Snake Mating Systems, Behavior, and Evolution: The Revisionary Implications of Recent Findings

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Sexual selection and mating systems profoundly influence the behavior and psychology of animals. Using their own studies of green anacondas (*Eunectes murinus*) and reviewing other recent studies, the authors conclude that incomplete data derived from a few well-studied snake species have led to general acceptance of polygyny as the dominant mating system in snakes. New data on behavior, paternity, and life history in a diverse taxonomic array of snakes support the view that polyandry is not only common in snakes but may have been the ancestral mating system. This interpretation helps to explain many seemingly paradoxical behavioral differences between lizards and snakes, such as the lack of territorial systems in most snakes and their frequent female-biased sexual size dimorphism.

Comparative studies are necessary for drawing conclusions on the role of ecology and evolution in the behavioral and psychological attributes of animals at different taxonomic levels. However, for these studies to be most informative, they must include appropriate samples of taxa evaluated in an unbiased manner. Recent literature has documented how cultural, sexual, and personal biases can cloud scientific judgment (Gowaty, 1994, 1997; Marsh & Hanlon, 2004; Rivas & Burghardt, 2002a; Ruse, 1999). In this contribution, we suggest that lack of balanced information about the mating systems of different taxa of snakes, along with uncritical interpretation of the data at hand, has prejudiced general conclusions about snake mating behavior and the resulting mating systems. We discuss recent data and reinterpret earlier findings that led to the prevalent notion that polygyny is the primary, if not universal, mating system in snakes. We also briefly discuss the implications of acceptance of these conclusions for understanding the evolution and comparative psychology of snakes.

Snakes have been suggested as a prime group for testing ecological and evolutionary hypotheses, including those on mating systems (Shine & Bonnet, 2000). However, despite the fact that there are more than 3,000 species of snakes (Greene, 1997), most of the detailed field and experimental literature dealing with mating behavior in snakes comes from limited taxonomic groups (e.g., natricines) studied in a limited distribution range (North America). In particular, in the far north of the United States and southern central Canada, there are large hibernacula of garter snakes (*Thamnophis sirtalis*). They emerge in large numbers in spring, and most mating takes place over several weeks at these sites. This expedites efficient collection of large data sets on mating behavior. It leads, however, to two potential problems. The first is that a disproportionate number of studies have been performed with only one species, often considered a model for serpent reproductive behavior and physiology, with a consequent handicapping of obtaining the diverse database needed for comparative studies (Rossman, Ford, & Seigel, 1996). The other problem is that most of the research on mating behavior in *T. sirtalis* has been done in only one geographic location at the extreme northern limits of the species' geographic range, which may not even be representative of this species' typical habitat and social environment. In fact, virtually no other snakes live in these cold climates.

The Status Quo: Polygyny in Snakes

Polygyny is typically represented by species in which a few males monopolize access to many females or in some way manage to gain the benefit of matings with multiple females, relegating most males in the population to bachelorhood. Classic representative examples would be northern elephant seals (*Mirounga angustirostris*) or the red deer (*Cervus elaphus*). In these cases, only a few males obtain mating, and most of the other males either do not mate at all or accomplish very few of the matings (Clutton-Brock, Albon, & Guiness, 1988; Le Boeuf & Reiter, 1988). In lizards and snakes (Squamata), a heavily documented example of this typical polygyny is the green iguana (*Iguana iguana*; Dugan, 1982; Rodda, 1992). The variance in mating success produces selection pressure for traits that give males a mating advantage in male–male competition as well as attractiveness to females. These

traits can include overall body size or secondary morphological, behavioral, or physiological attributes. In snakes, as well as in other taxa, adult male size relative to adult female size increases in those species with male–male combat (Shine, 1994). However, as we discuss below, there is no documented case of a male monopolizing access to several females in an equivalent manner to the cited mammalian or lizard taxa.

The influential Emlen and Oring (1977) framework for understanding the diversity of mating systems relies on the degree to which mates can be monopolized, the spatial distribution of resources (and thus the underlying ecology), and the availability of mates. Specifically addressing mating systems in snakes, several authors (Duvall, Arnold, & Schuett, 1992; Duvall, Schuett, & Arnold, 1993) proposed an alternative quantitative genetic-based model for the evolution of snake mating systems utilizing the *sexual selection gradient,* the regression of number of mates on fecundity. In this scheme (formally generalized to all animals in Arnold & Duvall, 1994), sexual selection is greater on the sex that benefits more from increased matings in terms of number of offspring. Thus, in polygamy and monogamy, the gradients are similar for both sexes; in polygyny, greater for males; and in polyandry, greater for females. On the basis of their understanding of snake biology, Duvall et al. (1993, p. 171) wrote, "because of the phylogenetic momentum for polygyny among the snakes, neither polyandry nor polygamy as defined in fig. 5.2 are likely to occur." However, no reference or source was provided for this statement. Within polygyny, these authors diagrammed and listed four types that they claimed encompass virtually all snakes: female defense polygyny (mate guarding), hotspot polygyny, prolonged mate-searching polygyny, and explosive mating assemblage polygyny. Territorial or resource defense polygyny was mentioned as

a possible, but not yet documented, fifth type. Lek polygyny was viewed as even less likely in snakes.

In fact, virtually all reports of mating systems of snakes regard them as polygynous (Duvall et al., 1992, 1993; Duvall & Schuett, 1997; Shine & Fitzgerald, 1995). Recent articles on snake reproduction that have reviewed or expanded the evidence of mating systems in snakes have continued to use polygyny as a framework to analyze their data (Pearson, Shine, & Williams, 2002; Shine, Langkilde, & Mason, 2003b). However, the requisite multiple matings with several females by individual males per breeding season have been largely assumed (Gibson & Falls, 1975; Schuett, 1982) and seldom documented. Alternatively, a male courting multiple females has been considered as evidence of multiple mating by males without confirmation as to whether those courtships were successful (Blanchard & Blanchard, 1942; Brown & Weatherhead, 1999b; Shine & Fitzgerald, 1995; Weatherhead, Barry, Brown, & Forbes, 1995). Other reports have documented multiple mating by both males and females (Madsen, Shine, Loman, & Hakansson, 1993) or have lacked supporting evidence that the males obtained exclusive access to the females (Blouin-Demers, Gibbs, & Weatherhead, 2005; Duvall & Schuett, 1997; Madsen, Shine, Loman, & Hakansson, 1992; Prosser, Weatherhead, Gibbs, & Brown, 2002). In short, polygyny requires copulation by a male with several females during the reproductive season, and such data from the field are sparse (see Table 1). Furthermore, few studies have shown that multiple matings lead to males siring offspring in multiple females (Prosser et al., 2002, is an exception). Thus, despite widespread evidence that females mate with multiple males and little evidence of multiple mating of females by males, snake biologist have persisted in viewing mating systems of snakes as polygynous.

Table 1

Snake Species That Breed in Multiple Breeding Aggregations and Snake Species in Which Multiple Mating by Females or Males in the Same Year Has Been Documented

Species	Multimale breeding aggregation	Multiple mating in females	Multiple mating in males	Multiple paternity confirmed	Source(s)
Boa constrictor	Y				Bertona & Chiaraviglio (2003)
Crotalus viridis viridis		Y			Duvall & Schuett (1997)
Elaphe obsoleta		Y		Y	Blouin-Demers, Gibbs, & Weatherhead (2005)
Eunectes murinus	Y	Y			Rivas (2000); Rivas & Burghardt (2001b)
Eunectes notaeus	Y				C. Strussman (personal communication, March 1999)
Laticauda colubrina	Y				Shetty & Shine (2002)
Morelia spilota	Y				Pearson, Shine, & Williams (2002); Slip & Shine (1988)
Nerodia sipedon	Y	Y			Brown & Weatherhead (1999a, 1999b)
Nerodia sipedon	Y	Y		Y	Barry, Weatherhead, & Philips (1992)
Nerodia sipedon	Y	Y	Y	Y	Prosser, Weatherhead, Gibbs, & Brown (2002); Weatherhead, Prosser, Gibbs, & Brown (2002)
Thamnophis butleri		Y		Y	Albright (2001)
Thamnophis sirtalis sirtalis		Y		Y	Gibson & Falls (1975); McCracken, Burghardt, & Houts (1999); Schwartz, McCracken, & Burghardt (1989)
Thamnophis sirtalis parietalis	Y				Many sources: e.g.,
Vipera berus		Y	Y		Madsen & Shine (1993c); Madsen, Shine, Loman, & Hakansson (1992, 1993); Shine, Langkilde, & Mason (2003a)
Vipera berus		Y		Y	Höggren & Tegelström (1995); Stille, Madsen, & Niklasson (1986)

Polygyny Versus Polyandry in Snakes

In a long-term field study, Rivas (2000) described the mating system of green anacondas (*Eunectes murinus*) as polyandrous (see also Rivas & Burghardt, 2001a, 2001b) based on over 45 mating aggregations in an intensively studied population with hundreds of marked individuals. One female lies on the mud or in shallow water, and males, up to 13 of them, approach and coil around her to court and attempt to mate. Such mating aggregations may last for up to a month, and males that find a female tend to stay with the same female until the end of her attractive period. There is no evidence of the males going out to look for other females after they mate. Although the female mates multiple times, there is thus no evidence of males mating with more than one female in a given season. Perhaps this is because the females are dispersed in the landscape and difficult to find. Rivas's (1998, 2000) and Rivas and Burghardt's (2001a, 2001b, 2002b) reports of polyandry in anacondas are unusual because individual anacondas were tracked for several years. It is interesting to note that anacondas are the first species in which the word *polyandry* has been used to describe, and best describes, the mating system observed. It is, perhaps, not the only or the first instance in which polyandry has been documented but was previously unrecognized.

Other than the work by Rivas and Burghardt (e.g., Rivas, 2000; Rivas & Burghardt, 2001b), the closest that some authors have come to acknowledging polyandry has been by using the word *promiscuity* (Shine & Fitzgerald, 1995), but no further discussion has been provided. Even in that study, all findings were analyzed in the light of "female defense polygyny" or "mate-searching polygyny" (Shine & Fitzgerald, 1995, p. 496). The work by Prosser et al. (2002) is an exception to this trend as they documented successful multiple mating by females as well as by males. However, they did not assign any label to characterize the mating system. We have presented data implicating polyandry in snakes in recent years at scientific meetings and conferences (Rivas, 1998; Rivas & Burghardt, 2001a, 2002b) to skeptical audiences. Interestingly enough, some colleagues aware of our arguments have recently mentioned polyandry when analyzing their work (e.g., Blouin-Demers et al., 2005).

We think that virtually all detailed studies of snake reproductive behavior, viewed objectively, show that snakes' reproductive biology is more consistent with polyandry than with polygyny. All evidence suggests that during reproduction, males spend extensive time and energy courting and mating. During this period, males feed rarely or not at all. Also, they often choose to mate with the females that are more fertile or more likely to breed (see Table 2). Males searching for and courting females may suffer high mortality in the wild as a result of their mating investment, which further raises the cost of courting several females (see Table 2). Male snakes show assortative mating in which they seek to mate with the larger, more fertile, or otherwise more attractive females (see Table 2). Males thus choose females selectively instead of mating indiscriminately, as would be expected in typical examples of polygyny, in which males typically do not make a large reproductive investment per mating. Such male choosiness that conflicts with multiple mating by male snakes is an important selection pressure because truly polygynous males should maximize the number of mates and minimize courtship duration and investment per mating event.

Table 2

Snake Species Reported With Traits Associated With Polyandry: Male Choice or Large Male Reproductive Investment (Through Energetic Investment, Forfeiting Feeding for Long Periods of Time, or Suffering Strong Predation Pressure During the Mating Season)

Species	Choosy males	Large male mating investment	Source(s)
Arizona elegans		Y	Aldridge (2001)
Coluber viridis viriflavus		Y	Bonnet, Naulleau, & Shine (1999)
Crotalus horridus		Y	O'Leile, Beaupre, & Duvall (1994)
Elaphe longisimus		Y	Bonnet, Naulleau, & Shine (1999)
Elaphe obsoleta	Y	Y	Blouin-Demers, Gibbs, & Weatherhead (2005)
Eunectes murinus	Y	Y	Rivas (2000); Rivas & Burghardt (2001b)
Eunectes murinus		Y	Rivas (2001); Rivas & Owens (2000); Rivas, Thorbjarnarson, Owens, & Muñoz (1999)
Laticauda colubrina	Y	Y	Shetty & Shine (2002)
Liasis fuscus		Y	Madsen & Shine (2000)
Morelia spilota		Y	Shine & Fitzgerald (1995); Slip & Shine (1988)
Natrix natrix	Y		Luiselli (1996); Madsen & Shine (1993b)
Nerodia sipedon	Y	Y	Prosser, Weatherhead, Gibbs, & Brown (2002); Weatherhead, Prosser, Gibbs, & Brown (2002)
Nerodia sipedon		Y	Brown & Weatherhead (1999a); Weatherhead, Barry, Brown, & Forbes (1995)
Thamnophis sirtalis parietalis	Y	Y	Shine, LeMaster, Moore, Olsson, & Mason (2001); Shine, O'Connor, LeMaster, & Mason (2003)
Thamnophis sirtalis parietalis	Y		Garstka, Camazine, & Crews (1982); Shine, Langkilde, & Mason (2003a, 2003b); Shine & Mason (2001); Shine, Olsson, Moore, LeMaster, & Mason (2000); Shine, Phillips, Waye, LeMaster, & Mason (2003)
Vipera berus		Y	Madsen, Shine, Loman, & Hakansson (1993)

The ratio of available females per male, or *operational sex ratio* (OSR), is far less than one to one for many snake species (Arnold & Duvall, 1994, preferred to use the *breeding sex ratio,* the ratio of breeding males to females, but the following argument is similar). Female snakes make very large reproductive investments and often cannot recuperate rapidly enough to reproduce every year, leading to male-biased OSR (Bonnet, Naulleau, & Shine, 1999; Madsen & Shine, 1993a; Rivas, 2000; Shine, Langkilde, & Mason, 2003a, 2003b). A male-biased OSR creates a great potential for reproductive females to mate multiple times (Barry, Weatherhead, & Philips, 1992) and reduces opportunities for many males. Finally, the most convincing argument that the dominant mating system in snakes is not polygyny is the fact that multiple mating and multiple paternity have been found in all the species in which they have been studied in detail (see Table 1). Thus, anaconda polyandry might not be just a rare exception to the Duvall et al. (1993) model; true polygyny might not be nearly as common in snakes as currently believed. When that model was developed, there was not enough empirical evidence to suggest how probable polyandry may be in snakes, but over the past 10 years, there has been a substantial increase in the literature dealing with snake reproductive biology. Currently, it is evident not only that polyandry might be more common than formally thought but also that sensu stricto polygyny (in the sense used for mammals and lizards cited above; see also Arnold & Duvall, 1994) might not even apply to snakes.

We should note at this point that our effort is not just about accepting a word or label, as new ones can become as constraining as the old, but to use an alternative lens to view and interpret empirical data. We also feel that within a population, it is possible for different mating systems to occur, such as in the human species, which can be typed as monogamous, serially monogamous, or moderately polygynous.

However, the problem with researchers resisting the hypothesis that the mating system of the snake may not be polygynous goes beyond the simple issue of terminology to how scientists interpret and direct their research. For instance, there have been several studies demonstrating that males obtain mating advantages for being larger, yet the males in those species are smaller than the females (Madsen & Shine, 1993c; Shine et al., 2000; Weatherhead et al., 1995). Sexual selection theory predicts that the sexual selection gradient is stronger in animals that obtain mating advantages from multiple mating. If the males were polygynous, they would be under stronger selection pressure (higher sexual selection gradient) than females because of the benefit of mating with multiple females (Arnold & Duvall, 1994) and would therefore grow larger if large size benefited their mating abilities. The research done by scholars trying to explain why males do not grow larger than females is a consequence of the mistaken assumption of polygyny. In a polyandrous system, mating advantage for large size in males is not expected to produce larger males, as the sexual selection gradient in males is lower than in females (Arnold & Duvall, 1994). The abundant literature documenting unsuccessful attempts to explain this apparent dilemma (Brown & Weatherhead, 1999a, 1999b; Madsen & Shine, 1993b; Prosser et al., 2002; Weatherhead et al., 1995; Weatherhead, Prosser, Gibbs, & Brown, 2002) suggests that this is more than a simple issue of terminology.

Evaluating Data on Mating Behavior in Snakes

The secretive nature of many snakes and other difficulties that snake researchers have had in obtaining valid data on snake mating behavior have contributed to the poor database available for snakes. In addition, however, snake researchers may have been misled by the voluminous sexual selection literature on organisms that do not grow much after adulthood (mammals, birds, and insects) and that also may have a size-independent clutch size, thus overlooking suggestive data that were available. This is, perhaps, a consequence of most snake biologists being male (Wilson, 1998), which may have biased their interpretations of data. Evidence of this possible bias in interpreting snake mating behavior can be found in an apparent double standard in documenting multiple mating. Observations of males courting several females have been considered as evidence of polygyny, but observations of a female being courted by several males have not constituted sufficient grounds to conclude polyandry or even multiple mating in females. In fact, unequivocal evidence of copulation with multiple males has not been enough to even suggest that females may be polyandrous, whereas scant field evidence of multiple mating in males has been grounds to conclude that they are polygynous. Although there were scattered reports (Gibson & Falls, 1975; Schuett & Gillingham, 1986), it was not until DNA and molecular studies conclusively proved several sires in the litters in the well-studied common garter snake, *Thamnophis sirtalis* (Schwartz, McCracken, & Burghardt, 1989), that the existence of multiple female mating and resulting multiple paternity of her offspring was seriously recognized; even that species is still being considered as polygynous. Since then, studies using molecular methods to assess paternity have found that multiple paternity is the norm in snakes across a wide variety of families, whereas molecular data for "multiple maternity" are singularly lacking in naturalistic studies (see Table 1). Even in the few documented cases, however, the word polyandry was seemingly avoided until very recently (see below). Such biases influencing the interpretation of data have been documented before in other taxa (Cunningham & Birkhead, 1997; Gowaty, 1994, 1997). As we have argued elsewhere (Rivas & Burghardt, 2001b, 2002a), such research bias can be reduced through attempting to take into account the attributes of the species under study and the way its members perceive and respond to the world, an approach called *critical anthropomorphism* (Burghardt, 1985). Nonanthropomorphic and allegedly objective approaches are not a sufficient safeguard against unwitting and uncritical anthropomorphism in interpreting data (Rivas & Burghardt, 2002a). However, as pointed out below, misleading comparative and evolutionary inferences are also involved.

We conclude that given the available evidence, the dominant mating system in snakes is not polygyny. The most common mating system in snakes is polygynandry or even polyandry in some cases. We prefer *polygynandry* instead of *promiscuity* because the latter really means lack of discrimination, and mating with multiple partners does not necessarily involve lack of discrimination, for several potential partners might meet the desired standards.

Snake Behavior, Size Dimorphism, and Evolution

The origin of snakes continues to be controversial although their placement as a derived squamate reptile aligned with lizards is accepted. A recent analysis (Greene & Cundall, 2000) contradicted the view that snakes originated in a marine environment (Caldwell & Lee, 1997) and supported early views that snakes as a group evolved in terrestrial environments (Greene & Cundall, 2000), probably in a subterranean (fossorial) habitat (Forstner, Davis, & Arévalo, 1995; Gans, 1975; Lee, 1997; Rieppel, 1988). The constrained mobility of these early snakes in a fossorial environment could account for a lower encounter rate with both mates and prey. In an aquatic habitat, it would also be harder for snakes to follow scent trails, and the encounter rate with mates would also be expected to be low (Shine, 1993). Thus, a low encounter rate with potential mates seems to be the most likely scenario in the evolutionary history of snakes.

One of the values of comparative studies is the opportunity to assess which traits are primitive for a clade and which ones are more derived. In trying to understand the evolution of the mating system, because squamate reptiles other than serpents have diverse evolutionary lineages, we focus on the accepted closest extant saurian relatives of snakes, the Varanoidea (monitors, *Varanus*, *Lanthanotus*; beaded lizards, *Heloderma*; Forstner et al., 1995; Lee, 1997; Pianka & Vitt, 2003). There are several traits of snakes as a group that differ from their sister taxa, that may support or enhance nonpolygynous systems, and that may be derived from a low encounter rate. For instance, snakes lack the territoriality and male-biased sexual size dimorphism (SSD) that are common in their squamate relatives (Phillips, 1995; Pianka & Vitt, 2003; Shine, 1994; Stamps, 1983; Wikramanayake & Dryden, 1988). Territoriality is less marked in Varanoidea than in many other groups of lizards (although injurious fights occur), but the lack of territoriality in snakes may also relate to the difficulty they have in defending feeding or mating sites because their visual and auditory abilities are often limited, and chemosensory vigilance may be impractical in the relatively large areas and complex environments in which many snakes live. Furthermore, typical male–male combat, so common in polygynous vertebrates, has been documented in only about 6% of all snake species and appears totally lacking in entire lineages, including the seven most basal families (Schuett, Gergus, & Kraus, 2001), which leads us to conclude that such combat is a derived trait in snakes. There are also a few other important differences between snakes and varanid (or other closely related) lizards that might be due to the same evolutionary path. First, snakes tend to make larger relative reproductive investments than do lizards. Second, snakes very seldom have multiple clutches or litters in a year (Seigel & Fitch, 1984). Third, all snakes are obligate carnivores, and most eat relatively large prey that are frequently dispersed, are vagile, and have large home ranges. Fourth, snakes average larger body masses than lizards in comparable habitats and often live at much lower densities than lizards (the exceptions are extreme temperate habitats where snakes, such as garter snakes and vipers, are more frequent). We conclude that an ancestral evolutionary environment with a low encounter rate with both prey and conspecifics is a likely scenario for the evolution of snakes as a group and could explain the evolution of these synapomorphies.

Retention of a polygynous mating system from the ancestral lizard was not likely in the earliest snakes because of the difficulty of finding or monopolizing females in a fossorial existence. A male might not easily find more than one female in a season thanks to the high costs of locomotion, the low rate of moving, the predation risk associated with surface searches, and the possibly high dispersion of females. This also offers an explanation for the switch in SSD from male biased to female biased. Perhaps the ancestral snake did not have male–male combat, which is present in virtually all lizards (Pianka & Vitt, 2003). Territoriality, which is present in most lizards, is reduced in the more chemosensory-dominated Autarchoglossa lizard lineages from which snakes apparently evolved and is undocumented in the most basal snake families. However, male lizards are still almost always larger, even in those groups of lizards that show monogamy (Pianka & Vitt, 2003). So, although the benefits of large size in female snakes continued (larger clutches, increased survival, wide range of prey), the costs of a male snake being large outweighed the benefits. Instead, being small was adequate and reduced metabolic expenses, including costs of locomotion for feeding and finding females. The probability of encountering other males with females during the reproductive season was so small that male combats were no longer a major selection pressure for the evolution or maintenance of large size. Additional support for the importance of the fossorial environment driving the system is found in the fossorial slow-worm lizard (*Anguis fragilis*), which displays female-biased SSD and multimale breeding aggregations (R. Platenberg, personal communication, August 2000).

We hypothesize that the ancestral condition of the snakes was female-biased SSD based on the general trend found in the group (Shine, 1994). Shine (1994) concluded that the most common scenario is female-biased SSD except in those cases in which males combat. Shine stopped short of hypothesizing that female-biased SSD was the ancestral condition, perhaps being unable to explain how it could have evolved from an ancestor with male-biased SSD and a polygynous mating system. We conclude that the original serpent mating system was not polygyny, as the ancestral lizards probably had a mating system somewhere between serial monogamy (when encounter rates were very low) and polyandry (if several males found the same female).

Parthenogenesis by females is expected to evolve in a situation of low encounter rate between males and female. It is interesting to note that the only obligatorily parthenogenetic snake is the blind snake (*Ramphotyplops braminus*), a basal snake that has a fossorial existence (Nussbaum, 1980). Further support for the idea of low encounter rate in the evolution of snakes is the fact that several snakes have been documented to show either long-term sperm storage or even facultative parthenogenesis (Schuett et al., 1997), including Burmese pythons (*Python molurus bivittatus*; Groot, Bruins, & Breeuwer, 2003). Both traits are expected to evolve in conditions of low encounter rate. Although today, many advanced (Macrostomata) snake species breed in multimale breeding aggregations, this does not challenge our suggestion that low male–female encounter rate was the ancestral condition. It is more likely a derived trait arising after the evolution of the streptostylic jaw that allowed snakes to successfully swallow large prey equaling 50% or more of their body mass. This low encounter rate with potential mates was not evident to early snake biologists (most of

them native to temperate zones) because congregations of north temperate snakes at hibernacula suggested a different scenario. So, their interpretation might have been biased to the particular scenario of a very common temperate snake and not something representative of the whole taxa. Even so, the high concentrations of common garter snakes in some parts of their extreme northern range are exceptional judging by the low occurrence of such aggregations across related taxa and even other populations of this most widely distributed species. Although northern hibernacula provide scientists a great opportunity to gather abundant information in a short time, these situations are most certainly highly derived and unrepresentative.

We endorse the call of several authors (Madsen & Shine, 1993c; Seigel & Ford, 1987; Shine, 1993; Weatherhead et al., 1995) for long-term field studies of individually marked snakes in different taxa and different geographic regions. These are needed to test and develop theories regarding mating systems and sexual selection in snakes. The fossorial basal snake families so little studied (Greene, 1997) need, in particular, to be studied to test the hypotheses advanced here.

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