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Chemosensory discrimination of social cues mediates space use in snakes, *Cryptophis nigrescens* (Elapidae)



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Keywords: chemical communication Cryptophis nigrescens male contest competition sexual selection small-eyed snake reptile retreat site selection social behaviour Snakes have traditionally been viewed as solitary, asocial animals whose habitat use is driven by temperature, prey and predators. However, recent studies suggest that snake spatial ecology may also be socially mediated. We examined the influence of conspecific chemical cues on refuge selection in a small nocturnal snake (the small-eyed snake) that engages in male contest competition. Females preferred refuges containing scent cues from conspecifics (of either sex) rather than scentless refuges. Males preferred female-scented rather than male-scented refuges, and preferred the scent of larger (and hence, more fecund) females than smaller females. Males spent more time in refuges containing the scent of smaller rather than larger males, but males that lost a contest did not avoid the refuge scented by the winner and therefore did not show evidence of the winner—loser effect. Females preferred refuges scented by larger males. Small-eyed snakes can distinguish conspecific sex and body size using chemical cues, and they use these cues to select alternative refuge sites. We suggest that social factors play a significant role in driving snake spatial distribution patterns in the wild and that snakes may exhibit more complex social systems than has generally been believed.

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Chemical communication is ubiquitous throughout the animal kingdom; more interactions are elicited by chemical cues than by any other signal (Wyatt 2003). This widespread use of chemical (rather than visual or auditory) stimuli may reflect the ability of chemical cues to convey detailed information (including individual identity, sex, size and reproductive condition), their potential long-term persistence in the environment, and their effectiveness at communication even in habitats where light and sound are unlikely to provide clear signals (Wyatt 2003). Organisms use scent cues in many types of social communication: to attract mates (Pandey 2005), to signal to rivals (Moore et al. 1997), to attract conspecifics to aggregations (Byers 1991) and to warn of danger (Hagman & Shine 2008).

For squamate reptiles (lizards and snakes), chemical cues play a key role in intraspecific signalling. Squamates possess a sensitive vomeronasal organ (Houck 2009) that processes information from the environment and, in many species, drives social as well as predator—prey interactions (Mason & Parker 2010). Lizards and

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snakes differ considerably in their social systems. Lizards have long been 'model organisms' for studies of social behaviour (Burghardt et al. 1977), and exhibit complex social systems including longterm monogamy (Bull 2000) and stable nuclear family structures with parental protection of offspring (O'Connor & Shine 2003), built upon a capacity for individual and kin recognition (Whiting 1999; Bull et al. 2000). In contrast, snakes have been considered highly asocial creatures, living solitary lives and only coming together briefly to mate, or to use spatially concentrated resources that provide prey, shelter or thermoregulatory opportunities (Brattstrom 1974). However, that conclusion may reflect logistical impediments to study: most snake species occur at low densities, and are cryptic and frequently inactive (Shine & Bonnet 2000). Thus, it is more difficult to observe social interactions in snakes than in many lizards (a notable exception is the garter snake Thamnophis sirtalis parietalis; see Shine 2012). However, the idea that snakes are socially 'simple' has come under increasing attack (Gillingham 1987; Clark 2004; Pernetta et al. 2009, 2011; Shine 2012).

Individuals of many snake species aggregate in the field (Gregory 2004; Shine et al. 2005a), but the proximate and ultimate causes for those groupings remain unclear. Such aggregations are

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METHODS

Study Species

rather than to any positive selection by snakes for sites that contain conspecifics. Chemical cues may play a significant role in the formation of these aggregations (Ford & Burghardt 1993). Individuals of many (probably most) snake species follow substrate-deposited chemical trails for reproductive benefit as well as prey location (Chiszar et al. 1983; Webb & Shine 1992; Greene et al. 2001; LeMaster et al. 2001; Fornasiero et al. 2007). Not only the presence of such a trail but also the specific information that it provides about the scent donor may influence snake behaviour (Shine 2003). From a single flick of its tongue, an individual snake can clarify the identity and phenotypic attributes (size, sex, reproductive potential) of conspecifics and heterospecifics (Shine et al. 2003; Fornasiero et al. 2011). Size is important: larger females produce larger litter sizes (Shine 1994), and, in species with male combat, contests are typically won by the larger individual (Madsen et al. 1993). Thus, chemical cues that convey information about fecundity and fighting ability may allow an individual to assess its social environment better.

typically attributed to limited availability of suitable retreat sites,

In species with male combat, assessing an opponent's fighting ability and experience can reduce costs associated with fighting (Whiting et al. 2003). For example, the outcomes of previous battles may influence the outcome of a current bout (Schuett 1997). Recent fighting experience can be conveyed through chemical communication. In bigclaw snapping shrimp, Alpheus heterochaelis, and American lobsters, Homarus americanus, losers avoid winners by detecting a chemical cue (Karavanich & Atema 1998; Obermeier & Schmitz 2003). In Pacific field crickets, Teleogryllus oceanicus, changes in social dominance affect cuticular hydrocarbons, which convey fitness information (Thomas & Simmons 2011). Similar social cues affect habitat selection by many taxa (Fletcher 2007), including birds (Etterson 2003; Doligez et al. 2004; Coulton et al. 2011), reptiles (Brown & Maclean 1983; Reinert & Zappalorti 1988; Clark 2007), fish (Lecchini et al. 2007) and insects (Jeanson & Deneubourg 2007). Thus, the spatial distribution of snakes within a population may be affected by social as well as nonsocial cues.

The small-eyed snake is a nocturnally active species that frequently shelters beneath exfoliated rocks on sandstone outcrops (Webb et al. 2004, 2009). Small-eyed snakes often aggregate in the wild (Greer 1997; J. K. Webb, unpublished data), but the proximate mechanisms that result in these aggregations remain unclear. Individuals select habitat using abiotic cues, and communal use of shelter sites is often attributed to a limited availability of suitable refuges (Webb et al. 2004). Snakes may also select specific sites based upon prey availability (Shine 1984; Goldsbrough et al. 2006) and avoidance of predators (Webb & Whiting 2005). An additional possibility (consistent with those other functions) is that snakes aggregate for social reasons. For example, they may actively search for scent cues from conspecifics, and prefer to shelter in crevices that contain such cues. To test this hypothesis, we conducted laboratory trials exposing captive (recently field-collected) small-eyed snakes to a choice of shelter sites differing in the scent cues they provided. More specifically, we tested the following predictions stemming from the hypothesis that snakes adaptively use social cues when selecting shelters. (1) Snakes use chemical cues to select between shelter sites based on the likelihood of conspecific presence. (2) Snakes have a scentbased preference for specific body sizes of conspecifics; for example, a male might prefer the scent of a smaller male (because larger males are more likely to win combat bouts; M. Scott, unpublished data), but a larger female (because larger females are more fecund: Shine 1984). (3) A male will avoid the scent of a rival that has recently defeated it in a physical struggle (winner-loser effect).

The small-eyed snake is a small nocturnal elapid found along the east coast of Australia (Cogger 1975). Both sexes are slate-grey in dorsal colour, and feed primarily upon diurnally active skinks (which they locate while the skinks are asleep in nocturnal refuges: Shine 1984). As their common name suggests, these snakes have relatively small eyes (see Shine 1984; Brischoux et al. 2010 for quantification) and use chemosensory cues to find their prey (Shine 1984; Llewelyn et al. 2005). In cooler months of the year, the snakes frequently shelter under thin rocks that provide a thermally optimal microhabitat (Webb et al. 2004). Sexual size dimorphism (SSD) is clear-cut: males grow to 600 mm in snout-vent length (SVL), whereas females rarely exceed 523 mm (Webb et al. 2003). Male combat has been recorded in this species in the wild (Shine 1984), as is common in snake species in which males attain larger body sizes than females (Shine 1978). As in other snakes, combat in small-eyed snakes is ritualized. Males raise and intertwine their forebodies, and each appears to try to push the other's head downwards. This typically occurs only briefly (seconds, at most a minute or so), at which time the loser retreats. There is no biting, and no overt damage whatsoever.

Collection and Husbandry

We collected 57 adult small-eyed snakes (31 males, 26 females) in July and September 2011, from crown lands near Nowra, 160 km south of Sydney, Australia. We located snakes by turning over cover items on westerly facing escarpments (Webb et al. 2004). We gently picked up snakes with gloved hands, and determined their sex by everting the hemipenes, and visually assessing tail shape (males have longer tails, thicker at the base). We measured each snake and injected a miniature PIT tag (Biomark HPT8, 8.4 × 1.4 mm; Boise, Idaho, U.S.A.) under the skin. We gently massaged the PIT tag away from the insertion point, and sealed the incision with nontoxic surgical glue (Vetbond, 3M; North Ryde, NSW, Australia). Longterm studies have shown no adverse effects of PIT tagging on snake health, nor have tags migrated from their insertion points (Webb et al. 2009). Each snake was placed in a numbered cloth bag and was placed in a styrofoam box for transport back to Sydney (2.5 h drive).

We housed snakes individually at Macquarie University in rectangular boxes ($300 \times 205 \text{ mm}$ and 95 mm high) with opaque walls, a transparent lid and ventilation holes. Each snake had access to water ad libitum, and a small rectangular plastic refuge $(150 \times 100 \text{ mm and } 40 \text{ mm high})$. We fed the snakes on freshly thawed lizard-scented mice every 2 weeks. Frozen mice were obtained from a commercial pet food supplier, and were thawed and rubbed with a dead lizard (a road-killed skink) prior to feeding to snakes. Enclosures were kept on a heat rack at night (2200-0500 hours), creating a thermal gradient (18-30 °C) to allow thermoregulation. To conduct trials by day, we reversed the usual light cycle. All windows were blacked out, and timers ensured that fluorescent light was only on at night (1700-0900 hours). Fieldwork was approved by the New South Wales National Parks and Wildlife Service (Licence A2686 to J. K. Webb). Laboratory experiments were approved by the Macquarie University Animal Ethics Committee (AEC Reference Number 2010/040). At the end of the study, all snakes were released at their site of capture.

Refuge Site Selection Based on Chemical Cues

We conducted trials inside plastic tubs $(350 \times 550 \text{ mm} \text{ and} 330 \text{ mm high})$ with a clear Perspex lid secured with clamps. We

filmed all trials from above using a Samsung Digital Camera under 25 W red lights. In each treatment, the focal snake was given a choice between two scented refuges, one at either end of the arena. Scents were acquired by leaving a large (180 mm diameter) piece of filter paper on the base of the donor's refuge for 48 h. This procedure was designed to simulate natural conditions where a snake leaves a substrate-deposited scent inside a refuge. We discarded any filter paper that was contaminated with faecal matter. Both the filter paper and the refuge were taken from the donor's enclosure and placed in the trial arena. We transported each focal individual from its enclosure to the trial arena by blocking the entrances to its refuge box. A large plastic spatula was then used to scoop up the refuge (containing the snake) and deposit it into the centre of the trial arena.

We conducted trials between 1000 and 1500 hours in a temperature-controlled room at 18 °C. Focal animals were given 30 min to habituate to the test arena before the onset of a trial. Trials commenced by lifting the refuge out of the tub (thus exposing the snake) while the observer remained out of sight. We then used the overhead video system to record any snake movements between the two scented refuges over the following 1 h. Videos were analysed by a single observer (M.L.S.) under 'blind' conditions (i.e. scorer had no knowledge of treatment), and a snake's location at any point in time was defined by the position of its head. We noted the presence or absence of tongue-flicking behaviour, but could not count tongueflicks when snakes were inside opaque shelters and obscured from view. Regardless, in all scented-refuge trials and contest trials individuals frequently tongue-flicked while in view, strongly suggesting a reliance on chemical cues. Focal snakes were used only once per treatment but were used across multiple treatments. The order of treatments for individual snakes was balanced to avoid order effects. Some donor snakes contributed to more than one trial (range 1-3 trials). We vigorously scrubbed test arenas between each trial using detergent followed by F10 Veterinary Disinfectant (Health and Hygiene Pty. Ltd., Sunninghill, South Africa). Tubs were thoroughly rinsed and then dried with a clean paper towel.

Pungency Control Test

We tested whether snakes would respond to a scent purely because of its presence (as opposed to the information it carries: see Table 1). The filter paper in one refuge was scented with three drops of eucalyptus oil, to mimic a scent that occurs naturally in the field but conveys little or no biologically relevant information about shelter site suitability. The filter paper in the other refuge was treated with distilled water (control). The refuges were left for 2 min to dry before being placed at either end of the arena. The mean time spent in the refuge scented with eucalyptus oil was not significantly different to that spent in the refuge scented with distilled water (Table 2). Therefore, pungency alone should not affect our results, and we used distilled water as the control for the remaining experiments.

Experiment 1: Male Refuge Site Preferences

A focal male was given the choice between two scented refuges in the following treatments: (1) smaller male versus control; (2) smaller male versus larger male; (3) larger male versus control; (4) female versus male; (5) female versus control; and (6) small female versus large female (Table 1).

Experiment 2: Female Refuge Site Preferences

A focal female was given the choice between two scented refuges in the following treatments: (1) relatively smaller female versus control; (2) relatively smaller female versus relatively larger female; (3) relatively larger female versus control; (4) male versus control; and (5) small male versus large male (Table 1).

Experiment 3: Scent-based Winner-Loser Effects

We staged encounters in the laboratory between rivals of various body sizes to obtain scents from winners and losers to be used in refuge selection trials. Rivals readily fought over a single heated refuge, so we did not need to include female scent as a stimulus. Because body size predicted the winner of a contest (M. Scott, unpublished data) we could manipulate the outcome of bouts for any given snake by choosing a rival of the appropriate size. Each focal male took part in two contests, winning one and losing the other. Contests were 2 days apart and outcome order was balanced across individuals (i.e. win first lose second, or lose first win second). Scented refuges from the winner (the snake that defeated the focal male) and the loser (the snake that was defeated by the focal male) were used in two-choice refuge trials under the same conditions as experiment 2. Thus, there were three treatments: (1) loser-scented refuge versus control; (2) loser-scented refuge versus winnerscented refuge; and (3) winner-scented refuge versus control.

Experiment 1, conducted beforehand, indicated that male smalleyed snakes could discriminate chemically between the body sizes

Table 1

Sample sizes (N) and mean body sizes of small-eyed snakes used in laboratory trials of refuge site preference

Experiment	Treatment	Focal snake			Stimulus snake 1			Stimulus snake 2		
		Sex	Ν	SVL (mm)	Sex	Ν	SVL (mm)	Sex	Ν	SVL (mm)
1	Pungency versus control	Male	11	409 (288-566)	_	_	_	_	_	_
		Female	10	369 (270-435)	_	_	_	_	_	_
2a	Smaller male versus control	Male	13	456 (372-515)	Male	9	354 (296-449)	_	_	_
2b	Smaller versus larger male	Male	13	456 (372-515)	Male	11	373 (288-470)	Male	10	523 (445-566)
2c	Larger male versus control	Male	13	456 (372-515)	Male	11	529 (489-566)	_	_	_
2d	Female versus male	Male	12	500 (306-566)	Female	10	398 (355-430)	Male	9	462 (418-545)
2e	Female versus control	Male	12	506 (418-555)	Female	8	392 (365-430)	_	_	_
2f	Small female versus large female	Male	13	490 (372-540)	Female	5	350 (300-375)	Female	5	411 (395-430)
3a	Smaller female versus control	Female	12	372 (345-412)	Female	10	319 (155-390)	_	_	_
3b	Smaller female versus larger female	Female	12	372 (345-412)	Female	10	319 (155–375)	Female	10	405 (375-435)
3c	Larger female versus control	Female	12	372 (345-412)	Female	10	409 (392-435)	_	_	_
3d	Male versus control	Female	11	381 (300-430)	Male	7	545 (530-555)	_	_	_
3e	Small male versus large male	Female	14	381 (325-430)	Male	7	361 (340-492)	Male	8	515 (449-555)
4	Winner/loser effect	Male	24	446 (297-566)	_		_	_	—	_

In each trial, a focal snake was given a choice between two refuge sites containing different scent cues. Focal individuals were used once per treatment, while some scent donors (stimulus snakes) were used more than once per treatment. Snout-vent length (SVL) includes mean and range.

of rival males. Therefore, to avoid confounding between cues for body size and contest experience, rival pairs were size matched (5–10% disparity in SVL).

Statistical Analysis

From the videos, we calculated the total time that each focal snake spent inside each of the two shelters during each trial. Data were non-normally distributed and arcsine and square-root transformations failed to achieve a normal distribution. Therefore, we used nonparametric Wilcoxon signed-ranks tests to analyse paired data (Quinn & Keough 2002). A Holm–Bonferroni sequential correction was used to avoid making a familywise type 1 error owing to having many trials of the same type. Treatments with the same-sex focal snake and same-sex donor were considered groups for this correction (Quinn & Keough 2002).

RESULTS

Experiment 1: Male Refuge Site Preferences

Male small-eyed snakes spent more time in refuges scented by other males than in control (unscented) refuges, regardless of whether those other males were smaller or larger than the focal animal (Fig. 1). However, this pattern was not significant following sequential HolmBonferonni correction (Table 2). When given a choice between malescented refuges, the focal male spent more time in the refuge scented by a smaller rather than larger male (Table 2, Fig. 1b).

When given the choice between a female-scented refuge and a male-scented refuge, the focal male spent more time in the female-scented refuge (Table 2, Fig. 1d). Males spent more time in refuges scented by larger females than in refuges scented by smaller females (Table 2, Fig. 1f).

Experiment 2: Female Refuge Site Preferences

Female small-eyed snakes spent more time in refuges scented by other females than in the control refuge, regardless of whether the female scent came from an individual that was smaller or larger than itself (Table 2, Fig. 2). The time spent by females in refuges scented by smaller females versus refuges scented by larger females was not significantly different (Table 2, Fig. 2).

Females spent more time in refuges scented with males than in the control and preferred refuges scented by larger males than refuges scented by smaller males (Table 2, Fig. 2).

Experiment 3: Scent-based Winner-Loser Effects

Following combat trials, a male was no more likely to spend time in the control refuge versus a refuge scented by a rival they



Figure 1. Mean \pm 1 SE amount of time spent by male small-eyed snakes over 1 h between two refuges scented by: (a) a relatively smaller male versus control; (b) a relatively smaller male versus a relatively larger male; (c) control versus relatively larger male; (d) female versus male; (e) female versus control; (f) small female versus large female.

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Table 2
Tests for significant differences in time (min) spent in two scented refuges (Wilcoxon signed-ranks test)

Figure	Focal snake	Scented refuges		Ν	Wilcoxon W	df	Р	Bonferroni correction	
		Refuge 1	Refuge 2						
_	Male and female	Eucalyptus oil	Control (distilled water)	21	69	20	0.106	_	
1a	Male	Smaller male	Control	13	9.0	12	0.019	0.057	
1b	Male	Smaller male	Larger male	13	9.5	12	0.021	0.042	
1c	Male	Control	Larger male	13	16.0	12	0.071	0.071	
1d	Male	Female	Male	12	9.5	11	0.037	0.037	
1e	Male	Female	Control	12	11.0	11	0.028	0.056	
1f	Male	Small female	Large female	13	3.0	12	0.0003	0.009	
2a	Female	Smaller female	Control	12	8.0	11	0.015	0.030	
2b	Female	Smaller female	Larger female	12	20.5	11	0.146	_	
2c	Female	Control	Larger female	12	0.0	11	0.002	0.006	
2d	Female	Male	Control	11	3.0	10	0.008	0.016	
2e	Female	Small male	Large male	13	15.0	12	0.018	0.018	

Significant P values following sequential Holm–Bonferroni correction are shown in bold font.

had defeated (W = 34, P = 0.69), or a refuge scented by a rival that had defeated them (W = 32, P = 0.58). When given a choice between refuges scented either by snakes they had defeated, or had been defeated by, the focal animals showed no significant preference (W = 20, P = 0.14; Fig. 3).

DISCUSSION

Small-eyed snakes detected differences in the phenotypic traits of conspecifics solely from chemical cues, and (at least in the laboratory) they adjusted their behaviour accordingly. When given the



Figure 2. Mean \pm 1 SE amount of time spent by female small-eyed snakes over 1 h between two refuges scented by: (a) a relatively smaller female versus control; (b) a relatively smaller female versus a relatively larger female; (c) relatively larger female versus control; (d) male versus control; and (e) small male versus large male.



Figure 3. Mean \pm 1 SE amount of time spent by focal male small-eyed snakes over 1 h between two refuges scented by: (a) male that recently lost to focal male (loser scent) versus control; (b) male that recently lost to focal male (loser scent) versus male that recently defeated focal male (winner scent); (c) male that recently defeated focal male (winner scent) versus control.

choice between male- and female-scented shelters, males spent more time in female-scented shelters. When given the choice between two female-scented shelters, males spent more time in the shelter scented by the larger female than the shelter scented by a smaller female. Female small-eyed snakes were attracted to scents of both males and females. Female snakes did not distinguish between scent cues from different-sized females when selecting retreat sites, but were attracted to the scents of larger rather than smaller males. The outcome of a previous contest did not affect a male's reaction to scent cues from his rival.

Evolutionary theory predicts that individuals that alter their behaviour in response to social cues will gain fitness benefits by doing so. Our results show that male small-eyed snakes, like males of at least two other snake species (Shine et al. 2003; Bryant et al. 2011; Shine 2012), can use scent cues to discriminate between females of different body sizes. Benefits to courting females of greater body size and condition include increased fecundity and increased probability of survival for offspring (Bonnet et al. 2000). Maternal body length and fecundity are correlated in small-eyed snakes (Shine 1984) and therefore it is adaptive for males to mate with larger females. Although the experimental design here was 'refuge based', our results also suggest that like other snake species, male small-eyed snakes may be able to trail high-quality females (Ford 1986; Greene et al. 2001).

Males chemically discern the relative body size of a rival, suggesting that chemical cues may be a mechanism by which contests are resolved or avoided. The small eyes that give this species its common name suggest that visual cues are likely to be less important for this species than are chemical cues. Additionally, males of this nocturnally active species may meet one another within narrow and poorly illuminated crevices. In this context, visual cues may be weak or unavailable. A male may avoid entering a refuge occupied by a larger rival if it is able to sample chemical cues deposited by the occupant. Other reptile species also use chemical cues to identify fighting ability in conspecific rivals and potentially mitigate the costs of fighting (Poschadel et al. 2006; Martin et al. 2007). In some snakes (Schuett 1997) and other animals (Rutte et al. 2006) there are short-term behavioural and hormonal changes that occur directly after a contest (i.e. 'winner and loser effects'), eliciting changes in the chemical cues produced by the combatants. In our study, however, the responses of male smalleyed snakes were not affected by whether the scent they encountered came from an animal that had recently won (versus lost) an intraspecific combat bout, implying that contest outcome does not affect a snake's chemical cues, or at least does not affect the retreat site selection behaviour of other male snakes. Winner-loser effects are generally short lived (Rutte et al. 2006), and male small-eyed snakes may not encounter each other often enough to benefit from detecting or responding to short-term scent differences.

Attraction to the scent of same-sex conspecifics may be advantageous for habitat selection. Small-eyed snakes may use these biotic cues in addition to abiotic (structural and thermal) cues when selecting diurnal refuges (Webb et al. 2004). In some squamates, aggregation provides thermoregulatory benefits by increasing effective mass and, thus, retarding cooling (Graves & Duvall 1995; Shah et al. 2003). Such benefits are unlikely to apply to small-eyed snakes, because animals in groups were only rarely in close contact (M. L. Scott & J. K. Webb, personal observation). During the cooler months, small-eyed snakes aggregate beneath thermally distinctive 'hot rocks' that are a limited resource (Webb et al. 2003, 2004). At night, individuals choose hot rocks with narrow crevices and snakes can detect subtle differences in the thermal quality of rocks (Webb et al. 2004). Small-eyed snakes have poor vision (reduced eyes; Shine 1984) and select retreat sites at night when they are vulnerable to avian predators (Webb & Whiting 2005). Thus, one advantage of choosing conspecific-scented shelters may be to reduce the costs of locating microhabitats that confer thermoregulatory benefits (Khan et al. 2010). A secondary advantage may be to increase the chance of locating prey such as sleeping skinks (Shine 1984), which are also found under 'hot rocks' (Goldsbrough et al. 2006). Other benefits from aggregation, such as enhanced predator defence, increased vigilance or the confusion of predators (Calvert et al. 1979; Andersson 1994; Wyatt 2003; Clark 2004) seem unlikely in this species.

Chemical discrimination can act as a mechanism for sexual selection (Andersson 1994). Male small-eyed snakes grow larger than females (Shine 1984; Webb et al. 2003) and this form of sexual size dimorphism in snakes is correlated with the occurrence of male– male combat (Shine 1978, 1994). An armament or ornament is a trait that increases the chance of reproductive success by overcoming rivals or being more attractive to mates, respectively (Whiting et al. 2003). Chemical cues indicating male body size may act as an armament to mediate contests, with larger males displacing smaller rivals and increasing their reproductive success.

Additionally, male scent could function as an ornament that females use to select among males. Female mate choice is uncommon in reptiles (Olsson & Madsen 1998), and although documented in some squamate species (Bajer et al. 2010) it has not been shown in snakes. Female small-eyed snakes preferred scents of larger males but does this carry any direct or indirect benefits? Although most snake species (including small-eyed snakes) lack male parental care (Shine 1998), females may still benefit directly by minimizing harassment from other males (in the field, females are more likely to group with larger males; J. K. Webb, unpublished data). Selecting one large male that will displace others may reduce the costs of harassment (Rich & Hurst 1998; Cordero & Eberhard 2003), such as physical injuries, energy loss, spread of disease and increased risk of predation (Partridge & Hurst 1998; East et al. 2003; Shine et al. 2005b).

Females may also derive genetic benefits from mating with larger rather than smaller males, if sons fathered by large fathers are likely to be larger and hence reproductively successful in this system ('sexy son' hypothesis; Fisher 1958). Female mate choice is further complicated by sperm competition, especially because larger male snakes may produce larger ejaculates (Moya-Larano & Fox 2006; Tourmente et al. 2009). Thus, a larger male may obtain a disproportionate share of paternity even if his partner mates with other, smaller males. For example, in slatey-grey snakes, *Stegonotus cucullatus*, larger males have a higher reproductive success per clutch, suggesting that the sperm of larger males outcompetes that of smaller males (Dubey et al. 2009).

Recent studies have documented parental behaviour, kin recognition and cryptic sociality in rattlesnakes, Crotalus horridus (Greene et al. 2002; Clark 2004; Clark et al. 2012), possible cryptic social organization in sea snakes, Emydocephalus annulatus (Shine et al. 2005a), and complex, pheromone-based alternative reproductive tactics in garter snakes (Shine 2012; Doody et al. 2013). Our results support the notion that proximate social interactions, mediated by chemical cues, influence snake spatial ecology and habitat use in the wild. A long-term (20-year) mark-recapture study on small-eyed snakes is consistent with our laboratory-based results: conspecific small-eyed snakes often aggregate, and adult aggregations consist of groups of females, or a single large male with multiple females, but males are almost never found together (J. K. Webb, unpublished data). For animals that live cryptic lifestyles such as snakes, chemical cues are a reliable and efficient mode of communication that facilitates adaptive habitat selection and social interactions. Future research may well reveal that we have erroneously classified many taxa as 'asocial' simply because their social systems are structured around chemical rather than visual or auditory signals.

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