CHAPTER 4

The evolution of sexual size dimorphism in reptiles

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4.1 Introduction

Reptiles figure prominently in both historical and current research on sexual size dimorphism (SSD), in part because of the considerable range of dimorphisms and life histories observed within this group. In this chapter, we describe the major patterns of SSD in reptiles and discuss the primary evolutionary hypotheses and ecological correlates proposed to explain these patterns. Our discussion of patterns in reptile SSD is based on a large dataset for which we compiled measures of adult SSD for 1314 populations representing 832 species (479 lizards, 277 snakes, and 76 turtles). To address the major evolutionary hypotheses for SSD, we focus our discussion on recent comparative studies that examine the relationships between SSD and various ecological and evolutionary correlates across multiple populations and species.

4.2 Phylogenetic distribution of reptile SSD

To date, the only comprehensive empirical review of SSD across reptiles is that of Fitch (1981). However, subsequent investigators have supplemented this monograph with new data and analyses for lizards (Stamps 1983; Carothers 1984; Braña 1996; Stamps et al. 1997; Butler et al. 2000; Cox et al. 2003), snakes (Shine 1994b), and turtles (Gibbons and Lovich 1990; Forsman and Shine 1995). Figure 4.1 summarizes our compilation of body-size measurements from these and other studies and provides the empirical basis for our descriptions of SSD in each reptile lineage. We

follow convention in the reptile literature by focusing our analyses and discussion on sex differences in length (i.e. snout–vent, carapace, or plastron length), since body mass typically varies with reproductive status, fat storage, and digestive state. We use the index of Lovich and Gibbons (1992) to express SSD as (length of larger sex/ length of smaller sex)–1, negative by convention when males are the larger sex and positive when females are larger than males.

4.2.1 Lizards

Males are larger than females in the majority of lizards, although female-biased SSD is common and occurs in nearly every family (Figure 4.1). Male-biased SSD reaches extremes in which males average 50% longer than females in some polychrotid anoles (*Anolis*), tropidurids (*Tropidurus*), marine iguanas (*Amblyrhynchus*), and varanid monitor lizards (*Varanus*). By contrast, females exceed males by as much as 20% in some polychrotids (*Polychrus*), skinks (*Mabuya*), and pygopodids (*Aprasia*). Male-biased SSD is the rule in several families (e.g. Iguanidae, Tropiduridae, Teiidae, Varanidae), whereas others exhibit considerable variation with no clear directional trend in SSD (e.g. Gekkonidae, Scincidae). At a finer taxonomic scale, many genera show consistent trends toward substantially larger males (e.g. *Ameiva*, *Leiocephalus*, *Microlophus*, *Tropidurus*) or females (e.g. *Phrynosoma*, *Diplodactylus*, *Aprasia*), whereas others show considerable phylogenetic lability in the direction of SSD (e.g. *Anolis*, *Lacerta*, *Mabuya*, *Sceloporus*).
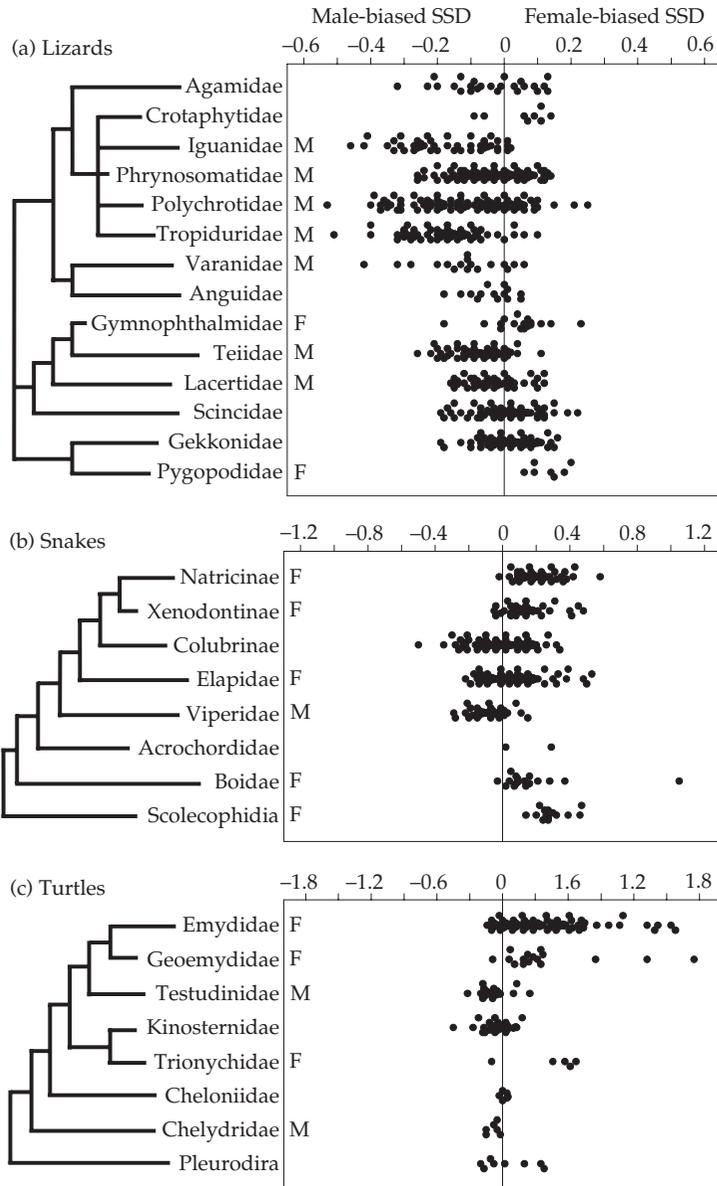
Figure 4.1 Distribution of SSD in major reptile lineages. SSD is calculated as (mean length of larger sex/mean length of smaller sex)–1, arbitrarily expressed as negative when males are larger and positive when females are larger. Lengths are snout–vent length (lizards and snakes) and carapace or plastron length (turtles). Each data point represents a single population or species. Letters indicate when mean SSD for a particular lineage is significantly ($P < 0.05$) male- (M) or female-biased (F). Phylogenetic relationships are provided for illustrative purposes. Axes are drawn to different scales in each panel on account of differences in the range of maximum SSD in each lineage. Snakes are actually a derived lizard clade (i.e. our depiction of lizards is paraphyletic with respect to snakes), but we have separated these lineages for graphical convenience.

4.2.2   Snakes

Although snakes actually comprise a derived lizard clade, they differ from lizards in that females are larger than males in the majority of species (Figure 4.1). Moreover, female-biased SSD is the rule in many lineages (e.g. Natricinae, Xenodontinae, Boidae, Scolecophidia) and only one family is characterized by ubiquitous male-biased SSD (i.e.

Viperidae). Males are also larger than females in many elapids and colubrines, but these groups exhibit a broad range of SSD with no consistent directional trend. The overall range in SSD across snakes is comparable to that observed in lizards. Females exceed males in length by more than 50% in some natricine water snakes (*Nerodia*), xenodontines (*Farancia*), elapid sea kraits (*Laticauda*), boids (*Morelia*), and scolecophidian blind snakes

(*Ramphotyphlops*). Sex differences in body mass are quite impressive in large pythons (*Morelia*, *Python*) and boas (*Eunectes*), with females exceeding males by an order of magnitude in some cases. Males may average as much as 50% longer than females in some exceptional colubrines (*Drymoluber*) and frequently exceed females by 20–30% in some other colubrines (*Coluber*, *Lampropeltis*) and viperid rattlesnakes (*Crotalus*).

4.2.3   Turtles

As with lizards and snakes, turtles exhibit a broad range in SSD, although females are larger than males in the majority of species (Figure 4.1). Female-biased SSD is the rule in several families (e.g. Emydidae, Geoemydidae, Trionychidae), and male-biased SSD is characteristic of others (e.g. Testudinidae, Kinosternidae). The magnitude of SSD in many turtles is greater than that of most snakes and lizards, with females exceeding males by 50–60% in mean shell length for many aquatic emydids (*Chrysemys*, *Trachemys*), trionychid soft-shell turtles (*Apalone*), and pleurodire side-neck turtles (*Podocnemis*). Even more impressive are some geoemydids (*Kachuga*) and emydids (*Graptemys*) in which females average two or nearly three times the length of males. Extremes in male-biased SSD are more modest, although several testudinid tortoises (*Geochelone*, *Gopherus*) and kinosternid mud turtles (*Kinosternon*) typically exceed females by 20–30% in mean shell length.

4.2.4   Crocodilians

Although comparative data are few for crocodilians, male-biased SSD is the rule in this group, with males exceeding females by 20–40% in length for some large alligatorids (*Alligator*, *Caiman*) and crocodylids (*Crocodylus*). However, females may be slightly larger than males in smaller species such as *Alligator sinensis* and the dwarf crocodile, *Osteolaemus tetraspis*.

4.3   Rensch's rule in reptiles

Rensch's rule states that SSD characteristically increases with size when males are the larger sex and decreases with size when females are the larger sex, such that logarithmic plots of male against female size across species have a slope greater than one (Abouheif and Fairbairn 1997; see also Chapters 2, 3, and 6 in this volume). Although many studies have found support for Rensch's rule in reptiles (Fitch 1978; Berry and Shine 1980; Shine 1994a; Wikelski and Trillmich 1997; Shine *et al*. 1998; Kratochvil and Frynta 2002; Cox *et al*. 2003), others have not (Gibbons and Lovich 1990; Braña 1996; Butler *et al*. 2000). On the basis of our extensive literature data-set, we investigated allometry in SSD within each major reptile family or subfamily. Although we did not account for phylogenetic relationships in our analyses, previous studies involving subsets of these data have generally found that allometric patterns are similar in both conventional and phylogenetically based analyses (Abouheif and Fairbairn 1997; Butler *et al*. 2000; Kratochvil and Frynta 2002).

Figure 4.2 reports major-axis slopes from the regression of $\log_{10}$-transformed measures of male size on female size. Out of 24 reptile lineages, eight exhibit significant allometry consistent with Rensch's rule and several others show nearly significant trends toward this pattern. Only natricine snakes exhibit significant allometry opposite Rensch's rule, although several other snake and turtle lineages tend toward this pattern. The average major-axis slope is significantly greater than unity across lizard families ($t = 5.20$, df $= 12$, $P < 0.01$) and across all reptile lineages ($t = 3.12$, df $= 23$, $P < 0.01$), providing support for general tendency toward Rensch's rule.

The ultimate explanations for both this general tendency and its notable exceptions are not clear. Among snakes, Rensch's rule occurs only in those lineages in which male combat and male-biased SSD are common, whereas converse Rensch's rule tends to occur when female-biased SSD is prevalent. The picture is less clear in lizards and turtles. Rensch's rule is evident in several lizard families characterized by territoriality and male-biased SSD, but is conspicuously absent from others with similar characteristics (e.g. Phrynosomatidae, Polychrotidae). Of the two turtle lineages in which male combat and male-biased SSD are common, kinosternids follow Rensch's rule,
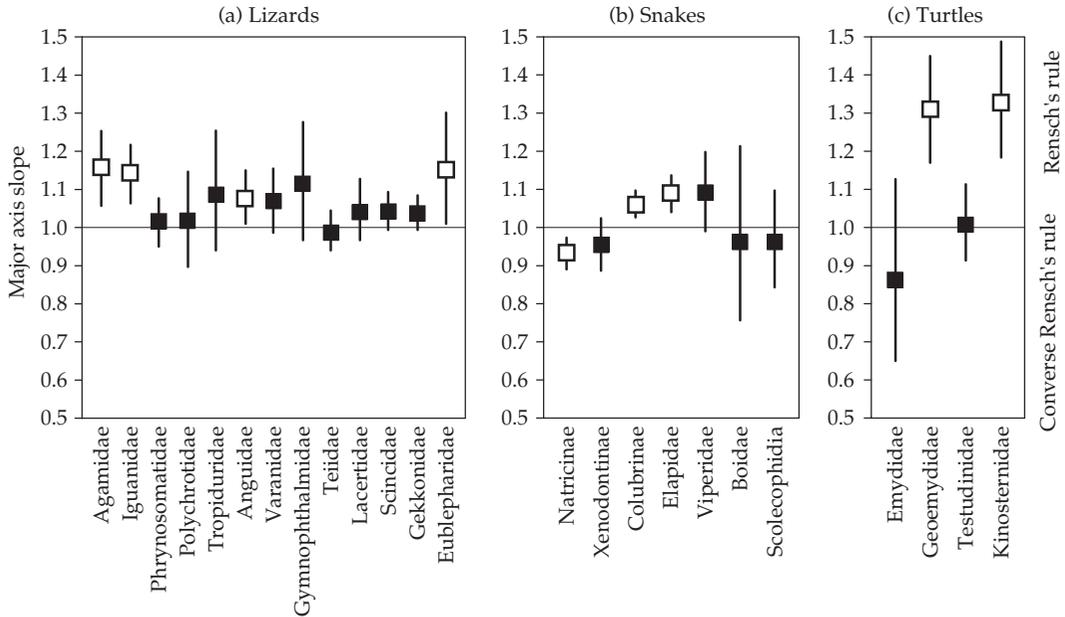
Figure 4.2 Tests for Rensch's rule in major reptile lineages. Symbols indicate slopes (±95% confidence intervals) from major-axis regressions of $\log_{10}$(male size) on $\log_{10}$(female size) within each lineage. Open symbols indicate significant deviations from isometric scaling of male and female body size, as determined by confidence intervals that do not include a slope of 1. These analyses do not account for phylogenetic relationships within lineages.

whereas testudinids do not. Although both emydids and geoemydids are characterized by extreme female-biased SSD, they differ dramatically with respect to Rensch's rule.

4.4 Geographic variation in reptile SSD

Shifts from male-biased SSD at low latitudes to monomorphism or female-biased SSD at higher latitudes have been found in the lizard genera *Sceloporus* (Fitch 1978) and *Leiocephalus* (Schoener *et al*. 1982), and across lizards in general (Cox *et al*. 2003). By contrast, higher latitudes are typically associated with male-biased SSD in *Anolis* lizards (Fitch 1976) and across snake species (Shine 1994b). In either case, these trends appear to be driven primarily by phylogenetic conservatism rather than any systematic tendency for the evolution of SSD in response to latitudinal range expansion within clades (Shine 1994b; Cox *et al*. 2003).

Considerable geographic variation in SSD also occurs *within* many reptile species. The Australian

carpet python (*Morelia spilota*) exhibits the largest known geographic variation in SSD for any vertebrate species. Males from northeastern populations exceed females by a modest 10% in length and 30% in mass, whereas females from southwestern populations are more than twice as long and 10 times as massive as their "dwarf" male counterparts (Pearson *et al*. 2002). In some reptiles, phenotypic plasticity in growth and body size interact with population differences in food availability to drive intraspecific variation in SSD (Madsen and Shine 1993b; Wikelski and Trillmich 1997). Geographic variation in SSD of the slider turtle, *Trachemys scripta*, is related to variation in proximate environmental factors, influencing juvenile growth and the timing of maturation (Gibbons and Lovich 1990). Intraspecific variation in SSD also correlates with population differences in latitude, altitude, climate, and geophysical features (Fitch 1978, 1981; Iverson 1985; Lappin and Swinny 1999). Roitberg (in Chapter 14 in this volume) provides a more detailed discussion of patterns and causes of intraspecific variation in reptile SSD, illustrated by

an extensive analysis of geographic variation in the widespread Eurasian sand lizard, *Lacerta agilis*.

4.5   Selective pressures influencing reptile SSD

Three major, non-exclusive selective pressures have received the majority of attention as ultimate explanations for SSD in reptiles: (1) sexual selection, which arises through variance in mating success and is usually invoked in the context of large male size conferring an advantage in male–male competition; (2) fecundity selection, which favors large female size when number of offspring increases with maternal size; and (3) natural selection for resource partitioning, which occurs when body size is related to resource use, such that SSD reduces intersexual competition. In turn, these distinct selective mechanisms may often vary

predictably with certain suites of characteristics related to habitat or ecological niche. Table 4.1 summarizes recent comparative studies examining the first two hypotheses.

4.5.1   Sexual selection

In lizards, body size often determines success in agonistic encounters between males, and male reproductive success is known to increase with body size in some species (reviewed in Stamps 1983; Cox *et al.* 2003). Further, comparative studies have revealed associations between SSD and the occurrence of male combat or territoriality. Carothers (1984) showed that iguanids with male aggression exhibit strong male-biased SSD, whereas those lacking male aggression are monomorphic. Across lizard families, Stamps (1983) found that the mean SSD is strongly male-biased in

Table 4.1   Summary of recent studies using comparative data-sets (multiple species or populations) to test for correlations between SSD and various measures of sexual selection for large male size and fecundity selection for large female size. Support refers to significant correlations, although we emphasize that many caveats (e.g. strength of correlations, methods of analysis) apply to our simple categorizations of support (see text for further details). Studies that have been superceded by more comprehensive recent analyses are not presented here.

Taxon	Support	Measure	Study
Sexual selection			
Across lizards	Yes	Male aggression	Cox *et al.* (2003)
	Yes	Territoriality	Figure 4.3
	Yes	Female home range area	
	Yes	Ratio of male:female home-range area	
Eublepharid geckos	No	Male combat	Kratochvíl and Frynta (2002)
Anolis sagrei *	No	Female density	Stamps (1999)
Anolis lizards	Yes	Female density	Stamps *et al.* (1997)
Across snakes	Yes	Male combat	Shine (1994b)
Fecundity selection			
Across lizards	Yes	Clutch size	Cox *et al.* (2003)
	No	Fecundity slope	Figure 4.3
	Yes	Reproductive frequency	
	Yes	Reproductive mode	
	No	Length of reproductive season	
Lacertid lizards	Yes	Fecundity slope	Braña (1996)
Emydid turtles*	No	Reproductive frequency	Forsman and Shine (1995)
Across snakes	No	Clutch size	Shine (1994b)
	No	Fecundity slope	
	No	Reproductive frequency	
	Yes	Reproductive mode	

*Phylogenetic relationships not explicitly taken into account.

territorial species, whereas non-territorial species show no overall directional trend in SSD.

Nonetheless, many territorial lizards do exhibit pronounced female-biased SSD, and many non-territorial species have strong male-biased SSD. Further, evolutionary changes in SSD are not associated with the evolution of male aggression in at least one lineage, the eublepharid geckos (Kratochvil and Frynta 2002; see also Chapter 15). In a comprehensive study across lizard families,

Cox *et al.* (2003) showed that evolutionary shifts in male aggression and territoriality are generally correlated with changes in SSD, but concluded that these variables fail to explain most of the inter-specific variance in lizard SSD (Figure 4.3). In part, this may reflect the weak explanatory power of these categorical surrogates for sexual selection, since stronger correlations are observed between SSD and continuous measures such as the ratio of male to female home-range areas (Figure 4.3) and
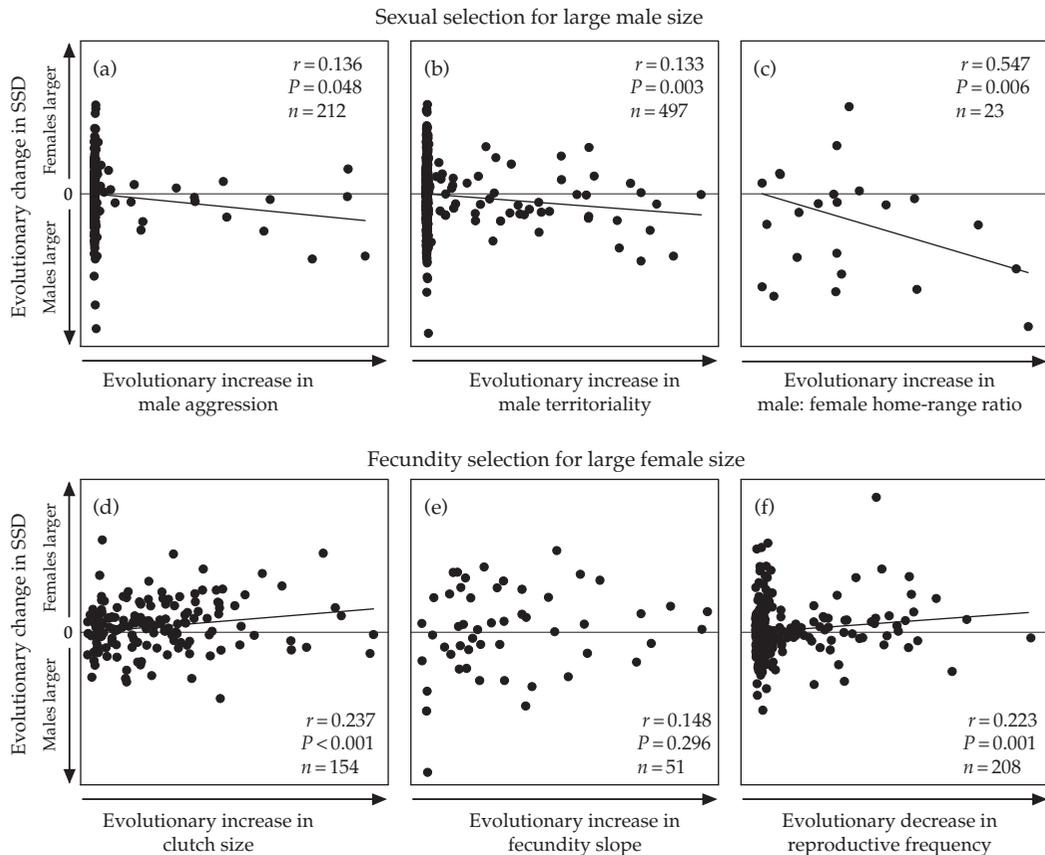

Figure 4.3 Comparative evidence for correlated evolutionary changes in SSD and several measures of sexual selection (top panels) and fecundity selection (bottom panels) in lizards. Values are 'positivized' independent contrast scores from phylogenetically based statistical analyses (see Cox *et al.* 2003 for details). The evolution of male aggression (a) and territoriality (b) are associated with shifts toward larger male size, but SSD also varies considerably in the absence of evolutionary change in either variable. The ratio of male to female home-range area (c) reflects the potential for a single male to defend multiple females within a territory (Stamps 1983). This measure of sexual selection yields a stronger correlation, but data are available for fewer species. The evolution of larger clutch size (d) and lower reproductive frequency (f) are associated with shifts toward larger female size, but SSD is not associated with fecundity slope (e), the slope of the regression of clutch size on maternal size within a population. Sample sizes indicate number of independent contrasts. Multiple regression including measures of sexual selection (territoriality) and fecundity selection (clutch size, reproductive mode, reproductive frequency) reveals that 84% of the intraspecific variation in lizard SSD is left unexplained even when simultaneously considering both hypotheses ($r^2 = 0.16$; $n = 84$; $P = 0.008$). Modified from Cox *et al.* (2003) with permission from *Evolution*.

female density (Stamps 1983; Stamps *et al*. 1997; Cox *et al*. 2003).

Recent intraspecific studies of lizards are revealing a complexity that challenges many of our conventional assumptions about sexual selection on male body size. For example, *Crotaphytus collaris* is a highly territorial, polygynous species in which Baird *et al*. (1997) found that large size confers success in male agonistic encounters for each of three populations with varying degrees of SSD. However, social organization varies with habitat structure, such that the opportunity for sexual selection is high in only a single population, and moreover one with a low index of SSD. Subsequent studies of this species using paternity analyses have revealed that male reproductive success is not correlated with body size, but rather with bite force, which provides a direct measure of performance in male contests (Lappin and Husak 2005). In other territorial species with male-biased SSD, paternity studies contradict the simplistic notion that sexual selection is uniformly directional with respect to male size: females of *Uta stansburiana* and *Anolis sagrei* mate with multiple males and then produce sons by large sires and daughters by small sires (Calsbeek and Sinervo 2004; R. Calsbeek, personal communication).

The majority of snake species exhibit female-biased SSD, with the occurrence of male-biased SSD restricted to derived lineages in which males engage in physical combat. Multiple evolutionary gains and losses of male combat are associated with evolutionary shifts in SSD (Shine 1994b), but considerable variation in the magnitude of SSD occurs even in the absence of variation in male combat. The python *Morelia spilota* is the only snake known to exhibit intraspecific variation in male combat. Interestingly, whereas males are slightly larger than females in the presence of male combat, females are more than twice as long and 10 times as massive as males in its absence (Pearson *et al*. 2002). Large body size generally confers an advantage in male combat (reviewed in Shine 1994b), and success in combat enhances mating success in some species (Madsen and Shine 1993c; Madsen *et al*. 1993; Fearn *et al*. 2005). Even when females are the larger sex and overt physical combat is absent, large male size may be advantageous for scramble competition (Madsen and Shine 1993a; Weatherhead *et al*. 1995), or forcible insemination of females (Shine and Mason 2005).

Turtles are similar to snakes in that the occurrence of male-biased SSD is primarily restricted to lineages with male combat, particularly tortoises, terrestrial emydids, and kinosternids (Berry and Shine 1980). Male combat usually occurs in the presence of receptive females, and large males dominate smaller males in some species (Kaufmann 1992; Niblick *et al*. 1994). The prevalence of male-biased SSD in crocodilians is also believed to result from sexual selection for large male size, which presumably confers an advantage in male aggression and territoriality (Fitch 1981). However, definitive comparative studies of sexual selection with respect to SSD are generally lacking for both turtles and crocodilians.

Historically, most attempts to explain reptile SSD in terms of sexual selection have focused on the advantages of large size in male–male competition. However, SSD may also be influenced by intrasexual competitive advantages of small male size (as in birds; see Chapter 3), sexual selection via female choice, and sexual selection on female size. For example, Zamudio (1998) concluded that patterns of female-biased SSD in horned lizards are consistent with the hypothesis that sexual selection favors small male size. Similarly, Berry and Shine (1980) hypothesized that small male size may favor efficient mate searching and agile precoital behaviors in aquatic turtles.

Although females mate preferentially with large males in some lizard species (Cooper and Vitt 1993; Censky 1997), the evidence for female choice related to male size is generally weak in reptiles (Olsson and Madsen 1995; Tokarz 1995), and available data are too sparse to support robust conclusions with respect to SSD. Interestingly, recent genetic data suggest that many lizards and snakes are polyandrous (Calsbeek and Sinervo 2004; Rivas and Burghardt 2005). Such promiscuity may seem paradoxical with respect to female preference, but may actually facilitate so-called cryptic female choice that resolves intersexual genetic conflict over body size and other traits (see Chapters 16 and 18). For example, females of

several lizard species with male-biased SSD use sperm from large mates to produce male offspring and that of small mates to produce female offspring (Calsbeek and Sinervo 2004; R. Calsbeek, personal communication). This complexity underscores the general point that attempts to explain SSD via sexual selection may often be confounded by inferences drawn solely from behavioral observations in the absence of genetic paternity data. Finally, we note that sexual selection may also influence female size, as in the case of the snake *Thamnophis sirtalis*, in which males mate preferentially with large females (Shine *et al*. 2006).

4.5.2 Fecundity selection

In the majority of reptiles, the number of offspring in a clutch or litter increases with maternal body size, so selection for increased fecundity should favor large female body size. Consistent with this hypothesis, comparative studies have documented evolutionary increases in clutch or litter size associated with shifts toward female-biased SSD in lacertid lizards (Braña 1996) and across lizards in general (Cox *et al*. 2003; Figure 4.3), but not in horned lizards (Zamudio 1998) or Australian snakes (Shine 1994b). The slope of the relationship between clutch size and maternal size within a population presumably offers a more informative estimate of fecundity selection than mean clutch size, since this relationship describes the extent to which selection on female body size is likely to increase fecundity within a given species. Braña (1996) found a strong relationship between this so-called fecundity slope and SSD even after controlling for phylogenetic relationships among lacertids. However, broad-scale analyses across lizards and snakes revealed that correlations between SSD and fecundity slope are no longer significant when phylogeny is taken into account (Shine 1994b; Cox *et al*. 2003). Further, several lizard lineages that have independently evolved invariant clutch sizes of one or two eggs show no systematic tendency towards relatively male-biased SSD when compared to related species with variable clutch size (Shine 1988).

Fitch (1978, 1981) suggested that fecundity selection should be particularly intense in species that reproduce infrequently, as in viviparous species with lengthy gestation periods or species that inhabit temperate regions with short breeding seasons. In lizards, the evolution of viviparity and reduced reproductive frequency are generally correlated with shifts toward female-biased SSD (Cox *et al*. 2003; Figure 4.3). However, evolutionary shifts in these variables explain only a small portion of the associated variance in SSD, and many species that reproduce infrequently nonetheless exhibit strong male-biased SSD. Further, there is no relationship between SSD and continuous measures of reproductive frequency such as length of the reproductive season. The evolution of viviparity is also associated with shifts toward female-biased SSD in snakes, but continuous measures of reproductive frequency do not correlate with SSD (Shine 1994b). Finally, the magnitude of female-biased SSD actually increases with reproductive frequency in emydid turtles, challenging the assumption that the intensity of fecundity selection varies inversely with reproductive frequency (Forsman and Shine 1995). On the whole, comparative data for reptiles provide only weak and inconsistent support for Darwin's (1871) fecundity-advantage hypothesis as an explanation for SSD (Table 4.1).

4.5.3 Ecological hypotheses for SSD

In considering ecological causes for the evolution of SSD, most authors have focused on the role of SSD in reducing competition between the sexes. In particular, sex differences in food type are often associated with SSD, especially in gape-limited predators such as snakes (Shine 1989, 1991). Sea kraits (*Laticauda colubrina*) provide a good example: in populations where multiple prey types are available, large females feed primarily on large conger eels, while small male kraits prey upon small moray eels. However, female-biased SSD remains substantial (50%) even in populations where dietary partitioning does not occur and head-size dimorphism is greatly reduced (Shine *et al*. 2002). Many snake species provide similar evidence that dietary partitioning has influenced the evolution of sexual dimorphism in trophic morphology, but the evidence for a relationship

with SSD is less clear (Shine 1991). Even when SSD and dietary differences are correlated, it is often difficult to determine the causal relationship between the two, since divergence in prey size would not be an unusual consequence of SSD resulting from other factors (Vitt and Cooper 1985). Furthermore, few studies have actually validated the assumption that SSD reduces intersexual competition. Interestingly, Stamps *et al.* (1997) found that intersexual competition coefficients in *Anolis aeneus* are actually predicted to be lower when males and females are the same size than when males are larger.

Even in the absence of intersexual competition, males and females may evolve to different body-size optima given a sufficiently complex adaptive landscape. Schoener (1969a) modeled optimal body size based on foraging energetics and showed that two size optima exist for "sit-and-wait" predators, whereas a single optimum is more likely for "active" foragers. The Lesser Antilles is a chain of small Caribbean islands that have either one or two species of *Anolis* lizards per island, and these lizards fit the assumptions of the sit-and-wait predator model. Across islands, various *Anolis* species follow a remarkably regular pattern of pronounced SSD, with male and female body sizes lying near the predicted body-size optima (Schoener 1967, 1969b, 1977). Although SSD is consistently male-biased, sexual selection alone is not sufficient to explain the similarity of SSD across islands (Schoener 1969b). In fact, if the strength of sexual selection were related to female density (Stamps *et al.* 1997), one would expect variability in SSD across islands. Pronounced SSD may allow solitary species to maximize population-level resource utilization and help explain the incredible densities observed (Rand 1967; Schoener 1967).

A very different situation exists in more complex *Anolis* faunas. With greater numbers of sympatric species, niche compression should result in reduced SSD (Schoener 1969a), which is indeed observed (Schoener 1969b). The most complex *Anolis* communities occur in the Greater Antilles. Each of the four major islands has been the site of an independent adaptive radiation producing the same suite of six "ecomorph" types characterized by different microhabitats and lifestyles. For example, species characterized as trunk-ground ecomorphs live close to the ground in relatively open habitat, use a sit-and-wait foraging strategy, and are generally territorial. In contrast, twig anoles live in the crowns of trees in dense matrices of thin twigs and tend to use an active foraging mode of searching for prey. This microhabitat specialization has resulted in the evolution of correlated differences in morphology, behavior, and—interestingly—SSD (Butler *et al.* 2000; Butler and King 2004). Trunk-ground and trunk-crown ecomorphs consistently evolve high SSD, whereas trunk, crown-giant, grass-bush, and twig anoles repeatedly evolve low SSD (Figure 4.4). The selective pressures driving the repeated evolution of convergent dimorphisms are not clear because precise information about mating system, niche breadth, and species and sex overlap in resource use are not available across all ecomorphs. However, the pattern is not an artifact of phylogenetic inertia, as SSD evolves repeatedly (Figure 4.4), and neither is it correlated with body-size evolution. Sexual dimorphism in shape is also partitioned by ecomorph type. When males and females are plotted in multivariate shape morphospace, the sexes form separate clusters in some ecomorphs (trunk-ground and trunk-crown), whereas the species/sex classes are interdigitated in the remaining ecomorphs (Butler *et al.* 2007). Thus, patterns of sexual dimorphism are not only highly convergent to microhabitat type, but also serve to increase "species packing" within these complex lizard assemblages.

Turtles provide another intriguing association between SSD and ecological specialization. Berry and Shine (1980) noted that most turtles could be placed into one of four major ecological categories: (1) aquatic swimmers, (2) semi-aquatic species, (3) aquatic bottom-walkers, and (4) terrestrial species. Females are larger than males in most aquatic swimmers, males equal or exceed female size in most semiaquatic species and aquatic bottom-walkers, and male-biased SSD reaches extremes in terrestrial tortoises and emydids. Berry and Shine (1980) suggested that male combat and forced insemination favor large male size in terrestrial, semi-aquatic, and aquatic bottom-walking species,
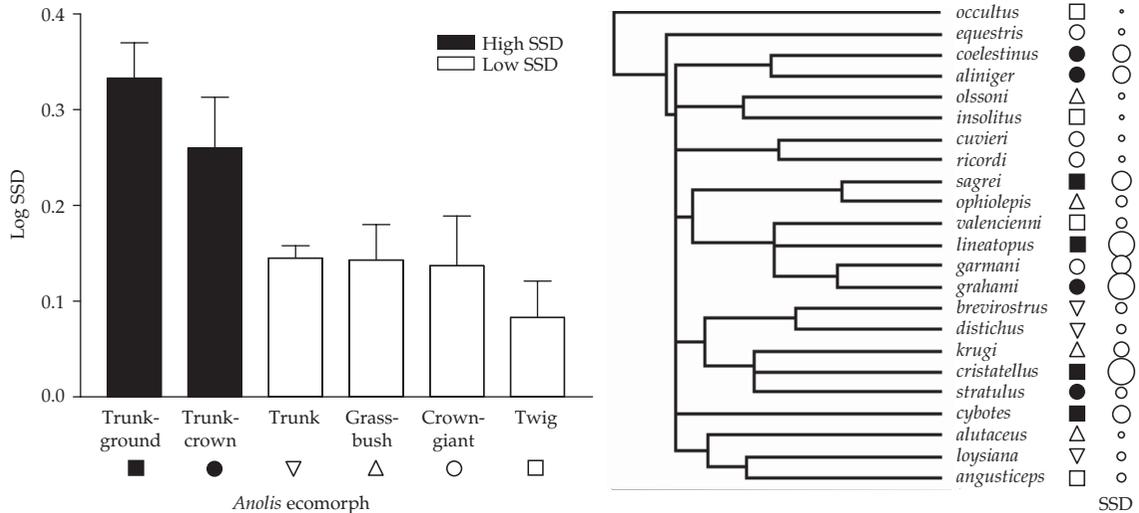
Figure 4.4   Association between ecomorph (habitat) type and SSD in 23 species of Greater Antillean *Anolis* lizards. The left-hand panel shows mean (±1 SE) log SSD for each ecomorph type. All species exhibit male-biased SSD, but the repeated convergent evolution of trunk-ground and trunk-crown ecomorphs (dark symbols and bars) is consistently associated with an increase in the magnitude of SSD (indicated by the size of the circles on the far right). Redrawn from Butler *et al.* (2000) with permission from *Evolution*.

whereas small male size confers an advantage in agile courtship behaviors and mate searching in aquatic species. However, Gibbons and Lovich (1990) suggested that size-dependent predation simply prevents most terrestrial males from maturing at the early ages and small sizes that are favored in aquatic species. Although there is some disagreement about the actual selective forces driving this correlation between SSD and habitat, the association remains striking.

4.6   Constraints on reptile body size

4.6.1   Female reproductive burden

In reptiles, the burden of a clutch or litter may impose substantial constraints on female morphology. An interesting example occurs in Asian flying dragons of the genus *Draco*, which glide from trees by extending their modified ribs and associated membranes to form crude airfoils. Despite the fact that males are territorial and large size enhances male reproductive success, many *Draco* species exhibit female-biased SSD, and *Draco melanopogon* females also exceed males in relative head size, wing size, and tail length. These atypical

dimorphisms may represent sex-specific adaptations to permit gliding when females are encumbered by a clutch (Shine *et al.* 1998). However, studies of live animals suggest that small size actually enhances gliding, and that gravid females are reluctant to glide (McGuire and Dudley 2005; J. McGuire, personal communication). Thus, an additional possibility is that selection for enhanced gliding has favored small size in males, but opposing advantages of large size or reduced frequency of gliding have prevented the complementary evolution of small female size.

Many arboreal lizards have evolved reduced clutch size, presumably as an adaptation to facilitate arboreal locomotion (e.g. *Anolis*, gekkonids, and some skinks). Andrews and Rand (1974) observed that these taxa use adhesive toe pads for climbing and suggested that their adhesive properties may fail if mass is greatly increased. One consequence of reduced clutch size is that fecundity selection should favor increased reproductive frequency over the per-clutch fecundity advantage of large female size. However, Shine (1988) found no consistent trend toward male-biased SSD in species with invariant clutch size when compared to related species with variable

clutch size. Arboreal species that rely on claws or grasping rather than adhesive toe pads tend to have relatively larger clutch and body sizes (e.g. *Polychrus*, *Iguana*, chameleons), indicating that mode of arboreal locomotion may influence both clutch and body size. However, implications with respect to SSD per se are less clear.

4.6.2   Energetic growth constraints

Most reptiles continue to grow after sexual maturation, such that energetic costs of reproduction may constrain energy allocation to growth. In some species, reproductive females expend nearly twice the total metabolizable energy as males, whereas in others males may have substantially greater respiratory expenditure than females during the mating season (Merker and Nagy 1984; Orrell *et al*. 2004). Given that males and females often differ in the timing and relative magnitude of reproductive investment, growth may often be differentially constrained in each sex, giving rise to SSD (see Chapter 19).

Adult male *Cophosaurus texanus* lizards average 10% larger than females because of a divergence in growth that occurs when females initiate reproduction. Estimates of the energetic costs of growth and egg production suggest that SSD would be essentially eliminated if females were to hypothetically allocate the energy content of a clutch into growth, rather than reproduction (Sugg *et al*. 1995). Similarly, male and female diamond-backed rattlesnakes (*Crotalus atrox*) grow at comparable rates until maturity, when females shift energy allocation to reproduction at the expense of growth, resulting in male-biased SSD (Duvall and Beaupre 1998). However, sex differences in growth are absent when captive snakes are raised on controlled diets, suggesting that proximate environmental factors predominate in the development of SSD (Taylor and DeNardo 2005). In several species of *Sceloporus* lizards, female-biased SSD may develop because male growth is constrained by metabolic costs (i.e. increased movement, activity, and home-range defense) associated with maturational increases in plasma testosterone (see Chapter 19).

Of course, even when the growth of one sex is constrained by energetic costs of reproduction, the continued post-maturational growth of the opposite sex implies that there is some additional selective advantage to large size. However, the important point is that the actual magnitude of SSD depends not only on the strength of selection on male or female size, but also the extent to which growth in each sex is constrained by energetic costs of reproduction. These constraints will depend upon the timing of maturation and the nature of reproductive investment in each sex, as well as the extent to which environmental factors (e.g. food availability) provide a context for energetic trade-offs. If such energetic growth constraints are prevalent in reptiles, this may help explain why so much of the interspecific variance in SSD is left unaccounted for by measures of sexual and fecundity selection (Cox *et al*. 2003).

4.7   Summary

Most studies interpret observed patterns of reptile SSD in light of sexual selection for large male size, fecundity selection for large female size, and natural selection to reduce resource competition. Although sexual selection for large male size has clearly influenced the evolution of reptile SSD, the broad explanatory power of this hypothesis is uncertain because we generally lack sufficient comparative data beyond simple categorizations of the presence or absence of male combat or territoriality. Future work would benefit from more precise descriptions of the intensity of sexual selection on male size and other traits, since recent paternity analyses have revealed complexity that goes beyond simple directional selection favoring large males, and that size may be less important than other traits in determining reproductive success.

Although fecundity increases with female body size in many reptiles, comparative data provide only weak and inconsistent support for the fecundity advantage of large female size as an explanation for SSD in this group. For most reptiles, we still lack quantitative data on lifetime fecundity as it relates to female growth and size, ecological determinants of optimal body size, and energetic costs of reproduction and their impact on growth of both males and females. Although broad

comparative studies have been valuable for suggesting major patterns and hypotheses, the relative importance of these processes will likely remain uncertain until we are able to develop more detailed predictions incorporating linkages between behavioral strategies for acquiring energy, rates of energy expenditure for growth and reproduction, mating system, and fitness. We believe that the key to further understanding lies in the integration of comparative, demographic, and experimental techniques designed to simultaneously address both the ultimate evolutionary causes and proximate developmental mechanisms for SSD.

4.8   Acknowledgments

4.9   Suggested readings

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