



Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards

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(Received 30 November 2003; initial acceptance 13 January 2004;
final acceptance 15 February 2004; published online 25 August 2004; MS. number: 7921)

Alternative territorial tactics may be part of a broader behavioural tendency that can influence the expression of other behavioural traits. We compared the exploratory and predator avoidance behaviours of territorial and floater male water skinks, *Eulamprus heatwolei*, to identify whether these alternative behavioural tactics are part of a broader behavioural dichotomy. Floater and territorial males differed in their tendencies to explore novel habitats. Floaters spent less time in the refuge, moved further and ate more mealworms when placed in a novel enclosure, suggesting that floaters were less wary of the novel environment and had greater exploratory tendencies. Predator avoidance behaviours also differed between the two groups of males. Territorial lizards were less likely to retreat to a refuge site during a simulated predator attack, returned faster to a basking site after this attack and as a result had a smaller net reduction in preattack body temperature. These results may be attributed to the trade-off that territorial lizards face between territorial defence and antipredator behaviour, which floaters do not experience. Our results suggest that territorial tactics may be part of a broader behavioural tendency that can influence the expression and evolution of other seemingly unrelated traits.

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Trade-offs between traits as a result of conflicting selection pressures represents a central component of evolutionary biology (Roff 2002). These trade-offs occur predominantly between correlated life history traits, but more recent studies have shown correlations between behavioural responses across different contexts. For example, in the spider *Agelenopsis aperta*, some individuals may be consistently more aggressive than others, independent of the situation (Riechert & Hedrick 1993), and some stream-dwelling salamander larvae, *Ambystoma barbouri*, are consistently more active than others (Sih et al. 2003). Correlations between behaviours have also been identified. Individual great tits, *Parus major*, that had greater exploratory tendencies dispersed further than did their more wary conspecifics (Dingemanse et al. 2003). Correlations have also been identified between behaviours that had been considered unrelated. For example, individual chaffinches, *Fringilla coelebs*, that were good foragers were also good at detecting predators (Cresswell et al. 2003). These studies show that behaviours may be linked, and

that the evolution of a behavioural trait may be constrained by selective forces acting on that trait in another context, ultimately limiting optimal expression of the behaviour (Sih et al. 2003). Identifying these behavioural correlations can provide insight into the selective pressures responsible for shaping the evolution of behavioural traits.

Behavioural dichotomies such as territorial strategies provide a useful system to investigate the presence of behavioural correlations (Sih et al. 2003). Beginning with a known behavioural dichotomy, we can test whether individuals that display different tactics also differ in other behaviours that are not directly related to mating. Alternative strategies are widespread and can manifest in the form of behavioural or morphological differences between individuals adopting alternative tactics (Gross 1996; Shuster & Wade 2003). Alternative behaviours, such as dominance and sneaker tactics, may be related to an overall fight–flight or shy–bold tendency (Wilson et al. 1994). If so, then they could influence a range of behaviours, including exploratory behaviours, predator avoidance behaviours, dispersal tendencies and feeding rates (Wilson et al. 1994; Sih et al. 2003). Individuals displaying alternative tactics may face different selective trade-offs between behaviours. For example, males that adopt

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territorial tactics may need to trade-off predator avoidance with territorial defence (Diaz-Uriarte 2001), but males that adopt a sneaker or floater tactic will not face such a trade-off. To our knowledge, this is the first study to investigate whether alternative territorial tactics are part of a broader behavioural tendency influencing the expression of other traits.

In the water skink, *Eulamprus heatwolei*, a behavioural dichotomy exists related to territoriality. Most individuals in our study population (61%) use a 'floater' tactic, while the rest use a 'territorial' tactic (Morrison et al. 2002). Territorial male lizards maintain core areas where other males are not tolerated, and frequent displays such as chases and combat bouts between males are observed (Morrison 1999). The males maintain the same territories over at least 2 years (Morrison et al. 2002; Stapley 2004). 'Floater' lizards, on the other hand, are characterized by few resightings and large movements after initial capture, and they are absent from the study site in subsequent years (Morrison et al. 2002; J. Stapley & J. S. Keogh, unpublished data). Although we did not measure age in these studies, it is unlikely that these tactics are age related, because snout-vent length (SVL) or condition did not differ between the two groups, and both of these variables are correlated with age in many reptiles (Andrews 1982). Our aim in this study was to identify whether alternative territorial tactics represent a broader behavioural tendency that can influence the expression of other traits. To address this question, we investigated whether territorial and floater males differed in their exploratory behaviours and their predator avoidance behaviours.

METHODS

We conducted the study in November 2002 with approval from the Australian National University Animals Experimentation Ethics Committee. Males were captured from the Koala enclosure at the Tidbinbilla Nature Reserve, near Canberra, Australia (Morrison et al. 2002). We captured by noosing 15 previously toeclipped males that were known territory holders in 2000 (Morrison et al. 2002) and 2002 (J. Stapley & J. S. Keogh, unpublished data), and 17 previously unmarked floater males. Noosing is a common capture method used for these lizards and does not harm them. Lizards were transferred to a cloth bag and brought back to the laboratory within a few hours of capture. We measured SVL (± 1 mm) with a ruler and weight (± 0.1 g) with an electronic balance. Each lizard was placed into an individual opaque plastic box (330 \times 510 mm and 260 mm high) with a paper substrate and a ceramic tile retreat site (100 \times 100 mm). The lizards were housed in a temperature-controlled room maintained at 21 °C and under a natural light regime. We established a temperature gradient in individual containers by placing heating tape under one-half of the container to allow animals to thermoregulate freely. The lizards were fed ad libitum with live food (crickets and mealworms) dusted with vitamin powder. Live food was used to reduce any acclimation of lizards to unnatural food items. Water

was also provided ad libitum. Only males with complete tails were used in the experiments to remove any variation in behaviour caused by tail loss (Wise & Jaeger 1998; Downes & Shine 2001). All animals were released back into the field at their point of capture approximately 3 weeks after capture.

Exploratory Behaviour

These experiments were conducted in an open-topped, plastic enclosure (same size as home enclosure). The enclosure had a paper substrate and a ceramic tile (100 \times 100 mm) that could be used as a retreat site. Four mealworms were placed into the enclosure in an open petri dish, just before the trial. Mealworms could move freely throughout the enclosure. Male lizards were placed into the novel enclosure under an opaque box and allowed to acclimate for 5 min; then the box was lifted from behind a blind so that the lizard could move freely through the enclosure. The activity of the lizard was monitored with a video camera suspended above and recorded for 30 min. During the analysis of the videotapes, we recorded the lizard's position every 20 s against a 500 \times 500 mm grid (30 min \times 3 observations/min = 90 observations). Analysis of the videos was carried out blind to each lizard's mating tactic (toeclips could not be identified from the tapes), and two behavioural measures were obtained. We calculated refuge use as the total number of scans in which the lizard was observed in the refuge. Overall movement was measured as the sum of the distances moved by the lizard between successive scans. We also recorded the number of mealworms eaten. Data were analysed with Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM). Refuge use was analysed with a GLM with a Poisson (P) distribution. The significance of a term in the model was estimated from the analysis of accumulated deviance and the associated *F* statistic. The influence of tactic on overall movement and the number of mealworms eaten were analysed with a GLMM with a Poisson model. In the model, refuge use was treated as a random factor to control for differences in time spent in the open between territorial and floater males. The influence of tactic on these variables was estimated with the Wald (*W*) test and associated *P* value.

Predator Avoidance Behaviour

In this experiment, we set out to quantify the predator avoidance behaviours of territorial and floater lizards and to measure body temperature before and after the predatory attack to calculate heat lost as a result of the antipredator response. To control for differences in habitat familiarity between territorial and floater males, which may influence their predator avoidance behaviour, experiments were conducted in the laboratory, in the home enclosure of the lizard, which was moved to a testing room. The testing room had the same temperature and lighting regimes as the animal's maintenance room. Lizards could thermoregulate using a temperature gradient

that we established by placing heating tape under one-half of the container. The refuge temperature was constant at 21°C and the heat tape was set at 36°C, which created a hot spot within the box of 35°C. After moving the lizard's enclosure to the testing room, we allowed the animals to acclimate for 30 min. In all cases, lizards had resumed basking and reached their preferred body temperature (31°C; Schwarzkopf & Shine 1991) within the acclimation period. We measured lizard body temperature remotely with a thermal imaging camera (FLIR ThermoCam SC2000 PAL), Boston, MA. U.S.A. Temperature readings were recorded live from the camera, and they were always taken from the same place on the lizard: on the dorsal surface, between the lizard's shoulders. During a preliminary study, several positions were tested, but the chosen position was easy to locate repeatedly and provided temperature measurement consistent with internal temperature readings taken from an anal probe (J. Stapley, unpublished data). The use of the thermal imaging camera was also robust to physiological changes related to heating and cooling phases (e.g. vascular dilation or constriction), providing accurate measurements of the lizard's internal temperature regardless of these states (J. Stapley, unpublished data).

The body temperature of the lizard was measured before and after the 'predator attack', which we simulated by walking directly towards the enclosure at about 2 m/s, stopping 0.5 m from the enclosure. We recorded the immediate response of the lizard from behind a blind. Humans have been used successfully to simulate predators in previous studies on lizards (Cooper 1998, 2000) thus enabling researchers to measure predator avoidance behaviours without endangering prey. In all cases, lizards fled the basking site and ran to the opposite end of the enclosure. Whether the lizard retreated under the ceramic tile was recorded. When the lizards returned to the basking site, the time and the lizard's body temperature were recorded. The difference in the likelihood that a lizard fled to the refuge between territorial and floater males was tested with a GLM with a binomial (B) distribution, because the data had two states (Yes/No). We analysed the effect of tactic on time taken to return to the basking site and the change in body temperature before and after the predatory attack with a GLM with a Poisson model.

RESULTS

There was no difference in SVL or condition (weight/SVL) between floater and territorial males (SVL: $t = -1.15$, $P = 0.260$; condition: $t = -1.35$, $P = 0.187$; Fig. 1). Exploratory behaviours of territorial and floater males differed. Territorial males spent more time in the refuge than did the floater males during the exploratory experiment (GLM(P): $F_{1,32} = 34.82$, $P < 0.001$; Fig. 2a). Floater males moved more overall within the enclosure (GLMM(P): $W_1 = 31.43$, $P < 0.001$) and consumed more mealworms than did territorial males (GLMM(P): $W_1 = 6.65$, $P = 0.010$; Fig. 2c).

The predator avoidance behaviour of territorial and floater males also differed. During the simulated attack,

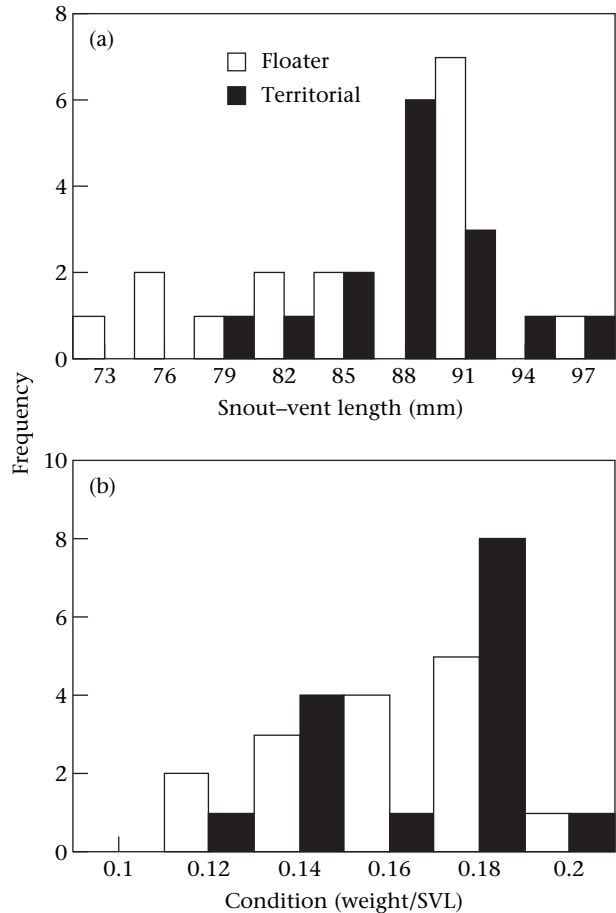


Figure 1. Frequency histograms of (a) snout-vent length (SVL) and (b) condition (weight/SVL) of territorial and floater males.

floater males were more likely to flee under the refuge than were territorial males (GLM(B): $F_{1,32} = 34.30$, $P < 0.001$; Fig. 3a). Floater males also took longer to return to the basking position (GLM(P): $F_{1,32} = 8769.1$, $P < 0.001$; Fig. 3b), and when they did return, they had a greater net reduction in body temperature than did territorial males (GLM(P): $F_{1,32} = 17.13$, $P < 0.001$; Fig. 3c). Body temperature before the simulated predator attack was not different between groups (GLM(P): $F_{1,32} = 0.07$, $P = 0.785$). The change in body temperature was directly related to the time spent in the thermally suboptimal habitat, because of the positive relation between the time taken to resume basking and the change in temperature (GLM(P): $F_{1,32} = 13.847$, $P < 0.001$).

DISCUSSION

The results show that territorial and floater males differed in their exploratory and predator avoidance behaviours. Floater males were less wary of a novel environment, spent more time in the open, moved further and ate more mealworms than did their territorial counterparts. The increased exploratory tendencies of floaters in this study are consistent with the lack of site fidelity and extensive movements of floaters in the field (Morrison et al. 2002;

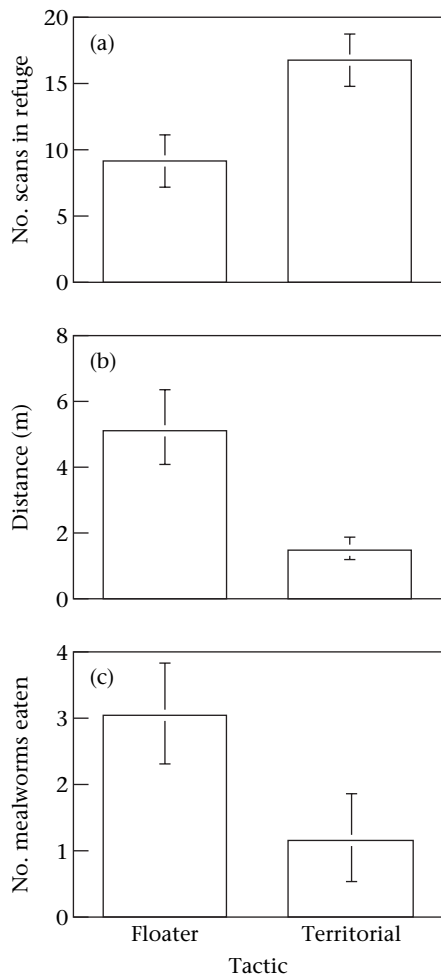


Figure 2. Mean behavioural responses ($\pm 95\%$ CI) of floater and territorial males when placed in a novel enclosure and observed for 30 min. (a) Refuge use, measured as the mean number of scans on which a lizard was observed under the retreat site; (b) mean distance travelled during the trial; (c) mean number of mealworms eaten over the course of the trial.

Stapley 2004). A tendency to explore novel environments is a trait fundamental to dispersal. In great tits, immigrants had higher exploration scores than did locally born birds (Dingemanse et al. 2003). Differences in dispersal between floater and territorial males may also influence immigration, emigration and patterns of gene flow between populations (Witlock 2001). Exploratory behaviour can also be correlated with an individual's ability to adjust to changes in its environment. In mice, *Mus musculus*, individuals that explored more were also more aware of their environment and adjusted their behaviour to environmental changes (Benus et al. 1987). In great tits, birds that explored the novel habitats comprehensively adjusted faster to changes in the position of feeding stations, but birds that explored little kept returning to the previous position of the feeding station and took longer to learn where the new feeding station was (Verbeek et al. 1994). In our study, floaters ate more mealworms. Although exploratory behaviour may be related to foraging efficiency, the difference between males in the number of mealworms

eaten was probably because of their increased movements in the novel arena rather than a difference between floater and territorial males in foraging efficiency per se.

Predator avoidance behaviours differed between territorial and floater males. During the simulated predator attack, territorial males were less likely to flee inside their refuge, but instead they fled beside or on top of it. Territorial males also returned faster to their basking site after the simulated attack, and because the refuge site was not optimal for thermoregulation, floater males had a greater net reduction in body temperature after the predator attack. The trade-off between territorial defence and antipredator behaviour may explain much of the variation between territorial and floater males in their antipredator behaviours. Territorial males may be under conflicting selection pressures when faced with a predator attack, because responding to the predator (e.g. hiding) will decrease the chance of detecting and chasing away an intruder (Diaz-Uriarte 2001). An intruding male can mate with resident females, and theory predicts that the longer the territorial male remains hidden, the greater will be the decrease in his reproductive success (Diaz-Uriarte 2001). In this study, territorial males were less likely to hide and returned to their basking position faster after a predator attack, which could facilitate their territory defence and maximize their reproductive success. In contrast, floater males remained hidden longer after the predator attack, which resulted in greater net reduction in body temperature. Studies have used indirect measures such as refuge, substrate and air temperature to predict the thermal cost of predator avoidance behaviours in lizards, but these studies did not measure lizard body temperature directly or control for initial body temperature (Martín & López 1999a, b). To our knowledge, this is the first study to show a thermal cost, in net reduction in body temperature, of predator avoidance behaviours. In ectothermic animals, body temperature can have a strong influence on behaviour and physiology (Angilletta et al. 2002). Territorial males that are warmer may have improved locomotor capabilities, which may help them to evict intruders and defend their territories more effectively.

Although territorial males at our study site have been caught more times than the floater males, it is unlikely that the differences in antipredator behaviour observed in this study were because territorial males had acclimatized to the presence of humans. All areas of the Tidbinbilla Nature reserve, not just the study site, receive heavy human traffic. Lizards within the study site, i.e. territorial males, and lizards moving in from outside the study site, i.e. floater males, receive similar exposure to human presence. Furthermore, considering that territorial males have been caught more than once, they might be expected to be more wary of humans, because they may experience stress and fear while being handled, i.e. the opposite effect on behaviour to what we observed in this study.

The behavioural differences between floater and territorial males identified in this study suggest that these alternative territorial tactics may be part of some broader behavioural tendency. The mechanisms underlying such behavioural tendencies are unclear. Considering the

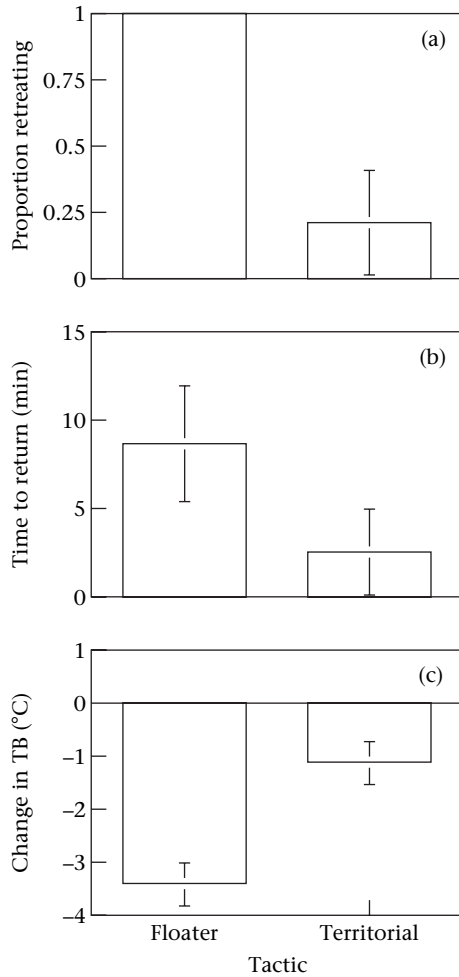


Figure 3. Mean behavioural responses ($\pm 95\%CI$) of floater and territorial males after a simulated predator attack. (a) Proportion of males fleeing under the refuge during the simulated attack; (b) mean time taken to return to the basking site; (c) mean change in body temperature (TB) before and after the attack.

overlap in body size and condition between males of these two groups, it is unlikely that alternative tactics are the result of ontogenetic shifts in behaviour (Andrews 1982). During previous studies of this population, and when males were removed from their territories for this study, no territory ownership changes were observed (Morrison et al. 2002; J. Stapley, unpublished data), suggesting that floater and territorial tactics are fixed for at least several years. Other mechanisms underlying these behavioural tendencies may be genetic, environmental or a combination of both (Sih et al. 2003), and these differences may be mediated through hormones (Knapp et al. 2003) or differences in metabolic rate (Metcalf et al. 1992). Differences in circulating hormonal levels can have wide-ranging effects on the behaviour of animals and are likely candidates mediating territorial behaviour (Tokarz 1995; Knapp et al. 2003). In tree lizards, *Urosaurus ornatus*, territorial and nonterritorial males differed in the sensitivity of testosterone levels to elevated corticosterone levels (Knapp et al. 2003). In free-living territorial males,

testosterone levels were resistant to suppression by corticosterone and territorial males did not show elevated corticosterone levels after agonistic encounters, but non-territorial males did (Knapp et al. 2003). In many vertebrates, elevated corticosterone can reduce aggressive behaviour and territorial defence and increase activity (Knapp et al. 2003). Similarly, floater male water skinks may be characterized by higher sensitivity of corticosterone suppression of circulating testosterone than territorial males, but experiments are needed to test this.

An important finding of our study is that individuals of either tactic may be under different selection pressures that can influence the expression of other behavioural traits. As a result of their extensive movements and exploratory behaviours, floater males may suffer greater risk of predation or end up in unfavourable habitats (Kokko & Lundberg 2001). In the subalpine environment, overnight temperatures below freezing are not uncommon, even in midsummer (Green & Osborne 1994), and in an unfamiliar habitat, floaters may not have access to suitable refuges from these conditions. In contrast, territorial lizards may suffer little risk from dispersal, but may be at greater risk on their territories because of the trade-off between predator avoidance and territorial defence. Few studies have identified selection acting differentially in males that use different territorial tactics. This study also identifies links between components of an individual's reproduction, survival and dispersal and provides information regarding trade-offs that can influence the evolution and maintenance of alternative tactics.

Acknowledgments

Many thanks go to Marilyn Ball and Katharina Siebke for use of the thermal imaging camera. Funding was provided by the Australian Research Council grants to J.S.K. and ASIH Gage Fund and the Ecological Society of Australia grants to J.S.

References

- Andrews, R. M. 1982. Patterns of growth in reptiles. In: *Biology of the Reptilia* (Ed. by C. Gans & F. H. Pough), pp. 273–320. London: Academic Press.
- Angilletta, M. J., Niewiarowski, P. H. & Navas, C. A. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, **27**, 249–268.
- Benus, R. F., Koolhaas, J. M. & van Oortmerssen, G. A. 1987. Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, **100**, 105–122.
- Cooper, W. E. J. 1998. Direction of predator turning, a neglected cue to predation risk. *Behaviour*, **135**, 55–64.
- Cooper, W. E. J. 2000. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia porpinqua*). *Behaviour*, **137**, 1299–1315.
- Cresswell, W., Quinn, J. L., Whittingham, M. J. & Butler, S. 2003. Good foragers can also be good at detecting predators. *Proceedings of the Royal Society of London, Series B*, **270**, 1069–1076.
- Diaz-Uriarte, R. 2001. Territorial intrusion risk and antipredator behaviour: a mathematical model. *Proceedings of the Royal Society of London, Series B*, **268**, 1165–1173.

- Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Behavioral Ecology*, **14**, 741–747.
- Downes, S. & Shine, R. 2001. Why does tail loss increase a lizard's vulnerability to snakes? *Ecology*, **82**, 1293–1303.
- Green, K. & Osborne, W. 1994. *Wildlife of the Australian Snow-country*. Sydney: Reed Books.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution*, **11**, 92–97.
- Knapp, R., Hews, D. K., Thompson, C. W., Ray, L. E. & Moore, M. C. 2003. Environmental and endocrine correlates of tactic switching by nonterritorial male tree lizards (*Urosaurus ornatus*). *Hormones and Behavior*, **43**, 83–92.
- Kokko, H. & Lundberg, P. 2001. Dispersal, migration and offspring retention in saturated habitats. *American Naturalist*, **157**, 188–202.
- Martín, J. & López, P. 1999a. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos*, **84**, 499–505.
- Martín, J. & López, P. 1999b. When to come out of a refuge: risk sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology*, **10**, 487–492.
- Metcalfe, N. B., Wright, P. J. & Thorpe, J. E. 1992. Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology*, **61**, 585–589.
- Morrison, S. 1999. Effects of male territoriality and body size on paternity in the alpine water skink (*Eulamprus heatwolei*). B.Sc. thesis, Australian National University.
- Morrison, S., Keogh, J. S. & Scott, I. A. W. 2002. Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus heatwolei*. *Molecular Ecology*, **11**, 535–545.
- Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Aranae, Agelenidae). *Animal Behaviour*, **46**, 669–675.
- Roff, D. A. 2002. *Life History Evolution*. Sunderland, Massachusetts: Sinauer.
- Schwarzkopf, L. & Shine, R. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus heatwolei*: why do gravid females bask more? *Oecologia*, **88**, 562–569.
- Shuster, S. M. & Wade, M. J. 2003. *Mating Systems and Strategies*. Princeton, New Jersey: Princeton University Press.
- Sih, A., Kats, L. B. & Maurer, E. F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, **65**, 29–44.
- Stapley, J. 2004. Behavioural trade-offs, traits and tendencies in two Australian skinks. Ph.D. thesis, Australian National University.
- Tokarz, R. R. 1995. Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: an experimental test. *Animal Behaviour*, **49**, 661–669.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**, 1113–1121.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, **9**, 442–446.
- Wise, S. E. & Jaeger, R. G. 1998. The influence of tail autotomy on agonistic behaviour in a territorial salamander. *Animal Behaviour*, **55**, 1707–1716.
- Witlock, M. C. 2001. Dispersal and the genetic properties of metapopulations. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 273–298. New York: Oxford University Press.