	species	SSD	M/F	SHSD	M/F	prey size	bite force	Reference
Agamidae	<i>Chlamydosaurus</i>	<i>kingii</i>	Yes	M	Yes	M			Shine et al. 1998d
Agamidae	<i>Ctenophorus</i>	<i>caudicinctus</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Ctenophorus</i>	<i>fionni</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Ctenophorus</i>	<i>maculosus</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Ctenophorus</i>	<i>nuchalis</i>	Yes	M	Yes	M	No	BF	Shine et al. 1998d
Agamidae	<i>Hypsilurus</i>	<i>boydii</i>	Yes	F	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Hypsilurus</i>	<i>spinipes</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Japalura</i>	<i>swinhonis</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Lophognathus</i>	<i>gilberti</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Lophognathus</i>	<i>temporalis</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Physignathus</i>	<i>lesueurii</i>	Yes	M	Yes	M	No	No	Shine et al. 1998d
Agamidae	<i>Pogona</i>	<i>vitticeps</i>	Yes	M	Yes	M	No	BF	Shine et al. 1998d
Agamidae	<i>Pogona</i>	<i>minor</i>	No		Yes	M	No	No	Shine et al. 1998d
Gekkonidae	<i>Hemidactylus</i>	<i>turcicus</i>	No		Yes	M	F = M	No	Saenz and Conner 1996; Johnson et al. 2005
Gekkonidae	<i>Ptenopus</i>	<i>garrulus</i>	No		Yes	M	F = M	No data	Hibbitts et al. 2005
Varanidae	<i>Varanus</i>	<i>salvator</i>	Yes	M	No		No data	No data	Shine et al. 1998c

resulted in faster processing of prey in the sex with the larger bite force (Verwajen et al. 2002), suggesting this approach to be a fruitful avenue for further research.

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