

# SEXUAL SIZE DIMORPHISM AND THE MATING SYSTEM OF THE GREEN ANACONDA (*EUNECTES MURINUS*)

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**ABSTRACT.**—We examined 50 breeding aggregations of Green Anacondas (*Eunectes murinus*) collected over an eight-year period. Aggregations were composed of one female and 1–13 males. *Eunectes murinus* shows a female-biased sexual size dimorphism (SSD), with females averaging considerably larger (32.6 kg) than males (7.0 kg). This is surprising because males mate in multiple-male breeding aggregations, where larger males seem to benefit from large size. However, larger females are courted by more and larger males. Females mate several times within a season and likely with several males. Males, on the other hand, do not appear to mate with more than one female per season. Males spend considerable time and energy in courtship ( $\bar{x}$  = 14 days) and the mating season is relatively short. Hence, we propose that *de facto* polyandry is the main mating system in this species.

## INTRODUCTION

A major gap in our knowledge of snake ecology, and especially mating systems, is the lack of information based on field research (Slip and Shine, 1988). Published studies of reproductive ecology are dominated by notes on animals in captivity (Carpenter et al., 1978; Barker et al., 1979; Gillingham and Chambers, 1982; Tolson, 1983, 1992; Hammond, 1988; Perry-Richardson, 1991; Schuett and Schuett, 1995). Studies on the reproductive ecology of West Indian boas (Tolson, 1992; Tolson and Henderson, 1993) and Australian pythons (Pearson et al., 2002a, b) are among the few investigations based on field studies of tropical snakes, but comparable information concerning mainland Neotropical species are lacking. Long-term field studies are required to understand the evolutionary forces acting on snakes and their behavioral ecology (Duvall et al., 1993). Generalizations about mating systems of snakes, generally thought to be polygynous in a manner comparable to those of most lizards, may be premature. We have discussed alternative views elsewhere (Rivas and Burghardt, 2005). Here we present detailed data on the mating system of the Green Anaconda (*Eunectes murinus*), a semi-aquatic vertebrate with one of the largest known sexual size dimorphism (SSD) indices (Rivas, 2000; Rivas and Burghardt, 2001).

## METHODS

### Study Area

The study was carried out on two cattle ranches (El Frío and El Cedral) in the Venezuelan llanos, Apure State (7° 41' N, 69° 03' W; 7° 30' N, 69° 18' W, respectively). The climate of the llanos is highly seasonal. The study area is a seasonally flooded savanna with low grassland. Rivas (2000) and Rivas et al. (2002) provided detailed descriptions of the habitat.

### Data Collection

We conducted fieldwork during the dry seasons of 1992–1999. Mating occurs during the dry season, when snakes are concentrated and easier to locate and capture (Rivas et al., this volume). We systematically searched remaining water bodies and detected animals with our feet, poles, or by visual contact (Rivas, 2000; Rivas et al., this volume). At the height of the dry season, we often found breeding aggregations composed of one female and several males (hereafter, breeding balls; Fig. 1). We captured all animals in and within 5 m of breeding balls, processed them, and released them within 24 h. For each animal captured, we recorded total length, tail length, mass, and sex.

While capturing animals in breeding balls, we were not always able to monitor all males that were mating or those nearest the cloaca of the female, which potentially had a better chance of mating. However, we managed to collect these data from 16 breeding aggregations. We considered males that were mating or in a mating position to be “successful.” We also calculated the probability of a male’s success in a breeding ball by dividing 1 by the number of males in the breeding ball. We then calculated the expected probability of a male mating as the average of the probabilities of mating among all the breeding aggregations.

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We monitored the development of several breeding balls by force-feeding radiotransmitters to 15 females (Rivas, 2000). We collected all snakes from four breeding balls and placed them in outdoor enclosures to observe mating behavior. In addition, we monitored the duration of the breeding balls in nature by visual observation of three unmarked breeding females, and, if they were not evident, by thoroughly searching places where they had been seen.

We force-fed radiotransmitters to 28 adult males captured opportunistically (Rivas, 2001) in order to study the duration of males in the breeding aggregations and to assess a male's breeding investment (Rivas, 2001; J. Rivas, unpublished). We collected data on the duration of courtship from 16 males captured more than once in a breeding ball, and from three males held in outdoors enclosures. Nine adult males found in breeding balls were force-fed transmitters and subsequently tracked. Seven of them rejoined the breeding ball after the animals were radio-equipped. We dropped the two males that did not rejoin the ball from the analysis, assuming that capture might have influenced their behavior. We also monitored the duration of 10 other males by following the radio-implanted females they were courting. Eleven other males were recaptured by chance in breeding balls. These data allowed us to determine the time they stayed in aggregations. Data analyses consisted of non-parametric correlations, and we performed mean and variance comparisons with SAS 6.10 (SAS Institute, Cary, North Carolina). Levene tests and coefficients of variation were used to

compare the variances of sizes of the animals (Sokal and Braumanm, 1980; Madansky, 1988).

## RESULTS

### Mating Aggregations

We often found mating aggregations of *Eunectes murinus* during the dry season. Males were found coiled around a female in shallow water, forming a mass that usually broke the surface through aquatic vegetation. Occasionally, females were encountered at the water's edge or partially buried in mud and drying vegetation. Large females often were found in shallow water or on dry land.

Males likely find females using chemosensory cues to track pheromone trails laid by the female. The chemicals are considered to be non-volatile molecules produced in the skin (Ford and Low, 1984; Ford and O'Blesness, 1986; Mason et al., 1989; Ford and Holland, 1990; Mason, 1992). However, males were often seen tongue-flicking during the mating season, seemingly detecting airborne molecules. These observations suggest that males can use airborne molecules to detect receptive females.

In breeding balls, males generally coil around the caudal quarter of a female, but sometimes nearly cover her entire body. While coiling around her body, males scratch the female with their spurs, moving them rapidly in a "tickling" fashion. Males also stimulate the female with their spurs and induce her to move, facilitating the opposition of their cloacae. The males' use of spurs occurs in bouts, typically 10–30 sec in duration.

Females often move or twitch in response, allowing males to maneuver into a copulatory position. Spur use seems to be an important feature of courtship in *E. murinus*.

Each breeding ball consisted of one female and one to 13 males ( $\bar{x}$  = 3.83; median = 3; N = 50; Fig. 2). When a new male joined a ball, he coiled around the female and started pushing his way toward the female's cloaca. Males already present responded to the arrival of a new male by tightening their coils and attempting to expel the newcomer with their bodies. On several occasions, we observed males coiling around a female's neck, apparently courting the "wrong end." On at least four occasions, we also saw males coiling



Fig. 1. A breeding female *Eunectes murinus* (410 cm TL; 44 kg) courted by 12 males.

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**Table 1.** Measurements of adult Green Anacondas (*Eunectes murinus*) involved in breeding aggregations. Means are presented  $\pm 1$  SD.

	Total Length (cm)	Snout-vent Length (cm)	Body Mass (kg)
Females N = 48	370.4 $\pm$ 70.6 (242.7–517.3)	326.2 $\pm$ 65.9 (210.7–477.0)	32.60 $\pm$ 18.59 (9.25–82.50)
Males N = 177	263.2 $\pm$ 28.3 (188.3–333.7)	225.9 $\pm$ 24.7 (159.3–293.7)	6.96 $\pm$ 2.07 (2.45–14.30)

around and “courting” the tail of a large male, apparently confusing him with the female due to his large size. In one instance, a very small female (275 cm TL, 11 kg) was courted by four males, two of which were relatively large (277 cm TL, 8.75 kg; 280 cm TL, 8 kg), which in turn were being courted by other males in the breeding ball. A similar example of males being mistaken for females was recorded by Rivas and Burghardt (2001).

Movement within a mating aggregation is not readily evident. We never saw actual or ritualized combat, as described for some species of snakes (Gillingham et al., 1983; Gillingham, 1987; Tolson, 1992). However, males can only copulate if their vent is near that of a female, so slow-motion wrestling may occur, with males pushing one another away from the vicinity of the female’s cloaca. Analysis of time-lapse video taken of a wild-caught breeding ball mating in an enclosure showed that males breathe heavily. Breathing is subtle and not usually apparent. Panting was not apparent either in real time or time-lapse footage of single-male mating couples filmed in captivity at the Bronx Zoo.

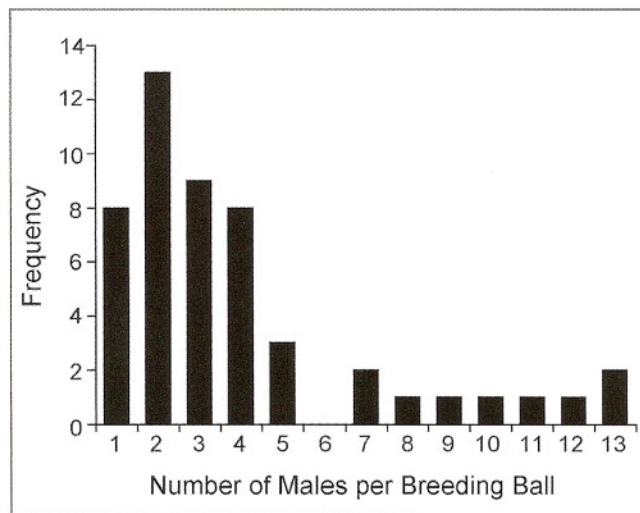
We documented copulation in 11 breeding balls by capturing the snakes and confirming intromission. In one instance, we noticed copulation occurring (i.e.,

hemipenis inside a female’s cloaca) before we disturbed the mating aggregation. Copulation continued for 100 min until dusk, when we disturbed the animals to collect body measurements. At the moment of capture, the copulating male tightened his coils to prevent the hand of the researcher (JAR) from getting between his body loops. When the male’s resistance was overcome, the female coiled her tail around the body of the male to prevent him from being removed from his copulatory position. Until then, because their heads and eyes were under muddy water, the animals did not seem to be aware of our presence. We interpret this behavior as an effort to prevent an arriving male from replacing the mating one. This observation also suggests that males resist the efforts of other males to replace them from the copulatory position, and that females are active participants in mating and do not passively accept a copulating male.

### Sexual Dimorphism

Adult females are longer ( $t = 15.67$ ,  $P < 0.001$ ,  $df = 223$ ) and heavier ( $t = 17.64$ ;  $P < 0.001$ ;  $df = 223$ ) than males. Males showed a smaller relative and absolute variance in sizes than females (Levene test,  $F_{1,233} = 71.51$ ;  $P < 0.0001$ ; Table 1; Rivas and Burghardt, 2001). Absolute lengths of tails of males are shorter ( $\bar{x} = 37.44$  cm) than those of females ( $\bar{x} = 49.06$  cm;  $t = 5.48$ ,  $P < 0.001$ ,  $df = 195$ ; Rivas and Burghardt, 2001). However, males have relatively longer and more slender tails than females. Relative tail length (RTL = tail length/SVL) differed significantly ( $t = 7.35$ ,  $P < 0.001$ ,  $df = 195$ ). The RTL of smaller males is significantly larger than that of longer animals ( $r = -0.39$ ,  $P < 0.001$ ,  $N = 177$ ). The variance in tail length also is smaller for males than for females (Levene test;  $F = 11.58$ ,  $P < 0.001$ ). The coefficient of variance (CV) of the tail length also is significantly different between males (0.155) and females (1.02;  $t = 28.54$ ,  $P < 0.0001$ ,  $df = 223$ ), with males showing much smaller variance than females.

Males have longer spurs ( $\bar{x} = 7.47$  mm) than females ( $\bar{x} = 5.13$  mm;  $t = 8.49$ ,  $P < 0.0001$ ,  $df = 51$ ; Fig. 3) despite the larger size of females. Variance in spur



**Fig. 2.** Frequency distribution of male Green Anacondas (*Eunectes murinus*) found in breeding aggregations.

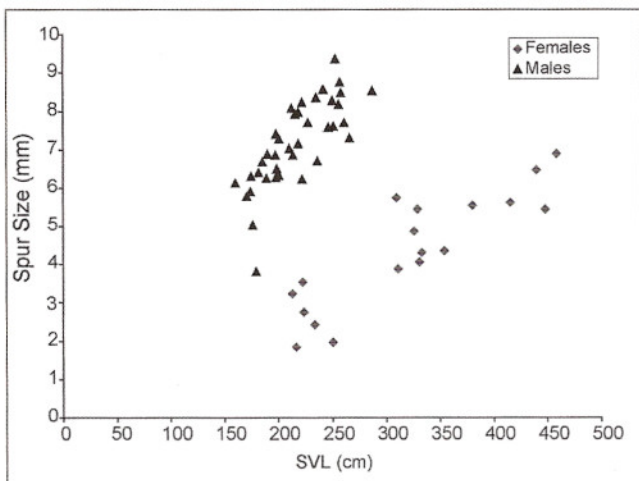


Fig. 3. Spur length (mm) and snout-vent length (cm) of males (triangles) and females (squares) in a sample ( $N = 56$ ) of adult Green Anacondas (*Eunectes murinus*) captured in the Venezuelan llanos.

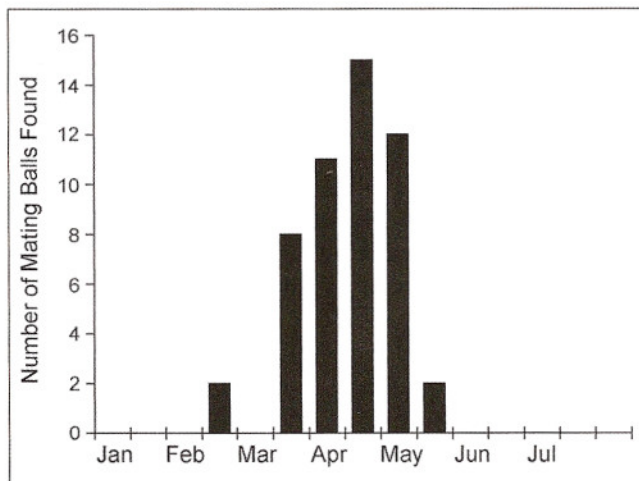


Fig. 4. Number of Green Anaconda (*Eunectes murinus*) breeding aggregations found during two-week intervals, from January to July, in the Venezuelan llanos.

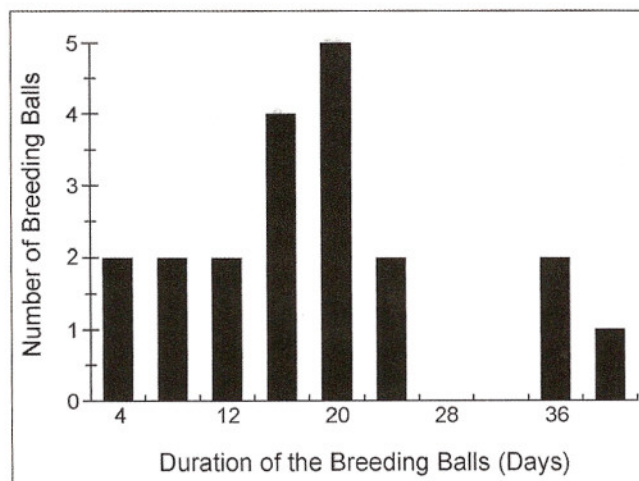


Fig. 5. Minimum number of days that breeding balls of Green Anacondas (*Eunectes murinus*) remained.

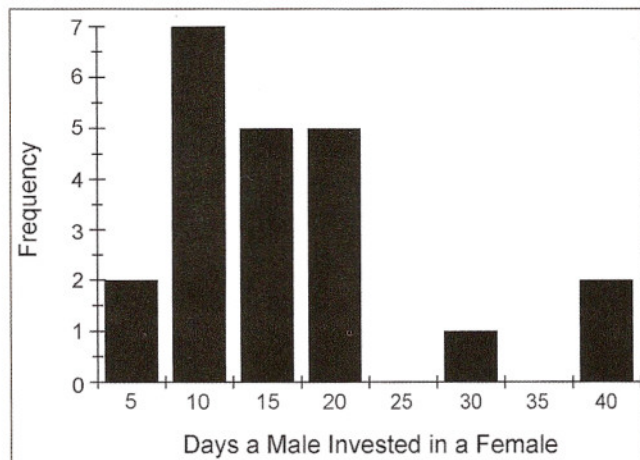


Fig. 6. Time spent by individual male Green Anacondas (*Eunectes murinus*) with a particular female. The time spent was determined by following radio-implanted animals or by recapturing males at different times.

lengths of the sexes did not differ significantly (Levene test;  $F = 1.39$ ,  $P < 0.24$ ), but the CV of males (0.78) is significantly smaller than that of females (0.98;  $t = 2.17$ ;  $P < 0.025$ ). Differences in spur length may be explained by selection favoring longer male spurs, and the lower variance of male appendages might be a byproduct of stabilizing selection for optimal male size (Shine et al., 1999c; Rivas and Burghardt, 2001). No obvious differences in coloration or pattern existed between the sexes at any size, although the largest individual of either sex tended to be dull.

### Breeding Season

We observed breeding balls from mid-February through the end of May (Fig. 4). Early in the dry season (January–March), males commonly moved overland while actively tongue-flicking, presumably tracking females across bodies of water. Rivas (2001) found breeding females by radiotracking searching males, which move frequently, often more than 1 km during the mating season (Rivas, 2000). Breeding balls lasted an average of 18 days (2–46 days,  $N = 21$ ; Fig. 5).

Snakes in most breeding balls were captured when first sighted in order to record data. Individual males stayed in breeding balls an average of 14 days (5–40 days; Fig. 6), although some males stayed with the female until the end of the period of attraction (we have no information about receptivity of females to males; so, by “period of attraction,” we mean the period during which males gathered around females). Most animals found were in breeding aggregations, so the reported duration probably underestimates the actual time each male invests in a female.

The operational sex ratio (OSR) in breeding aggregations was 1:3.83 (F:M). However, the sex ratio of adult snakes captured throughout the years was nearly even (Rivas, 2000; Rivas et al., this volume), suggesting that not all adult females in the population are participating in breeding balls every year.

Males that mated successfully or wrapped their tails around the cloaca of a female usually were larger than the average male in that group. In nine of 16 observed breeding balls, the largest male was the most successful. Since average breeding-ball size was 4.3, a pooled binomial test revealed that the largest-male advantage was highly significant ( $P < 0.01$ , two-tailed). In the two largest balls (with 11 and 13 males, respectively), the largest male was successful and each of these were significant on their own ( $P < 0.05$ , two-tailed).

### Mating System

We documented several instances of multiple males copulating with one female. We found sperm plugs in nine captured females. Sperm plugs are made of a friable white mass that produces a strong scent. Mean dimensions from two plugs that looked relatively complete were  $7.5 \times 1.9 \times 0.8$  cm; one plug weighted 7.5 g. Microscopic and pathological analysis revealed the presence of acellular protein and a moderate amount of spermatozoa. These nine females were being courted at the time of capture, and thus the presence of a sperm plug did not prevent the females from being courted. We observed one plugged female mating in captivity. Two days later, the sperm plug came loose while the female was being courted by two males (including the male that mated). We also collected five sperm plugs in the water 12 days after another female was in an enclosure with 11 males (an original breeding ball

collected in nature). These sperm plugs were probably dropped by the female after mating (e.g., Schwartz et al., 1989).

Despite our efforts to follow males in breeding aggregations, we did not document instances of males mating with more than one female during the same year. Two males were found in two different breeding balls during the same year, but due to our intervention (capturing the animals), we cannot be certain that the male would have joined the second ball without having being interrupted the first time. The seven radio-implanted males that were successful in finding females, which we followed during the entire mating period, each found only one female. Unlike females, males seem to mate with only one partner in a given season. On the other hand, males appear able to breed every year; three males were found in breeding balls in consecutive years, something we never found in females. Females seem to breed every other year, or less frequently in the case of larger animals (Rivas, 2000).

We found a positive correlation between female body mass and the average body mass of the males courting her ( $r = 0.38$ ,  $P = 0.01$ ,  $N = 45$ ; Fig. 7). Larger females also were courted by a larger number of males ( $r = 0.48$ ,  $P = 0.001$ ,  $N = 46$ ; Fig. 8). Smaller breeding females often were found in mud or aquatic vegetation and were likely to bite and ready to flee. Larger individuals, however, usually were found in shallow water or on dry land and were calm and sedate.

### DISCUSSION

#### Breeding Balls and Operational Sex Ratios

Breeding balls show a highly male-biased OSR (1:3.83), despite the fact that the adult sex ratio apparently is fairly even (Blomberg, 1956; Lopez, 1984;

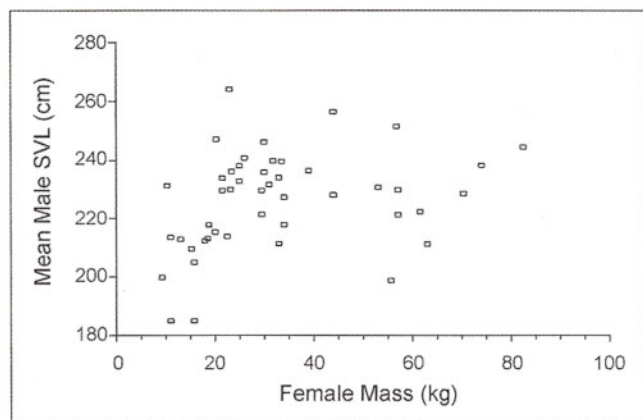


Fig. 7. Relation of body mass of a female Green Anaconda (*Eunectes murinus*) and the average length of the males in a breeding ball ( $r = 0.38$ ,  $P = 0.009$ ,  $N = 45$ ).

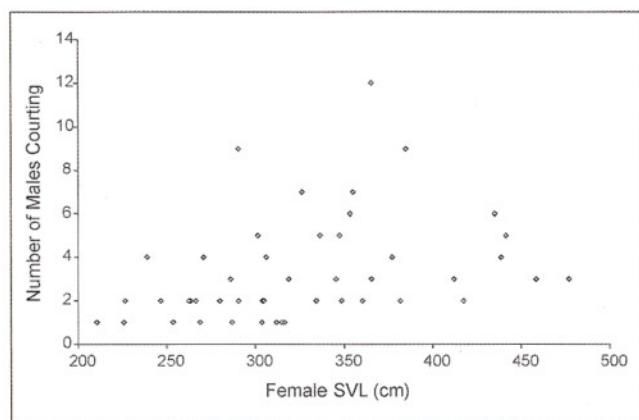


Fig. 8. Relationship between the number of male Green Anacondas (*Eunectes murinus*) in a breeding ball and the length of the female ( $r = 0.48$ ;  $P = 0.001$ ;  $N = 46$ ).

Rivas, 2000). Females make a large reproductive investment that averages almost 40% of their post-birth body mass, which prevents them from breeding every year (Rivas, 2000). Male-biased OSR increases intra-sexual selection in males and competition for access to females.

Observing activity in a breeding ball is difficult. From our observations, however, we speculate that males use spurs to stimulate females and to locate a female's cloaca and manipulate her into position for mating. Females clearly react to males by moving and allowing them to maneuver with their tails. Spur movement was similar to that described during courtship for other species of snakes (Carpenter et al., 1978; Gillingham and Chambers, 1982; Charles et al., 1985; Slip and Shine, 1988; Tolson, 1992).

Duration of copulation varies among the few boids that have been studied. In captive *Epicrates* spp., courtship can last about two weeks and copulation from 30 min to 9 h (Tolson, 1992). In *Morelia spilota*, mating aggregations can last 4–6 weeks (Slip and Shine, 1988; Shine and Fitzgerald, 1995). Strimple (1996) reported that mating in captive *E. murinus* can last up to 2 h. Hence, Green Anacondas in nature fall within the range reported for other large-sized species. For smaller species, the risk of predation might limit mating time and formation of mating aggregations. The large size of *E. murinus* also plays a role in the duration of copulation by decreasing the frequency of eating, which allows snakes to endure the long fasts associated with extended courtship and mating (Rivas, 2000, 2001).

### Male-male Competition

The extent of SSD in *E. murinus* is exceptional in snakes and other terrestrial vertebrates (Rivas and Burghardt, 2001). What is the nature of competition among males? When several males coil around one female, only the individual nearest the cloaca seems able to mate at any given time. This male apparently prevents other males from mating by physically blocking access to the female's vent. The panting of males evident in the video footage suggests that they were physically struggling. Furthermore, the apparent advantage for larger males to mate supports the notion that physical competition is at play. If competition occurs, and the largest males have an advantage, selection would favor larger males and large male size would be expected to evolve (Shine, 1978, 1993, 1994; Shine and Fitzgerald, 1995). However, the magnitude and direction of the SSD suggest that competition among males may not be physical. The dynamic of

breeding aggregations might result in stabilizing selection that leads to an optimal size. Larger males might be mistaken for females and courted. Consequently, males would benefit by attaining an optimal size that allows them to compete effectively with other males and still be small enough to not be mistaken for a female (Rivas and Burghardt, 2001).

The positive correlation between female size and the average size of males courting her (Fig. 7) suggests that smaller males are excluded from breeding balls with large females. A mechanism to explain this trend is assortative mating; smaller males court smaller females with which they have a better chance of breeding successfully. Male garter snakes (*Thamnophis* spp.) show size-assortative mating that is not necessarily due to larger males displacing smaller ones (Shine et al., 2001). Larger males might select larger females to maximize their breeding effort, as larger females have much larger litters (Rivas, 2000). Whether due to exclusion of smaller males or an ontogenetic switch in mating strategy, the correlation between the size of males and females can be interpreted as further evidence of physical competition among males. However, habitat selection is an alternative scenario that might explain such a correlation. Smaller males might be limited to searching for females in deeper water covered by aquatic vegetation to lower the risk of detection by predators. There they are more likely to find smaller females that, for the same reason, also use these habitats.

Breeding aggregations are relatively common among large boid snakes. Starin and Burghardt (1992) reported a seasonal occurrence of groups of Central African Rock Pythons (*Python sebae*), and they speculated that these groups were mating aggregations. Similar mating aggregations have been reported in Carpet Pythons (*Morelia spilota*; Slip and Shine, 1988), except that Green Anacondas coil around each other, whereas male *M. spilota* remain in the same area as females with little physical contact. This seems to explain why some populations of *M. spilota* show no evidence of male combat; the presence of other males increases the risk that a third male might mate while two others are fighting. Instead, they mate with the female without combat or guarding (Slip and Shine, 1988). However, other populations of the same species show male-male combat without male aggregation (Shine and Fitzgerald, 1995).

Interestingly, long-term captive *E. murinus* mate without the male coiling around the female (W. Holmstrom, pers. comm.; Rivas, 2000). In the field, however,

even in single-male mating pairs, the male coils his tail around that of the female. Coiling might give males more leverage to hold their position when other males attempt to displace him from a female's cloaca, but differences in body size probably preclude any coercion of the female by the male, which has been reported in some populations of garter snakes (Shine et al., 2003b).

Males need not fight over a female to prevent other males from mating. The use of sperm plugs by male Common Garter Snakes (*T. sirtalis*) might prevent other males from mating through physical interference (Devine, 1975) or the presence of "turn off" pheromones that discourage other males (Ross and Crews, 1997). Nevertheless, multiple insemination in garter snakes is common (Schwartz et al., 1989). Subsequent work falsified the notion of turn-off pheromones associated with sperm plugs, but sustained the presence of turn off pheromones associated with mated females (Shine et al., 2000). We have no evidence of chemical deterrence for mating, since nine females that were being courted had sperm plugs, suggesting they had mated already. In a species with a lengthy breeding period, such as *E. murinus*, a plug probably would not prevent other males from mating, primarily due to the short time the plug remains in place. Furthermore, considering their strength and constricting abilities, males might be able to remove a plug by squeezing the female near her cloaca (assuming that the female is neutral). In fact, in a captive breeding ball involving 11 males, the female dropped five sperm plugs in 12 days.

Wild males that mated in captive trials did not leave the breeding ball, remaining instead with the females and apparently preventing other males from mating or recovering to mate with her again. Nevertheless, due to the metabolic constraints of ectothermy and the presence of many other males, males probably cannot retain an optimal breeding position throughout the entire mating period, regardless of size. Mating males might alternate physical competition and sperm competition by leaving a sperm plug when they can no longer maintain the copulatory position. After recovery, males might reenter the struggle. This scenario would account for the permanence of males in breeding balls. Even at the height of the dry season, females seem to be too dispersed for males to have a good chance of locating other females during the same season. Thus, males that mate more frequently and prevent other males from mating by maintaining the breeding position for long periods or by using sperm plugs would have a higher probability of siring offspring.

### Male Strategy

If males mated with the first female that they found, we would expect to find no correlation between the size of the female and the number and sizes of males courting her, unless both males and females are segregated by size in the same habitats. The positive correlation between female size and the number of males, as well as the positive correlation between average male size and female size, suggest that males actively chose to court larger females, enhancing the likelihood of both larger clutches and larger offspring (Rivas, 2000). Rivas (2000) described observations indicating that a male was highly selective, following the best females and disregarding animals of lower quality. This phenomenon has been seen in other snakes (Ford and Seigel, 1989; Madsen and Shine, 1992, 1994, 1998; Brown and Shine, 2005), and appears to be a consistent trend when we analyze the available body of data (Rivas and Burghardt, 2005).

Are the males making a large investment per individual female? A sperm plug that was removed relatively intact from a female's vent represented 0.1% of the male's body mass. This value is fairly high if we consider that the sperm plug represents only a portion of the sperm that the male ejaculated and the short time he has to replenish his sperm reserves within the mating season — however, it is much lower than the almost 40% of body mass that a female might invest (Rivas, 2000). In the llanos, the breeding period for *E. murinus* is restricted to the driest part of the dry season (ca. 2 months), when males most easily locate receptive females. The time when males are courting an individual female can occupy much of the breeding season. Such a long time devoted to a single female prevents males from looking for other receptive females during the same season (Figs. 3, 6).

We hypothesize that the proximate mechanism for male choice might be based on: (1) larger females producing more pheromones, and thus manipulating male behavior, (2) larger females being easier to find, which results in more frequent encounters with more males (Luiselli, 1996), (3) males looking for females of a particular size in areas where they occur most frequently (larger females in shallow water, smaller females in relatively deep water), (4) individual recognition and preference, or (5) qualitative differences in the scents of larger females that trigger a mechanism in the male vomeronasal system or brain, which remains poorly understood (Shine et al., 2003a). More long-term studies of individually marked animals are needed to discriminate between these possibilities.

Larger males apparently have reproductive advantages over smaller males for several reasons: (1) larger males might be able to outcompete other males in an aggregation, (2) larger males might be able to search for females in different habitats with less risk of predation (Rivas et al., 1999; Rivas and Owens, 2000), or (3) larger males have larger testes and consequently more sperm, and thus an advantage in sperm competition (Shine et al., 1999a). Furthermore, Rivas (2000) noted strong selection for large size in females, so females might select larger males that would provide genes for large size for her daughters ("sexy daughters"; Weatherhead and Robertson, 1979). Homologous morphological traits in males and females are expected to show high genetic correlation (Halliday and Arnold, 1987); hence, any selection for large size in females should also increase the size of males. Males might suffer some disadvantages by being too large (Rivas and Burghardt, 2001), but benefits seem to outweigh the disadvantages.

### Female Strategy

Larger females produce more and larger offspring, which are expected to have a better chance of survival (Madsen and Shine, 1998; Rivas, 2000). Females would benefit by mating with larger males if they provide genes for large female size, which would enhance survival of offspring and the reproductive success of daughters (Brown and Shine, 2005). If females select larger males, larger (more attractive) sons are the byproduct of female preference and an added benefit of mating with a large male. Females also would benefit by producing offspring with males that have high ability to find females or that have higher courting success (Weatherhead and Robertson, 1979).

Female *E. murinus* often mate more than once in a season, and potentially with several males. This is suggested by the fact that several females with sperm plugs were being courted. The long duration of the breeding ball and the strongly biased OSR creates opportunities for multiple mating by females (Barry et al., 1992). Females are not expected to engage in multiple matings when a mating event increases the risk of injury or death (Arnqvist, 1989). The large size of females, however, lowers the risk of injury while mating. This is consistent with the sedate behavior exhibited by large individuals and the increased exposure of larger females when basking and laying on dry land or shallow water. Multiple mating and insemination have been reported in several species of snakes (Stille et al., 1986; Slip and Shine, 1988; Schwartz et al., 1989; Barry et

al., 1992; Höggren and Tegelström, 1995; McCracken et al., 1999). If females mate with many males, sperm competition should be operative. Sperm competition might decrease the benefits of physical competition accruing to larger males. However, larger males can compensate by having larger testes that produce more sperm, as has been noted in Australian pythons (Shine et al., 1999a; Shine et al., 1999b).

Madsen and Shine (1998) reported that the survival of a litter was determined by its quality and not its size. If true, selecting good mates might be a critical trait for females (Barry et al., 1992). Male snakes apparently are unable to forcibly copulate with females due to the elongate body shape (Shine, 1993). Also, hemipenes are not designed for forcible penetration (Devine, 1975, 1984). In *Epicrates*, copulation cannot be accomplished if the female does not open the cloaca to allow intromission (Tolson, 1992). Similar circumstances seem to prevail in *Agkistrodon contortrix* (Schuett and Gillingham, 1988) and *Crotalus atrox* (Gillingham et al., 1983).

Females are known to be highly selective in mating aggregations. Perry-Richardson et al. (1991) found that female Checkered Garter Snakes (*Thamnophis marcianus*) reject some males, even after intromission has occurred. While breeding several generations of the Mexican garter snake, *T. melanogaster*, in the laboratory, we noted that females accept some males and not others. Perry-Richardson et al. (1990) suggested that some individual males may be consistently more successful than others, highlighting the importance of female choice. However, recent evidence suggests that forcible copulation may be possible in garter snakes that mate in very large breeding aggregations where females emerging from hibernacula are too cold to resist males (Shine et al., 2003b, 2005; Shine and Mason, 2005). Nevertheless, female choice may be even more important in robust constrictors, in which females are much larger than males (to the point that they are capable of cannibalizing males; Rivas and Owens, 2000). The massive size difference between males and females undoubtedly precludes male coercion of females. On many occasions, while trying to collect males in breeding balls, females responded to our proximity (especially if the female had been captured previously) and slipped through the embrace of all the males. This leads us to think that she was there willingly. Furthermore, our observation of females actively preventing a mating male from being removed from his position suggests that female choice plays an important part in the process.



### Sexual Size Dimorphism

*Eunectes murinus* has one of the largest SSD reported in any amniote. The largest female found in a parallel demographic study was 97.5 kg, 40 times heavier than the smallest adult male (Rivas, 2000; Bryden, 1972). This large SSD can be explained by selection for very large size in females or very small size in males.

Female-biased SSD is the most common scenario among snakes, including basal macrostomatans (Shine, 1994), and might be the ancestral condition among the group (Rivas, 2000; Rivas and Burghardt, 2005). Phylogenetic inertia would explain the female-biased SSD unless strong selection pressure for large size in males was operative. Smaller adult male size also can be explained by the benefits of enhanced mobility, which may offer advantages in locating females and moving on dry land or shallow water, lower conspicuousness, and lower energetic requirements. Another explanation for the maintenance of small male size in species where larger males mate more frequently is that some smaller males may experience mating success in some years due to fluctuations in the OSR (Madsen and Shine, 1993b). The reproductive investment of males might be relatively low and they forfeit little growth by breeding early (Bell, 1980). Consequently, males would benefit from maturing early in life as this could allow them to breed at a young age (Madsen and Shine, 1993a; Weatherhead et al., 1995).

The possibility of cannibalism is another important element that might influence SSD, since mating females occasionally eat adult males (Rivas and Owens, 2000). Presumably, larger males would be less likely to be eaten by females. However, the size differential between males and females is such that an increase in male size might not be sufficient to save him; females are known to eat relatively large prey (Rivas, 1998; Rivas, 2000). Also, if male size is constrained for the other reasons (mobility, early maturation, dynamics of the breeding ball), males might benefit by being too small to be a profitable meal for a female (larger females are known to drop smaller prey from their diet; Rivas, 2000). This scenario also would help explain the small size variance in males compared to adult females.

In some species, SSD is evident at birth, with males slightly smaller than females (Weatherhead et al., 1995; King et al., 1999). This does not seem to be the case in *E. murinus* (Rivas, 2000). An explanation for a mechanism favoring strong SSD and small variance in male size is that males grow fast (like females) until they reach an optimum size and essentially cease to grow

(Beaupre et al., 1998). Fast growth rates allow males to escape predation and enter the breeding arena earlier, retarding growth at a point where size is optimal for breeding. This is supported by parallel mark and recapture data that suggest that many adult males did not experience perceptible growth in as many as eleven years (J. Rivas, unpublished).

Diets of small *E. murinus* consist primarily of birds. Males maintain this diet throughout life, whereas females do so only until they reach reproductive size (ca. 3 m TL). Around sexual maturity, females switch to mammalian and reptilian prey. This shift in diet might be related to the increase in energy that allows them to grow larger and keep up with the energetic demands of reproduction (Rivas, 2000). Birds are a relatively low-fat, low-energy prey resource. Males might maintain smaller size by relying on a lean bird-based diet and feeding infrequently. In fact, a captive-born male at the Bronx Zoo was fed *ad libitum* with mammalian prey and developed an exceptional mass of 40 kg (W. Holmstrom, pers. comm.), which is remarkably greater than the size attained by any wild-caught individuals of which we are aware. Sadly, the origin of this captive animal is unknown, since it came from the pet trade or a donation to the zoo. Trophic niche segregation as a cause of SSD also has been reported in other species where males specialize in smaller, less nutritious prey items (Pearson et al., 2002a; Shine et al., 2002). However, this is an unlikely scenario for *E. murinus*, as both sexes consume a variety of similar items and the prey supply is plentiful (Rivas, 2000). Instead, sexual identification in reproductive aggregations seems to be at play. Rivas and Burghardt (2001) used critical anthropomorphism to explain the dilemma of those species of snakes where males fight over the females and still attain smaller adult size. They argued that larger males can be confused for females in the breeding ball, which lowers their odds of success. Thus, the reason for the extreme SSD in *E. murinus* is that females are subject to selection for large size and males for a size at which they can exclude rivals but are not confused for females.

The lower variance recorded in male tail length also supports this idea. This stabilizing selection acting on tail size has been demonstrated in other snakes (Shine et al., 1999c; Shine and Shetty, 2001). Stabilizing selection in male size has been found in Northern Water Snakes (*Nerodia sipedon*; Brown and Weatherhead, 1999).

Here we propose a plausible scenario for the evolution of this system involving differential maturation. Females delay maturation because they must invest a

greater breeding effort. Males start breeding earlier and at a smaller size than females, since females need to gather more energy to start breeding, and the fecundity-independent costs of reproduction are too high to produce a small clutch (Bell, 1980; Madsen and Shine, 1994). This differential maturation sets the scenario for natural selection to act, and SSD can be selected as a method of sex discrimination. Once females are larger, the stage is set for natural selection to target SSD as a mechanism of sex discrimination.

Most snakes have great chemosensory ability, and scent trails of females are a key mechanism that allows males to find prospective mates (Ford and Holland, 1990; Shine et al., 2003c). Males undoubtedly can tell the sex of another individual by using their chemosensory abilities, but the conditions in the breeding balls may render chemosensory information unreliable. Heads are facing in one direction and tails are intertwined in a manner that no chemosensory discrimination of the female appears possible. How does the female decision work? In a breeding ball, females are courted by several males at the same time. One way a female can discriminate and choose among males is by relying on tactile cues. Does she have the ability to differentiate, based on displays given by the head of a snake at her back or neck, which tail is worthy of her favors? Observing a mating ball as a three-dimensional underwater matrix might be necessary to fully understand the processes involved; using genetic markers to determine which males are successful would only be a first step.

### The Mating System

Why do breeding balls last so long? A lengthy mating period involves greater exposure to predators, reduces foraging efficiency, and, in males, forfeits other mating opportunities. Explanations include: (1) females may be randomly receptive throughout the period and mate with different males without much discrimination, in which case a female is encouraging sperm competition among males (Madsen and Shine, 1992; Schuett, 1992; Wesneat, 1996); (2) a female may not be initially receptive to males, but emits pheromones and attracts several males that compete physically, and she is receptive only at the end of the period when selecting the stronger males that endured the struggle; (3) females in shallow mud result in breeding balls that are conspicuous to predators; a female is safe due to her larger size, but the smaller males are at risk of predation; thus, the handicap principle is at work, which also selects for larger or bolder males (Zahavi, 1975); or (4) a female entices courtship that allows her to select the best males in the

ball by mating selectively with the most appropriate male(s) using some criteria unknown to us (perhaps assessing some aspects of courtship related to spur movement). Future studies should address these issues.

In species where the female mates with many males, sperm competition is at work (Parker, 1970). Some theoretical models predict that males that mate last obtain reproductive benefits (Wesneat, 1996). Much controversy remains, but the last-mate advantage model may explain the extensive time males spend in breeding aggregations. Males that stay after they mate might prevent other males from mating or might mate again, if they can. However, cannibalism might pose a considerable risk for the last male that copulates (Rivas and Owens, 2000; O'Shea, 1994), resulting in a dilemma for males: the longer they stay with a female, the more likely they are to sire her offspring and prevent others from doing so — but they also suffer a greater risk of being eaten at the end of the breeding period. This scenario would select for refined abilities of males to detect the mood of the female, and an abrupt, as opposed to a gradual dissolution of the ball. The latter hypothesis is not supported by field observations. In the only controlled study of mate order on paternity of a snake, eight female Adders (*Vipera berus*) mated to three different males on three consecutive days gave birth to litters heavily skewed in paternity to the first mating male (Höggren and Tegelström, 2002). Size of male had no influence on this first-male effect. However, this species does not normally mate in breeding balls, but, when several males are present, they fight, and large males have more success in mating (Madsen and Shine, 1993b).

The long duration of breeding balls enhances the low probability of encountering other females. Females are not clumped and have rather unpredictable distributions. Consequently, males looking for females must travel relatively long distances, during which they face the risk of predation. Leaving a ball and trying to find another female may not be profitable. Duvall et al. (1992) argued that if the chances of a male of finding a female are low, a male should improve his convincing abilities once he finds a female. Shine and Fitzgerald (1995) found that males were more insistent in courting females in areas where the density of animals (and thus the encounter rate) was low.

Duvall et al. (1992, 1993) proposed a model for the evolution of mating systems that predicts the mating system expected based on the female spatial predictability and female temporal availability. Several types of polygyny can evolve from female-defense polygyny: prolonged mate-search polygyny, explosive

mating assemblages, and hotspot polygyny. They also speculated on the possibility of resource defense polygyny, as present in other taxa, and argued that polyandry is constrained in snakes due to phylogenetic reasons. Recent work, however, challenged this notion (Rivas and Burghardt, 2005). Green Anacondas do not fit into any of the patterns described by Duvall et al. (1992). The *E. murinus* mating system in the llanos appears to be different, with low spatial predictability and a lengthy receptive period, and possibly is labeled best as "prolonged breeding-ball polyandry."

We believe that the reason for this polyandrous system might be related to the low encounter rates of males with females. We see no reason why a male would not opportunistically mate with two females if two breeding balls were contiguous. Although polygyny has long been thought to be the dominant mating system in snakes, a recent evaluation of the evidence shows that polygyny is rather uncommon, if it occurs at all (Rivas and Burghardt, 2005). Other authors have documented multiple mating in females, but males often mate many times as well (Shine and Fitzgerald, 1995; Duvall and Schuett, 1997; Prosser et al., 2002; Blouin-Demers et al., 2005). Our study provides what might be the first documented instance of polyandry in snakes from a wild population.

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