



## FORUM

# Understanding sexual size dimorphism in snakes: wearing the snake's shoes

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Sexual size dimorphism (SSD) is widespread in almost every group of animals, generating great scientific interest (Andersson 1994). Most research has been on species in which males are larger than females. Explanations tend to focus on the advantages of size for direct male–male competition over access to fertile females or resources needed by females for reproduction. However, this explanation has been more difficult to apply to snakes where SSD is often extreme and female biased and in which intraspecific aggression, dominance hierarchies and territoriality are rare. Although relatively large males have been shown to have a greater mating success in some species (Shine 1978; Shine 1993; Madsen & Shine 1994), they have not in others (Madsen & Shine 1993; Madsen et al. 1993; Weatherhead et al. 1995). Recently Shine et al. (2000) and Crews (2000) discussed conflicting evidence on the role of male body size in mating success in common garter snakes, *Thamnophis sirtalis*, in this forum, but were unable to resolve the different empirical results. Sometimes scientific assumptions or ingrained points of view may hinder recognition of other possibilities. Here we discuss an alternative approach to generating testable hypotheses: critical anthropomorphism (Burghardt 1991). By using critical anthropomorphism we propose a new hypothesis that has the potential to settle this controversy.

Jacob von Uexküll (1909/1985) advocated studying the behaviour of animals by considering both their inner world (Innenwelt) and how they perceived and responded to their environment (Umwelt). A major aspect of this approach was to evaluate differences among species in the salience of biologically relevant perceptual cues (Tinbergen 1951; Burghardt 1985). Recent proposals to study animal cognition focus on the ways that animals

perceive, interpret and experience the world (Griffin 1978; Cheney & Seyfarth 1992; Glotzbach 1992; Burghardt 1997; Bekoff & Allen 1997). An important component of this approach, although often understated, is to consider the animal being studied as an active participant, with the researcher trying to put him or herself in the animal's situation. This is especially true for those studying primate behaviour (Herzog & Galvin 1997). Timberlake & Delamater (1991) proposed that to understand the behaviour of an animal 'Experimenters not only need to put themselves in the subject's shoes, they need to wear them—walk, watch, hear, touch and act like the subject' (page 39). One approach to doing this and still maintaining scientific rigour is to apply a critical anthropomorphism in which hypotheses are based on existing scientific knowledge about the species being studied as well as considering the 'shoes' (point of view) of other organisms (Burghardt 1991). We apply this method to the maintenance of female biased SSD in snakes, where males compete physically for access to females in the context of actual mating.

In most snake species females are larger than males, reversing the typical terrestrial vertebrate pattern where males are of equivalent or larger size than females (Shine 1994). Large size in female snakes is considered adaptive in species that grow throughout life with little or no parental care, and in which larger females produce more and/or larger offspring. Larger offspring have higher survival rates and can store more yolk or fat for their development (see Ford & Seigel 1989 for a review). Natural selection should, therefore, favour large size in females. Male snakes, on the other hand, benefit from traits that enhance their ability to find and successfully court females (Table 1). Thus, refined chemosensory senses, high mobility, being inconspicuous to predators, early maturation, small size and decreased costs of locomotion would be adaptive (Duvall et al. 1993; Madsen et al. 1993; Shine 1993; Andersson 1994).

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**Table 1.** Possible benefits and disadvantages of large size in males and females; the benefits and disadvantages of small size can be inferred from the opposite reasons mentioned

	Benefits of large size	Disadvantage of large size
Both sexes	<ol style="list-style-type: none"> <li>1. Increased number of potential prey species</li> <li>2. Ability to subdue prey</li> <li>3. Less frequent feeding on often risky prey</li> <li>4. Fewer predators</li> <li>5. Lower energetic cost per unit of body mass</li> <li>6. Greater body temperature stability</li> </ol>	<ol style="list-style-type: none"> <li>1. More easily detected by predators</li> <li>2. Greater energetic needs</li> <li>3. More conspicuous to their prey</li> <li>4. Higher costs of locomotion</li> </ol>
Females only	<ol style="list-style-type: none"> <li>1. Increased fecundity due to increased coelomic capacity that allows larger clutches</li> <li>2. Possibility of larger offspring with greater chances of survival</li> </ol>	
Males only	<ol style="list-style-type: none"> <li>1. Increased number of matings and fitness in males if there is male–male physical competition for mating access</li> </ol>	<ol style="list-style-type: none"> <li>1. Higher costs for locomotion and tracking of females during mating season</li> </ol>

Female biased SSD is probably the ancestral condition of snakes as a group (Rivas 2000). Thus, smaller size in males can be explained by the lack of selection pressure towards large body size (Semlitsch & Gibbons 1982). Unlike lizards, their sister squamate taxa, territoriality has not been reported in snakes, and male–male fighting is also uncommon. Thus, selection forces for large male size are generally lacking (Shine 1993). However, in conditions of high density, where females are very easy to track, or where females do not breed every year, several males would encounter each other while courting a female and male–male combat is likely to evolve (Shine 1978, 1993; Duvall et al. 1992). The relationship between male–male fighting and male size in snakes has been discussed broadly (Shine 1978, 1993; Madsen et al. 1993; Madsen & Shine 1994). If larger males are more successful in combat and obtain more matings than smaller males, large size in males would be favoured by selection. Male combat is much more frequent in snake species where males are larger than females or where SSD is absent (Shine 1994).

There are, however, some species where sexual selection appears to favour male biased SSD, yet males are not larger than females (Madsen et al. 1993; Madsen & Shine 1993; Weatherhead et al. 1995). Grass snakes, *Natrix natrix*, breed in mating balls where males wrestle with the tail in subtle combat and larger males obtain more matings than small males (Madsen & Shine 1993). A similar scenario has been found in northern water snakes, *Nerodia sipedon*, where larger males accomplish more matings than smaller males in multiple-male breeding aggregations (Weatherhead et al. 1995; Brown & Weatherhead 1999). On the other hand, there are data showing that male common garter snakes, *T. sirtalis*, do not obtain an advantage by being larger (Joy & Crews 1988). However, recent studies on the same population reveal that larger male garter snakes do obtain more matings than smaller males (Shine et al. 2000). Madsen & Shine (1993) argue that if females obtain more benefits from large size than

males, males may remain smaller than females. However, the selection gradient for increased size for males obtaining multiple matings is both proportional to, and higher than, the comparable selection gradient for females due to the increased fecundity of larger females (Duvall et al. 1993; Madsen et al. 1993; Shine & Fitzgerald 1995; Weatherhead et al. 1995). Thus, it is not clear how an increase in the fecundity of larger females would not increase even more the fitness of males that can obtain more matings in the polygynous system considered the dominant mating system in snakes (Duvall et al. 1992, 1993; but see Rivas 2000). Furthermore, homologous morphological traits in males and females are expected to show high genetic correlations (Halliday & Arnold 1987); if true, any selection for large size in females should also increase the size of the males. Predictions from these models do not appear plausible when faced with the extent of the dimorphism seen. Perhaps we have been overly influenced by the behaviour of lizards, birds and mammals, in which size and strength seem to be major determinants in mating success, and have inappropriately applied the evolutionary logic proposed for these groups to snakes.

In the literature regarding SSD it has not been hitherto proposed that males could suffer a sexual selection disadvantage from being too large. Consider the problems of being a male snake in search of potential mates, putting ourselves in the 'animals shoes'. Being too large could actually be a disadvantage in multimale breeding aggregations. Males search with their tails for the female's cloaca (as described by Gillingham 1979, 1987; Madsen & Shine 1993; Weatherhead et al. 1995). With their heads (and chemoreceptors) facing away from the female's cloaca, vision and chemoreception are of limited use to males. Males are more likely to rely heavily on tactile cues to identify the female and secure intromission, as has been demonstrated in some species (Pisani 1976; Perry-Richarson et al. 1990). Thus, a male as large and thick as the female could mislead other males into mating



**Figure 1.** Breeding female anaconda (Ashley, 475 cm TL) at the shore of a lagoon in the Venezuelan llanos, being courted by 11 males. Photo Jesus Rivas.

with him. The result would be that a very large male might have to spend time and effort fighting off other males that might attempt to mate with him. If this is so, in species that mate in large multimale breeding aggregations, smaller male body size could be a cue for sex recognition for other males as well as for the female. A courted male, as well as the males that court him, would be at a disadvantage compared with smaller males that do not mislead other males. This constraint on large male body size may lead to a local size optimum, where males are large enough to win combats with other males in the breeding aggregation, and yet be small enough to be distinguished from breeding females. In those snake species that do show male–male combat, breeding aggregations are not common and sex recognition during courtship is not a selection pressure limiting male size. Thus, selection for large male size in species that engage in male–male combat is fully expressed.

To seek and court large bulkier animals is adaptive for a male, since larger and thicker females have more offspring (Ford & Seigel 1989) and are more likely to breed (Rivas 2000). Such females are also older and more experienced. Hence, it would benefit males to court the animals with the largest girth, both for certainty of courting the right sex (and individual) and for increase of fitness. Thus, SSD could be the key for sex identification in situations where the chemosensory organs are not involved or the pheromones of the females and scents of the males have impregnated all the animals in the

seething breeding ball. Success may belong to the male who can best discriminate males from females, manoeuvre into position for copulation, and simultaneously thwart other males from doing likewise.

The above scenario can be applied and partially tested by studies of green anacondas, *Eunectes murinus*, which also breed in multiple-male aggregations where a female is courted by several males. In these aggregations males coil around the female and search for her cloaca with their tails; visual or chemical cues do not appear to be involved (Fig. 1; Rivas 2000). If one male is very large it can be mistaken for a female by other males and be courted (Fig. 2). Selection would favour large size in males in order to outcompete other males, as larger males are more likely to be found mating with the larger and more fecund females (Rivas 2000). However, there is an optimal size where males start being confused with females by other males; this imposes a limit on male size. The result would be stabilizing selection on males, producing a population structure where all the males have a very similar adult size and the overlap of size between males and females is minimal (Fig. 3). We predict that this sort of confusion between large males and females could be present in most, if not all multimale breeding aggregations. In particular it seems to apply to the experiment of Madsen & Shine (1993) with grass snakes (*N. natrix*), where they report that ‘Males seemed to become confused between the female’s tail and those of other males, and the tails of rival males often became entwined’ (page



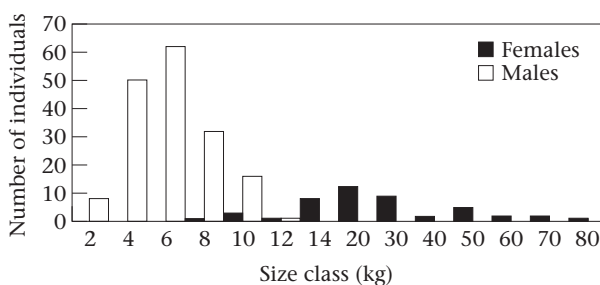
**Figure 2.** Mating aggregation of anacondas involving a very large female (Ashley) and 11 males. The female moved out of the water and dragged with her some of the males that were coiled around her (A). Other males were removed from their positions and tried to find the female again to continue courtship. However, some smaller males have mistakenly coiled around a very large male and are courting him (B).

562). That size cues by males to the female's presence is also suggested in the report of Noble (1937) on two small male *T. sirtalis* that, for half an hour, courted a large male from another region where the animals were not reproductively active at the time. In his recent reply to Shine et al. (2000), Crews (2000) argued that the number of males involved in a breeding aggregation may lead to different outcomes in the competition between males; this could be the reason why his results (Joy & Crews 1988) differ from those of Shine et al. (2000). Shine et al. used only a relatively small number of males (perhaps a more common scenario in the mating system of garter snakes throughout North America), whereas Crews

worked with a larger number of males per aggregation (simulating the scenario of the particular dense breeding aggregations found in southern Canada). We believe that in large breeding aggregations males may, in fact, be more likely to be mistaken for females, thereby decreasing the benefit of large male size. In small aggregations, however, the size advantage in displacing other males from the female's vent is more effective and larger males tend to be more successful.

This mechanism of sex identification may have evolved through the differential sexual maturation of males and females. Females often delay sexual maturation and become relatively larger before breeding, allowing larger clutches. Males start breeding earlier and at a smaller size, increasing their reproductive output since the fecundity-independent costs of reproduction are lower (Bell 1980; Madsen & Shine 1994) and territorial defence and establishing dominance are not prerequisites for mating. This differential maturation sets the scenario for natural selection to act and SSD could thus be selected as a method for sex discrimination.

To this point we have approached the actual courtship events from the male's perspective; the female's perspective must also be considered. Since larger males are either older or more successful foragers, females should prefer larger males over smaller males. Females are known to be selective in mating aggregations. Perry-Richardson et al. (1990) found that female *T. marcianus* rejected some males, even after intromission had occurred. In breeding



**Figure 3.** Size distribution of the adult population of anacondas from the Venezuelan llanos. The criteria to determine adulthood was finding them involved in a breeding aggregation. Notice the change in the scale of the X axis after 14 kg.

several generations of *T. melanogaster* in our laboratory, we also have noted females accepting some males and not others. Joy & Crews (1988) suggested that some individual males may be consistently more successful than others. Female choice might make a large difference in the fitness of offspring. Drickamer et al. (2000) report that female house mice, *Mus domesticus*, mated with males they preferred and, as a result, had more fit offspring than females that mated with nonpreferred males. Comparable phenomena may occur in snakes. What decision processes are female snakes using to accept or reject a male's advances? In a breeding ball several males court a female at the same time. It is very likely that the only way she can discriminate and choose among the males is, again, by relying on tactile cues. Does she have the ability to differentiate from the displays given by the anterior end of the snake (typically directed at the dorsum of her neck), to determine which tail is worthy of her favours? It may be necessary to observe a mating ball three dimensionally from the interior to better understand the processes involved. A focus on mechanisms of female choice is needed.

Female ethologists have correctly emphasized the value that taking a female perspective has added to our understanding of social behaviour, especially in primates (Small 1993; Gowaty 1994; Cunningham & Birkhead 1997). If a von Uexküllian approach to behaviour had been applied in the past, errors such as neglecting, presumably unconsciously, the role of females in social systems might never have occurred. Similarly, we feel that through applying a critical anthropomorphism it is possible to analyse the snake's Umwelt, and obtain testable, and perhaps more valid, insights about both the processes involved in these events and how sexual selection might be operating. Unfortunately, we currently have little data on the specific stimuli used by females to select males or the extent of female choice in snakes.

Too often ethologists and herpetologists regard snakes and other reptiles as robot-like machines or as animals so alien from us that attempting to put ourselves into their world, even heuristically, is both useless and a scientifically dangerous conceit. On the contrary, approaching unresolved issues by considering the perceptual world and the perspective of the target animal may generate testable hypotheses that were previously unconsidered. This may prove to be true in research on snake mating systems as well as on the evolution and maintenance of SSD.

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