

Nonlinearity in the predation risk of prey mobility

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Odorous waste products such as urine and faeces are unavoidable for most animals and are widely exploited by predators and their prey. Consequently, waste accumulations can be risky and prey which increase their mobility in order to disperse and dilute their waste should avoid a high predation risk until this benefit is balanced by the increasing risks of random predator encounter. This hypothesis was tested for voles (*Microtus* spp.) in Finland which are vulnerable to predation due to the scent and ultraviolet attractiveness of their urine. The mortality and mobility of radio-collared voles showed a U-shaped relationship, regardless of vole sex, species or population cycle phase. The low risks for prey making intermediate movements suggest that predation risk can exert strong selective pressures on prey such that they have little respite from the risk of being killed.

Keywords: movement behaviour; prey odour; stabilizing selection; signal exploitation; territoriality; trade-offs

1. INTRODUCTION

Odour and olfaction play pivotal roles in species interactions and strongly influence ecological and evolutionary processes. For most animals, odour is an unavoidable consequence of excretory processes but is often used as an essential means of sexual (Blaustein 1981; Wedekind *et al.* 1995; Penn & Potts 1998) and social communication (Moore *et al.* 1997). However, chemosensory abilities for detecting the excretions of other species have also evolved as a key weapon in the chemical arms race between predators and prey (Zuk & Kolluru 1998; Agrawal *et al.* 1999). Many prey organisms, from protists to primates, exploit the odour and social markings of their predators in order to reduce their risks of predation (Perot-Sinal *et al.* 1996, 1999; Kats & Dill 1998). For example, snowshoe hares (*Lepus americanus*) reduce feeding and strongly avoid places with the urine and faeces of their predators (Sullivan & Crump 1984; Sullivan 1986), whereas white-tailed deer (*Odocoileus virginianus*) seek refuge from predation near accumulations of scent markings at the borders of wolf (*Canis lupus*) territories where kills are rare (Lewis & Murray 1993). More generally though, there is a positive linear relationship between mobility and the likelihood of being killed (Norrdahl & Korpimäki 1998) and prey typically move less in response to predator odours (Kats & Dill 1998). Indeed, this relationship is a basic assumption of the theoretical models which analyse the optimal trade-offs between survival and reproduction (Werner & Anholt 1993): reduced movement increases survival but also hinders feeding and mating opportunities which in turn decreases reproductive output.

Existing work on chemical signal exploitation is strongly biased towards prey detecting predators. However, emerging evidence has suggested that predators also exploit incidental chemical cues in the odour (Weissburg & Zimmer-Faust 1993; Zuk & Kolluru 1998) or social markings (Magnhagen 1991) of their prey in order to focus their hunting efforts (Rebach 1996). Olfaction is

a primary sense by which many terrestrial and aquatic predators detect prey (Weissburg & Zimmer-Faust 1993; Rochette *et al.* 1994; Zimmer-Faust *et al.* 1996; Halpern *et al.* 1997; Zuk & Kolluru 1998), whereas many avian species use the ultraviolet (UV) reflectance of prey urine in order to find patchily distributed food (Viitala *et al.* 1995; Koivula & Viitala 1999). The way in which prey can reduce the predation risks resulting from their own body excretions is unknown.

Based on these observations, we predicted that a lowered prey mobility, which results in concentrations of chemical, predator attractants, should lead to a higher predation risk. However, higher mobility also results in higher probabilities of encounters with mobile predators (Anholt & Werner 1995), as do longer movements in unfamiliar areas where the escape routes and risks are less well known (Nelson & Mech 1991). Therefore, we propose a two-component, conceptual model in order to address the odour-induced mobility trade-offs faced by prey hunted by actively foraging predators (figure 1). A high predation risk at high levels of prey mobility and again at very low prey mobility should lead to stabilizing selection for nonlinearity in the predation risk of movement behaviour for prey vulnerable to attack due to their body odours and excretions (figure 1).

2. MATERIAL AND METHODS

We tested this model for cyclic voles in the Alajoki farmland area of western Finland (63° N, 23° E) where the principal rodent predators, small mustelids and kestrels, are major modifiers of vole dynamics (Hanski *et al.* 1993; Norrdahl 1995; Korpimäki & Norrdahl 1998). Unlike lemmings, voles do not hide their faeces in underground latrines (Boonstra *et al.* 1996) but deposit scats and urine throughout their runways as part of social communication (Rozenfeld *et al.* 1987; Rozenfeld & Rasmont 1991). Concentrations of these waste products attract terrestrial and avian predators due to their scent (Cushing 1985) and UV reflectance (Viitala *et al.* 1995; Koivula & Viitala 1999), respectively. In particular, least weasels (*Mustela nivalis nivalis*) are specialist predators of voles and cause most vole kills (Norrdahl & Korpimäki 1995), hunting primarily by smell in the narrow subterranean runways of rodents where voles have limited

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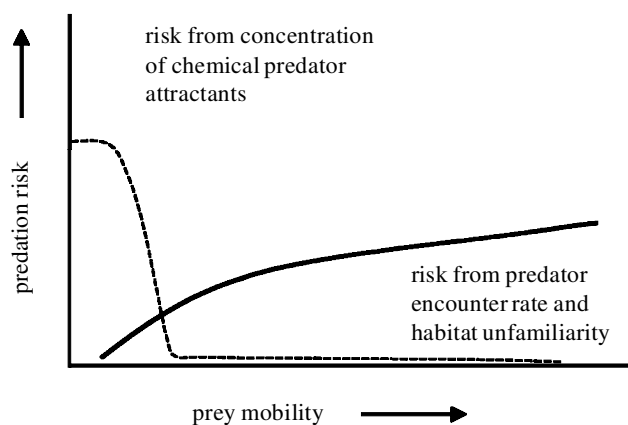


Figure 1. Hypothetical model relating two components of the predation risk of mobility for prey vulnerable to predators attracted to prey body odours or excretions. In the first component (dashed line), we propose that low mobility leads to concentrations of prey scent and, hence, concentrations of predator hunting activity and higher risks of predation. Thus, the risk should rapidly decline as prey mobility increases. In the second component (solid line), the predation risk increases with prey mobility due to a higher likelihood of predator encounter and movements in unfamiliar areas where refugia and escape routes are less well known. These two components intersect to form a nonlinear relationship between prey mobility and predation risk which we here test for cyclic voles and their predators.

chances of survival once detected (Erlinge 1975; Korpimäki *et al.* 1991; Jędrzejewska & Jędrzejewski 1998).

We used radio tracking for assessing the voles' movement behaviour, their sources of mortality and their vulnerability to predation risk. Vole tracking was conducted in six 0.5 km² sites, three with experimental predator reduction and three controls with no manipulation (Korpimäki & Norrdahl 1998). Resident adult field voles (*Microtus agrestis*) and sibling voles (*Microtus rossiaemeridionalis*) were live-trapped and fitted with miniature radio collars (1.5 g). In total, we used 29 mature male and 24 female voles weighing 19.5–46.0 g for the field voles and 19.0–42.0 g for the sibling voles. The voles were tracked in spring 1992 ($n = 18$) and 1995 ($n = 12$) (decline phases of the vole cycle) and in autumn 1998 ($n = 23$) (early increase phase). The data available for 1994 (Norrdahl & Korpimäki 1998) (peak phase) were not used as very few voles were killed, thereby restricting any analysis of the nonlinearity between risk and mobility. The animals were radio tracked for three weeks and located morning and evening and causes of death were determined from the condition (e.g. bite marks) and location of the vole remains and their radio collars (Norrdahl & Korpimäki 1995). Typically, mustelids took killed voles to subterranean nests whereas avian predators ate the voles in some high, open place.

Individual mobility (an estimate of movement and activity behaviour) (Norrdahl & Korpimäki 1998) was calculated as the mean distance between consecutive radiolocations during the three-week study period. The mobility estimates excluded the first 36 h while the voles adjusted to their new collars (Korpimäki *et al.* 1996). Killed animals naturally had fewer fixes (eight to 30) for the mobility estimates than voles which survived (16–56). However, there was no difference in the mean interfix distance when including all fixes and data from the first five days only (when 30% of killed animals had died) (paired *t*-test, $t_{51} = 0.14$ and $p > 0.8$). In addition, as the mean interfix distance

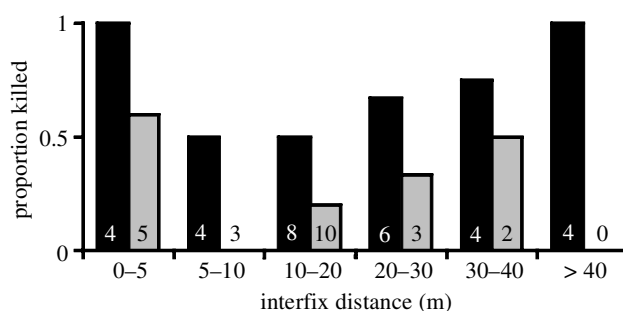


Figure 2. Proportion of radio-collared *Microtus* voles killed according to their mobility during the crash phase (solid bars) and early increase phase (shaded bars) of the vole cycle. The numbers of voles in each movement class are shown in the bars.

and number of fixes showed an asymptote at $n = 4$ fixes for the combined data set, the first four fixes were excluded. We collected our data set using a consistent methodology over three years and from areas with and without predator reduction (Korpimäki & Norrdahl 1998; Norrdahl & Korpimäki 1998) and included year, predator reduction, body mass, sex and species as predictors of vole mortality in the analyses.

We used generalized additive modelling (GAM) (Hastie & Tibshirani 1990) in S-Plus to test for nonlinearity in the relationship between mortality (died or survived) and mobility. This approach fits smoothing splines in order to allow the data to reveal the relationship between the response and explanatory variables rather than forcing significance to be based on linear or other fitted functions. The variables and nonlinearity were excluded in a stepwise model-fitting procedure if their exclusion led to no significant difference ($p > 0.05$) in the deviance explained (Hastie & Tibshirani 1990). We also used a permutation test in S-Plus in order to test for the presence of a U-shaped relationship between the proportion of voles killed and the interfix distance class. We calculated a test statistic (U) of the U-shape as the difference between the minimum proportion of voles killed with either the lowest or two highest movement classes and the maximum proportion of voles killed with intermediate movement classes. A positive value of U means that the voles in the low and high mobility classes had higher mortality than the voles in the intermediate classes. This value was then compared with the results of 5000 permutations of the test statistic generated from the random assignment of vole fates in the data set to distance classes.

3. RESULTS

Out of the 53 radio-collared voles, 25 (12 male) were killed by mammalian predators, three (all male) were killed by avian predators and 25 (14 male) survived. The final model predictors after stepwise model fitting were the interfix distance (as an additive term with d.f. = 4), body mass (as an additive term with d.f. = 4) and year. Smoothing splines were used for mobility and body mass with the conservative option of four degrees of freedom in order to avoid overinterpretation of the curve properties. As predicted by our conceptual model, predators were more likely to kill voles which had either concentrated activity (low mobility) or very high mobility, whereas individuals which made intermediate-distance movements

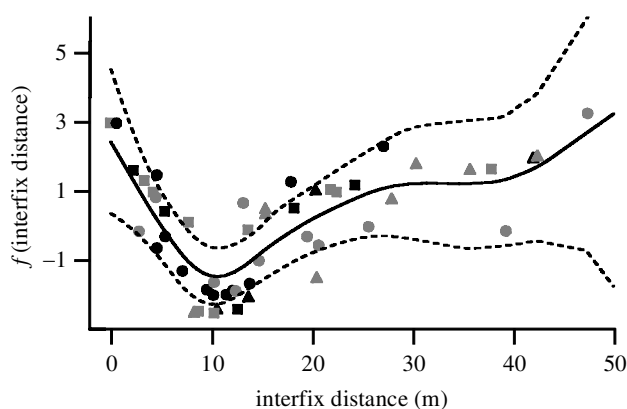


Figure 3. Modelled relationship of the contribution of vole mobility (interfix distance) to vole mortality due to predation showing the nonlinear effects of vole movement behaviour. The solid line represents the partially fitted function of vole mobility generated from the GAM model of vole mortality due to predation shown with pointwise $\times 2$ s.e. curves (broken lines). The symbols represent the partial residuals for males (black) and females (grey) from 1992 (squares), 1995 (triangles) and 1998 (circles). Two highly mobile males killed by weasels (interfix distance < 70 m) were included in the modelling but excluded from the figure for clarity.

had the lowest risks of predation (figure 2). Animals which, on average, changed location by 5–15 m every 12 h survived best and were no different in mass than voles with lower (< 5 m) or higher (> 15 m) mobility ($F_{2,49} = 1.34$ and $p = 0.27$) (figures 2 and 3).

GAM analysis confirmed that this nonlinear relationship between mobility and survival was highly significant ($\chi^2_{2,9} = 11.82$ and $p < 0.001$) and explained significantly more variance than a linear relationship (analysis of deviance, $\chi^2_{2,8} = 14.6$ and $p < 0.001$) (figure 3) which was non-significant. Body mass improved the fitted model (analysis of deviance, $\chi^2_{2,8} = 7.14$ and $p = 0.05$) but was non-significant as a partial explanatory variable of the vole mortality ($\chi^2_{3,0} = 6.4$ and $p = 0.09$). As expected, year influenced the vole mortality ($p < 0.01$), which was greatest during the crash phase when the predator:prey ratios were high and lowest during the early increase phase when predators are less common (Norrdahl & Korpi-mäki 1998). However, the general U-shaped relationship between mobility and mortality was consistent across years, vole sex and vole species (figure 4). Pointwise $\times 2$ s.e. curves (broken lines) show that the U-shaped fitted curve is reliable through low to high prey mobilities, but less reliable at the highest mobility where there are fewer data. Furthermore, the permutation test for a U-shaped relationship confirmed that the voles in the low and high mobility classes had higher mortality rates than the voles in the intermediate mobility classes ($U = 0.44$) and that only one result from 5000 random permutations of the data set had $U > 0.44$.

4. DISCUSSION

In accordance with our conceptual model, the vole mortality and mobility showed a significant, nonlinear, U-shaped relationship which explained significantly more

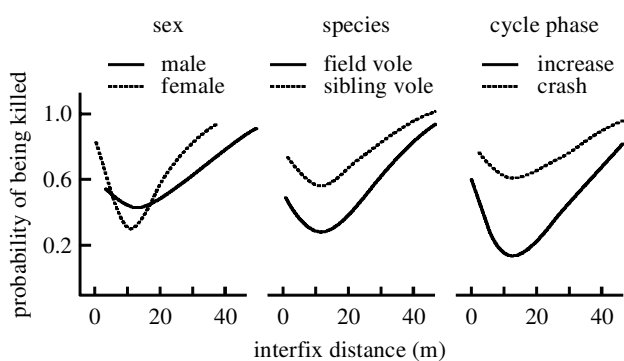


Figure 4. Fitted risks of predation for voles as a function of mobility conditioned by sex, species and cycle phase demonstrating consistent nonlinear effects of mobility and lower risks for voles with intermediate mobility behaviour. The lines represent the same smoothing spline used in the GAM (with d.f. = 4), here calculated for each variable in the conditioning factors. As demonstrated elsewhere, the risks of predation tended to be lower for males and field voles and in crash years. However, the final model (in figure 3) showed no significant reduction in the residual deviance with the inclusion of sex (analysis of deviance, $\chi^2_{1,14} = 2.33$ and $p = 0.15$), species ($\chi^2_{1,15} = 1.94$ and $p = 0.19$) or predator reduction ($\chi^2_{1,16} = 1.31$ and $p = 0.30$).

of the variance in the data than a simple linear one. At one extreme, animals with high mobility had a high probability of being killed (see also Norrdahl & Korpi-mäki 1995, 1998) which was most probably due to the increased probability of encounter with an active predator. At the other extreme, voles which moved very little also had a high probability of being killed. This latter result is in accordance with the prediction from our model that low mobility causes concentrations of chemical, predator attractants leading to higher probabilities of being found and killed. Consequently, voles with intermediate mobility had the lowest probability of being killed.

Coevolution of predator-prey signal exploitation should lead to prey responses which reduce the extent of signal exploitation by predators; however, the nature of these responses has been poorly understood. Prey which are vulnerable to signal exploitation by predators typically alter their duration or timing of signal production, particularly amongst acoustic and visual signalers (Zuk & Kolluru 1998). Similarly, insects which produce airborne, mate-attracting pheromones which also attract parasitoids can vary the duration or content of pheromone production in order to reduce their risks of detection (Aldrich *et al.* 1989; Raffa & Dahlsten 1995). However, the long-term persistence of odour is essential in effective signalling of territory markings and, hence, remains attractive to predators. Our model and results suggest that some voles which use territorial markings may address this dilemma by using spatial behavioural shifts and maintaining higher movement distances in order to reduce predation risk.

Whereas these data fitted the prediction that low prey mobility leads to scent accumulations which cause higher mortality, it is possible that some voles had traits not measured by us which coincidentally caused low mobility and high vulnerability to being killed. However, we

purposely chose animals as similar as possible in order to reduce the potential for bias in the relationship between mobility and mortality and used only adult animals. Furthermore, these relationships were independent of the differences in the voles' species or sex. Similarly, body mass, which is closely related to vole age and, hence, experience showed no relationship to mobility and both mobility and mass exerted independent influences on mortality. Unfortunately, we were unable to determine how disease status may have influenced mobility or predation mortality posthumously as mustelids and raptors typically consumed their prey entirely, leaving only the radio collar.

By looking beyond simple linear relationships, our analyses provide novel evidence that the predation risk of movement behaviour is nonlinear for prey which are vulnerable to attack due to their body odours and excretions. Until recently, the ecological and evolutionary consequences of predators exploiting prey excretions have received little attention (Zuk & Kolluru 1998). However, as many predatory organisms use chemical signal exploitation in hunting and few prey are without odorous excretions, our model and results probably represent a widespread phenomenon in many predator-prey systems, with diverse implications for existing ecological and evolutionary theories. Although individuals make unique decisions about mobility based on their requirements for maintaining their condition and breeding opportunities (McNamara & Houston 1996), heavy predation upon individuals which move little would exert substantial selective pressure for higher mobility in the prey in order to dilute and disperse their chemical, predator attractants. Similarly, theoretical models which examine the costs of territory maintenance may need to consider the predation risk as well as the social role of scent dispersal. Life-history models which assume that prey can reduce their movement linearly in order to trade-off access to resources for safety optimally (Oksanen & Lundberg 1995; Anholt & Werner 1998) may need to consider the limits to such linearity and how prey find refuge by changing their mobility. Indeed, our results suggest a new type of non-structural refuge from predation involving regular and constant mobility within prey ranges such that they can have little respite from the risk of predation.

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REFERENCES

- Agrawal, A. A., Laforsch, C. & Tollrian, R. 1999 Trans-generational induction of defence in animals and plants. *Nature* **401**, 60–63.
- Aldrich, J. R., Lusby, W. R., Marron, B. E., Nicolaou, K. C., Hoffman, M. P. & Wilson, L. T. 1989 Pheromone blends of green stink bugs and possible parasitoid selection. *Naturwissenschaften* **76**, 173–175.
- Anholt, B. R. & Werner, E. E. 1995 Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**, 2230–2234.
- Anholt, B. R. & Werner, E. E. 1998 Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evol. Ecol.* **12**, 729–738.
- Blaustein, A. R. 1981 Sexual selection and mammalian olfaction. *Am. Nat.* **117**, 1006–1010.
- Boonstra, R., Krebs, C. J. & Kenney, A. 1996 Why lemmings have indoor plumbing in summer. *Can. J. Zool.* **74**, 1947–1949.
- Cushing, B. J. 1985 Estrous mice and vulnerability to weasel predation. *Ecology* **66**, 1976–1977.
- Erlinge, S. 1975 The feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos* **26**, 378–384.
- Halpern, M., Halpern, J., Erichsen, E. & Borghjid, S. 1997 The role of nasal chemical senses in garter snake response to airborne odor cues from prey. *J. Comp. Psychol.* **111**, 251–260.
- Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. 1993 Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* **364**, 232–235.
- Hastie, T. J. & Tibshirani, R. J. 1990 *Generalized additive models*. London: Chapman & Hall.
- Jedrzejewska, B. & Jedrzejewski, W. 1998 *Predation in vertebrate communities*. Heidelberg, Germany: Springer.
- Kats, L. B. & Dill, L. M. 1998 The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* **5**, 361–394.
- Koivula, M. & Viitala, J. 1999 Rough legged buzzards use vole scent marks to assess hunting areas. *J. Avian Biol.* **30**, 329–335.
- Korpimäki, E. & Norrdahl, K. 1998 Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* **79**, 2448–2455.
- Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. 1991 Responses of stoats and least weasels to fluctuating vole abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* **88**, 552–561.
- Korpimäki, E., Koivunen, V. & Hakkarainen, H. 1996 Do radiocollars increase the predation risk of small rodents? *Ethol. Ecol. Evol.* **8**, 377–386.
- Lewis, M. A. & Murray, J. D. 1993 Modelling territoriality and wolf-deer interactions. *Nature* **366**, 738–740.
- McNamara, J. M. & Houston, A. I. 1996 State-dependent life histories. *Nature* **380**, 215–221.
- Magnhagen, C. 1991 Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183–186.
- Moore, P. J., Reagan-Wallin, N. L., Haynes, K. F. & Moore, A. J. 1997 Odour conveys status on cockroaches. *Nature* **389**, 25.
- Nelson, M. E. & Mech, L. D. 1991 Wolf predation risk associated with white-tailed deer movements. *Can. J. Zool.* **69**, 2697–2699.
- Norrdahl, K. 1995 Population cycles in northern small mammals. *Biol. Rev.* **70**, 621–637.
- Norrdahl, K. & Korpimäki, E. 1995 Mortality factors in a cyclic vole population. *Proc. R. Soc. Lond.* **B 261**, 49–53.
- Norrdahl, K. & Korpimäki, E. 1998 Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology* **79**, 226–232.
- Oksanen, L. & Lundberg, P. 1995 Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. *Evol. Ecol.* **9**, 45–56.
- Penn, D. & Potts, W. K. 1998 Chemical signals and parasitoid-mediated sexual selection. *Trends Ecol. Evol.* **13**, 391–396.
- Perot-Sinal, T. S., Heale, V. R., Ossenkopp, K. P. & Kavaliers, M. 1996 Sexually dimorphic aspects of spontaneous activity in meadow voles (*Microtus pennsylvanicus*). *Behav. Neurosci.* **110**, 1126–1132.

- Perot-Sinal, T. S., Ossenkopp, K. P. & Kavaliers, M. 1999 Brief predator odour exposure activates the HPA axis independent of locomotor changes. *Neuroethology* **10**, 775–780.
- Raffa, K. F. & Dahlsten, D. L. 1995 Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* **102**, 17–23.
- Rebach, S. 1996 Role of prey odor in food recognition by rock crabs, *Cancer irroratus* SAY. *J. Chem. Ecol.* **22**, 2197–2207.
- Rochette, R., Hamel, J. F. & Himmelman, J. H. 1994 Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odor, current and feeding status. *Mar. Ecol. Prog. Ser.* **106**, 93–100.
- Rozenfeld, F. M. & Rasmont, R. 1991 Odour cue recognition by dominant male bank voles, *Clethrionomys glareolus*. *Anim. Behav.* **41**, 839–850.
- Rozenfeld, F. M., Le Boulange, E. & Rasmont, R. 1987 Urine marking by bank voles (*Clethrionomys glareolus*, Schreber, 1780; Mircotidae, Rodentia). *Can. J. Zool.* **65**, 2594–2601.
- Sullivan, T. P. 1986 Influence of wolverine (*Gulo gulo*) odor on feeding behaviour of snowshoe hares (*Lepus americanus*). *J. Mamm.* **67**, 385–388.
- Sullivan, T. P. & Crump, D. R. 1984 Influence of mustelid scent gland compounds on suppression of feeding by snowshoe hares (*Lepus americanus*). *J. Chem. Ecol.* **10**, 1809–1821.
- Viitala, J., Korpimäki, E., Palokangas, P. & Koivula, M. 1995 Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* **373**, 425–427.
- Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. J. 1995 MHC-dependent mate preferences in humans. *Proc. R. Soc. Lond. B* **260**, 245–249.
- Weissburg, M. J. & Zimmer-Faust, R. K. 1993 Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. *Ecology* **74**, 1428–1443.
- Werner, E. E. & Anholt, B. R. 1993 Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**, 242–272.
- Zimmer-Faust, R. K., O'Neil, P. B. & Schar, D. W. 1996 The relationship between predator activity state and sensitivity to prey odor. *Biol. Bull.* **190**, 82–87.
- Zuk, M. & Kolluru, G. R. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**, 415–438.