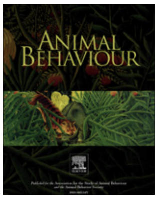
Animal Behaviour 82 (2011) 263–270

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Determinants of homing in nest-guarding females: balancing risks while travelling through unfamiliar landscapes

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ARTICLE INFO

Article history:
Received 7 January 2011
Initial acceptance 29 March 2011
Final acceptance 26 April 2011
Available online 26 May 2011
MS. number: 11-00018R

Keywords:
chemosensory cue
displacement experiment
Eutropis longicaudata
long-tailed skink
Mabuya longicaudata
nest guarding
nest location
parental care
trade-off
visual cue

Determining the context in which animals move through unfamiliar landscapes helps elucidate the risks associated with returning to known resources and the factors that outweigh those risks. For example, females that become separated from their nests can return to protect their offspring from predation, thereby increasing fitness, but also risking having the nest preyed upon or being preyed upon themselves. We predicted that after being displaced, long-tailed skinks, *Eutropis longicaudata*, guarding eggs would adjust their homing behaviour to minimize these risks. Nest-guarding females reduced the likelihood of encountering predators by homing at night, when lizard predators were inactive. Homing success rates decreased with increasing displacement distance (50–300 m), probably because homing took longer from further away, which may increase the chances of nest predation during the female's absence. However, large clutches were associated with successful homing at distances over 50 m, suggesting that increased fitness benefits provided by having more eggs outweighed the risks of returning. Females were more likely to return to a nest with freshly laid eggs, possibly because fresh eggs are easier for predators to locate, and thus more susceptible to predation. Finally, when females were exposed to an egg predator prior to displacement, they homed almost 50% faster, reflecting the ability to adjust homing behaviour according to the risk of nest predation. As predicted, nest-guarding mothers adjusted their homing behaviour so that the fitness benefits of returning to protect a nest outweighed the risks associated with becoming preyed upon or returning to an empty nest.

Most animals are dependent upon spatially distinct resources during different parts of their life cycle, such as overwintering sites (reviewed in Southwood & Avens 2010), shelter sites (Webb & Shine 1997), nesting microhabitat (Brown & Shine 2007) or mates (Bull et al. 1993). Once these resources are located initially, they may be relatively easy to relocate in the future because many animals have the ability to navigate complex spatial environments (Pike 2005; Russel et al. 2005; Gould 2006). However, locating resources becomes vastly more difficult when animals travel through unfamiliar landscapes, such as when dispersing from natal sites (Lohmann et al. 2004), nesting (Guyer 1991), or when displaced involuntarily (e.g. during flooding or following attempted predation). Travelling through unknown areas is risky because individuals can become disoriented and end up in unsuitable habitat (Massot et al. 2002), encounter predators (Gruber & Henle 2004) or be exposed to extreme conditions from which they are unable to seek refugia (e.g. unsuitable temperatures). Theory predicts that animals should move through unfamiliar landscapes only when such risks are outweighed by the benefits provided by the resource.

Appropriate nest sites are crucial for reproduction in oviparous species, and by facilitating egg survival, enhance fitness (Huang & Pike 2011). Often, however, predation on nests is high, and consequently some parents remain with the eggs during incubation (Shine 1988; Huang 2008). In some species both parents guard the nest, allowing one to leave (e.g. to forage) while the other guards the eggs. In many ectotherms, however, only one parent guards the eggs (Shine 1988; Clutton-Brock 1991). This means that when the guarding parent leaves the nest, the eggs are vulnerable to predation until the parent returns. Therefore, parents should minimize the time away from the nest to reduce the possibility of nest predation. In some situations, however, the parent becomes involuntarily separated from the nest (e.g. after being carried away by a predator, during flooding, etc.) and may be unable to return in a timely manner. In these instances, the parent should return to the nest only when the risks of doing so (e.g. disorientation, potentially encountering predators, exposure to extreme environmental

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doi:10.1016/j.anbehav.2011.04.023

conditions) are outweighed by the fitness benefits gained by protecting the eggs. In the worst-case scenarios, the female could become disoriented or preyed upon, and therefore be unable to return to the nest. Alternatively, females could find the nest preyed upon after returning, and therefore waste time and energy on the return journey.

Homing ability may depend on the mobility of the study organism; for example, birds and medium to large mammals generally have large home ranges and are relatively mobile as compared to most ectotherms. This gives them the advantage of being able to cover large areas in relatively short amounts of time, and being generally familiar with a wide geographical area. By contrast, most reptiles are less mobile, but many consistently home to important resources, such as hibernacula or nesting grounds (Brown & Shine 2007). Evidence from lizards suggests that homing through unfamiliar landscapes following experimental displacement is not ubiquitous, however. In homing experiments of 16 lizard species in five families, only 69% successfully returned home, and most of these took several days to cover distances of only a few hundred metres (Table 1). Five of 16 species (31.3%) failed to return home at all (Table 1). Despite these differences, there has been little investigation of the circumstances under which individuals trade the risks of returning home with the benefits of successfully returning. Such work can elucidate how and why species choose to home.

Over most of its geographical range, gravid female long-tailed skinks, *Eutropis* [formerly *Mabuya*] *longicaudata*, lay eggs beneath rocks or under the soil. The female then leaves the nest site and provides no further parental care (Huang 1994). However, some females on Orchid Island nest inside holes running through a concrete retaining wall. These females aggressively defend their nests from intruding egg-eating snakes, *Oligodon formosanus*, which are major reptile egg predators (Huang 2006a, 2007). When long-tailed skinks leave the nest to forage, the eggs remain exposed and are thus vulnerable to predation (Huang 2007). Because lizard nest defence is extremely successful at deterring egg predators (Huang 2006a, 2007), the longer that a female is away from the nest, the greater the opportunity there is for an egg predator to find and consume the unguarded eggs. Females should therefore minimize the time spent away from the nest to reduce the chances of egg predation. Additionally, because numerous, virtually identical holes distributed within a small area contain nests, accurate homing behaviour is essential to ensure that the mother returns to her own nest, rather than that of a conspecific. We used field experiments to investigate the homing ability of long-tailed skinks to determine whether: (1) there are sex differences in homing ability; (2) displacement distance, body size and clutch size influence homing success and return time; (3) egg age influences homing; (4) the threat of egg predation alters homing speed; and (5) visual or olfactory cues are mechanisms used for homing. Based on putative trade-offs between the cost of returning home and the fitness benefits gained by returning to familiar resources, we predicted that: (1) nest-guarding females will benefit more by returning to protect their eggs, and thus should be more likely to return than either males or females without eggs; (2) as distance increases, the likelihood of lizards returning will decrease, either because of the difficulty in finding their way home and/or because the cost of the journey outweighs the benefit of returning; (3) females with larger clutches should be more likely to return than females with relatively smaller clutches because of the relative fitness gain of protecting more eggs; (4) females should home more often to relatively older eggs because of the substantial time and energy already put into guarding the eggs, which are also closer to hatching; (5) the immediate threat of nest predation will decrease homing time because of an increased risk of losing the eggs to predators.

Table 1
Review of lizard displacement distances and the time needed to return home (if successful)

Species	Distance displaced (m)	Days to return	Source
Gekkonidae			
Cyrtodactylus philippinicus	100–150	2–51	Marek et al. 2010
Iguanidae			
Anolis lineatopus	~180	–	Rand 1967
Anolis cristatellus	11–62	(3)	Jenssen 2002
Dipsosaurus dorsalis	50–274	10–40 (20)	Krekorian 1977
Sauromalus obesus tumidus	50–500	1–2	Prieto & Ryan 1978
Phrynosomatidae			
Phrynosoma douglassi	~148	–	Guyer 1978, 1991
Sceloporus graciosus	~280	–	Guyer 1978, 1991
Sceloporus jarrovii	50–200	1–44 (20)	Ellis-Quinn & Simon 1989
Sceloporus occidentalis	<100	–	Fitch 1940
Sceloporus orcutti	~150	~20	Mayhew 1963
Sceloporus undulatus	~270	7–18	Noble 1934
Uta stansburiana	49–122	–	Spoecker 1967
Lacertidae			
Takydromus tachydromoides	<180	3	Ishihara 1969
Scincidae			
Eutropis longicaudata	50–300	0.25–6 (1.4)	This study
Oligosoma grande	25–75	2–34	Stanley 1998
Tiliqua rugosa	~800	>3	Freake 1998

Data are presented as ranges with means in parentheses when available. *Eutropis longicaudata* was the only species tested that guards eggs during incubation.

METHODS

Study Area and Field Methods

We studied diurnal long-tailed skinks on Orchid Island (22°02′N, 121°34′E), Taitung County, Taiwan from 2004 to 2010. The study area was a concrete retaining wall bordering a mountain road (100–150 m in elevation). A series of holes extend through the wall to facilitate water drainage during rainfall, and are commonly used by long-tailed skinks for nesting (Huang 2006a, b). There are nearly 1200 identical holes spread along 3 km of road. During the nesting season (May–August) we searched all holes for nests and/or lizards at 6 h intervals (i.e. four times in each 24 h period). During nightly surveys we used a red-filtered light to minimize disturbance to sleeping lizards. We attempted to capture all lizards by gently picking them up. We recorded clutch size and whether a female lizard was present at the nest site, and measured the body size of the female (when present; snout–vent length, SVL, to 0.1 mm). We marked females using PIT tags to facilitate long-term identification, and gave each a temporary mark by affixing a 1 cm^2 plastic tag to the dorsum using veterinary surgical glue (temporary marks fell off when the lizards shed their skin, typically within 1–2 months). Temporary marks were used in addition to PIT tags to allow us to distinguish individual lizards without disturbing them for the current set of experiments, and PIT tags were necessary for permanent identification as part of our long-term studies. Factory-sterilized PIT tags were injected intraperitoneally into the lateral trunk to the body between a fold of skin gently grasped by the researcher; this prevented damage to internal organs. Within a short period, PIT tags become attached to abdominal fat bodies via connective tissue and thus do not move around in the body (Keck 1994). PIT tags do not appear to influence growth, survival or mobility of small vertebrates (Keck 1994). Most females already contained PIT tags when captured for our current study; we thus affixed the temporary tags to the lizards and immediately used them in our trials.