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Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating

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Data on over 950 natural matings of red-sided garter snakes, *Thamnophis sirtalis parietalis*, in Manitoba revealed size-assortative pairing: large males tended to mate with large females, and small males with small females. Unlike previously reported cases of size-assortative mating, the causal mechanism in these snakes involved a size-related shift in active mate selection by males. In the field, courtship as well as mating was size assortative (albeit, with considerable scatter around the trend line). Staged trials in outdoor arenas showed that males of all sizes preferred to court large rather than small females, but this preference was stronger in large males. Males adjusted their courtship intensity in response to the numbers and sizes of females and competing males, but did not change their preferences with respect to female body size. Thus, size-assortative mating was not a direct consequence of large males excluding their smaller rivals from large females. Males may be selective courters in this species because they have a limited supply of sperm and mating plugs, and hence can copulate effectively only a few times within the mating season. Given intense competition from large males (which primarily court large females), small males may benefit from focusing on small females. Alternatively, small males may be less capable of inducing sexual receptivity from large females. Mark–recapture data confirmed that males grow rapidly from one year to the next. Thus, the size-related shift in male mate choice was due to an ontogenetic change rather than the existence of multiple male morphs differing in both body size and courtship preference.

Darwin's theory of sexual selection is based on the premise that phenotypic traits influence the mating success of organisms. There is abundant evidence that many traits do indeed affect an animal's probability of obtaining a mate, and the quality of mate that is obtained (e.g. Andersson 1994). One aspect of the phenotype that is often implicated in this respect is body size. An animal's body size may influence its mating success via various processes, of which the most obvious is enhanced physical prowess in sexual battles (Clutton-Brock 1991; Andersson 1994). More subtle but probably of equal importance is the possibility of size-based mate choice. If either sex strongly prefers mating partners of a particular size, this behaviour may substantially modify the relationship between mating success and body size (and, hence, the trajectory of evolutionary change in genes that influence body size: e.g. Jennions & Petrie 1997).

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Ever since Darwin, the 'conventional wisdom' in this field has been that females are the 'choosy' sex whereas males are less discriminating (e.g. Williams 1966). None the less, theory suggests that these sex roles can be modified by a variety of factors. For example, selection may favour males to be highly selective about their choice of partners in species where male parental investment is substantial, sperm competition is intense, or where female quality is very variable (e.g. Sargent et al. 1986; Schwagmeyer & Parker 1990; Olsson 1993). A crucial factor in this equation is likely to be the extent to which engaging in one mating compromises a male's ability to obtain other copulations. If males are essentially unlimited in their ability to mate multiply (i.e. 'sperm is cheap'), they are not likely to be highly selective in mate choice. However, males that can afford to invest in only a few matings may be more selective about the attributes of their partners (Dewsbury 1982).

Mate choice based on body size is widespread, and can have numerous consequences. One such consequence is the possibility of size-assortative mating: that is, larger males will tend to mate with larger females, and smaller

males with smaller females. For example, if all males prefer large (and thus fecund) females, and large males can physically exclude small ones from mating with these 'preferred' females, an overall trend for coupling of small with small and large with large may result (e.g. Olsson 1993; Cooper & Vitt 1997). The mechanism for the male–male interaction could be direct (i.e. large males attack and drive away their smaller rivals) or indirect (i.e. because smaller males are less likely to be able to mate with large females, selection favours a shift in mate preference so that smaller males preferentially court smaller females).

Reptiles potentially offer excellent systems in which to investigate this topic. Like most other ectotherms, reptiles continue to grow after maturation (Andrews 1982). Hence, a reptile population typically contains adult individuals over a much wider range of body sizes than would be the case for endothermic taxa such as mammals and (especially) birds (Andrews 1982; Calder 1984). This wide size range provides considerable opportunity for natural and sexual selective forces to act on body size. Indeed, there is good evidence that larger male reptiles of several taxa are more likely to win combats, and thus obtain matings (Schuett & Gillingham 1989; Madsen et al. 1993; Luiselli 1996; Cooper & Vitt 1997). Similarly, larger females are likely to reproduce more often, and produce more (and often, larger) eggs per clutch (Fitch 1970; Seigel & Ford 1987).

The existence of size-based mate choice in reptiles is much less well understood. Because male parental care in reptiles is essentially unknown (Shine 1988; Somma 1990), we might expect mate choice by males to be rare. None the less, the strong link between female body size and reproductive output may favour a male preference for large (and, hence, fecund) females. Such a preference has been demonstrated in several species of lizards (e.g. Olsson 1993; Cooper & Vitt 1997; Whiting & Bateman 1999) and one species of snake (Aleksiuk & Gregory 1974; Hawley & Aleksiuk 1976; Gartska et al. 1982). Size-based mate choice by males results in size-assortative mating in at least two of these lizard species (Olsson 1993; Cooper & Vitt 1997). Our field studies reveal size-assortative mating in snakes, and our experimental studies (using outdoor arenas) clarify the determinants of mate choice in these animals.

METHODS

Study Species and Area

Red-sided garter snakes, *Thamnophis sirtalis parietalis*, are small nonvenomous colubrid snakes found over a large geographical range in North America (e.g. Rossman et al. 1996). In the Interlake region of Manitoba, Canada, these snakes aggregate in huge numbers (>10 000 animals per den) in suitable hibernation sites (e.g. Gregory 1974, 1977; Gregory & Stewart 1975; Shine et al. 2001, in press). The snakes court and mate in early spring, before they disperse from the den. This situation facilitates behavioural studies, with the result that these populations have become a 'model system' for studies on snake reproduction (Duvall et al. 1993).

We have been studying these Manitoba populations for several years. Data in the present paper were gathered at two sites. First, from 1992 to 1998 we worked at the massive Narcisse dens also used by several earlier workers (e.g. Whittier et al. 1985; Mason 1993). Mass freezing-induced mortality during the winter of 1998–1999, apparently caused by atypically low snow cover (D. Roberts, personal communication), greatly reduced snake numbers at these dens. Thus, in May 1999 we worked 30 km further south, at a large den in a gravel quarry 1.5 km north of the town of Inwood, 0.5 km east of Highway 17 (50°31.58'N, 97°29.71'W). Individual snakes may travel up to 20 km from the den during their summer movements (Gregory & Stewart 1975; Larsen 1987), and genetic differences between nearby dens are minor (M. LeMaster, unpublished data). Hence, there is unlikely to be any significant genetic difference between snakes using the two denning areas.

Methods for Field Studies

Narcisse dens, 1992–1998

Throughout May each year, we conducted a variety of studies at the dens. Some of the work was descriptive, whereby we gathered large samples of snakes close to the dens each day to quantify temporal variation in the sizes of snakes that were active. Body length (snout–vent length, SVL) and mass were recorded for each animal. Some of these snakes were found singly, but many were in large courting groups of males focused on a single female (Gregory 1974; Shine et al. 2001). We kept each group separate so that we could compare the phenotypic traits of males with those of females that they were courting when captured. Whenever we found pairs of snakes in copulo, we captured them, kept them in bags until they had separated, and then recorded their body sizes. A subset of males was scale clipped individually before release to provide information on growth rates between years.

We also carried out a series of experimental trials with open-topped nylon arenas measuring 1.1 × 1.1 m, 90 cm high. Combinations of males and females were placed into each arena so that we could record which male was successful in obtaining the mating. These trials were conducted to explore issues such as the role of male body size and relative tail length in determining mating success (Shine et al. 1999, 2000b), the behavioural 'tactics' of female mimics ('she-males': Mason & Crews 1985, 1986; Shine et al. 2000a, d), and factors influencing the mass of mating plugs deposited by male snakes (Shine et al. 2000c). However, data from these trials can also clarify the question of whether courtship and mating are influenced by the relative body sizes of males and females.

Inwood den, 1999

In the same way as in earlier years at the Narcisse dens (above), we walked around the Inwood den on sunny

days throughout May 1999 looking for courting and mating activity. Snakes engaged in these activities were collected, and placed in cloth bags for later measurement and weighing.

We also erected open-topped arenas (as above) adjacent to the Inwood den to conduct staged encounters between male and female snakes of various numbers and body sizes. These trials were specifically designed to investigate the possibility of size-assortative courtship. In an initial set of 36 trials, each arena contained the following snakes: six large males (SVLs >50 cm); six small males (SVLs<40 cm); one female-mimic (she-male); one small female (SVL<45 cm); one medium-sized female (SVL 45–55 cm); and one large female (SVL>55 cm). Females of all sizes had their cloacas taped shut to prevent mating during the trials. Results for she-males have been analysed separately (Shine et al. 2000d), and will not be considered in the present paper. We scored courtship behaviour at 10-min intervals for the next 60 min, recording the numbers and sizes of males courting each female. Courtship was scored as occurring if a male's body was aligned with that of the female, with his chin firmly adpressed to her (e.g. Whittier et al. 1985). We recorded the total number of observations (summed across time periods) of each possible combination of snake sizes in courtship (e.g. number of times that small males were recorded as courting large females).

We then expanded these trials to investigate the effects of different numbers and sizes of males and females. Thus, further trials were run with all males (N=12) in each arena being either small (N=30 trials) or large (N=30 trials). Another 36 trials had half the numbers of males per arena (i.e. three small plus three large). Lastly, we ran 36 trials where all females within the arena (N=3) were small rather than ranging over a wider size range. Of these 36 trials, 12 had 12 large males per arena, 12 had 12 small males per arena, and 12 had six large plus six small males per arena.

We did not observe any aggression in the trials. The research was conducted under the authority of the Oregon State University Institutional Animal Care and Use Committee and in accord with the U.S. Public Health Service 'Policy on Humane Care and Use of Laboratory Animals' and the National Institutes of Health 'Guide to the Care and Use of Laboratory Animals'. For further ethical considerations see Shine et al. (2000a).

Statistical analysis of the data from all these trials was designed to avoid pseudoreplication. In particular, (1) records of courtship by the same male snake at consecutive 10-min periods within a 60-min trial are not independent; and (2) the activities of one male might modify the intensity of courtship of other males within the same enclosure (although we never saw any overt sign of such an interaction). To avoid pseudoreplication, we calculated mean intensities of courtship (number of times that males were recorded as courting females) for each size class of males within each enclosure, over the entire 60-min period of each trial. Our statistical analysis of courtship intensity was thus based on a single number from each size class of males for each trial. All snakes were used only once, in a single trial, before being released.

RESULTS

Size-assortative Mating in the Field

There was a highly significant trend to size-assortative pairing in natural matings at both the Narcisse and Inwood dens: larger males generally mated with larger females, and smaller males with smaller females. We have data on body sizes of the partners in 65 mating pairs at the Narcisse dens from 1992, 301 from 1995, 155 from 1996, 155 from 1997 and 91 from 1998, as well as 109 pairs from Inwood in 1999. A one-factor ANCOVA with year as the factor, male SVL as the independent variable, and female SVL as the dependent variable confirms that there was a consistent trend for larger males to mate with larger females (covariate $F_{1,957}$=16.64, P<0.0001). The intercepts for this relationship, that is, the values for female SVL relative to male SVL, also varied between years ($F_{5,957}$=5.66, P<0.0001), but the slopes of the regression lines did not differ significantly between years ($F_{5,952}$=1.54, P=0.18). An earlier study on the Narcisse snakes also revealed significant size-assortative mating in 1 of 2 years (Joy & Crews 1988).

Despite the highly significant overall relationship between male and female SVLs within mating pairs, the scatter around the regression lines was very wide (regression of female SVL against male SVL for Inwood data: r^2=0.092, N=109 pairs, P<0.0015; Fig. 1a). That is, there were many instances of small males mating with large females, and large males mating with small females (Fig. 1). Although the slope of the regression line between male and female SVLs was positive in all years for which we have data, these regressions generally explained relatively little variance in female size (r^2 values for each year ranged from 0.002 to 0.083). Hence, it is of interest not only to determine why size-assortative mating occurs, but also why there is so much 'noise' in the relationship between male and female body sizes.

Size-assortative Courtship in the Field

Why do these snakes display size-assortative mating? The mechanism might involve active mate selection (i.e. small males actively court small females, whereas large males court large females) or interactions within courting groups (i.e. all males court large females, but only large males are able to obtain matings with them). Our data on courting groups around the den support the former hypothesis. Data gathered in 1997 on the Narcisse snakes show that larger males tended to court larger females (r^2=0.019, N=211 groups, P=0.046). Analogous data from Inwood in 1999 provided a similar result (r^2=0.096, N=47 groups, P=0.034; Fig. 1b).

Body Sizes and Times of Activity

Size-assortative courting by garter snakes (above) is not necessarily due to active mate choice. Instead, a snake's body size might affect the times or places in which it is active, because of thermal biology or vulnerability to predation (Peters 1983; Peterson et al. 1993; Shine et al.

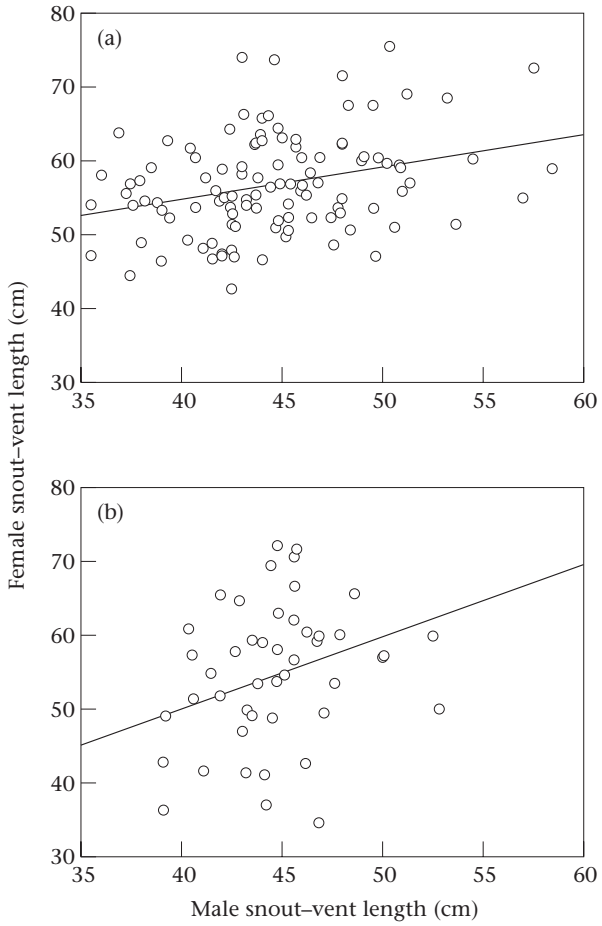

Figure 1. Size-assortative courtship and mating in red-sided garter snakes in the field. All data were gathered at the Inwood den in May 1999. (a) Body sizes of males and females found in copulo in the field. (b) Body sizes of females and the mean body sizes of the males found courting them. Each courting group is represented by a single data point.

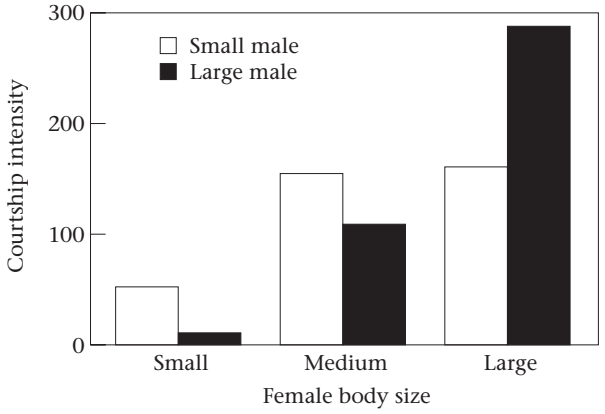

Figure 2. Relative intensity of courtship by small (<40 cm snout–vent length) and large (>50 cm SVL) garter snakes to females of three different body sizes (small <45 cm; medium 45–55 cm; large >55 cm SVL). The courtship intensity is the sum of all recorded observations of courtship (i.e. total number of time periods when such courtship was observed) over trials with equal numbers of each size class of male, and equal numbers of each size class of female. See text for further explanation and statistical analysis.

2000e). Such size-related shifts in activity could generate correlations between male and female body sizes within courting groups, regardless of any active mate choice. We can test this possibility with data from surveys of the Narcisse dens, where we captured and measured every snake that we could find near the den over a 1-week period in 1997. Data were available for six 1-h periods during the snakes' daily activity period (0800–0900; 0900–1000; 1000–1100; 1400–1500; 1600–1700; 1700–1800 hours). A two-factor ANOVA with time period and sex as the factors shows that the sexes differed in mean SVL ($F_{1,1865}$=365.72, P<0.0001), and that mean body sizes varied significantly between hours ($F_{5,1865}$=4.24, P=0.0008). Mean SVLs of males versus females were significantly correlated in a comparison across these different time periods (r^2=0.78, N=6, P=0.02). Thus, the times when large females were active were also the times that large males were active. There are two possible interpretations of this result. Either size-assortative courtship is due to these correlated activity patterns; or the correlated activity patterns may be a consequence rather than a cause of size-assortative courtship (i.e. males are active only when appropriately sized females are active). To test between these two propositions, we carried out the experimental tests at the Inwood den in 1999, in which we could control the numbers and sizes of snakes (see below).

Size-assortative Courtship in Arena Trials

Each arena contained three females of different sizes, plus equal numbers of small and large males. We calculated the total number of records of courtship by small and large males to females of each size class (Fig. 2). These data revealed the following.

(1) The overall intensity of courtship was very similar in the two size classes of males (Fig. 2: overall scores of 372 versus 411).

(2) Both size classes of males showed size-selective courtship. We used chi-square analyses to compare the numbers of courtship attempts to those expected under the null hypothesis of equal numbers of courtships directed to each of the three size classes of females. The results are highly significant both for small males (χ^2_2=61.18, P<0.0001) and for large males (χ^2_2=285.42, P<0.0001).

(3) The two size classes of males differed in their relative intensity of courtship to different size classes of females. Small males devoted approximately equal courtship to large and medium females (44 and 42%, respectively), with less effort (14%) directed to small females. In contrast, large males concentrated heavily on courting the largest females (70%), with less interest in medium-sized females (27%) and almost none in small females (3%). Thus, the distribution of courtship attempts among the three size classes of females differed significantly between large versus small males (for 12-male trials: χ^2_2=35.05, P<0.0001; for 6-male trials: χ^2_2=33.72, P<0.0001; Fig. 2).

Size-assortative Mating in Arena Trials

Does this strongly size-assortative courtship in arena trials (above) result in size-assortative mating? First, we look at trials conducted in 1997 at the Narcisse dens, in which each arena contained one female and either two, four or 24 males (see Shine et al. 2000b for more details). Males were allocated to arenas such that both the mean and the variance in male body size were equivalent across enclosures. These arena trials resulted in a significant (and positive) male–female size correlation among the mating pairs (r^2=0.13, N=36, P=0.033).

Remarkably, we see the same pattern even when we examine data from trials with only one male and one female per enclosure. Males and females were combined into pairs randomly with respect to size, so the only opportunity for size selection came from the fact that under these circumstances, some females did not mate. Such females were removed after 30–60 min, and replaced with other females. Despite this relatively limited opportunity for size-assortative mating (mean=1.36 females tried per male), larger males consistently mated with larger females (r^2=0.10, N=43 trials, P=0.035). This result shows that male–male rivalry is not necessary for size-assortative mating.

Factors Influencing Mate Choice by Males

Given that small and large males differ in their relative preference for different sizes of females (above), how flexible are such preferences? In particular, do small males court small rather than large females only because of the presence of large males? The 1999 arena trials at Inwood clarify this issue. Males modified their intensity of courtship depending on the numbers and sizes of competitors and potential partners (Fig. 3), but did not change their relative degree of preference for small versus large females (Fig. 4). Total courtship intensity of small males differed between trial types (one-factor ANOVA with trial type as the factor: $F_{4,37}$=4.97, P=0.0026). Post hoc tests (Fisher's PLSD) show that small males courted most intensely when the arena contained: (1) few other males (compare 6-male versus 12-male trials in Fig. 3); and (2) large females (compare 3-small-female versus small+medium+large female trials). Despite this increase in courtship when large females were present, the small males none the less continued to direct considerable courtship to small females (Fig. 3). Similar ANOVAs to examine the proportion of courtship directed to small, medium and large females under various trial types where all three female sizes were present, revealed no significant variation (separate ANOVAs for each size class of female yield P values>0.20 in each case; Fig. 4). That is, small males courted more vigorously under some conditions than others, but their relative allocation of courtship to the three size classes of females was not affected.

Large males showed similar responses to smaller ones. Their overall intensity of courtship was modified by trial conditions ($F_{4,37}$=38.20, P=0.0001; Fig. 3). Post hoc tests (Fisher's PLSD) show that the intensity of courtship of large males was affected by: (1) female body size, because

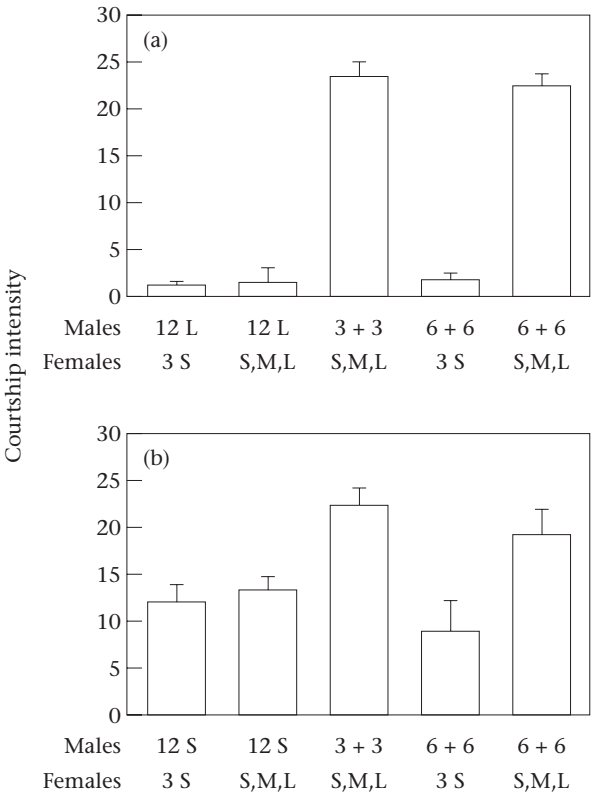

Figure 3. Intensity of courtship (see Fig. 2 legend for definition) by male garter snakes in arena trials with different combinations of male and female numbers and body sizes. (a) Large males (>50 cm SVL) and (b) small males (<40 cm SVL). Trials represent the following combinations. (1) Twelve large or small males, three small females, N=4 trials; (2) 12 large or small males, one small, one medium and one large female, N=10 trials; (3) three large and three small males, one small, one medium and one large female, N=12 trials; (4) six large and six small males, three small females, N=4 trials; (5) six large and six small males, one small, one medium and one large female, N=12 trials. Vertical lines show SE.

these males virtually ignored the small females; (2) the number of competing males; and (3) the body size of competing males. This latter effect can be seen by comparing courtship levels in the trials with all large males versus with a combination of large and small males (Fig. 3). The presence of other large males suppressed courtship by these animals to a greater degree than did the presence of small males. As was the case for the small males, the relative intensity of large-male courtship to the three size classes of females was not significantly affected by trial conditions (with proportional courtship to each size group as the dependent variables in separate one-factor ANOVAs, all P values>0.09; Fig. 4).

Ontogenetic Changes

Both correlative and experimental studies showed size-assortative courtship and mating in garter snakes (above). This pattern suggests an ontogenetic shift in mate preference within the lifetime of a single male, but our cross-sectional data do not provide direct evidence of

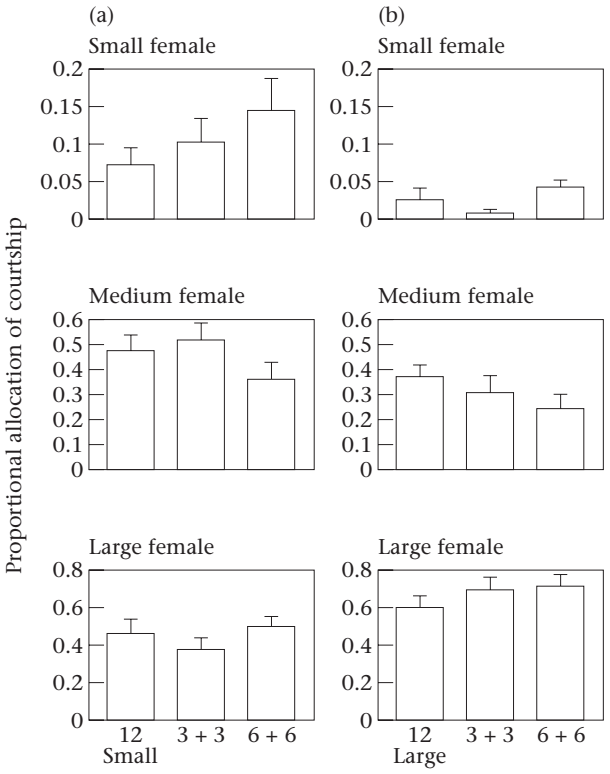

Figure 4. Proportional allocation of courtship by small (<40 cm snout–vent length) and large (>50 cm SVL) male garter snakes to small (<45 cm SVL), medium (45–55 cm SVL) and large (>55 cm SVL) females, in arena trials with different numbers and sizes of competing males. (a) Small males and (b) large males. Each arena contained one small female, one medium female and one large female. Trials represent the following combinations. (1) Twelve males, either all large or all small, N=4 trials in each case; (2) three large and three small males, N=12 trials; and (3) six large and six small males, N=4 trials. Vertical lines show SE.

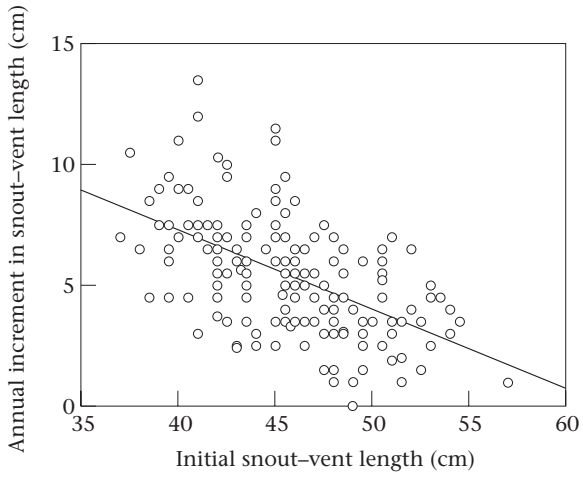

Figure 5. Growth rates of male garter snakes that were individually marked during the mating season at the Narcisse dens and then recaptured a year later in the subsequent mating season. Linear regression line fitted by least-squares method (r^2=0.30, N=162, P<0.0001); note that the relationship may well be curvilinear, and we fitted a linear regression only for simplicity.

such a shift. Instead, it is possible that males are polymorphic for both body size and mating preference. In such a case, some males would be small throughout their lives, and court small as well as large females. Others would delay courtship until they are large, and thereafter direct almost all of their courtship to large females. These two hypotheses make contrasting predictions about growth rates after maturity, and so we can test between them with growth data from a mark–recapture study. Figure 5 shows growth rates of males recaptured 1 year after they were first marked at the Narcisse dens. These data support the hypothesis of an ontogenetic shift in male mate preference. The small males that were captured as they were actively courting females had grown very substantially by the time that they were recaptured a year later (Fig. 5), moving from our 'small' to 'large' categories within 1–2 years.

DISCUSSION

Male red-sided garter snakes exert size-based mate choice. This result accords with previous work on the same species, which documented a general preference for larger females (Aleksiuk & Gregory 1974; Hawley & Aleksiuk 1976; Gartska et al. 1982). However, our study also revealed a stronger preference in large males than in small males. Mark–recapture data on this population show that males grow from 'small' (<40 cm) to 'large' (>50 cm) in 1–2 years (Fig. 5; see also Gregory 1977). Thus, the difference in mate preference is not attributable to subsets of males that differ in their response to cues from females as well as in body size (as reported in some fish, Sumner et al. 1994). Instead, these snakes offer a clear example of an ontogenetic shift in mate choice. We are unaware of any previous examples of this phenomenon, although theoretical models suggest that such complexities may eventually prove to be common (e.g. Galvani & Johnstone 1998) and size-based choice in females has been well documented (Sullivan et al. 1995).

Why do male garter snakes display mate choice? Theory suggests that a male should be an unselective suitor unless he allocates parental care to the offspring, or unless each mating reduces his future mating opportunities (Dewsbury 1982). For most snakes, neither condition is likely to be fulfilled. Parental care is not known in male snakes (Shine 1988; Somma 1990), and males of most snake species are presumably capable of producing sperm rapidly enough that any mating-induced depletion of their sperm stores does not impact on future mating opportunities. However, two aspects of garter snake reproductive biology may alter this scenario such as to increase the 'costs' of a current mating (i.e. incur reductions in the male's ability to inseminate other females). First, the male's testes are inactive during the mating season, so he cannot replenish his sperm supply until the following summer (Rossman et al. 1996). Second, he deposits a large gelatinous 'mating plug' during copulation, to occlude the female's reproductive tract (Devine 1977). Plug mass declines with successive matings by the same male (Shine et al. 2000c). Perhaps for this reason,

plus the high metabolic costs of courtship, the majority of males leave the mating area after a few weeks (Shine et al. 2001). Thus, male garter snakes are likely to be capable of only a limited number of effective copulations during the mating season. Under these circumstances, we might expect male garter snakes to be 'choosy' about their mates.

Given that male garter snakes exhibit mate preferences, why do they favour larger rather than smaller females? From the perspective of male reproductive success, a larger female is more likely to reproduce, and will produce more and larger offspring when she does so (Gregory 1977). This fitness advantage to the male would be reduced if larger females mated with more partners, but we have no evidence that this is the case. In keeping with these ideas, large females are actively preferred by small as well as large males (Fig. 2).

Although all males prefer to court large rather than small females, a male's body size affects the strength of that preference. Small males courted small females more vigorously than large males, both in the field and in the arena trials (Fig. 2). The most plausible reasons for this size-related shift in male preferences involve: (1) mate selection by females; (2) competition from other males; or (3) physical constraints. We examine these hypotheses below.

Female Choice

Small males may court and mate small females because large females will not copulate with them. This hypothesis is difficult to test, but is supported by the persistence of size-assortative mating in the absence of male–male interaction (i.e. when each enclosure contained only one male plus one female). However, it is difficult to imagine how a female garter snake could exert such a choice, especially when she is simultaneously courted by dozens of males. As soon as she gapes her cloaca open, several males move rapidly to insert a hemipenis; female control over this process is difficult to envisage. Alternatively, small males may be unlikely to achieve matings with large females if the process of 'courtship' involves a male somehow forcing the copulation on the female. However, we doubt that forcible insemination is physically possible in elongate, flexible animals such as snakes (Devine 1984; Shine et al. 2000f).

Male–Male Interactions

Small males may court and mate small females because they are unable to win copulations in direct physical competition with larger males. Large males are indeed able physically to exclude mating by their smaller rivals (Shine et al. 2000b; contra Joy & Crews 1988). The presence of large males also suppresses courtship by other males (above). None the less, such an effect clearly cannot be a direct one, because size-assortative mating was seen even in the absence of any opportunity for male–male interaction (single-male arena trials, above). If male–male interactions play some role, it must be an indirect one whereby the presence of larger competitors has favoured the evolution of size-specific mate preferences in male garter snakes (a behavioural analogue to 'the ghost of competition past': Connell 1961). Courting small females may well enhance the reproductive success of small males, because it reduces the amount of effort they expend on (ultimately unproductive) courtship to larger females.

Under this scenario, smaller males will court most vigorously to large females, but only when there are no large males in the vicinity. The presence of large rival males tends to suppress courtship by all other males, regardless of their body size. In the absence of large females, the small (but not large) males court smaller females. The reward of such courtship in terms of paternity (fitness) will be lower, but the lack of competition from large males means that a small male's probability of mating will be higher. Because of spatial and temporal heterogeneity in the locations of snakes around the den, small males may sometimes encounter large females, and court them unopposed. Such circumstances may generate much of the 'noise' around the general pattern of size-assortative mating in this population (Fig. 1).

Physical Constraints

Size-assortative mating might arise because of physical constraints. For example, large males might be physically unable to copulate with small females (Brown 1993); males may have to carry females about (Hatcher & Dunn 1996); or mating may occur within a confined space that limits the body sizes of both participants (Christy 1983). None of these possibilities is plausible for garter snakes. Measurements of the dimensions of the relative reproductive organs (hemipenes and female cloacal vestibules) show that all adult females can physically accommodate the hemipenis of any-sized male (Shine et al. 2000f). Mating occurs in the open, and copulating pairs rarely move about in any way that would place a premium on physical strength of the male (personal observation).

Conclusions

Our results differ in significant respects from those of most other reports on size-assortative mating. For example, size-assortative mating in lizards appears to result from (1) a universal male preference for large females, combined with (2) larger males actively excluding smaller males from these 'preferred' mates (e.g. Olsson 1993; Cooper & Vitt 1997). The same situation has been described in invertebrates (Brown 1990). This offers a strong contrast to the size-assortative courtship seen in our snakes. Size-assortative mating in amphibians generally seems to result from active preference by females (e.g. Orense & Tejedo-Madueno 1990; Sullivan et al. 1995), because fertilization success depends on the size disparity between male and female (Robertson 1990; Sullivan et al. 1995). None the less, active male preferences contribute to size-assortative mating in some amphibian taxa with male parental care (Boll &

Linsenmair 1998). Urodele amphibians provide an interesting parallel with garter snakes. Males of at least four species demonstrate an active choice for larger partners (reviewed by Sullivan et al. 1995), possibly for the same reason that we propose for garter snakes. Male salamanders produce a gelatinous spermatophore at mating, and males may thus be unable to mate repeatedly in quick succession (Verrell 1988). This constraint may favour the evolution of male choosiness (Dewsbury 1982). The situation has been taken to an additional level of complexity in garter snakes, by the evolution of ontogenetic shifts in mate preference among males.

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