

Chemoreception and kin discrimination by neonate smooth snakes, *Coronella austriaca*

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The study of chemoreception by squamate reptiles has become integral to understanding many aspects of their behaviour. However, previous studies of snakes have concentrated on its importance in prey choice and few studies have examined its role in kin discrimination. We examined the role of chemoreception not only in prey selection by ingestively naïve neonate smooth snakes, but also as a mechanism for discrimination between kin. We tested the responses of neonate smooth snakes to cotton-tipped applicators labelled with odours of potential prey species and control substances, both before and after their natal shedding events. Neonates tested prior to their natal shedding event were able to discriminate between potential prey species and an odourless control but not between potential prey and a pungent control. In contrast, neonates tested after their natal shedding event showed a significantly increased tongue-flick response towards the scent of nonkin conspecifics, lizard (*Anguis fragilis* and *Zootoca vivipara*) and mammalian prey (*Mus musculus*) compared to that towards both pungent and odourless controls. However, scents of invertebrate prey species and kin, while eliciting more tongue-flicks than the odourless control, did not elicit more than the pungent control. The apparent ability of smooth snake neonates to differentiate between kin and nonkin using chemoreception was confirmed during 'blind' trials. The mechanism by which kin discrimination occurs is discussed.

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Vomeranaseal chemoreception, in which environmental chemical stimuli are transferred to the vomeronasal receptor (Jacobson's organ) typically during tongue flicking and predatory strikes (Burghardt 1993), is important in many aspects of squamate ecology (Young 1993), including reproduction (Cooper & Pèrez-Mellado 2002; Lemaster & Mason 2002), predator avoidance (Burger 1989; Downes 2001), microhabitat use (Downes 1999; Van Damme & Quick 2001) and prey location (Greenbaum 2004; Vincent et al. 2005).

Chemoreception is particularly important for newborn animals that lack parental care after birth, as it can provide a heritable mechanism for identifying potential predators and prey (Burghardt 1970; Burghardt & Krause 1999). In snakes, chemosensory perception of preferred prey types is innate in ingestively naïve

neonates of a number of colubrid species (e.g. Burghardt 1968, 1970; Arnold 1981; Henderson et al. 1983; Cooper 1992). However, these studies have been geographically restricted, to North America, and often examined dietary specialists. Despite these study limitations, results suggest that chemoreception may be important for other neonate snake behaviours, in addition to predator and prey identification. Kin discrimination, and its role in lizard behavioural ecology, has attracted attention recently in attempts to explain observed patterns of sociality. Species known to use vomeronasal cues in kin discrimination include skinks of the *Egernia* genus (Bull et al. 1994, 2001; Main & Bull 1996; O'Conner & Shine 2005), *Lacerta vivipara* (Léna & de Fraipont 1998) and *Iguana iguana* (Werner et al. 1987). Research has indicated that the social behaviour of snakes may also be more complex than was previously thought (Clark 2004; Shine et al. 2005). Despite research showing the importance of chemosensory cues for other snake behaviours, such as ambush site selection (Clark 2007), there have been no studies, to our knowledge, that have examined their use in kin discrimination by snakes. This is surprising given their importance in some lizard species (Léna & de Fraipont 1998; Bull et al. 2001).

The ability of an animal to alter its behavioural response towards kin, compared to nonkin, has been the subject of intense research (Tang-Martinez 2001) and as a result has been widely recognized in

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many animal groups (reviewed in Pfennig 1997). Despite this, the mechanisms by which this discrimination occurs remain unclear (Sherman et al. 1997). There are, however, clear benefits to kin discrimination. By altering its behaviour towards kin versus nonkin, an animal has the potential to preserve inclusive fitness (Roberts et al. 2003) through the display of nepotistic behaviour and/or optimal mate choice (Mateo 2003).

Adult smooth snakes, despite being ambush predators, can readily distinguish the chemical cues of a known prey species (*Podarcis muralis*) in experimental situations (Amo et al. 2004). They typically feed on small mammals and lizards (Rugiero et al. 1995; Drobenkov 2000) but cannibalism is also known to occur (Drobenkov 2000). Feeding observations made by Spellerberg (1977) also suggest that juvenile smooth snakes may feed primarily on lizard prey. However, there have been no studies examining whether this is a result of an innate feeding response.

Since studies on individual recognition by snakes lag far behind those of other vertebrate species (Gillingham 1987), we designed an experiment to investigate (1) whether ingestively naïve neonate smooth snakes have an innate preference for prey species that constitute a large proportion of their adult diet and (2) whether chemoreception is used as a mechanism for kin discrimination in a snake species in which cannibalism occurs.

METHODS

Study Animals

We collected all gravid female smooth snakes observed between 15 August and 15 September of 2006 ($N = 2$) and 2007 ($N = 7$) at field sites within Wareham Forest, Dorset U.K. ($2^{\circ}7'W$, $50^{\circ}41'N$). Captured females were individually housed in plastic vivaria (38×28 cm and 16.5 cm high) furnished with a paper towel substrate and artificial refugia, in a dedicated facility at the Centre for Ecology and Hydrology (CEH), Dorset, U.K. A natural light:dark cycle was observed. The room temperature was raised during the day to a peak of $26^{\circ}C$ and allowed to reach ambient levels at night. Water was provided ad libitum and defrosted commercially available domestic mice, *Mus musculus*, were offered every 2 days. The females were released, at their point of capture, within 48 h of parturition. The study was carried out under licence from Natural England.

Within 24 h of parturition the neonate snakes were weighed and measured, before being housed individually in plastic vivaria (21×15 cm and 8 cm high). Furnishings were the same as those provided for females with the addition of two or three rough stones to provide an abrasive surface to aid sloughing during the natal shedding event. Water was provided ad libitum but food was withheld to ensure the snakes were ingestively naïve prior to experimentation.

Potential prey species were also collected during fieldwork either by hand (slow worm, *Anguis fragilis*; common field grasshopper, *Chorthippus brunneus*, and the dark bush cricket, *Pholidoptera griseoptera*) or with a noose (common lizard, *Zootoca vivipara*). These were also maintained in plastic vivaria, but located in a different room within CEH to ensure snakes were not exposed to prey vomodors (vomeronasally sensed equivalents to odours, Cooper & Burghardt 1990) prior to experimentation. Slow worms and common lizards were fed dark bush crickets. All prey species remained healthy during the trials and were released at their point of capture after the experiment. We attempted to capture long-tailed field mice, *Apodemus sylvaticus*, in 2006 and 2007 using baited Longworth traps but were unsuccessful and so a mammalian prey species was not used in the 2006 experiments. In 2007, commercially available pre-killed newborn *M. musculus* were used as the mammalian prey species. All neonates were released at the

point of their parental female's capture, within 24 h of the experiments terminating.

Pre- and Postshedding Prey Response Experiments

We investigated the lingual responses of ingestively naïve neonates to cotton-tipped applicators (CTA) bearing chemical stimuli from the two invertebrate, two lizard and one mammalian (only used in 2007) prey species in addition to conspecific siblings and nonsiblings. The two invertebrate species were chosen as potential prey species because of their abundance on the field sites from which the females were collected (A. P. Pernetta, personal observation). In addition to potential prey items, an odourless control (deionized water) and a pungent control (1:4 dilution of Calvin Klein Eternity cologne) were used. Preparation of chemical stimuli involved dipping the CTA into deionized water before rolling it across the dorsal and ventral surfaces of the prey item's head and body, taking care to ensure that it did not touch the researcher's hand at any point. A single animal was used in the preparation of CTAs for each prey species to reduce any potential variation in stimuli, as a result of intraspecific variation in pheromonal or other chemical products (e.g. Gonzalo et al. 2004). A new CTA was used for all individuals with all chemical stimuli. Every snake was exposed to each stimulus in a randomized order with a maximum of three stimuli per individual per day. A minimum of 30 min was left between trials. In 2006, all trials were conducted for all individuals ($N = 9$) prior to their first (natal) shedding event (i.e. within 7 days of birth). The trials were repeated in 2007 with the difference that neonates ($N = 19$) were exposed to vomodors after their natal shedding event.

Experimental trials were conducted within each individual's vivarium by gently opening the lid and moving it to a position so that half of the enclosure remained covered. A period of 5 min elapsed before the stimulus was presented to the subject to minimize interference. The stimulus was slowly positioned to a point approximately 1 cm anterior to the snake's snout and the number of tongue-flicks directed and not directed to the CTA was recorded for a period of 60 s following the first tongue-flick.

Kin Discrimination Experiment

To examine the role of chemoreception in kin discrimination, we recorded lingual responses of three clutches of neonates ($N = 15$) in blind trials. Preparation of chemical stimuli was as previously described. However, to prevent recorder bias influencing the observations made, the CTAs bearing sibling and nonsibling scents were reassigned a label (either A or B) by a second researcher out of sight of the observer, before the trials. In these trials each neonate was presented with only four stimuli: an odourless control (deionized water), a pungent control (cologne), a sibling's scent and a nonsibling's scent.

Data Analysis

To examine the difference in the number of tongue-flicks observed between stimuli, we used a general linear mixed model (GLMM). In addition to the stimuli a clutch effect and an effect of individuals nested within their clutch of origin were included to account for the testing of multiple litters. Both clutch and individual were treated as random effects in the GLMM. When significant differences were observed between treatments, pairwise comparisons were made using Tukey's honestly significant difference tests (Tukey's HSD). To meet the assumptions of the analyses (i.e. normally distributed and homogeneous variances) both the total number of tongue-flicks and the number of directed tongue-flicks were square-root transformed prior to analysis for all trials. All

statistical analyses were conducted with Minitab v14 (Minitab Inc. State College, PA, U.S.A.).

RESULTS

Preshedding Prey Response Experiment

All neonates ($N = 9$) responded by tongue flicking when presented with CTAs but no snakes attempted to bite any CTA in any treatment. The mean number of total tongue-flicks observed for each stimulus ranged from 11.89 with *A. fragilis* scent to 21.33 in the presence of *C. brunneus* scent (Fig. 1a.) The total number of tongue-flicks observed in the 60 s test period showed a minor significant difference between treatments (GLMM: $F_{7,56} = 2.24$, $P = 0.044$). However, post hoc analyses did not find any significant pairwise differences between stimuli (Table 1). Although tongue-flick responses also differed significantly between individuals (GLMM: $F_{7,56} = 2.71$, $P = 0.017$), there was no significant difference between clutches (GLMM: $F_{1,56} = 1.28$, $P = 0.296$).

Analysing the number of observed tongue-flicks directed at the CTA showed a significant difference between stimuli (GLMM: $F_{7,56} = 6.62$, $P < 0.001$; Fig. 1b). Responses to all stimuli, with the exception of sibling scent and cologne, were significantly higher than to the deionized water control (Table 1). However, only *C. brunneus* elicited a significantly higher

response than cologne and this response was also significantly higher than the response towards sibling scent (Table 1). None of the other pairwise comparisons were significantly different. Again, there was a significant difference between individuals in directed tongue-flicks (GLMM: $F_{7,56} = 2.84$, $P < 0.001$), but there was no significant difference between clutches (GLMM: $F_{1,56} = 1.65$, $P = 0.240$).

Postshedding Prey Response Experiment

This experiment used 19 subjects from four clutches. However, one individual consistently fled when presented with the stimuli and did not tongue-flick at all during their presentation. As a result, this individual was excluded from the analysis. The remaining 18 individuals all responded by tongue flicking when presented with the stimuli. No incidences of biting the stimuli were observed during the trials. As recorded in 2006, there was a significant difference in the total number of tongue-flicks observed between stimuli (GLMM: $F_{8,135} = 6.83$, $P < 0.001$; Fig. 1c). Post hoc analysis showed only *A. fragilis* and *Z. vivipara* stimuli resulted in significantly more tongue-flicks than the odourless control (Table 2). In addition, *A. fragilis* and *Z. vivipara* stimuli resulted in significantly more tongue-flicks than *C. brunneus*, *P. griseoptera* and nonsibling stimuli (Table 2). The total number of observed tongue-flicks showed significant individual variation (GLMM: $F_{8,135} = 2.06$,

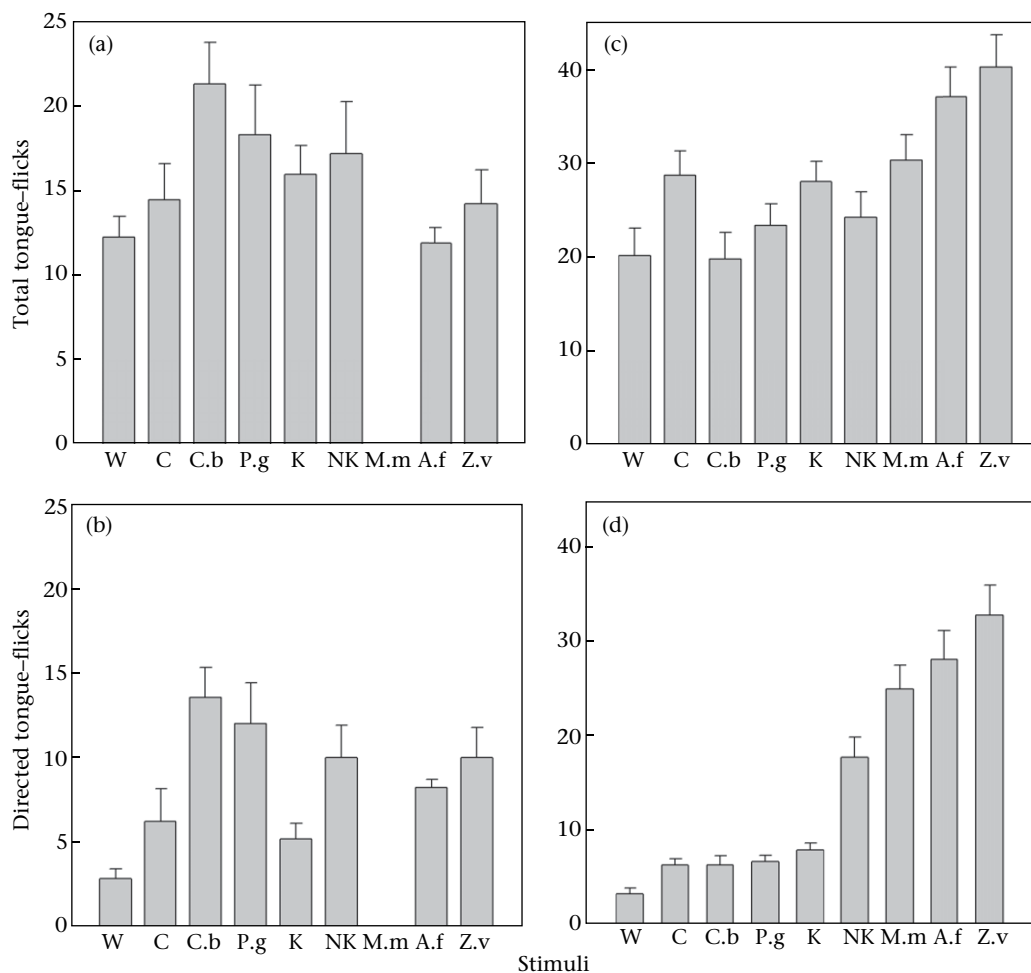


Figure 1. Mean (\pm SE) total tongue-flicks and directed tongue-flicks by ingestively naïve neonate smooth snakes during 60 s trials involving exposure to cotton-tipped applicators bearing chemical stimuli from potential prey species, kin, nonkin and two control substances. Data in this figure are from individuals tested both before (a and b) and after (c and d) their natal shedding event. Abbreviations refer to stimuli: W: deionized water; C: cologne; C.b: *Chorthippus brunneus*; P.g: *Pholidoptera griseoptera*; K: kin; NK: nonkin; M.m: *Mus musculus*; A.f: *Anguis fragilis*; Z.v: *Zootoca vivipara*.

Table 1
Results of Tukey's pairwise comparison tests between stimuli for total tongue-flicks (above dashes) and directed tongue-flicks (below dashes) by ingestively naïve neonate smooth snakes prior to their natal shedding event

Stimuli	Water	Cologne	<i>C. brunneus</i>	<i>P. griseoptera</i>	Kin	Nonkin	<i>A. fragilis</i>	<i>Z. vivipara</i>
Water	—	0.9963	0.064	0.488	0.859	0.792	1.000	0.998
Cologne	0.540	—	0.294	0.898	0.997	0.992	0.992	1.000
<i>C. brunneus</i>	0.0003	0.015	—	0.966	0.791	0.712	0.052	0.258
<i>P. griseoptera</i>	<0.001	0.089	0.997	—	1.000	0.999	0.431	0.869
Kin	0.594	1.000	0.012	0.073	—	1.000	0.816	0.995
Nonkin	0.009	0.5970	0.654	0.959	0.543	—	0.741	0.987
<i>A. fragilis</i>	0.014	0.700	0.549	0.918	0.647	1.000	—	0.996
<i>Z. vivipara</i>	0.003	0.353	0.868	0.997	0.308	1.000	0.999	—

Figures in bold indicate statistically significant pairwise comparisons ($P < 0.05$).

$P = 0.017$), but there was no significant difference between clutches (GLMM: $F_{3,135} = 0.72$, $P = 0.555$).

In contrast to this result, analysis of directed tongue-flicks showed a clear chemosensory response by neonate smooth snakes to potential prey stimuli (GLMM: $F_{8,135} = 42.02$, $P < 0.001$; Fig. 1d). All potential vertebrate prey stimuli elicited significantly more directed tongue-flicks than the deionized water control (Table 2). However, neither of the invertebrate stimuli nor the sibling stimuli elicited significantly more directed tongue-flicks than the pungent control. In contrast to previous experiments there was no significant difference in directed tongue-flicks between individuals (GLMM: $F_{14,135} = 1.26$, $P = 0.240$) or clutches (GLMM: $F_{3,135} = 1.07$, $P = 0.395$).

Kin Discrimination Experiment

A total of 15 individuals from three clutches were used in 'blind' kin discrimination trials. All subjects responded to stimuli by tongue flicking and none attempted to bite the CTAs. The mean number of total tongue-flicks observed during trials showed a significant difference between stimuli (GLMM: $F_{3,42} = 3.56$, $P = 0.022$; Fig. 2a) and there were no individual or clutch effects (GLMM: $F_{12,42} = 1.49$, $P = 0.166$ and $F_{2,42} = 2.17$, $P = 0.157$, respectively). Post hoc analysis showed the total number of tongue-flicks by snakes was significantly larger with the cologne stimuli than with water (Tukey's HSD: $P = 0.048$) and significantly smaller with the sibling stimuli than with the cologne (Tukey's HSD: $P = 0.047$). However, there were no other significant differences in pairwise comparisons of stimuli.

Analysis of directed tongue-flicks also showed a significant difference between stimuli (GLMM: $F_{3,42} = 25.47$, $P < 0.001$; Fig. 2b) but no individual or clutch effects (GLMM: $F_{12,42} = 1.17$, $P = 0.338$ and $F_{2,42} = 1.24$, $P = 0.325$, respectively). Both the pungent control and the two snake stimuli resulted in significantly elevated tongue-flick rates in comparison to the odourless control (Tukey's HSD: cologne: $P = 0.005$; sibling: $P < 0.0001$; nonsibling: $P < 0.001$). However, the mean number of directed tongue-flicks from neonates was significantly larger towards nonsibling scents

than towards either the pungent control or the sibling scent (Tukey's HSD: $P = 0.0001$ and $P = 0.0003$, respectively) and no significant difference was found between responses towards the pungent control and sibling stimuli (Tukey's HSD: $P = 0.933$).

DISCUSSION

The results of these experiments clearly show that ingestively naïve neonate smooth snakes use chemoreception in distinguishing potential prey species. This result complements that of Amo et al.'s (2004) experiments, which found that adult smooth snakes could distinguish *P. muralis* scent from controls. However, the change in responses to stimuli between the pre- and postshedding experiments suggests that the neonates may not actively feed during the first preshed phase. One possible reason for the reduced chemosensory response may be that neonate smooth snakes aggregate prior to their first shedding event (C. J. Reading, personal observation). Neonate rattlesnakes (*Crotalus* spp.) will often stay in natal aggregations prior to the first shedding event as a means of reducing evaporative water loss (Tu et al. 2002). The neonatal integument is thought to be more permeable in viviparous species, such as the smooth snake, to allow the passage of nutrients to the young from the amniotic fluid during gestation (Graves & Duvall 1987; Ball 2004).

The results of the 2007 postshedding experiment, however, showed a clear elevated response by neonate smooth snakes towards nonsibling, lizard and mammalian chemical stimuli. This result suggests that neonate smooth snakes have an innate preference for the prey species that constitute most of the adult snakes' diet (Goddard 1984; Rugiero et al. 1995; Luiselli et al. 1996; Drobenkov 2000). The observed elevated responses towards lizard and mammalian prey complement the results of Spellerberg (1977), who found that a single captive neonate smooth snake could only be encouraged to feed by providing live lizards (*A. fragilis* and *Z. vivipara*) or newborn *M. musculus*. The lack of biting of the CTAs by any snakes in this study suggest that movement is required in addition to chemical stimuli to initiate a full feeding response as suggested by Spellerberg (1977). Innate chemosensory responses as

Table 2
Results of Tukey's pairwise comparison tests between stimuli for total tongue-flicks (above dashes) and directed tongue-flicks (below dashes) by ingestively naïve neonate smooth snakes tested following their natal shedding event

Stimuli	Water	Cologne	<i>C. brunneus</i>	<i>P. griseoptera</i>	Kin	Nonkin	<i>M. musculus</i>	<i>A. fragilis</i>	<i>Z. vivipara</i>
Water	—	0.166	1.000	0.962	0.261	0.920	0.071	0.0004	<0.001
Cologne	0.127	—	0.137	0.849	1.000	0.916	1.000	0.642	0.230
<i>C. brunneus</i>	0.226	1.000	—	0.943	0.221	0.890	0.057	0.0003	<0.001
<i>P. griseoptera</i>	0.126	1.000	1.000	—	0.926	1.000	0.644	0.027	0.003
Kin	0.008	0.986	0.944	0.987	—	0.965	1.000	0.543	0.174
Nonkin	<0.001	<0.001	<0.001	0.0001	0.003	—	0.751	0.043	0.005
<i>M. musculus</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.224	—	0.848	0.427
<i>A. fragilis</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.027	0.379	—	0.999
<i>Z. vivipara</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.0002	0.996	0.887	—

Figures in bold indicate statistically significant pairwise comparisons ($P < 0.05$).

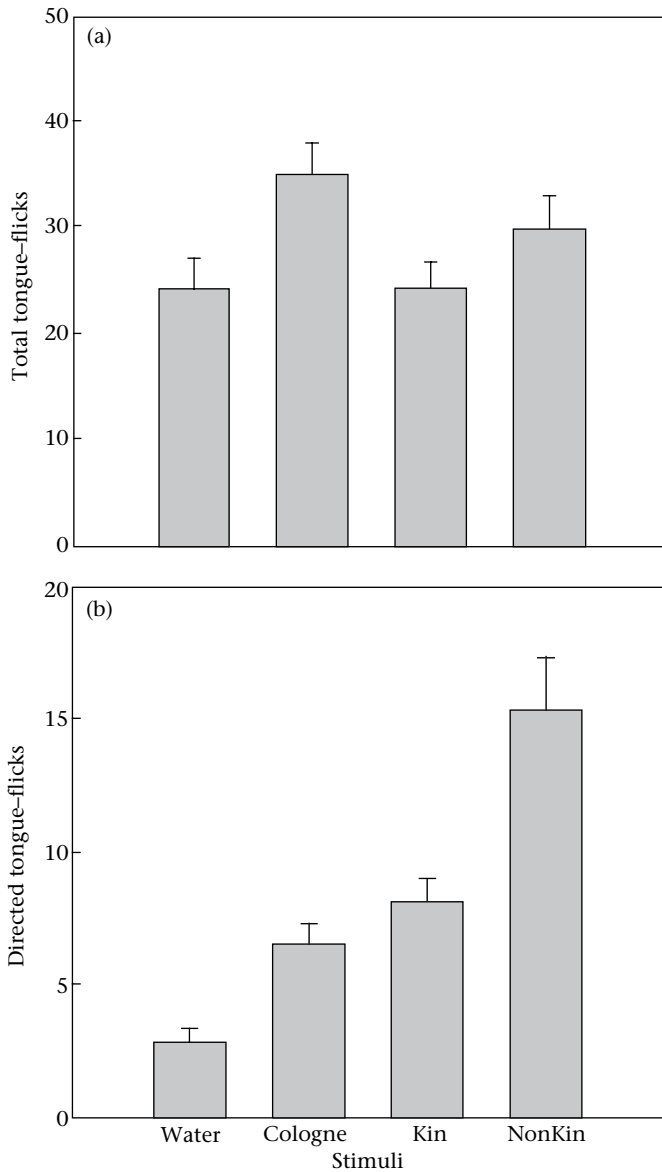


Figure 2. Mean (+SE) (a) total tongue-flicks and (b) directed tongue-flicks by ingestively naïve neonate smooth snakes directed towards cotton-tipped applicators bearing chemical stimuli from odourless and pungent control substances, as well as kin and nonkin skin secretions during blind trials.

recorded here have been shown to vary geographically as a result of prey distribution in neonatal garter snakes (*Thamnophis* spp.; Burghardt 1970; Arnold 1992; Burghardt & Krause 1999). However, whether the responses observed for smooth snakes are subject to geographical variation remains unknown, since all the clutches originated from within a single study area. One important caveat to our results is that the experimental design was confounded by sampling year. This is due to the small number of juveniles obtained in 2006, making the comparison of pre- and postshedding responses limited. In addition, the impact of intraspecific variation in prey species' chemical secretions on neonate smooth snake chemoreception requires more detailed analysis since this was beyond the scope of this study. Further work investigating this shift in chemoreceptive responses by neonate snakes is required to confirm our results. Perhaps the most important result from these experiments is the finding that neonate smooth snakes have an innate ability to discriminate between kin and nonkin individuals, based on chemical stimuli. Prior to this work kin recognition has

previously only been shown to occur in captive-raised adult timber rattlesnakes, *Crotalus horridus*, by measuring the mean separation distance between pairs of individuals housed together (Clark 2004), although the mechanism by which recognition occurred was unclear. To our knowledge ours is the first study to document kin discrimination in neonate snakes and is the first to show that chemosensory perception is important in the recognition process. The fact that the blind trials were conducted with animals that had been individually housed suggests that recognition of siblings may occur by phenotype matching (the use of a reference characteristic (phenotype) against which other individuals are judged; Halpin 1991), since this allows discrimination between unfamiliar kin and nonkin (Beecher 1982) and would be expected to occur in such species that lack parental care (Mateo 2003).

Based on the results of these experiments it appears that the functional significance of kin recognition by neonatal smooth snakes is likely to be preventing the loss of inclusive fitness through sibling cannibalism. Cannibalism has previously been recorded in smooth snakes from Belarus (Drobenkov 2000) and at a nature reserve in Dorset near our study site (B. P. Pickess, unpublished data). The fact that the increased responses towards nonsibling scents were recorded after the natal shedding event suggest that this behaviour was likely to be elicited by a feeding response. Food availability is potentially the single most important ecological factor influencing the occurrence of cannibalism (Dong & DeAngelis 1998) and kin recognition has been shown to determine its frequency during periods of limited food supply (Bilde & Lubin 2001).

In summary, this study provides evidence that ingestively naïve neonate smooth snakes show an innate feeding response towards chemical stimuli from both lizard and mammalian prey that constitute most of the adult diet. However, the observed response is not apparent until after the natal shedding event suggesting that there is an initial period, following parturition, during which feeding does not occur. In addition to this, neonate smooth snakes showed a significantly different response to chemical stimuli from sibling and nonsibling snakes. The lack of familiarization, as a result of individual housing, suggests that the mechanism used by smooth snakes may be self-referent phenotype matching and therefore indicative of a heritable basis for this behaviour. These results reinforce the idea that cryptic social behaviour may be more common in snakes than had been previously thought (Clark 2004; Shine et al. 2005).

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