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ORIGINAL ARTICLE

Territoriality in a snake

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Abstract Territorial behaviour, whereby dominant animals gain priority access to critical resources, is widespread in some animal lineages, but rare in others. Theory suggests that territoriality will evolve only when animals can economically defend sites that contain critical resources (typically mates, sometimes food). In striking contrast to their close relatives the lizards, male defence of territories for access to mates has not been reported in snakes. In south-eastern Australia, receptive female small-eyed snakes thermoregulate under "hot rocks", concentrating mating opportunities and thus, potentially allowing males to enhance their fitness by defending these rocks from rivals. We videotaped staged contests between resident and intruder males and analysed data on cohabitation patterns from a long-term (21 years) mark-recapture study. In staged contests, males actively defended hot rocks from intruder males; and thus, larger males actively displaced their smaller rivals. In the wild, larger males were found under rocks with more or larger females. These results suggest that the thermally driven concentration of female small-eyed snakes has rendered hot rocks economically defensible, and thus favoured the evolution of territoriality in a snake.

Keywords Behaviour · Residency · Territory · Elapidae · *Cryptophis nigrescens*

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Introduction

Territorial behaviour—whereby dominant individuals gain access to key resources while excluding subordinates, is widespread in frogs, salamanders, birds, mammals, and lizards (Kaufmann 1983). Despite the widespread occurrence of territoriality among lizards (Stamps 1983), territorial behaviour in snakes has been documented only once (Huang et al. 2011). In this instance, territoriality evolved because of the benefits of defending a key food resource. Female Taiwanese kukrisnakes (*Oligodon formosanus*) aggressively defend sea turtle nests because of the high pay-offs of consuming turtle eggs. The absence of territorial behaviour for access to mates, in snakes, is puzzling given that many species display ritualized male-male combat (Shine 2003). Nevertheless, the likely reason for this lack of territoriality in most snakes is economic defensibility: territorial behaviour is expected to evolve only in species that use spatially discrete resources that are economical to defend (Brown 1964). In many vertebrate species, for example, males defend resources required by females for reproduction. If resources are clumped, and hence defensible, dominant males may gain exclusive access to such sites and thereby increase their encounter rates with females while excluding or constraining rival access to females (Emlen and Oring 1977; Kim and Grant 2007). When multiple females use the same breeding site, a male that defends that site can increase his reproductive success by mating with more than one female. The ability of males to defend breeding sites depends on traits such as body size, weapons, and fighting ability (Archer 1988).

Here, we investigated whether males of the nocturnal small-eyed snake *Cryptophis nigrescens* defend "hot rocks" from rival males. In this species, males engage in ritualized combat and attain larger body sizes than females (Shine 1984; Webb et al. 2003). In southeast NSW, small-eyed snakes rarely bask in the open; instead, during the cooler months (autumn to late spring), small-eyed snakes thermoregulate beneath small sun-exposed "hot rocks" (Pringle et al. 2003; Webb et al. 2004). Small-eyed snakes feed year round (Shine 1984), and snakes that shelter underneath sun-exposed rocks can maintain high body temperatures (Webb et al. 2004), which facilitate digestion and other physiological processes (Huey 1991). In Morton National Park, hot rocks occur on exposed rock outcrops adjacent to cliffs where predatory birds are common. Field experiments with black Plasticine model snakes revealed that basking snakes had a much higher risk of avian predation than snakes hidden under rocks (Webb and Whiting 2005). Thus, snakes sheltering under rocks likely accrue thermal and fitness benefits. Due to encroachment and overshadowing of rock outcrops by vegetation, hot rocks are a limited resource for snakes on sandstone plateaux in this region (Pringle et al. 2003, 2009). During the mating season (autumn to spring), reproductive females and males require access to hot rocks to facilitate vitellogenesis and spermatogenesis, respectively. Adult females typically use one or two rocks as shelter sites during this period (JKW, unpublished data) and are more sedentary than males (Keogh et al. 2007). If females aggregate under hot rocks, males could potentially increase their fitness by excluding rival males from such sites. To explore this possibility, we evaluated patterns of resource use by small-eyed snakes by analysing data from a 21-year field study. We then staged male-male contests in the laboratory to determine whether resident males defend hot rocks against intruders.

Materials and methods

Study species

The small-eyed snake *C. nigrescens* is a small (to 757 mm snout-vent length) nocturnal venomous snake with a large geographic distribution in eastern Australia (Shine 1984; Cogger 2000). Small-eyed snakes are habitat generalists, occupying a wide diversity of vegetation types, including coastal heaths, open eucalypt woodlands, closed eucalypt woodlands, paper bark forests, and rainforests (Cogger 2000). Small-eyed snakes are active at night, and they feed mostly on small skinks (Shine 1984). In the Nowra region, both sexes attain maturity at age 2 years, but males attain larger body sizes (mean snout-vent length=448 mm) than females (mean snout-vent length (SVL)=391 mm). Females are viviparous and produce small clutches (mean clutch sizes of 4) each year (Shine 1984; Webb et al. 2002, 2003).

Long-term field study in Morton National Park

One of us (JKW) conducted a long-term (1992–2013) demographic study of *C. nigrescens* in Morton National Park, 160 km south of Sydney. Each year in spring, three study sites on the western side of a sandstone plateau were surveyed by turning sun-exposed rocks adjacent to cliffs. Snakes under rocks were captured, identified (via PIT tags), measured (SVL, tail length, head length, head diameter, and mass), and released at the site of capture. We considered males >287 mm SVL and females >300 mm SVL to be sexually mature (Shine 1984). Detailed descriptions of the study sites and sampling dates are presented elsewhere (Webb et al. 2003; Keogh et al. 2007). In order to obtain tissue samples for subsequent genetic analyses of dispersal (Keogh et al. 2007), we carried out additional searches for snakes on the plateaux surrounding our study sites during the period 2001–2012.

Do males defend "hot" rocks in the laboratory?

We collected 24 adult males (mean SVL=498 mm, range 358–610 mm; mean mass=45 g, range 18–72 g) from the study sites and transported them to the University of Sydney. We housed snakes individually in ventilated plastic containers (31×22×10 cm) containing a shelter (PVC pipe cut in half), water dish, and paper substrate. We placed cages on timer controlled heating racks (1000–1600 h) to create a thermal gradient (17–32 °C) to allow snakes to thermoregulate. Lighting in the room matched the natural photoperiod (12:12 light dark)

We staged 14 contests in a room (18 °C) illuminated by a 25-W red light bulb. We randomly paired each snake with another snake, and each snake was tested only once, except for two snakes that were tested twice (once as residents, and once as non-residents). In five contests, residents were 2.1 % larger in SVL than non-residents (range 1.0–3.7 %); in five contests, residents were 27 % larger than non-residents (range 12.5–32.7 %); and in four contests, non-residents were 14 % larger than residents (range 11.2–16.6 %). Two days prior to testing, we placed a male inside a ventilated plastic test arena (60×40×40 cm high with translucent lid) with a "hot" rock consisting of two rectangular concrete paving stones (230×180×40 mm thick) stacked on top of each other with a crevice between them. These 2 days allowed this male to become the resident. We suspended a timer-controlled (1000–1600 h) 40-W light globe above the hot rock to create temperatures similar to those of rocks used by reproductive females (Webb et al. 2004).

One hour prior to trials commencing, we added a cold rock (two concrete paving stones, with crevice between them, and light bulb suspended above, but switched off) to the test arena. Thus, the non-resident had the choice between a cold, unoccupied rock versus an occupied hot rock. Fifteen minutes prior to dusk, we painted a small (ca. 10 mm) white stripe on the neck and mid-body of the non-resident (with a non-toxic paint pen) to distinguish it from the resident and placed it inside a holding box (20×10×10 cm high). At dusk, we activated the video camera and connected the holding box to the middle of the test arena (allowing the non-resident to enter the test arena or remain inside the holding box). Thus, we did not place two males into sudden direct physical contact. Trials were run overnight, and the holding box allowed fleeing snakes to exit the test arena, and minimised the risk of snakes injuring one another. No snakes sustained any injuries in the trials.

From the videotapes, we recorded (a) chasing, (b) biting, (c) lunging, (d) combat, and (e) fleeing. Combat bouts ended with the winner chasing the loser from the hot rock. We identified losers because they would flee rapidly from winners, attempt to escape by wall climbing, or exit the arena.

Results

Groupings of snakes in the wild

From 1992 to 2013, we captured 373 individual small-eyed snakes (566 captures) at the three study sites, consisting of 54 juveniles, 160 adult males, and 159 adult females. We captured another 118 snakes (12 juveniles, 48 adult males, 58 adult females) during opportunistic searches on surrounding plateaux. Of 425 adult snakes, 273 were found alone (153 males, 120 females) and 152 were found in groups. Of the 94 groups of adult snakes found sharing the same rock, there were 23 female pairs, 4 female trios, 1 female quartet, 46 male-female pairs, 16 male-female trios (one male and two females), two male-female quartets (one male and three females), one group of two males with two females, and one male-male pair (two small snakes under the same large rock but spaced 1 m apart). Therefore, we detected multiple males in the same group in only two instances (2.1 %). Groupings involving mixed sexes (males and females) were more common than expected by chance, whereas groups involving two males were less common than expected by chance (χ^2=13.21, df=1, p<0.001).

Male body size versus the number and size of females in groups

In small-eyed snakes, female fecundity increases with female body size (SVL) (Shine 1984). Thus, males could enhance their reproductive success by mating with larger females or by mating with multiple females. If male body size is linked to resource holding potential, then larger males should gain access to larger females or larger groups of females. As predicted, larger males were found with larger females (r=0.35, $F_{1,56}$=7.93, p=0.007, Fig. 1a) and with more females (r=0.32, $F_{1,56}$=6.24, p=0.015, Fig. 1b).

Defence of "hot" rocks by males in the laboratory

In 13 of 14 trials, the intruder male attempted to refuge under the "hot" rock occupied by the resident male. Body size was an important predictor of contest success; when residents were larger than non-residents, they successfully expelled non-residents from the hot rock in 9 of 10 trials, whereas when non-residents were larger than residents, they expelled residents from hot rocks in all 4 trials (χ^2=10.08, 1 df=1, p<0.01). In trials where residents were slightly larger than non-residents (mean size difference 2 %), residents won 4 of 5 trials. In 2 trials, residents lunged, bit, and chased the intruders away, and non-resident snakes exited the test arena or exhibited submissive postures (coiling with head hidden). In 3 trials, males engaged in vigorous combat, intertwining their

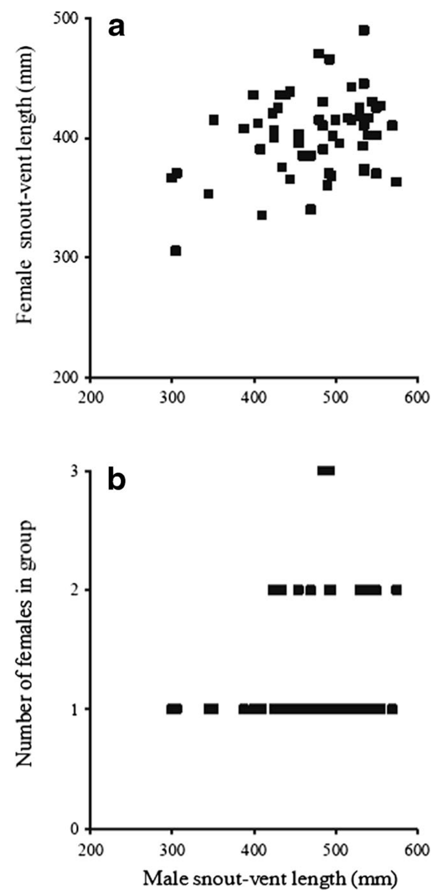

Fig. 1 Snout-vent lengths of male small-eyed snakes found in groups with females, as a function of **a** female snout-vent length and **b** the number of females with which they were found

bodies and attempting to push their rival's head down. No biting was observed in these prolonged combat bouts. These escalated fights began 60–120 s after intruders entered the hot rock refuge, lasted up to 330 s, and ended with winners chasing losers away from the hot refuge. When residents were 27 % larger than non-residents, they won 5 of 5 trials; combat bouts occurred in 3 trials, (duration 20–480 s), and four residents chased non-residents away from the hot rock. Biting (by the larger resident) was observed in 1 trial, while loser snakes adopted submissive coiling postures in 2 trials. When non-residents were 14 % larger than residents, they won 4 of 4 trials, 3 of which involved combat bouts (duration 150–222 s) and 3 of which involved the larger snakes chasing the smaller snakes away from the hot rocks.

Discussion

Our field and laboratory results provide compelling evidence that male small-eyed snakes actively defend "hot" refuges from rival males, consistent with territorial behaviour. During the 21-year field study, we found males together under a rock on only two occasions. By contrast, females often shared rocks with conspecifics of either sex. Larger males were more likely to share rocks with reproductive females, suggesting that larger males gain priority access to hot rocks—and thus, to the females that use these resources. Our behavioural experiments suggest that male agonistic behaviour is the proximate mechanism responsible for these patterns of co-occurrence. Intriguingly, males fought for rocks in the absence of females; all previous records of male-male combat in snakes involve males fighting for access to a female, rather than the resources used by females (Duvall et al. 1993). In our study system, males that can defend hot rocks in the absence of females will also gain thermal benefits, particularly when basking in the open increases the likelihood of avian predation (Webb and Whiting 2005).

Our results suggest that male body size (and perhaps, residency) influences contest outcome in small-eyed snakes. Our sample size was small and designed to ask whether snakes defend a resource, consistent with territoriality and not what factors predict contest outcome per se. Nevertheless, when residents were slightly larger (1–3.7 % larger) than non-residents, they won 4 of 5 bouts. When there was a greater divergence in size, larger snakes evicted smaller snakes from hot rocks, irrespective of residency status. Larger male size enhances combat success in other snake species also (Schuett and Gillingham 1989; Madsen and Shine 1993). In small-eyed snakes, larger males likely can gain increased reproductive success by excluding smaller rivals from refuges used by females, thereby promoting male-biased sexual size dimorphism (Shine 2003). We used male-female association as an index for male reproductive success, based on the inference that males and females found beneath the same rock were likely to have copulated. Because mate choice can occur both pre- and post-copulation (Fedina and Lewis 2008; Brooks and Griffith 2010), future work using genetic evidence to quantify paternity could test the assumption that males in aggregations achieve higher reproductive success (Gibbs and Weatherhead 2001).

Our results support the hypothesis that the evolution of territoriality in vertebrates has been driven by the spatial distribution of resources and their economic defensibility (Brown 1964; Emlen and Oring 1977; Duvall et al. 1993). For small-eyed snakes, hot rocks are critical thermal resources that are spatially predictable. Previous studies concluding that snakes lack territorial behaviour have focused on diurnal species that bask and occupy large areas. In these species, it may be uneconomical for males to defend large territories (Duvall et al. 1993). By contrast, in nocturnal species where thermal resources are limited and can be defended, males may enhance their fitness by controlling such resources. Although we did not explicitly test whether males can defend hot rocks occupied by females, our field data suggests that this is the case. However, further studies are necessary to determine whether the spatial distribution of thermal resources, or females occupying such resources, has led to the evolution of territoriality in this species. Nonetheless, our study provides the first evidence for territorial behaviour of male snakes whereby control of a key resource used by females is likely to be adaptive. Detailed field studies of other nocturnal snake species would help to clarify the generality of our findings.

Ethical approval

The research was in compliance with ethical guidelines and the current laws of Australia. Snakes were studied under protocols approved by the University of Sydney Animal Ethics Committee and permits obtained from the New South Wales National Parks and Wildlife Service.

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Conflict of interests The authors declare that they have no conflict of interest.

References

Archer J (1988) The behavioural biology of aggression. Cambridge University Press, Cambridge

Brooks RC, Griffith SC (2010) Mate choice. In: Westneat DF, Fox CW (eds) Evolutionary behavioural ecology. Oxford University Press, Oxford, pp 416–433

Brown JL (1964) The evolution of diversity in avian territorial systems. Wilson Bull 76:160–169

Cogger HG (2000) Reptiles and amphibians of Australia. Reed New Holland, Sydney, Australia

Duvall D, Schuett GW, Arnold SJ (1993) Ecology and evolution of snake mating systems. In: Seigel RA, Collins JT (eds) Snakes: ecology and behavior. McGraw-Hill, Inc., New York, pp 165–200

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Fedina TY, Lewis SM (2008) An integrative view of sexual selection in *Tribolium* flour beetles. Biol Rev Camb Philos Soc 83:151–171

Gibbs HL, Weatherhead PJ (2001) Insights into population ecology and sexual selection in snakes through the application of DNA-based genetic markers. J Hered 92:173–179

Huang WS, Greene HW, Chang TJ, Shine R (2011) Territorial behavior in Taiwanese kukrisnakes (*Oligodon formosanus*). P Natl Acad Sci USA 108:7455–7459

Huey RB (1991) Physiological consequences of habitat selection. Am Nat 137:S91–S115

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biol Rev Camb Philos Soc 58:1–20

Keogh JS, Webb JK, Shine R (2007) Spatial genetic analysis and long-term mark-recapture data demonstrate male biased dispersal in a snake. Biol Lett 3:33–35

Kim JW, Grant JWA (2007) Effects of patch shape and group size on the effectiveness of defence by juvenile convict cichlids. Anim Behav 73:275–280

Madsen T, Shine R (1993) Male mating success and body size in European grass snakes. Copeia 1993:561–564

Pringle RM, Webb JK, Shine R (2003) Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. Ecology 84:2668–2679

Pringle RM, Syfert M, Webb JK, Shine R (2009) Quantifying historical changes in habitat availability for endangered species: use of pixel- and object-based remote sensing. J Appl Ecol 46:544–553

Schuett GW, Gillingham JC (1989) Male-male agonistic behaviour of the copperhead, *Agkistrodon contortrix*. Amphibia-Reptilia 10:243–266

Shine R (1984) Reproductive biology and food-habits of the Australian elapid snakes of the genus *Cryptophis*. J Herpetol 18:33–39

Shine R (2003) Reproductive strategies in snakes. Proc R Soc Lond B 270:995–1004

Stamps J (1983) Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW (eds) Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, pp 169–204

Webb JK, Whiting MJ (2005) Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. Oikos 110: 515–522

Webb JK, Brook BW, Shine R (2002) What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecol Res 17:59–67

Webb JK, Brook BW, Shine R (2003) Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from south-eastern Australia. Austral Ecol 28:601–610

Webb JK, Pringle RM, Shine R (2004) How do nocturnal snakes select diurnal retreat sites? Copeia 2004:919–925