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Animal behaviour

Like mother, like daughter: inheritance of nest-site location in snakes

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A trait can be passed from parents to offspring even if it has no genetic basis. For example, if daughters return to reproduce at the same sites where they were hatched themselves, nest-site location is consistent within matrilineages. Most cases of natal homing (nest-site philopatry) across generations have been inferred from molecular evidence rather than directly demonstrated, and involve species with low dispersal abilities. However, some animals disperse long distances but then return to their own place of birth to reproduce, based on cues imprinted early in their own development. Our field studies on tropical natricine snakes (*Tropidonophis mairii*, Colubridae) show that when they are ready to nest, females return to the sites where their mothers were captured pre-nesting, and where they themselves were released as hatchlings.

Keywords: heritability; nesting; philopatry; reptile

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1. INTRODUCTION

Offspring frequently resemble their parents. The mechanisms generating this resemblance may involve genetic transmission, environmental effects or some interplay between the two. One interesting case involves culturally inherited trait transmission (Boyd & Richerson 1983). In many human societies, 'traditional knowledge' is handed down from one generation to the next, either in written form (such as this journal) or by oral tradition. Other species similarly transmit fitness-relevant information from one generation to the next (Richerson & Boyd 1984; Freedberg & Wade 2001). In species with prolonged contact between parent and offspring, such information (about predator recognition, location of critical resources and so forth) can be transferred by learning. Through this route, parents and offspring may resemble each other (and differ from conspecifics) in a range of behaviours and in the sensitivity of those behaviours to external cues. The mechanisms that generate such parent–offspring resemblance presumably involve an interaction between genetic factors (e.g. reflecting selection on learning ability) and non-genetic factors (e.g. the specific cues to which the offspring are taught to respond). Importantly, such 'cultural' transmission of information can occur even without parent-offspring contact. Perhaps the most striking cases involve nest-site philopatry (natal homing), where offspring disperse during their juvenile life but return to their own site of birth as adults to reproduce (Freedberg & Wade 2001).

Most cases of natal homing have been inferred from molecular evidence (Freedberg *et al.* 2005) and involve species with low dispersal abilities (so that return to the natal site may not require extensive migration). However, some aquatic animals (salmon, sea turtles) disperse long distances but then return to their own birthplace to reproduce (Lohmann *et al.* 1997; Stewart *et al.* 2003). Our field studies on tropical snakes reveal that nesting females return to the area where their own mother was captured prior to nesting (and where the daughters were released post-hatching), suggesting that hatchling snakes imprint on specific sites encountered early in their life.

2. MATERIAL AND METHODS

Keelbacks (*Tropidonophis mairii*) are small (to 0.8 m) non-venomous snakes (Brown & Shine 2005*a*, 2007). On the flood plain of the Adelaide River in tropical Australia, female keelbacks mature at about eight months of age and produce 1–3 clutches of eggs each year (Brown & Shine 2005*a*). As in most snakes, there is no parental care of eggs: females leave the nest after oviposition (Somma 2003). Adult keelbacks are highly vagile: females that we radio-tracked for two months had home ranges up to 1 km in diameter, and moved up to 900 m nightly (Brown & Shine 2005*a*, unpublished data 2001). Immediately before egg laying, females migrate to higher ground providing well-drained nesting sites (Brown & Shine 2005*a*).

We hand-captured gravid females along a 1.5 km earthen dam wall 3 m high and 5 m wide. We spray-painted markings on the ground atop the wall to delineate its length into 50 m increments. This wall constitutes one of the only areas of high ground in our flood plain study site and hence, acts as a major focus for oviposition (Brown & Shine 2005*a*,*b*). Following capture, we kept female snakes in captivity until they oviposited 1–18 (mean = 6.4, s.d. = 3.1) days later. The eggs were incubated in moist vermiculite in our laboratory, and the offspring individually marked (by branding ventral scales) before release in the same 50 m section of the dam wall as their mother's site of capture. We have recaptured many of these animals as reproductive adults about to lay their own eggs, enabling us to compare their oviposition sites with those of their mothers. Analyses in this paper are based only on females that oviposited soon after capture (see above). Indeed, some animals were captured while laying their eggs. In nine cases where we released gravid females and recaptured them the following night while they were still gravid, most had moved less than 50 m and none more than 250 m from the previous night's capture site. Thus, the places where we captured these females probably were close to their oviposition sites. Such sites tend to be consistent for repeated clutches by the same female. For 67 females that were captured while gravid for two clutches, the locations of their two captures were highly correlated (distance from the eastern end of the dam wall, $r = 0.39$, $p = 0.0012$).

3. RESULTS AND DISCUSSION

Like spawning salmon and nesting sea turtles (Lohmann *et al.* 1997; Stewart *et al.* 2003), keelback snakes ready to lay their eggs tend to return to the area where their gravid mother was captured. A linear regression of nest-site location (distance from the eastern end of the dam wall) for mothers versus daughters reveals a highly significant effect ($n = 69$, $r^2 = 0.24$, slope = 0.49, $p < 0.0001$; see figure 1*a*).

Because visual inspection suggested that two outliers might influence the statistical significance of the relationship (figure 1*a*), we repeated our analyses using non-parametric correlations. These confirmed significant associations between a mother's pre-nesting capture location and her daughter's pre-nesting capture location ($p = 0.0013$), and between a daughter's original release site (as a hatchling) and her capture location as a nesting adult ($p = 0.0001$). Both of these relationships remained significant after removal of the two potential outliers (mother capture site versus

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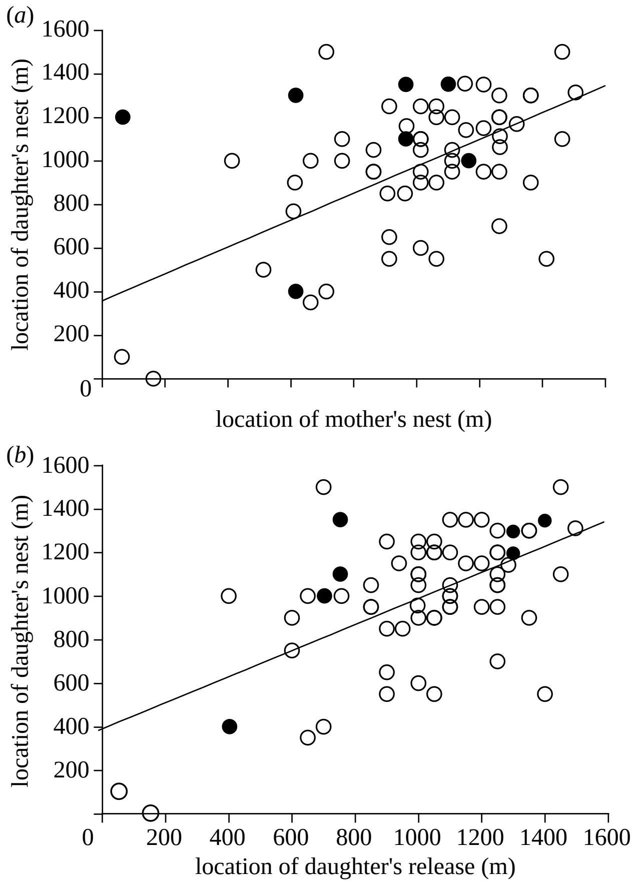

Figure 1. The relationship between location of capture sites for gravid female keelback snakes (likely to approximate nesting locations) and (*a*) collection sites of the mothers of those snakes when captured prior to nesting a year or two earlier and (*b*) the sites where the daughters were released as hatchlings. The two sites (*a*) and (*b*) generally coincide, but in a few cases (shown by filled circles) we inadvertently released hatchlings at a site distant from the mother's capture. Locations are expressed as distances along the earthen wall of Fogg Dam (beginning from the eastern end, so 100=100 m west of the eastern end). When they reach adulthood, female keelbacks about to nest return to sites close to where their mother was collected as she was about to nest (and hence, where they themselves were released as hatchlings).

daughter capture site $p=0.0075$; daughter capture versus daughter release $p=0.001$).

The trend for nesting females to return to the site where their own mother was captured prior to nesting cannot be due to low vagility; radio-tracked snakes moved long distances (above) and 12 females that we released as hatchlings (see below) were found an average of 150 m from their release site when recaptured as juveniles, versus 66.7 m when recaptured as they were about to oviposit (i.e. they returned to the natal nest-site, rather than remaining close to it). The potential selective advantage of natal homing is clear (i.e. this nesting area produced successful hatchlings previously, so is likely to do so again) but what mechanism drives this remarkable homing behaviour? The eggs in our study were laid and incubated in the laboratory, therefore any cue must come either from intrinsic factors (genetics, or maternally deposited cues within the egg) or from the hatchlings' experience of their post-release environment. Seven cases where we inadvertently released hatchlings at the wrong nest-site enable us to test between these ideas. These animals later returned close to the sites where we released them ($n=7$, $r^2=0.55$, $p=0.055$) rather than to the sites where their mothers had been collected ($n=7$, $r^2=0.02$, $p=0.78$). Accordingly, the location of a daughter's capture site when gravid is better explained by where she was released as a hatchling than by the location of her mother's capture ($n=69$, $r^2=0.33$, $p<0.0001$; see figure 1*b*). Thus, natal homing in keelbacks reflects spatial learning by hatchlings rather than encoding of spatial information within the egg.

The most plausible interpretation of our results is that hatchling keelback snakes imprint on an area experienced post-hatching and return to that area when they are ready to reproduce. The location of nests is affected by weather conditions and flooding levels (Brown & Shine 2005*a*) but female keelbacks prefer to oviposit in sites containing old eggshells (Brown & Shine 2005*b*). Hence, keelbacks may often deposit their own eggs close to the shell of the egg that they hatched from themselves at least a year earlier.

Extreme fidelity to natal nesting locations has strong implications. First, this behaviour confounds simple interpretations about inheritance: offspring may resemble their parents because they encounter similar environments during early life, as well as owing to genetic factors. In keelbacks as in many other reptiles, the thermal and hydric conditions inside a nest modify the phenotypic traits of offspring (Deeming 2004; Brown & Shine 2005*a*). Thus, any matrilineal consistency in nest-site location probably will result in similar nest conditions and hence, in similar hatchling phenotypes. Hence, we might expect offspring to resemble their mothers more than that would be expected from genetics alone. Second, nest-site philopatry may affect the evolution of traits such as environmental sex determination, owing to sex-specific fitness effects (Reinhold 1998; Freedberg & Wade 2001). That is, mothers selecting good nest-sites (i.e. that produce highly viable offspring via incubation-mediated effects) may enhance their fitness by overproducing daughters (the sex that benefits most from 'inheriting' the maternal nest-site). In contrast, females which select poor nest-sites would benefit by overproducing sons (the sex that pays a lower cost, because they do not return to the same nesting area; Reinhold 1998). No snake species has been recorded to show environmental sex determination, however (Valenzuela & Lance 2004), so this implication remains speculative. Third, the ability of ectothermic vertebrates to retain early memories poses questions about sensory and neural mechanisms in these putatively 'simple' creatures. Fourth, disturbance to traditional nest-sites may have severe ecological consequences. But fifth, the modified nesting preferenda of our inadvertently relocated hatchlings suggests that we could exploit this imprinting to facilitate translocation of threatened species.

In summary, our field study of snakes reveals a high level of similarity between mother and daughter for capture sites prior to nesting, and hence presumably for nest-site location. The mechanisms generating that resemblance remain unknown, but probably reflect a combination of genetic traits (such as the ability to remember and relocate sites encountered early in life) and phenotypically plastic (learned) responses to spatially variable environmental cues. The parallel to ‘traditional knowledge’ in other species, including our own, suggests that social systems and reproductive behaviour in snakes are far more complex than is generally assumed (Greene *et al.* 2002).

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