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Do mountain log skinks (*Pseudemoia entrecasteauxii*) modify their behaviour in the presence of two predators?

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Abstract Prey often adopt antipredator strategies to reduce the likelihood of predation. In the presence of predators, prey may use antipredator strategies that are effective against a single predator (specific) or that are effective against several predators (nonspecific). Most studies have been confined to single predator environments although prey are often faced with multiple predators. When more than one predator is present, specific antipredator behaviours can conflict and avoidance of one predator may increase vulnerability to another. To test how prey cope with this dilemma, I recorded the behaviours of lizards responding to the nonlethal cues of a bird and snake presented singly and simultaneously. Lizards use specific and conflicting antipredator tactics when confronted with each predator, as evidenced by refuge use. However, when both predators were present, lizards' refuge use was the same as in the predator-free environment, indicating that they abandoned refuge use as a primary mechanism for predator avoidance. In the presence of both predators, they reduced their overall movement and time spent thermoregulating. This shift in behaviour may represent a compromise to minimize overall risk, following a change in predator exposure. This provides evidence of plasticity in lizard antipredator behaviour and shows that prey responses to two predators cannot be accurately predicted from what is observed when only one predator is present.

Keywords Predator avoidance · Multiple predators · Scincidae · *Drysdalia*

Introduction

Behavioural mechanisms used to avoid predation can have marked effects on interactions between predator and prey. Numerous studies have investigated how a single predator can affect prey behaviour (for review see Lima and Dill 1990). However, prey often share their environments with a myriad of predators and can be confronted with the possibility of having to avoid multiple predators simultaneously (Soluk 1993; Sih et al. 1998). Given this, it is surprising that so few studies have considered the response of prey to multiple predators. Those that have demonstrate that simultaneous exposure to more than one predator can result in antipredator strategies that are not predicted from exposure to either predator alone (Soluk 1993; Krupa and Sih 1998). Therefore, studies investigating how prey respond to the simultaneous threat posed by multiple predators can provide insight into our understanding of predator-prey relationships.

Predator-avoidance strategies can be categorized as specific and nonspecific defences. Nonspecific antipredator tactics, such as reduced activity, are effective against several predators (Matsuda et al. 1994). In contrast, predator-specific antipredator tactics are behaviours that are effective against a single predator only, such as predator-specific vigilance (Matsuda et al. 1994). It is conceivable that, in the presence of multiple predators, these antipredator behaviours may conflict such that avoidance of one predator can increase vulnerability to the second (Power 1984; Soluk and Collins 1988; Kotler et al. 1992). The opportunity for this potential conflict has been shown in mayflies (Soluk and Collins 1988), desert rodents (Kotler et al. 1992) and fish (Power 1984).

How do prey cope with multiple predators when avoidance behaviours conflict? If predators differ in predation risk, prey could allocate more antipredator effort to the single most dangerous predator (Kotler et al. 1992; Weber and Declerck 1997; Stapley 2003). If predators are equally dangerous, predicting prey-defence strategies is more difficult because a specific avoidance response can increase overall vulnerability (Sih et al. 1998). When

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strategies conflict in that way, prey may adopt an alternative strategy. For example, water striders (*Aquarius remigis*) in the presence of a fish or a stonefly predator can alter microhabitat use to avoid predation. However, in response to multiple predators, the water striders reduced overall activity, a behaviour not observed in the presence of either predator alone (Krupa and Sih 1998). Hence, water striders were able to respond adaptively to multiple predators by switching from species-specific defence to a nonspecific strategy (Krupa and Sih 1998). This study provided evidence of flexibility in antipredator strategies in the face of multiple predators, but no additional studies have been conducted to test the generality of this finding.

In this study, I test how the mountain log skink (*Pseudemoia entrecasteauxii*) copes with two predators, a bird and snake, when their principal antipredator behaviours conflict. Snakes like the white-lipped snake (*Drysdalia coronoides*) often ambush lizards from retreat sites. Lizards use chemical cues from snakes to detect and avoid these retreat sites (Stapley 2003). During attacks from birds, however, lizards often flee to refuges. Observations in the field suggest that a lizard basks on a log and has access to a single suitable refuge site that is used during repeated predatory attacks. If a snake were to enter the refuge, a lizard would be faced with conflicting antipredator responses when a bird attacked. Therefore, *P. entrecasteauxii* provides an ideal study system to investigate how prey cope with multiple predators and conflicting antipredator tactics. This study aims to: (1) investigate the behavioural response of lizards to nonlethal cues of two predators presented singly and simultaneously, and (2) test whether these behaviours are learned or innate.

Methods

Study system

The mountain log skink (*P. entrecasteauxii*) is a small (up to 60 mm) diurnal lizard from southeastern Australia and Tasmania (Cogger 1996). Two groups of skinks differing in age and experience with predators were chosen for the study: wild-caught adults that had prior experience living in a predator-rich environment, and naïve juveniles born in the laboratory from wild-caught adults. Naïve juvenile lizards were approximately 10 weeks of age, born from different females caught in the field approximately 2 months prior to parturition. Juveniles were housed individually prior to the experiment in the same manner as the adults (see below). Two experienced groups of lizards were used to test whether antipredator behaviours are innate or learned. During the experiment, nonlethal cues from two predators, a bird and a snake, were used to simulate the presence of each predator. Paper towels impregnated with the scent of the white-lipped snake (*D. coronoides*) were used to simulate the presence of this reptilian predator. The white-lipped snake is the most common snake species found in alpine regions of Australia. Its distribution overlaps the lizard's distribution extensively (Bennett 1997). Small lizards compose over 90% of its diet (Shine 1981). Lizards avoid microhabitats containing white-lipped snake odours (Stapley 2003). To simulate the presence of a bird, I used an artificial model having the size and shape of the grey currawong (*Strepera versicolor*), a generalist predatory bird that feeds on *P. entrecasteauxii* (Simpson and Day 1993).

Lizards and the two snakes used in the study were collected from Namadgi National Park in the Australian Capital Territory. All animals were housed individually in plastic containers 420 mm (L)×320 mm (W)×220 mm (H) in a temperature-controlled room maintained at 18–20°C. The floor of the container was covered in mulch, and a ceramic tile was provided as a retreat site. Heat was supplied by heat tape that ran under one half of each container. The room was under a 12:12 h light:dark cycle. Animals were provided water and food ad libitum. All animals maintained weight and behaved normally over the course of the experiment, showing no signs of undue stress. All animals used in the study were released back into the field at their point of capture.

Experimental procedure

During trials, lizards were placed into experimental plastic tubs (420 mm (L)×320 mm (W)×220 mm (H) that contained a ceramic tile placed at one end, to serve as retreat site. The tile was separated from the substrate by 4 cardboard squares approximately 20 mm thick. The refuge was accessible from three sides, and the fourth side was flush against the enclosure wall. A strip of heat tape ran under the floor of the enclosure at the opposite end from the retreat, allowing lizards to thermoregulate. Eighty lizards were tested, 40 adult females and 40 naïve juveniles (sex unknown). Adult females were used in the study because males vary in breeding coloration, which may affect their vulnerability and antipredator behaviours (Olsson 1993; Martín and Lopez 2001). The experiment consisted of one predator-free control and three predator treatments. In the predator-free control treatment, no predator cues were present and a piece of clean paper towel was placed under the ceramic tile. In the snake treatment, a piece of paper towel containing snake odours was placed under the tile. The snake odour was obtained by placing a piece of damp paper towel in the snake's enclosure 2 days prior to the experiment. In the bird treatment, a piece of clean paper towel was placed under the tile, and every 5 min the bird model was flown over the enclosure. The bird model was suspended 1 m above the enclosure and was flown at a speed of 2 m s⁻¹, which is equivalent to the speed of a slow diving bird (Fine 1999). In the snake and bird treatment, snake-treated paper towel was placed under the tile, and every 5 min the bird model was flown over the enclosure to simulate a two-predator environment.

Lizards were tested with each of the four treatments on 4 separate days. Lizards were allocated to treatments using a Latin Square design. Thus, lizards were tested with different treatments on different days in a different order. A lizard was tested only once per experimental day, and experimental days were separated by 2 rest days to minimize potential carry-over effects. Experiments were conducted at approximately the same time each day between 9.30–11.30 a.m., when the lizards were most active. Activity in the enclosure was recorded for 20 min using miniature surveillance cameras. During the analysis of the videotapes, I scanned once every minute and recorded the position of the lizard against a 500 mm×500 mm grid. The total number of times the lizard was observed under the retreat site was a measure of refuge use. The overall movement was measured as the sum of the distances moved by the lizard between successive scans. The proportion of total time outside the refuge spent thermoregulating was measured. I recorded a lizard as thermoregulating when it was lying flat against the substrate with its limbs flush against the sides of its body. The proportion of time spent thermoregulating was chosen as a variable instead of total time spent thermoregulating in order to control for the difference in time spent in the open between treatments. The response of lizards immediately following the presentation of the bird stimulus was also recorded to quantify the proportion of lizards that retreated during presentation of the bird.

Data analysis

Refuge use and overall movement variables were tested for normality, transformed and analysed using an ANOVA. A square

root transformation was performed on refuge use and logarithmic transformation was performed on movement. Proportion of time spent thermoregulating could not be transformed to meet normality, and was analysed using Kruskal-Wallis nonparametric ANOVA. To test for significance of differences between means, I used t -tests and Mann-Whitney U -tests. Alpha values were 0.05, except in the case of multiple tests for which I used a sequential Bonferroni correction to determine the alpha value (α_1) (Quinn and Keough 2002). Only significant interactions are reported in the text. Lizard response following presentation of the bird stimulus was analysed using a generalized linear model with a binomial distribution because the data are binary (yes/no) (Quinn and Keough 2002). Other nonparametric methods such as binomial tests would be inadequate because they cannot test for multiple factor effects (treatment, age and bird stimulus number), which can be easily incorporated into a single generalised linear model.

Results

Lizards altered their refuge use in the presence of the predators (Fig. 1, treatment: $F_{3,320}=17.49$, $P<0.001$). The response differed between adult and naïve juvenile lizards (age: $F_{1,320}=17.55$, $P<0.001$). In comparison to the predator-free control, refuge use decreased in the presence of the snake-scented retreat site (adult: $t_{78}=-2.44$, $P=0.005$, $\alpha=0.016$; naïve juvenile: $t_{78}=-2.72$, $P<0.005$, $\alpha_1=0.0125$), increased in the presence of the bird stimulus (adult: $t_{78}=3.38$, $P<0.005$, $\alpha_1=0.0083$; naïve juvenile: $t_{78}=3.04$, $P<0.005$, $\alpha_1=0.01$), and was not significantly different when both predators were present (adult: $t_{78}=0.99$, $P=0.327$; naïve juvenile: $t_{78}=0.08$, $P=0.934$).

The overall movement of lizards was affected by treatment and experience (Fig. 2, treatment: $F_{3,320}=3.59$, $P=0.014$; age: $F_{1,320}=12.78$, $P<0.001$). In both age groups, lizards' overall movement was similar to the control treatment in the snake (adult: $t_{78}=-0.68$, $P=0.498$; naïve juvenile: $t_{78}=-0.90$, $P=0.337$) and bird treatments (adult: $t_{78}=1.60$, $P=0.113$; naïve juvenile: $t_{78}=1.46$, $P=0.149$). However, lizards reduced their overall movement in the

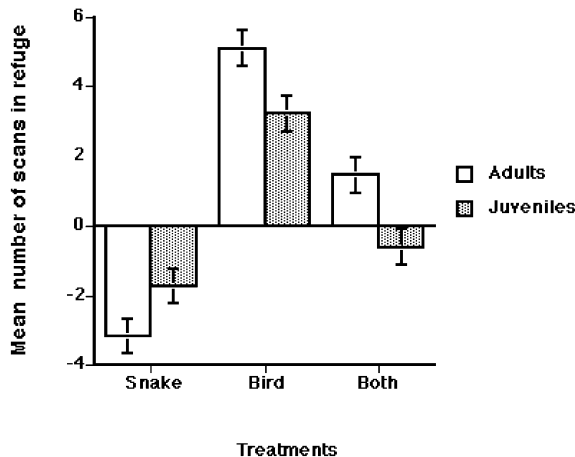


Fig. 1 The mean number of 1-min scans \pm standard error of differences (SED=0.53) in which lizards were observed under the retreat site in each treatment compared to the control mean (zero line). Mean number of scans for the predator-free control for adults 7.17 and juveniles 5.10

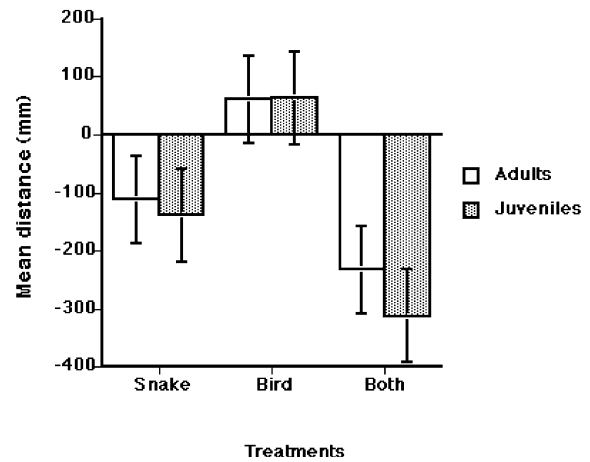


Fig. 2 The mean distance (mm) moved \pm SED (141.4) during each predator treatment compared to the predator-free control mean (zero line). Mean total distance travelled in predator-free control for adults 827.0 and juveniles 1131.3

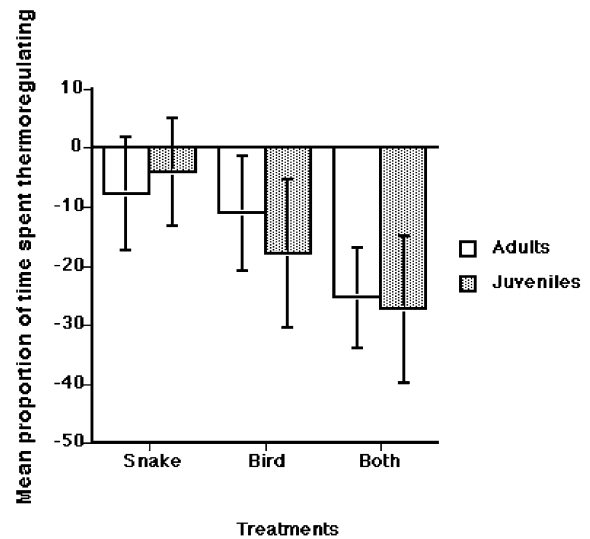


Fig. 3 The mean proportion of time spent thermoregulating \pm SED compared to the control mean (zero line). Mean proportion of time spent thermoregulating \pm SED during the predator-free control: adults 66.37 \pm 11.56, juveniles 80.75 \pm 12.79

two-predator treatment compared to the predator-free control (adult: $t_{78}=-2.87$, $P<0.005$, $\alpha=0.01$; naïve juvenile: $t_{78}=-3.01$, $P<0.005$, $\alpha_1=0.0083$).

Lizards altered the proportion of time spent thermoregulating in the presence of predators (Fig. 3.). This behaviour varied with treatment and age (treatment: $H=8.84$, $P=0.03$, $df=3$; age: $H=9.23$, $P=0.026$, $df=1$). In comparison to the control, the proportion of time spent thermoregulating was similar in the snake (adult: $U=0.88$, $P=0.379$; naïve juvenile: $U=0.73$, $P=0.465$) and bird treatments (adult: $U=0.72$, $P=0.470$; naïve juvenile: $U=1.79$, $P=0.73$). However, the proportion of time spent thermoregulating was reduced in the two-predator treat-

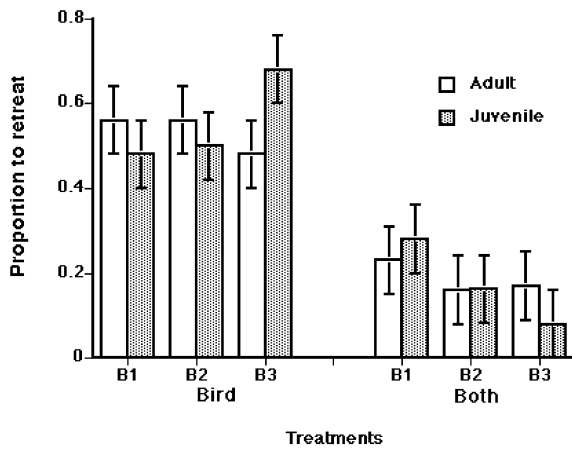


Fig. 4 The mean proportion of lizards that fled to the refuge \pm 95% CI immediately following each of the three presentations of the bird stimulus (B1, B2, B3)

ment (adult: $U=3.00$, $P<0.005$, $\alpha=0.0083$; naïve juvenile: $U=2.69$, $P=0.007$, $\alpha=0.01$).

The response of lizards immediately following presentation of the bird stimulus differed between the bird and the two-predator treatment (Fig. 4.). The proportion of lizards that retreated immediately following the bird stimulus did not differ between adults and naïve juveniles, was greater in the bird-only treatment and did not differ between each presentation of the bird [Wald (treatment)=7.29, $P=0.026$, $df=3$; Wald (age)=0.27, $P=0.605$, $df=1$, Wald (bird presentation number)=0.12, $P=0.942$, $df=3$].

Discussion

The results of this study demonstrate that lizards alter their behaviour in the presence of predators and these behavioural shifts are dependent on the predator type, as well as the presence/absence of a second predator. Lizards adopted specific antipredator tactics when predators were presented singly; they avoided the refuge when the snake odour was present and fled to the refuge when the bird stimulus was presented. However, when both predators were presented simultaneously, lizards did not alter their refuge use in comparison to the control, were less likely to flee to the refuge, reduced their overall movement and allocated less time to thermoregulating. Both snakes and birds use movement as a cue to detect prey when foraging (Greene 1988; Scanlon 1998; Downes and Shine 2001). Therefore, a reduction in movement may represent a compromise to minimize overall risk from both predators, which can be described as a non-specific antipredator response. The results demonstrate plasticity in lizard antipredator behaviours following a change in predator exposure.

Antipredator tactics of wild-caught adults and captive-born juveniles did not differ, suggesting that they are innate. Previous studies have shown that differences in

body size and, consequently, maximal sprint speed may influence vulnerability and predator-avoidance behaviours in lizards (Bauwens et al. 1995). As a result, it can be argued that factors relating to differences in body size rather than experience may cause antipredator behaviours of adults and naïve juveniles to diverge. However, several considerations suggest that the behaviours recorded in this study may be innate. First, despite differences in behaviour between adults and juveniles in the absence of predators, the direction and magnitude of change in behaviour in the presence of predators were similar in the two groups. Second, a previous study demonstrated that prey vulnerability to predation (Van Damme and Van Dooren 1999), suggesting that although smaller animals are slower, they are not necessarily more vulnerable. Third, innate predator-avoidance behaviour appears to be widespread in several taxa, including lizards (Smith 1975; Van Damme et al. 1995; Veen et al. 2000; Stapley 2003; Vilhunen and Hirvonen 2003).

Avoidance of a snake-scented refuge by lizards is similar to results of other studies. Downes and Shine (2001) and Cooper and Burghardt (1990), for example, demonstrated that lizards were able to detect and avoid snake-scented microhabitats. Increased refuge use when the bird stimulus was presented is also consistent with the work of Martín and López (2001), who showed that lizards often retreat to refuges when attacked by birds. A previous study on this species identified that lizards prioritized avoidance based on risk, preferentially avoiding the most dangerous predator (Stapley 2003). In this study, however, refuge use in the presence of two predators was similar to that in the predator-free environment, suggesting that when faced with two predators that pose a significant predation risk, *P. entrecasteauxii* modifies behaviour to minimize overall risk.

Considering that specific antipredator behaviour can increase vulnerability when both predators are present, adopting an alternative strategy that enables them to avoid both would be advantageous. In this regard, the results for *P. entrecasteauxii* are consistent with those reported for water striders (Krupa and Sih 1998). In contrast, a study of mayflies failed to identify a shift in prey defences in the presence of multiple predators (Soluk and Collins 1988). Soluk and Collins (1988) attributed an increase in prey mortality rates to conflict between antipredator strategies when both predators were present. Further studies are needed to identify the generality of these findings. However, plasticity in responses of prey to multiple predators is likely to influence the development of theory in this area. If prey defences are specific and conflicting, then the presence of one predator can increase the availability of prey to the second, resulting in competitive mutualism (Matsuda et al. 1993). Within Matsuda et al.'s (1993) theoretical framework, prey can use either specific or nonspecific antipredator defences, and plasticity in prey response as found in this study is not

considered. Future studies need to identify the prevalence of such plasticity.

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References

- Bauwens D, Garland TJ, Castilla AM, Van Damme R (1995) Evolution of sprint speed in lacertids lizards: morphological, physiological and behavioural covariation. *Evolution* 49:848–863
- Bennett R (1997) Reptiles and frogs of the Australian Capital Territory. National Parks Association of the ACT, Canberra
- Cogger HG (1996) Reptiles and amphibians of Australia. Reed, Sydney
- Cooper WEJ, Burghardt M (1990) A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *J Chem Ecol* 16:45–65
- Downes S, Shine R (2001) Why does tail loss increase a lizard's vulnerability to snakes? *Ecology* 82:1293–1303
- Fine PVA (1999) Aerial predator recognition by free-ranging *Sceloporus occidentalis*. *J Herpetol* 33:128–131
- Greene HW (1988) Anti-predator mechanisms in reptiles. In: Gans C (ed) *Biology of the reptilia*, vol 16. Liss, New York, pp 1–152
- Kotler BP, Blaustein L, Brown JS (1992) Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann Zool Fenn* 29:199–206
- Krupa JJ, Sih A (1998) Fishing spiders, green sunfish, and a stream-dwelling water strider: male-female conflict and prey responses to single versus multiple predator environments. *Oecologia* 117:258–265
- Lima AP, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–634
- Martín J, López P (2001) Risk of predation may explain the absence of nuptial coloration in the wall lizard *Podarcis muralis*. *Evol Ecol Res* 3:889–898
- Matsuda H, Abrams PA, Hori H (1993) The effect of adaptive anti-predator behavior on exploitative competition and mutualism between predators. *Oikos* 68:549–559
- Matsuda H, Hori H, Abrams PA (1994) Effects of predator specific defence community complexity. *Evol Ecol* 8:628–638
- Olsson M (1993) Nuptial coloration and predation risk in model sand lizards, *Lacerta Agilis*. *Anim Behav* 46:410–412
- Power ME (1984) Depth distributors of armoured catfish: predator induced resource avoidance? *Ecology* 65:523–528
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Scanlon J (1998) Prey-scaring by visual pursuit predators: a new use for tail-waving in snakes. *Herpetofauna* 28:5–10
- Shine R (1981) Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). *Copeia* 1:14–25
- Sih A, Enlund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Simpson K, Day N (1993) *Field guide to the birds of Australia*. Penguin Australia, Ringwood
- Smith SM (1975) Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759–780
- Soluk DA (1993) Multiple predator effects: predicting combined functional responses of stream fish and invertebrate predators. *Ecology* 74:219–225
- Soluk DA, Collins NC (1988) Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52:94–100
- Stapley J (2003) Differential avoidance of snake odours by a lizard: evidence for prioritised avoidance based on risk. *Ethology* 109:785–796
- Van Damme R, Van Dooren TJM (1999) Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim Behav* 57:347–352
- Van Damme R, Bauwens D, Thoen C, Vanderstighelen D, Verheyen R (1995) Responses of naive lizards to predator chemical cues. *J Herpetol* 29:38–43
- Veen T, Richardson DS, Blaakmeer K, Komdeur J (2000) Experimental evidence for innate predator recognition in the Seychelles warbler. *Proc R Soc Lond Ser B Biol Sci* 267:2253–2258
- Vilhunen S, Hirvonen H (2003) Innate antipredator responses of Arctic charr (*Salvelinus alpinus*) depend on predator species and their diet. *Behav Ecol Sociobiol* 55:1–10
- Weber A, Declerck S (1997) Phenotypic plasticity of *Daphnia* life history traits in response to predator kairomones: genetic variability and evolutionary potential. *Hydrobiologia* 360:89–99