Familiarity with a female does not affect a male's courtship intensity in garter snakes *Thamnophis sirtalis parietalis*

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Abstract   In many animal species, males direct more intense courtship towards females they have not previously encountered, than towards females with which they have previously mated. To test the factors responsible for this "Coolidge Effect", we need studies on a wide range of taxa – including those with mating systems in which we would not expect (based on current theory) that such an effect would be evident. The Coolidge Effect has been documented in several lizard species, but has not been looked for (and would not be expected) in snakes. We conducted experimental trials with red-sided garter snakes *Thamnophis sirtalis parietalis* at a communal den in Manitoba, to see whether previous exposure to a female (either courting, or courting plus mating) modified male mate choice or courtship intensity. In keeping with prediction from theory (but contrary to an early anecdotal report), male garter snakes did not modify their courtship behaviour based upon their familiarity (or lack thereof) with a specific female. At least in large courting aggregations, male snakes may maximize their fitness by basing mate-choice upon immediate attributes of the female (body size, condition, mated status) and the intensity of competition (numbers and sizes of rival males) rather than information derived from previous sexual encounters [*Current Zoology* 58 (6): 805–811, 2012].

Keywords   Coolidge Effect, Courtship, Mate choice, Mating system, Reptile

Males of many animal species direct courtship in a highly selective fashion, exhibiting strong preferences for specific females and ignoring others (Andersson, 1994). Many of these forms of mate choice clearly relate to phenotypic traits of females that predict probable fitness benefits from a mating: for example, males of many fish, amphibian and reptile species selectively court larger rather than smaller females, presumably reflecting the enhanced fecundity of larger partners (Olsson, 1993; Luiselli, 1996; Ptacek and Travis, 1997; Basolo, 2004). However, some examples of male courtship selectivity involve individual mate recognition rather than a broader bias with respect to female morphology. One of the most striking and widespread such phenomena comprises a preference for novel partners: that is, if given an appropriate opportunity, a male will direct courtship to a female with which he has no previous experience, rather than a female with which he has extensive previous experience (e.g., in pair-bonding species, his usual mate: Dewsbury, 1981a; Cohn et al., 2004). This form of mate choice has been dubbed the Coolidge Effect, after a former US president who referred to the phenomenon in humans and chickens (Dewsbury, 1981b; Malin, 1983; Pizzari, 2002; Steiger et al., 2008).

Preferences for unfamiliar partners occur in females as well as males of some taxa (Lisk and Baron, 1982; Hughes et al., 1999; McLaughlin and Bruce, 2001). The mechanisms underlying the Coolidge Effect might be adaptive (e.g., mating with a novel female offers a greater enhancement of the male's fitness than yet another mating with his usual partner) or a non-adaptive consequence of proximate factors (e.g., habituation of the sexual response to an existing partner). Although the Coolidge Effect has been demonstrated in a range of vertebrate taxa, research on this topic has concentrated on mammals and birds (Dewsbury, 1981b; Pizzari, 2002), presumably in the belief that the capacity for individual recognition required for such a choice likely is more common in the "higher" vertebrates (Steiger et al., 2008). However, extensive data now reveal that lineages such as amphibians and reptiles contain many taxa in which animals have highly-developed abilities to recognize specific other individuals (Bull et al., 1994; Cooper, 1996). Accordingly, we might expect to find the Coolidge Effect in some species within such lineages. In keeping with this prediction, the Coolidge Effect has been documented in salamanders (Donovan and Verrell,

1991) and a phylogenetically diverse array of lizard species (Cooper, 1985; Tokarz, 1992; Cooper and Steele, 1997; Steele and Cooper, 1997; Orrell and Jenssen, 2002). The obverse effect also occurs, whereby male lizards selectively court or associate with their prior partner in preference to a novel female (Censky, 1995; Olsson and Shine, 1998; Bull, 2000). Regardless, in all of these cases the inference is the same: males target courtship to specific females based on familiarity with that individual rather than her phenotypic traits *per se*.

Studies on a phylogenetically and ecologically broader array of taxa have great potential to clarify not simply the occurrence of familiarity-based mate choice, but also its functional significance. For example, if a simple proximate response to novelty is involved then we might expect the Coolidge Effect to be virtually ubiquitous. In contrast, adaptive hypotheses suggest that we should see no such effect in situations where there is no fitness benefit to males that base mate choice on familiarity (Pierce et al., 1992). Thus, we need research on a wide array of taxa to evaluate the generality of individual recognition as a mate-choice criterion. Importantly, we need to study not only taxa with mating systems that should favour the Coolidge Effect, but also taxa that do not conform to these conditions. Only by analysing a wide variety of systems can we hope to test among hypotheses on the causal mechanisms responsible for such phenomena. No such study has yet been conducted on snakes, primarily reflecting (1) logistical difficulties associated with behavioural studies on these animals, and (2) a general belief that because snakes rarely if ever form longterm pair-bonds (but see de Haan, 1984, 2003a,b), we would not expect to see males basing courtship choice upon familiarity.

Familiarity with individual females is likely to be especially limited in snake taxa that aggregate in large numbers for courtship and mating. Cold-climate populations of garter snakes *Thamnophis sirtalis parietalis* are the most extreme case of this phenomenon, with courtship occurring in groups of hundreds or even thousands of individuals (e.g., Gregory, 1974). However, in their landmark studies on garter snake mating systems, Blanchard and Blanchard (1941) suggested that male snakes focus their courtship on particular females. Specifically, they say (p. 218) that "although there may be several females in a group, and though the male may temporarily lose touch with the one he has started to court, he usually finds the original female again and persists with that one exclusively, ignoring the others. In a group of females he may become temporarily con-

fused, his body rippling over the body of another in the group; but shortly he becomes oriented. If the female moves away he follows her, leaving the others, even gliding over them, without hesitation. This is so usual as to justify the statement that snakes have individuality to one another". Most of the Blanchards' empirical statements have been verified by subsequent research, suggesting that these observations warrant further study. We exploited the opportunities offered by massive aggregations of courting garter snakes around communal overwintering dens in central Canada (Mason, 1993) to examine whether or not male snakes in these courting aggregations modify their mate-choice criteria or courtship intensity based upon their prior interactions with specific females, as suggested by Blanchard and Blanchard (1941) but contrary to prediction from current theory (Donovan and Verrell, 1991).

1　Materials and Methods

1.1　Study species and area

Red-sided garter snakes penetrate further north into severely cold areas than do any other North American snakes (Rossman et al., 1996). The harsh winter temperatures in Manitoba force adult snakes into deep caverns to avoid freezing, so that snakes from a wide area congregate in communal dens in autumn (Gregory and Stewart, 1975). Some dens contain many tens of thousands of snakes (Gregory, 1974; Gregory and Stewart, 1975). Courtship and mating occur early in spring, after the snakes emerge but before they disperse to their summer feeding ranges (Gregory, 1974). Adult males average smaller than females (mean snout-vent lengths [SVLs] 45 vs. 60 cm respectively) and remain longer near the den after spring emergence than do females (Shine et al., 2001a). Thus, courting aggregations near the den are highly male-biased, with any emerging female immediately courted by many males (Gregory, 1974; Shine et al., 2001a). We worked in May 2004 at a large communal den containing >50,000 snakes 1.5 km north of Inwood in central southern Manitoba (50°31.58'N, 97°29.71'W; see Shine et al., 2003b for more information on this den).

Copulations are followed by deposition of a gelatinous mating plug that occludes the female cloaca and prevents remating for about two days (Shine et al., 2000b), by which time many females have left the vicinity of the den (Shine et al., 2001a). Although remating at the den thus is rare, some females remain long enough for multiple mating before dispersal (Shine et al., 2001a). Recently-mated females attract little courtship,

because copulatory fluids act as pheromones to discourage male attention (Shine et al., 2000b). However, the deterrent effect generally lasts only a few hours, so that many courting groups form around already-mated females (R. Shine, pers. obs.).

To examine whether or not a male's prior familiarity with a female influences his intensity of courtship towards her, we need to remove impediments to courtship and mating. Based on previous research, we know that female attractivity can be restored simply by washing a recently-mated female to remove the copulatory fluids (Shine et al., 2000b). The gelatinous mating plug also must be removed, because otherwise it provides a physical impediment to intromission (Shine et al., 2000b). We used these methods to investigate whether or not familiarity with a female (either courtship alone, or courtship plus mating) affects the intensity of courtship by a male garter snake.

1.2   Effects of prior courtship

We collected recently-emerged unmated females (recognized by their muddy appearance and lack of a mating plug) from the den on the morning we conducted these trials. We placed one unmated female (with her cloaca taped shut to preclude copulation) with six males, in an open-topped nylon arena ("Space Pop", Smash Enterprises, Melbourne; circular with 48 cm diameter, 56 cm deep) in a room at 20°C. This air temperature, group size and density of males is typical of natural courting groups at the dens (Shine et al., 2001a). Males were marked with non-toxic paint for individual identification; each male was used in only a single trial. We ran 20 replicates of this procedure, and thus scored courtship intensities of 120 males in total. After five minutes to allow the animals to settle, we scored the intensity of courtship of each male on a four-point scale (0 = no courtship, 1 = alignment, 2 = chin-rubbing, 3 = caudocephalic waving: see Whittier et al., 1985 for more detail) at 3-minute intervals for the next 15 min. We then removed the female, and either immediately returned her to the arena 10 sec later, or replaced her with another, similar-sized female from a similar trial being conducted in an adjacent arena. In all cases, courtship recommenced as soon as the female was added. Our experimental design meant that all females in the second part of each trial had been exposed to similar levels of courtship in the preceding period; the only difference was that in some trials the males encountered a novel female whereas in others they encountered the same female as they had been courting previously.

1.3   Effects of prior courtship plus mating

We collected copulating pairs in the Inwood den, and kept them in open-topped arenas (as above) until they had separated. We then placed each pair together in a clean cloth bag and kept them overnight at low ambient temperatures (10–15°C) in our field laboratory; snakes are inactive under these conditions (R. Shine, pers. obs.). The following morning we washed females with clean water, removed their mating plugs, then placed a single male plus two of these females (one of them his previous partner, the other a novel female of the same body size [± 2 cm SVL] as his previous partner) into an arena. All arenas were washed between trials. The two females were presented simultaneously. We recorded which female he courted, and his intensity of courtship (on the same 4-point scale as above) at 1-min intervals for the next 15 min. We ran 24 replicates of this series (i.e., obtained responses on courtship by 24 males, to each of two females).

Each female in the "prior mating" experiment was used in trials with two males (once with its previous sexual partner, and once with a novel male). Apart from this exception, each snake was used in only a single trial; this was true for both sets of experiments described above. We used the software programs Statview 5 and JMP 5.01a (SAS Institute, 1998, 2002) for statistical analysis. Data were tested for conformity to the assumptions of parametric analyses prior to testing, and were ln-transformed if necessary. For P-values between 0.05 and 0.20, we calculated the power of the test to evaluate the probability that the non-significance was due to unacceptably low power (Day and Quinn, 1989; Peterman, 1990).

2   Results

2.1   Effects of prior courtship on male courtship intensity

We analysed data from these trials (20 replicates, each with 6 males) using a repeated-measures ANOVA, with treatment (female changed or not) as the factor, time period (before vs. after the "change" of females) as the repeated measure, and male courtship intensity as the dependent variable. Two measures of courtship intensity were used for each male: the maximum value recorded during the 15-min observation period, and the proportion of observations (out of 5) on which the male was actively engaged in courtship. Preliminary analyses revealed that courtship intensity was not significantly different among trials, so we treated each male as independent for the purposes of statistical analysis, rather

than including trial # as a nesting factor. Courtship intensity was similar in the two observation periods (before *vs.* after the female was removed and then either replaced or changed). This lack of difference was evident both for the maximum intensity of courtship observed per male ($F_{1,118} = 1.84$, $P = 0.18$; power = 0.26) and for the number of observation periods in which courting was seen ($F_{1,118} = 2.24$, $P = 0.13$; power = 0.31). Whether the female was changed or replaced had no significant effect on either the maximum intensity of courtship ($F_{1,118} = 2.62$, $P = 0.11$; power = 0.34) or the number of observation periods in which courting was recorded ($F_{1,118} = 0.07$, $P = 0.79$). No significant interactions were apparent between these factors (all $P > 0.50$; see Fig. 1).

2.2 Effects of prior mating on male mate choice and courtship intensity

We conducted 24 trials in which a male snake was given the opportunity to court either a female with which he had copulated the previous afternoon, or a novel female. Of 15 observation periods per trial, males courted their previous partner on 0 to 9 occasions (mean = 2.58, SD = 2.56) compared to 0 to 10 occasions for the novel female (mean = 3.31, SD = 2.68). These two rates did not differ significantly from each other (paired $t = 1.04$, $df = 25$, $P = 0.31$). The maximum courtship intensity observed per male was equal for courtship directed to his previous partner versus the novel female in 10 cases, greater to his previous partner in six cases, and greater to the novel female in eight cases (against a null hypothesis predicting equal numbers in either direction, $\chi^2 = 0.29$, $df = 1$, $P = 0.60$).

3 Discussion

Although previous studies have indicated that sexual novelty (provision of a novel partner) can enhance courtship intensity in both males and females of a variety of taxa (Dewsbury, 1981a,b; Lisk and Baron, 1982; Malin, 1983; Pizzari, 2002; Steiger et al., 2008), including lizard species (Cooper, 1985; Tokarz, 1992; Cooper and Steele, 1997; Steele and Cooper, 1997; Orrell and Jenssen, 2002), our experiments provided no evidence for such an effect in red-sided garter snakes. Males did not court more intensely to females that they had recently been courting, or had previously mated. Hence, we suspect that Blanchard and Blanchard's (1941) report of individually targeted courtship by males of this species represents cases where females differed sufficiently in sexual attractiveness that a given male focused his courtship only to the female emitting
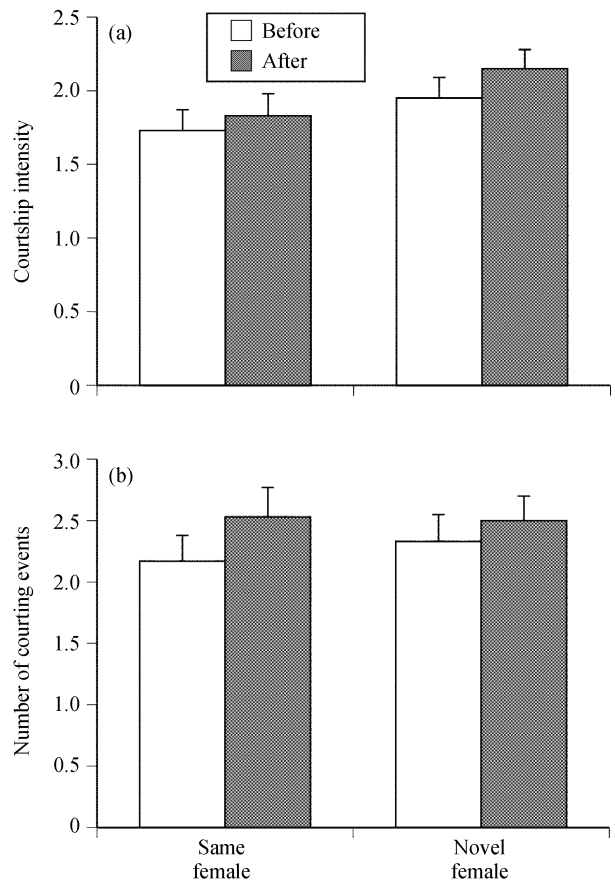

Fig. 1   Effects of introducing a novel female on the courtship intensity of male garter snakes
Halfway through the 30-minute trial, the female was removed from a group of courting males and then either returned to the same arena, or replaced with a female that had been subject to the same period of courtship from a different group of males. The upper graph shows courtship intensity (scored on a four-point scale: see text) of males before and after this halfway point, separately for males that courted the same female in both periods and for those that courted different females each time. The lower graph shows the number of observation periods during which each male was recorded as courting, again divided into trials where the female was returned to the same arena and those in which she was replaced by a different female. Histograms show mean values and associated standard errors. The upper graph is based on a sample size of 120 male snakes (20 replicate females each courted by 6 males) and the lower graph is based on a sample size of 24 male snakes (24 replicate males, each of which was scored for courtship intensity to each of 2 females).

the most powerful pheromonal signals. Given the strongly non-random mate choice by males of this species (Shine and Mason, 2001; Shine et al., 2001b, 2003b), such selectivity would not be surprising.

Both theory (Malin, 1983) and empirical data (Pierce et al., 1992) indicate that a novel sexual partner will not always modify the intensity of sexual response; thus, the Coolidge Effect may be common but is not ubiquitous. The mating system may exert a major influence in this respect, with a novel sexual partner most likely to attract

increased sexual response in taxa that are polygynous but with well-established pair-bonding (i.e., monogamous but with extra-pair copulations). In such cases, an additional copulation with the usual partner is likely to enhance the organism's reproductive success less than would a copulation with a novel partner. The underlying mechanism might involve paternity of an additional clutch (or part thereof) for a male, and additional genetic diversity among oviductal spermatozoa for a female (Pizzari, 2002).

In large communal breeding aggregations of garter snakes, it may be difficult in mechanistic terms for a male to discriminate among specific sexual partners (given that the den may contain >20,000 female snakes: Shine et al., 2006), and in any case such discrimination is unlikely to enhance male fitness. Most females mate only once before dispersing from the den, so the probability of a male encountering the same sexually receptive female twice in succession is low. Additionally, the gelatinous mating plug generally persists for at least 24 hours, precluding remating over that period (Shine et al., 2000b). Thus, although repeated encounters with the same female might plausibly occur in and around smaller dens, this is vanishingly unlikely in the large aggregations.

Our previous studies have shown that the intensity of courtship that a male garter snake directs to any given female conspecific depends upon his evaluation of a wide range of phenotypic traits of that female (Shine et al., 2001b, 2003c). Presumably, this information about the female's body size, condition, and recent mating history may predict the likely fitness benefits to courtship and successful mating. Similarly, males adjust their courtship intensity relative to the numbers and sizes of rival males; and also tailor their sexual behaviour to their own phenotypic traits (body size, condition: Shine et al., 2000a, 2003a, 2004). In contrast, whether or not the male has previously courted a specific female provides less useful information about the probable fitness increments arising from courtship.

We end with two caveats. First, the method used in the second set of trials involved washing a female with water to remove copulatory fluids. Could this washing remove cues that males need in order to recognise individual females? Males of this species identify the sex, body size and body condition of other snakes based on water-insoluble lipids (methyl ketones: Shine et al., 2003b,c), so that washing with water will not remove these cues. The only cues that would be removed are the scents of the male's own copulatory fluids; the mole-cules conveying this information are small and not lipid-based (Shine and Mason 2012). Removal of those substances might eradicate an underlying preference for novel females if males base their discrimination upon such cues. Such a preference would not, however, be a true "Coolidge Effect" (i.e., discrimination between familiar and unfamiliar females), but simply a male's response to information about his own prior activities. Our second caveat involves the generality of our results. Our data relate only to one snake species, and to a population that forms atypically dense aggregations during the breeding season; thus, its mating system may differ in important ways from those of many other snake taxa (Seigel and Ford, 1987). Accordingly, it would be premature to conclude that the Coolidge Effect does not occur in snakes. Research on taxa in which males and females cohabit for long periods during the mating season (such as the diamond python, *Morelia spilota* – Slip and Shine, 1988; or the colubrid *Malpolon monspessulanus* – de Haan, 1984) would be of special interest in this respect.

More generally, recent studies have revealed both diversity and complexity in the social systems of squamate reptiles. In snakes, that complexity includes a capacity for mutual recognition between siblings (Clark, 2004), between adults and their offspring (Greene et al., 2002) and between paired adults (de Haan, 2003a,b). Recognition of specific individuals and/or kin vs. non-kin also has been reported among lizards, the sister-group of snakes (Bull et al., 1994; Bull, 2000), suggesting that individual recognition may play a more important role in reptile sociality than heretofore has been envisaged. Given that familiarity influences courtship intensity in a variety of lizard species (Cooper, 1985; Tokarz, 1992; Cooper and Steele, 1997; Steele and Cooper, 1997; Orrell and Jenssen, 2002), and that recognition of individual conspecifics is likely to be widespread in snakes as well as lizards, future studies may well discover that some taxa of snakes also base courtship intensity upon familiarity with specific mates. Logistical impediments mean that studies such as our own, on free-ranging animals, are unlikely to be feasible for most snakes. However, controlled trials with captive animals should be feasible, and would provide valuable insights into mechanisms of mate choice in these poorly-understood animals.

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