



Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered

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Why do males exert strong mate choice in some taxa but not others? Theory suggests that mate discrimination will enhance male fitness when encounter rates with potential mates are high, when those potential mates vary in the fitness consequences likely to accrue from an attempted insemination, and when courting one female reduces the male's opportunity to court other females. One widespread form of mate choice involves a trend for males of many ectothermic species to court larger (and thus, more fecund) females. To test whether such preferences are dynamically adjusted to local conditions, we studied male preference for larger females in red-sided garter snakes, *Thamnophis sirtalis parietalis*, near a communal den in Manitoba, Canada. Courting a small female imposes a high opportunity cost for a male in the centre of the den, because many large and easily located females are nearby. In the surrounding woodland, in contrast, a male that neglects a small female is unlikely to encounter a larger substitute partner. In arena trials, male snakes from the den selected larger females more than did males from the surrounding woodland. Manipulating a den male's exposure to females (none, large, small) for 60 min led males to adjust their criteria for courtship depending upon the sizes of females encountered. Hence, the local environment can modify courtship criteria, with male garter snakes adjusting their mate choice selectivity based upon spatial and temporal factors that affect the opportunity costs of courtship.

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In almost all sexually reproducing species, individuals encounter numerous members of the opposite sex and hence have the opportunity to exert some degree of mate choice. Darwin's theory of sexual selection suggests that reproducing animals can increase their evolutionary fitness by selecting a mate (or mates) that will maximize the output of viable offspring likely to result from that mating (Darwin 1871). In support of this prediction, a substantial literature documents nonrandom allocation of courtship effort and/or sexual receptivity depending upon phenotypic traits of potential mates (Ghiselin 1974; Andersson 1994). Many of the mate choice criteria identified by these studies correlate with enhanced reproductive output (i.e. higher fecundity or offspring viability), again in accord with Darwinian predictions (Basolo 2004). However, the degree of mate choice exerted often differs between the sexes, is weaker overall within some populations than in others, and varies through space and time within a single

population (Jormalainen et al. 1992; Andersson 1994; Gowaty 2004).

Evolutionary theory suggests a reason for this diversity in 'choosiness': nonrandom mate choice is most likely to enhance individual fitness (1) if there is substantial variation in 'quality' among individuals of the other sex, generating equivalent variation in the fitness benefits accruing from a mating, (2) if investing effort in courting one potential partner reduces the animal's ability to invest in others, and (3) if rates of encounter with potential mates are high (Dewsbury 1982; Hubbell & Johnson 1987; Crowley et al. 1991; Berglund 1994). Thus, highly developed mate choice is predicted to occur most often in organisms that fulfil these requirements (Hubbell & Johnson 1987; Jennions & Petrie 1997). These attributes are widespread, so that to test the underlying model, we need to identify a study system with variation in either the benefits or costs of mate choice.

Although most studies on mate choice have focused on females as the 'choosy' sex, males can also exercise mate choice, in ways that significantly enhance their reproductive success (Drickamer et al. 2003; Gowaty 2004). Perhaps the most general such phenomenon

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involves a preference for courting larger rather than smaller females. The selective advantage of using female body size as a criterion for mate choice presumably involves a consistent trend for fecundity to increase with maternal body size (perhaps simply because of physical constraints on clutch volume: Ghiselin 1974; Vitt & Congdon 1978; Qualls & Andrews 1999). Thus, a wide range in female body size within a single population, as is typical of ectotherms (Pough 1980; Shine et al. 1998), will translate into massive differentials in fecundity and, thus, fitness benefits of mating. If the time, energy or risk invested in courtship reduces a male's opportunities to court other females, males should prefer larger females as sexual partners. In support of this prediction, increased courtship to larger females has been documented in a diverse array of organisms, including molluscs (Erlandsson & Johannesson 1994), crustaceans (Rahman et al. 2002; Gosselin et al. 2003), insects (Jormalainen et al. 1994; Mallard & Barnard 2003), fish (Sargent et al. 1986; Berglund & Rosenqvist 1993; Dosen & Montgomerie 2004), anuran amphibians (Berven 1981), urodele amphibians (Verrell 1986, 1989), lizards (Olsson 1993; Cuadrado 1998), snakes (Luiselli 1996; Shine et al. 2001b) and birds (Johnson 1988). None the less, there are also many cases where no male preference for larger females is evident (Pyron 1996; Rahman et al. 2004), or where such a preference is evident only in a subset of males (Basolo 2004), or only under particular conditions (Jormalainen et al. 1992; Berglund 1994). An increase in mating rates with increasing female body size may also be driven by factors other than male preference (Brown 1993), so direct experimental evidence is necessary for any confident interpretation of male mate choice.

Snakes offer a particularly interesting lineage with which to investigate male mate choice, and a striking contrast to their sister taxon, the lizards. Mate choice by females has been shown for many lizard species, whereas male mate choice has been documented only rarely (Andrews 1985; Andersson 1994; Olsson et al. 2003). In contrast, several empirical studies have revealed mate choice by male snakes (Luiselli 1996; Shine et al. 2001b), but none have demonstrated mate choice by females (but see Schuett & Duvall 1996). In the most intensively studied system, male red-sided garter snakes, *Thamnophis sirtalis parietalis*, adjust their intensity of courtship to a female based on not only her body length (Shine et al. 2001b), but also her body condition (Shine et al. 2003b), whether she has mated recently (Shine et al. 2000c), how long since she has emerged from hibernation (Shine et al. 2005b), and from which den population she comes (LeMaster & Mason 2003). These subtle mate discrimination choices are based upon sex-specific skin lipids on the female's skin (LeMaster & Mason 2002; Shine et al. 2003c). Why are male snakes so choosy? Theory suggests that the most likely reason is that male snakes experience high 'opportunity costs': locating and courting a female is a long and risky process that can substantially reduce the male's ability to locate and court alternative potential mates (Duvall et al. 1993; Shine et al. 2001b). Thus, selection may have

favoured male abilities to discriminate between potential mates based upon traits that predict the probable fitness benefits accruing from a mating, and to focus their courtship effort disproportionately towards larger, more fecund females.

To test the hypothesis that opportunity costs drive the evolution of male mate choice, a study system is needed where such costs vary in time and/or space. In such a system, we predicted that males would show corresponding variation in their degree of 'choosiness', with strong selectivity evident only under circumstances where courting one female directly compromises the male's ability to court another, perhaps larger, female. In contrast, males should be relatively nonselective (e.g. court even a small female) if they are unlikely to encounter a larger potential mate, either because densities of females are low or because most females in the local area are small. Communal dens of red-sided garter snakes provide an ideal opportunity to test this prediction. Courtship and mating occur both at the den itself, with high densities of large females, and in the surrounding woodland where both densities and mean body sizes of females are lower (Shine et al. 2001a). Thus, we predicted that male snakes at the den would be more selective (show stronger size-based mate choice) than would males in the surrounding woodland. Using the same system, we also tested whether any such modification of mate choice criteria is hard-wired or facultative; that is, does changing the density or body size distribution of females encountered by a male snake modify his criteria for mate choice? We conducted experimental studies at a garter snake den to answer these questions.

METHODS

Study Species and Area

Red-sided garter snakes are small (mean snout-vent length, SVL: males: 45 cm; females: 60 cm) nonvenomous colubrid snakes widely distributed across southern Canada and the northern U.S.A. (Rossman et al. 1996). Towards the northern limit of their range in south-central Manitoba, severely cold winters force the snakes to aggregate in communal overwintering sites for about 8 months each year (Gregory 1974). Most adult snakes within a wide area overwinter in these large communal dens, but smaller (juvenile) individuals spend the winter in other sites, probably in smaller groups (Gregory & Stewart 1975). Mating begins in the vicinity of the den as soon as the snakes emerge in spring (May), before they disperse to their summer ranges. Females ovulate about a month after dispersing from the den, give birth in early autumn in their summer ranges, and then migrate back to the den to overwinter (Gregory & Stewart 1975; Mason 1993). The large numbers of snakes at these dens, and the animals' tolerance to disturbance by observers, provide a unique opportunity for research on behavioural ecology and the mating system (Mason 1993). We worked at a den containing more than 50 000 snakes 1.5 km north of Inwood, 250 m east of Highway 17 in central southern

Manitoba (50°31.58'N, 97°29.71'W) in May 2003 and 2004. The den is an open rocky area beside a limestone quarry, bordered by aspen woodland interspersed with grassy areas (Shine et al. 2003a). The research was conducted under the authority of Oregon State University Institutional Animal Care and Use Committee.

Surveys of Female Body Sizes

To quantify the size distributions of female snakes in the den itself versus in the surrounding aspen woodland, we took daily samples of animals from both sites during May 2003. Den females were collected by hand soon after they emerged, whereas woodland snakes were captured in funnel traps set along a wire drift fence 50 m from the den (Shine et al. 2005a). Sex of captured snakes was assessed by tail shape and confirmed by manual eversion of the hemipenes in any doubtful cases. All snakes were measured (SVL) before immediate release at their site of capture (for woodland snakes, on the opposite side of the fence from which they had been caught). Given that the den contained more than 50 000 snakes (from mark-recapture studies: R. Shine, unpublished data), and the short duration of female residency in and near the den (Shine et al. 2001a), it is unlikely that any individual snakes were recaptured at the same site in more than one sample. However, some 'den' females might have been recaptured later, as they dispersed through the woodland. This minor level of inadvertent pseudoreplication should have little effect on our estimates of the size distributions of females in these two sites.

'Opportunity Costs' for Mate Location

A dramatic reduction in snake densities with increasing distance from the den, coupled with an increase in the proportion of already mated females (Shine et al. 2001a, 2005a), suggests that males in the woodland should take longer to find a potential mate than males at the den. Already mated females are unable to remate for at least 24 h, because mating males deposit a gelatinous plug that occludes the female cloaca (Devine 1977; Shine et al. 2000c). To quantify the time taken to find a female, we removed the female from a courting group (with minimal disturbance) and then followed one randomly selected male from that group until he found another female. Trials were terminated after 5 min if the male was still mate searching at that time.

Effects of Female Size on Male Courtship

We measured intensity of courtship by recently captured males in open-topped nylon arenas (1 × 1 m and 0.8 m high) erected in a grassy area near the Inwood den. Two sets of trials were conducted, with different experimental designs for logistical reasons. Trials with a single male and a single female per arena always produced vigorous courtship. To generate variation in courtship intensity, we added a second male in the first set of trials;

and to obtain a direct comparison of mate choice, we added a second female in the second set of trials.

Den versus woodland males

We placed two males and a single unmated female (with her cloaca taped shut to preclude copulation) within each arena, and scored whether each male courted the female (i.e. aligned with her body, chin pressing, caudocephalic waving; Whittier et al. 1985) at 1-min intervals for 20 min. Both males within a single trial were taken from the same location (either den or woodland); all females were recently collected from the den.

Experimental manipulations

Each arena contained one male from the den and two unmated females, one large (>55 cm SVL) and one small (≤55 cm SVL); female cloacas were taped shut to prevent mating. We scored whether either female was courted during five observation periods (10 s each) at 5-min intervals. For 60 min before these trials of courtship intensity, males were kept in groups of 10 in similar arenas containing either no females, five large females (>55 cm SVL), or five small females (≤55 cm SVL). Again, all females were taped to preclude copulation. In all experiments, an individual snake was used in only a single trial.

RESULTS

Surveys of Female Body Sizes

Among our sample of 2469 female snakes, den females averaged significantly larger than did woodland females (ANOVA: $F_{1,2467} = 160.36$, $P < 0.0001$; Fig. 1). For the categories of 'large' and 'small' female subjects, 52% (496/959) of females in the den were small (≤55 cm SVL) versus 67% (1017/1510) in the woodland (chi-square test: $\chi^2_1 = 59.73$, $P < 0.001$). Temporal (day-to-day) variation in mean female body sizes was also significant, both at the den (range of daily mean values 49.9–60.0 cm SVL; ANOVA: $F_{16,892} = 7.26$, $P < 0.0001$) and at the drift fence in the woodland (range of daily mean values 44.8–57.0 cm SVL: $F_{15,1494} = 2.24$, $P < 0.0001$).

'Opportunity Costs' for Mate Location

When we removed the female that the den males had been courting, they located another female and recommenced courting after a mean ± SD of 22.5 ± 23.62 s (range 3–67 s), and after travelling a mean ± SD of only 1.99 ± 2.21 m. In contrast, only four of the 10 woodland males located another female within the allotted 5-min period (range 60 to >300 s) and they travelled much further (12.55 ± 8.29 m) in the process. The den males required significantly less time to relocate a female than did woodland males (ANOVA: $F_{1,18} = 49.06$, $P < 0.0001$) and did not have to travel as far to do so (distance travelled: $F_{1,18} = 15.16$, $P < 0.001$).

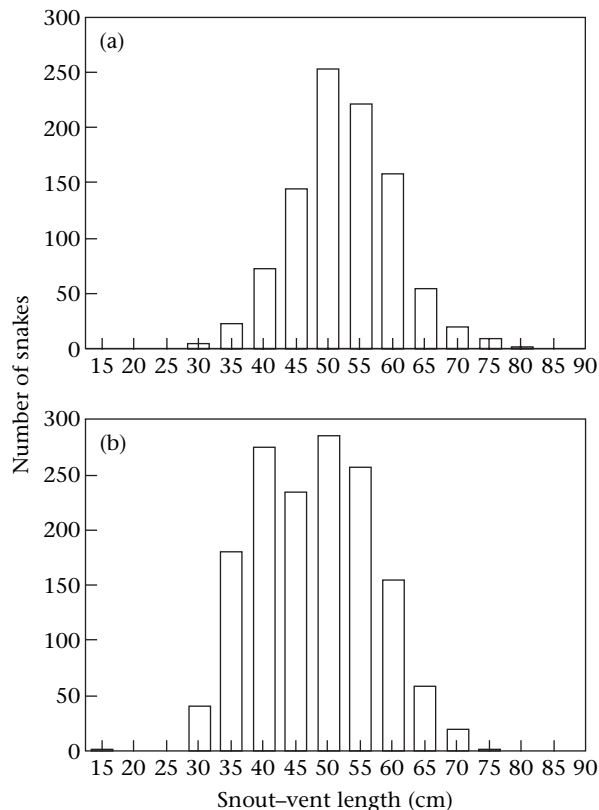


Figure 1. Snout-vent length distributions of female garter snakes collected in (a) the den and (b) the surrounding woodland.

Effects of Female Size on Male Courtship

Den versus woodland males

ANCOVA with male location as the factor, female SVL as the covariate and courtship intensity as the dependent variable showed that larger females attracted more courtship overall ($F_{1,138} = 5.49$, $P < 0.03$), and that den males courted at a higher rate than did woodland males ($F_{1,138} = 5.01$, $P < 0.03$). More importantly, a significant interaction between female SVL and male location ($F_{1,138} = 6.05$, $P < 0.02$) means that female body size affected the intensity of courtship by den and woodland males differently. Woodland males did not modify their courtship intensity based on female body size, whereas den males courted larger females more intensely than smaller ones (Fig. 2). Including male body length as a covariate in these analyses did not explain significant additional variance ($F_{1,134} = 0.51$, $P = 0.48$; all interactions NS).

Experimental manipulations

When two females of different sizes were present within the same arena, the larger female generally attracted more courtship. Thus, the proportion of observation periods when the male courted the smaller rather than the larger female was significantly less than expected under the null hypothesis of equal courtship intensity regardless of female body size (overall = 32.7% of courtship to the smaller female; chi-square test: $\chi^2_1 = 97.79$, $P < 0.0001$).

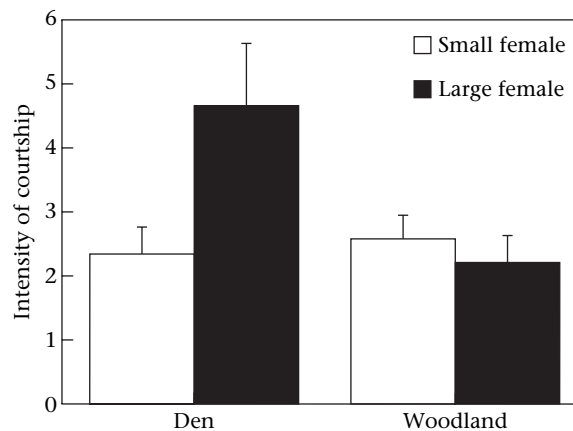


Figure 2. Mean number of observation periods (out of 20) + SE at which male garter snakes collected either at the den or in the surrounding woodland were recorded courting smaller-than-average females (≤ 55 cm snout-vent length) versus larger-than-average females (> 55 cm snout-vent length) in outdoor arenas. Sample sizes (left to right) = 42, 30, 26 and 44 trials.

However, the magnitude of this bias was stronger for males that had been housed only with large females than for males that had been housed only with small females (ANOVA with arcsine percentage of courtship to small female as the dependent variable: $F_{2,58} = 3.33$, $P < 0.05$; Fig. 3). Including male body size as an additional covariate in this analysis showed that larger males were more likely to court larger rather than smaller females (ANCOVA: $F_{1,57} = 4.14$, $P < 0.05$), but with no significant interaction term between treatment and male body size ($F_{2,55} = 0.99$, $P = 0.38$); the significance of the treatment effect was not changed by including this additional covariate ($F_{2,57} = 3.61$, $P < 0.04$). Thus, male snakes adjusted their intensity of courtship to smaller versus larger females

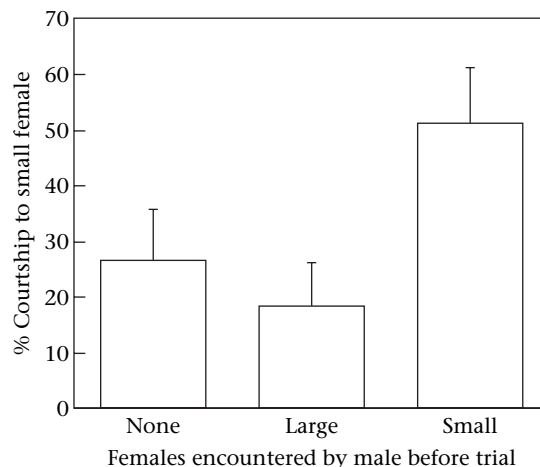


Figure 3. Mean percentage of observation periods (out of 5) + SE at which a male garter snake was recorded courting the smaller rather than the larger of two females placed in his outdoor arena. Sample sizes (left to right) = 22, 18 and 21 trials.

based on the body size distribution of females that they had encountered over the preceding 60 min (Fig. 3).

DISCUSSION

The current study reinforces a major conclusion from previous research: male red-sided garter snakes are highly selective courters in ways that are likely to enhance male fitness. Studies to explore the mechanistic basis of this choosiness have revealed that courting males use multiple criteria (e.g. the female's length, condition, pheromonal profile, appearance and body temperature) and that such criteria can differ even between small and large males within the same population (Shine et al. 2001b; LeMaster & Mason 2002). Our field studies have also revealed that males in the den differ from those in the surrounding woodland in several aspects of mating tactics (mate location modalities, movement patterns, response of courtship intensity to operational sex ratio: Shine et al. 2001a, 2005a). The present study adds another variable, size selectivity of courtship, to that list of spatial divergences in male mating tactics.

The overall preference for larger females is also consistent with previous results on garter snakes (Gartska et al. 1982; Shine et al. 2001b) and may be one of the most widespread mate choice criteria used by males throughout the animal kingdom (see above). The proximate mechanism by which male red-sided garter snakes assess female body size involves vomeronasal detection of body-size-related changes in the chemical composition of the skin lipids of females (Shine et al. 2001a, 2003b, 2005a). Consistent with a priori predictions, males facing higher opportunity costs (i.e. in the den rather than the woodland) were more selective courters based on female body size. However, our results also reveal an unsuspected flexibility in mate choice in male snakes, because the body sizes of females previously encountered by a male induced a rapid shift in the degree to which he subsequently courted larger rather than smaller females.

Why did males shift courtship preferences in this way? At a proximate level, one possible explanation is familiarity; that is, males court females that provide stimuli similar to those they have encountered during recent (albeit unsuccessful) courtship. Alternatively, males may modify their courtship criteria based on a relative rather than an absolute scale, ignoring, for example, females that are smaller than most of the potential mates they have encountered over some previous period. Regardless of the proximate mechanism involved, the end result is a facultative adjustment of courtship intensity to the temporal and spatial distribution of potential mates of differing body sizes.

This kind of facultative mate choice is likely to enhance male fitness if, and only if, the numbers and body sizes of females encountered by a mate-searching male garter snake vary significantly over small spatial scales (e.g. between the den and the woodland) and/or short temporal scales (e.g. day to day). Our sampling reveals exactly this kind of variation (e.g. Fig. 1). Mean body sizes of female snakes also vary over even shorter temporal scales (hour

to hour) at the same site in a den during the same day (Shine et al. 2001b). Why are female body sizes so variable? Sexual conflict drives much of this spatial and temporal variation in mean body sizes of females, with smaller females avoiding potentially costly courtship by males by selecting times and places for activity that minimize rates of encounter with males (Shine et al. 2000b, 2004). As a result, small females are rarely found in the den, and they emerge and disperse primarily on days too cold for courtship (Shine et al. 2000b). The consequent small spatial and temporal scales for variation in female abundance and body size favour rapid facultative shifts in male mate choice criteria. More dramatic variations in female numbers and sizes can occur over other scales; for example, numbers and mean body sizes of female snakes at one den fell precipitously in a year after most of the large adult snakes died in very cold weather (Shine & Mason 2004).

The specific cues eliciting less discriminating courtship by woodland males include a shift in the body size distribution of females encountered (Fig. 3). Do other factors, such as low overall encounter rates with females, also play a role? Males kept away from females did not show unselective courtship (i.e. they tended to court larger rather than smaller females; Fig. 3), suggesting that the lower encounter rate was not a proximate cue for shifting selectivity. Similarly, the intensity of competition from rival males (lower in the woodland than in the den, based on sizes of courting groups; Shine et al. 2001a) might influence criteria for male mate choice. However, when numbers and sizes of courting males were manipulated, there was no evidence of such a shift (Shine et al. 2000a and unpublished analyses of those data). Thus, the size distribution of females that a male encounters may be a more important influence on his mate choice criteria than any shift in encounter rates or operational sex ratio. In contrast, operational sex ratio has been reported to influence the degree of male preference for larger females in isopods (Jormalainen et al. 1992) and fish (Berglund 1994; Pyron 1996). Our results indicate that male preference for larger females can occur despite highly male-biased sex ratios, as seen also in the moth *Operophtera brumata* (Van Dongen et al. 1998).

Despite interspecific differences in the determinants of male mate choice criteria, there is broad consensus that males adjust such criteria not only to spatial and temporal variation in mating opportunities, but also to phenotypic traits of the male in question. One major determinant of the degree of male preference for larger females in garter snakes is the male's own body size (larger males are more selective; Shine et al. 2003a), a trend also seen in studies of poeciliid fish (Ptacek & Travis 1997; Basolo 2004). Such behavioural analogies across disparate phylogenetic lineages encourage the search for general patterns in the types of fitness costs and benefits that drive the evolution of mate choice. None the less, our study also provides a cautionary tale for the methodology of future studies. If the degree of a male's mating preference for larger females is sensitive to the numbers and/or sizes of conspecifics that he encounters beforehand, as in our snakes, then experimental trials need to control the encounter rates of their test animals immediately before conducting trials.

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