Sex- and concentration-dependent effects of predator feces on seasonal regulation of body mass in the bank vole Clethrionomys glareolus

Wendy L. Tidhar a,⁎,1, Frances Bonierb, John R. Speakmana

a Aberdeen Centre for Energy Regulation and Obesity (ACERO), School of Biological Sciences, University of Aberdeen, Aberdeen AB14 2TZ, Scotland, UK

b Department of Biological Sciences, University of Idaho, Moscow, ID 83844, USA

Received 13 February 2007; revised 8 June 2007; accepted 9 June 2007
Available online 30 June 2007

Abstract

Increased perception of predation risk can cause changes in activity, feeding and reproductive behavior in a wide range of taxa. Many small mammals in the temperate zone exhibit fluctuations in body mass in response to changing photoperiod. Bank voles lose body mass in winter which they regain when photoperiod increases in the spring. To determine if predation risk affects seasonal changes in body mass (BM), bank voles were exposed to two concentrations (low: LC and high: HC) of weasel feces. Food intake (FI) and daily energy expenditure (DEE) were measured to establish if differences in body mass were due to adjustment in energy intake or expenditure. Fecal corticosterone (CORT) was measured to assess whether the voles had detected and responded to predator feces as a physiological stressor. Voles of both sexes had higher levels of fecal CORT in the groups exposed to weasel feces compared to controls. Voles responded to the predator feces in a sex- and concentration-dependent manner. Males responded to LC feces by gaining less mass following the change in photoperiod. This was mediated by reduced FI and higher DEE. Female voles also gained less BM in response to HC feces, but increased both FI and DEE. We hypothesize that males may gain a short-term advantage by lowering BM in response to predation risk, which may be regained without affecting reproductive success. The consequences of mass loss in females may be more significant as this may delay the onset of breeding or reduce the size or number of young, thereby negatively affecting breeding success.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Predation risk; Daily energy expenditure; Photoperiod; Least weasel; Bank vole; Fecal corticosterone; Mustela nivalis; Clethrionomys glareolus

Introduction

Many small mammals show seasonal fluctuations in body mass. It is suggested that species such as the bank vole, Clethrionomys glareolus, reduce body mass in winter to lower their metabolic requirements at a time when food may be of lower quantity or quality (Dark and Zucker, 1983; Nagy and Negus, 1993). Regulation is primarily mediated through changes in photoperiod that are transduced into the secretion of melatonin via the pineal gland (Petterborg, 1978; Morgan and Mercer, 2001; Mercer and Speakman, 2001; Bartness et al., 2002). Over the past two decades, research on the control and regulatory mechanisms associated with photoperiod-induced body mass change has focused on factors such as thyroid activity (Pistole and Cranford, 1982), reproductive hormones (Kriegsfeld and Nelson, 1996) and more recently neuroendocrine responses (Morgan and Mercer, 2001).

Although photoperiod is a primary signal involved in body mass regulation, individuals may fine-tune their responses using additional cues (such as ambient temperature or food availability) that vary with the current environmental conditions (Heldmaier et al., 1982; Banks and Dickman, 2000; McDevitt and Speakman, 1994a,b, 1996; Bairlein, 2002; Zhang and Wang, 2006; Zhao and Wang, 2005). Local variation in resource levels, ambient temperature or predation risk is common (Ekman and Hake, 1990; Lima and Bednekoff, 1999; Sih et al., 2000; Speakman, 2001).
et al., 2000); therefore, one might expect animals to assess their local environment and respond appropriately (McNamara and Houston, 1986; Kats and Dill, 1998; Wingfield, 2003). In addition to reducing energy demands in winter, body mass reduction in prey species may further serve to lower the risk of predation at a time when risk may be high due to elevated predator population levels (Graham and Lambin, 2002) as well as the increased energetic demands placed on predators (Gosler et al., 1995; Sundell and Norrdahl, 2002). Weasels, Mustela nivalis, are prolific predators of rodents and have evolved a long, thin body shape to access their prey’s burrow systems and nests (Jędzrejewska and Jędzrejewski, 1998). This morphological adaptation comes at a cost of higher energetic demands in winter compared to animals of a similar weight but with a more conventional body shape (Brown and Lasiewski, 1972). Weasels do not store endogenous energy reserves, although they may store food when necessary, and must therefore spend a large proportion of their time hunting to satisfy these high-energy demands (Jędzrejewska and Jędzrejewski, 1998). Energetic demands of the predator, combined with seasonal changes in weasel population density, are likely to affect the risk of predation in the prey species at this time of the year (Graham and Lambin, 2002).

While physiological responses to predation risk have been well studied in birds (Witter and Cuthill, 1993; Clinchy et al., 2004; McNamara et al., 2005), much less is known for small mammals (but see Boonstra et al., 1998). Predator-related studies on rodents have concentrated on either behavioral adaptations (Ylönen and Ronkainen, 1994; Jędzrejewska and Jędzrejewska, 1990; Korpinäki et al., 1996; Koskela et al., 1996) or interactions relative to prey population cycles (for reviews see Ylönen et al., 1992; Norrdahl and Korpinäki, 2000), rather than those relative to the prey individual per se. Birds deposit fat at levels below those physiologically possible (King, 1972), suggesting a cost to fat storage that must be traded off against the benefits of reduced starvation risk or enhanced reproductive success (Lima, 1986; Adriaensen et al., 1998). Increased fat mass impedes the ability of a bird to escape attack by affecting flight maneuverability (Hedenstrom, 1992), and birds carrying migratory levels of fat have reductions in both flight velocity and angle of ascent (Kullberg et al., 1996; Burns and Ydenberg, 2002). Increased fat deposition may also be costly due to increases in energy expenditure in flight (Ward et al., 2001, 2004), resulting in extended foraging times and hence exposure to predators (Witter and Cuthill, 1993; Brodin, 2001).

It is presently unknown whether terrestrial mammals store fat with a similar trade-off as birds. Field voles, Microtus agrestis, exhibit a reduction in body mass in response to simulated predation risk in the laboratory (predator feces) and in field experiments (avian predator enclosure areas; Carlset al., 1999). Furthermore, rabbits, Oryctolagus cuniculus, increased body mass in areas where foxes, Vulpes vulpes, had been removed (Banks et al., 1999). Sundell and Norrdahl (2002) concluded that weasel predation might impact the mean body size of voles (Microtus sp.) due to small voles being able to seek refuge in tunnels not large enough for a chasing weasel. However, this impact on body size was not a result of voles responding directly to higher predation risk but weasels selecting larger prey, thereby influencing the mean body size of the population. Whether individual bank voles regulate body mass directly in response to predation risk, and possible mechanisms involved are, at present, unknown.

It seems unlikely that voles and other small mammals respond to predators as a result of direct encounters with the predators themselves, since any encounter between a vole and a weasel is likely to end fatally for the vole affording it no opportunity to respond. Animals are likely to utilize indirect cues to modulate their body mass. Indeed, as noted above, photoperiod may be one such cue that serves to synchronize body mass cycles of voles with changes in predator population densities to minimize predation risk. An additional factor that may allow the voles to more closely link their body mass to actual predation risk is to assess predator population density from predator odors. Accordingly, predator odors have become a common method of simulating predation risk in the laboratory. Olfaction is a widespread method of communication among mammals (Eisenberg and Kleiman, 1972). Although chemical signaling is primarily associated with intraspecific communication, such as pheromones relaying reproductive information, odors may be used by members of other species to gauge, for example, the presence of predators or prey (Stoddart, 1975; Kats and Dill, 1998; Koivula and Korpinäki, 2001). Many studies have taken advantage of interspecific communication to examine the effect of perceived predation risk on behaviors of small rodents (mobility: Jędzrejewski et al., 1993; Borowski, 1998a; activity patterns: Perrot-Sinal et al., 1996, spatial and microhabitat use: Merkens et al., 1991; Korpinäki et al., 1996; Fey et al., 2006; feeding: Calder and Gorman, 1991; Borowski, 1998b). Behavioral changes in response to predator odor may serve to reduce the risk of predation and one would expect prey species to respond conservatively to any suggestion of increased predation risk since a liberal response could lead to increased mortality (Lima and Dill, 1989; Frid and Dill, 2002; Bouskila and Blumstein, 1992). Voles that are more mobile have a higher risk of predation (Norrdahl and Korpinäki, 1998; Banks et al., 2000); so by reducing activity levels in the presence of predator odor, the likelihood of encounter and subsequent capture is potentially lowered. This effect is complicated by the fact that increased rates of movement may dilute the accumulation of their own odor which may act as a predator attractant (Banks et al., 2000; Pastro and Banks, 2006).

This study aimed to determine whether, like many bird species and some mammals, bank voles respond to increased perceived predation risk by reducing body mass. Since bank voles exhibit seasonal fluctuations in body mass (Peacock et al., 2004), the experiment aimed to establish whether the photoperiod-stimulated increase in body mass could be modulated by exposure to an indicator of predation risk—predator feces. Perceived predation risk is known to affect foraging behavior (Borowski, 1998b), activity levels (Jędzrejewski et al., 1993) and blood stress hormone levels (Table 1) in prey species. Any or all of these factors are underlying mechanisms that may affect body mass, therefore food intake and daily energy expenditure, using doubly labeled water, were measured to determine whether any differences in body mass
were mediated by energetic changes in feeding or activity pattern. Furthermore, fecal corticosterone levels were measured to assess whether the voles perceived weasel feces as a stressor, and to begin to determine an underlying mechanism by which voles may regulate their body mass.

Material and methods

Animals

Thirty-five bank voles were taken from a laboratory colony maintained in a 12 h light/12 h dark photoperiod at a temperature of 20±2 °C. The bank vole colony at the University of Aberdeen was established in 1996 from wild caught voles. Voles were weaned at 18 days old and housed in 28×11 ×12 cm. Voles were assigned to one of three groups, matched for body mass: low concentration (LC) feces (6 males/7 females); high concentration (HC) feces (6 males/7 females); control (5 males/4 females). After a further 5 weeks, a reliable estimate of DEE in small mammals over periods of 1–3 days (Speakman et al., 1994; Bertaux et al., 1996) and has been validated for use in voles (Speakman and Król, 2005). Individuals were weighed (±0.01 g Sartorius) and labeled with an intraperitoneal injection of approximately 0.2 g of water containing enriched deuterium (4.63 at.%) and Θ-oxygen (9.44 at.%) to the precise mass prescribed. The syringe was weighed before and after the injection (±0.0001 g Ohaus Analytical Plus) to obtain an accurate measurement of the amount of isotope injected. An initial 50–100 μl blood sample was collected by tail tipping 1 h after the injection, the time required for the isotopes to reach equilibrium (Krol and Speakman, 1999; Visser et al., 2000; Kerstel et al., 2006). Blood samples were immediately flame-sealed into pre-calibrated 50-μl pipettes (Vitrex, Camlab Ltd) until analysis. A final blood sample was collected 24 h after the initial sample to minimize any effects of circadian variation in metabolism (Speakman and Racey, 1988). Blood samples were vacuum-distilled into glass Pasteur pipettes (Volac, John Poulten Ltd) (Nagy, 1983) and the distillates used for mass spectrometric analysis of stable isotopes. Mass spectrometric analysis of deuterium enrichment was performed using H2 gas, produced by reacting water, distilled from the blood, with LiAIH4 (Ward et al., 2000). For analysis of Θ-oxygen enrichment in the blood samples, the water distilled from the blood was equilibrated with CO2 gas using the small sample equilibration technique (Speakman et al., 1990). Background enrichments were established from samples taken from unlabelled individuals (Speakman and Racey, 1987: Method C). Energy expenditure was calculated using a single pool model as recommended for animals weighing less than 2 kg (Speakman, 1993). There are several alternative approaches for the treatment of evaporative water loss in the calculation (Visser and Schekkerman, 1999). We chose the assumption of a fixed evaporation of 25% of the water flux (equation (7.17): Speakman, 1997) which has been established to minimize error in a range of conditions (Visser and Schekkerman, 1999; Van Trigt et al., 2002).

Hormone extraction and corticosterone radioimmunoassay

Vole feces (wet mass 0.2 g) were collected and stored in 1.5 ml 95% EtOH at −20 °C until corticosterone extraction. Extraction followed Harper and Austad (2000). The fecal sample, including the storage EtOH, was boiled twice in 10 ml 95% ethanol for 20 min. Solvents from each extraction were combined in a glass culture tube and dried under nitrogen in a water bath in a fume cupboard. After drying each tube was rinsed with 3.0 ml ethyl acetate: hexane (3:2 vol./vol.) solution, vortexed for 30 s and dried again. The residue was resuspended in 4.0 ml 95% EtOH and stored at −20 °C until assayed. Samples were assayed in triplicate using a double-antibody 125I-corticosterone radioimmunoassay kit for rats and mice (MP Biomedicals, Inc., formerly ICN Pharmaceuticals) according to manufacturer’s instructions, but at half-volume and counted on a gamma counter (Hewlett-Packard). To reduce the effect of pipetting error, the outlier of the triplicate was removed and the covariate of the remaining duplicate samples was calculated. Samples were removed if the CV was greater than 20%.

Experimental protocol

Following baseline measurements, each vole was weighed and given approximately 100 g of food; the photoperiod in the room was switched to 16 h light/8 h dark and temperature remained at 6°C (Day 0). Individuals in the control group were moved to a room similar in all respects to the first so that they were not exposed to the predator odor. Body mass and food intake were recorded every 3 days and a second vole fecal sample was taken on Day 7. We searched the cage for pieces of food that had been removed from the hopper but not eaten and replaced these into the food hopper. Food intake was then recorded from the calculated amount of food missing from the hopper compared to the previous measurement. The hoppers were periodically topped up to ensure the animals were always given an excess of food (100 g). On Day 8, groups were exposed to the following treatments:

Daily energy expenditure

DEE was measured using the doubly labeled water technique (Speakman et al., 1990; Speakman, 1998) which has been previously established to generate

<table>
<thead>
<tr>
<th>Study citation</th>
<th>Protocol</th>
<th>Control</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blanchard et al. (1998)</td>
<td>Exposed prey species to live predator for 60 min on 5 test days spread 5 days apart</td>
<td>Soft toy cat</td>
<td>Higher blood corticosterone in cat-exposed rats</td>
</tr>
<tr>
<td>Eilam et al. (1999)</td>
<td>Exposed prey species to 3 min human voice, 2 min owl calls, 5 min silence</td>
<td>5 min human voice, 5 min silence</td>
<td>Higher blood cortisol in mice exposed to owl calls</td>
</tr>
<tr>
<td>Zhang et al. (2003)</td>
<td>Smear 0.05 mg predator anal gland secretion onto the oronasal groove of prey species daily for 28 days</td>
<td>Distilled water</td>
<td>Higher blood cortisol in predator odor-exposed hamsters</td>
</tr>
<tr>
<td>Monclús et al. (2005)</td>
<td>Predator feces in a bowl next to food bowl for 4 days</td>
<td>Sheep feces in bowl for 4 days</td>
<td>Higher blood corticosterone in rabbits exposed to fox odor</td>
</tr>
<tr>
<td>Ylönen et al. (2006)</td>
<td>Sprayed a liquid (1 l predator bedding soaked in 5 l water) at 5, 9, 12, 15, 24, 27, 30, 36, 54 h into arena where prey species were housed</td>
<td>Distilled water</td>
<td>No difference in fecal corticosterone between groups</td>
</tr>
<tr>
<td>This study</td>
<td>Predator feces in pots throughout room or smeared inside of prey species cage, applied weekly for 7 weeks</td>
<td>Rabbit feces smeared on inside of cage</td>
<td>Higher fecal corticosterone in predator odor-exposed voles</td>
</tr>
</tbody>
</table>
Weasel feces were collected from wild-caught weasels from an ongoing large-scale population study in Kielder Forest in the north of England. Feces were collected from live traps and stored at −20 °C until required, at which time they were defrosted. Rabbit feces were collected fresh from a domestic rabbit. We used exposure to feces of a non-predator to control for the possibility that the responses of the voles were to a novel odor rather than the odor of a predator. Over the next 6 weeks, predator and control feces were replaced weekly and vole feces samples were collected for stress hormone analysis using the following protocol. At 00:20 h, weasel or rabbit feces were placed in or beside vole cages. Fresh bedding was placed in vole cages at 05:20 h and the vole fecal samples were collected for stress hormone analysis using the following protocol. At 00:20 h, weasel or rabbit feces were placed in or beside vole cages. Fresh bedding was placed in vole cages at 05:20 h and the vole fecal samples removed from bedding at 09:20 h. This protocol allowed a sample of vole feces to be taken containing levels of hormone corresponding to when the predator feces was placed in the cage (Harper and Austad, 2000). This period was during the dark phase so the voles were not disturbed by any other animal care activities during this time. Lights were not switched on during this time; however, the door was left open briefly to allow dim light to enter the room. Body mass and food intake were measured every 3 days for the 6 weeks and DEE was measured for a second time by DLW on Days 49–52.

Statistical analysis

Data were analyzed using the statistical package Minitab Version 11 (Ryan et al., 1985). All data were tested for normality prior to analysis using the Anderson–Darling test (p<0.05). Time and group effects on body mass were analyzed using general linear models (GLMs) on data relative to baseline. To determine significant group effects, a one-way ANOVA was carried out using the residuals calculated from the regression of body mass and day, followed by post hoc Tukey’s test. Time and group effects on food intake were analyzed using repeated measures GLM. Least squares regression (LSR) was used to determine if significant time effects were due to general trends or daily variation. Time and group effects on DEE were analyzed using paired t-tests and one-way ANOVAs, respectively, followed by post hoc Tukey’s tests.

Results

There was no significant difference between the three groups in any variable measured prior to experimental manipulation. Males: body mass $F_{2,16}=0.01, p=0.99$; food intake $F_{2,16}=0.77, p=0.48$; DEE $F_{2,13}=0.02, p=0.98$; fecal corticosterone $T^*_8=1.66, p=0.16$. Females: body mass $F_{2,17}=0.19, p=0.83$; food intake $F_{2,17}=0.33, p=0.73$; DEE $F_{2,17}=0.12, p=0.89$; fecal corticosterone $T^*_8=0.94, p=0.39$.

Body mass

As expected, all three groups increased their body mass significantly over time following the increase in photoperiod (Fig. 1; (a) males GLM; $F_{15,271}=15.5, p<0.001$; (b) females $F_{15,287}=45.5, p<0.001$). Male LC voles gained 39.2% less weight over the duration of the experiment than voles from the control group (ANOVA; $F_{2,271}=4.35, p=0.01$). This amounted to a gain of 1.24±0.23 g compared to 1.93±0.46 g by HC and control voles, respectively. In contrast, female HC voles gained between 12% and 28% less weight than either the control or the LC voles (ANOVA; $F_{2,287}=7.31, p=0.001$); amounting to 2.14±0.25 g in the HC group compared to 2.45±0.35 g and 2.96±0.43 g by the LC and control groups, respectively.

Food intake

Male LC voles significantly decreased their food intake from Day 7 to 47 (GLM; $F_{2,186}=9.37, p<0.001$, LSR; $F_{1,10}=5.84, p=0.04$). There was no analogous effect of time on the other two groups (LSR; HC $F_{1,10}=0.08, p=0.78$; control $F_{1,10}=1.00, p=0.34$). There was no significant difference in mean food intake per day or total food intake between groups over the duration of the experiment (Table 2; ANOVA; per day $F_{2,16}=0.82, p=0.46$; total $F_{2,16}=0.81, p=0.47$). Females in all three groups exhibited a significant increase in food intake over time (Fig. 2; GLM; $F_{10,197}=16.0, p<0.001$, LSR; LC $F_{1,10}=10.0, p=0.01$; HC $F_{1,10}=8.63, p=0.02$; control $F_{1,10}=10.2, p=0.01$). There was no

<table>
<thead>
<tr>
<th>Sex</th>
<th>Group</th>
<th>Food intake (g/day)</th>
<th>Total food intake (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Control</td>
<td>4.64±0.12</td>
<td>265±4.76</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>6.11±0.19</td>
<td>251±7.66</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>6.33±0.23</td>
<td>260±9.36</td>
</tr>
<tr>
<td>Female</td>
<td>Control</td>
<td>5.51±0.12</td>
<td>226±4.94</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>5.72±0.19</td>
<td>234±7.86</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>5.94±0.28</td>
<td>244±11.4</td>
</tr>
</tbody>
</table>

Values are expressed as means±S.E.M.
difference in mean food intake per day or total food intake between groups (ANOVA; per day $F_{2,17}=0.75, p=0.49$; total $F_{2,17}=0.74, p=0.49$).

**Daily energy expenditure**

There was a general increase in DEE in male voles from all three groups, however, this only reached significance for LC voles (Fig. 3a; paired $t$-test LC $T=5.11, p=0.02$; HC $T=1.28, p=0.27$; control $T=1.82, p=0.14$). These voles increased their DEE from $70.6\pm3.23$ kJ to $106\pm3.78$ kJ, a rise of 49.3%. Following exposure, LC also had a DEE 26.9% higher than that of the control group (ANOVA; $F_{2,13}=4.19, p=0.04$).

Females in all three groups increased their DEE following exposure to weasel or rabbit feces (Fig. 3b; paired $t$-test; low $T=3.41, p=0.02$; high $T=3.71, p=0.01$; control $T=3.97, p=0.02$). This equated to increases of approximately 30% in all groups.

**Fecal corticosterone**

Due to feces being collected from only a sub-sample of LC and HC voles, these results were pooled and compared to the control group. Intra-assay CV (mean±S.E.M.) was $5.43\pm0.40\%$ (range 0.07–13.1). Voles exposed to weasel feces had significantly higher levels of fecal corticosterone than controls (Fig. 4; GLM; $F_{1,19}=6.17, p=0.02$). In both experimental and control groups, female voles had significantly higher levels of fecal corticosterone than male voles (GLM; $F_{1,19}=7.49, p=0.01$); this resulted in male voles exposed to weasel feces having similar levels of corticosterone as female controls. The response to weasel feces by females was almost twice as large as that of male with mean corticosterone increasing by 92 and 50 ng/g, respectively.
Discussion

Bank voles gained less body mass when exposed to increased perceived predation risk in a manner consistent with studies on birds (Witter and Cuthill, 1993; Gosler et al., 1995) and some other mammals (Carlson et al., 1999; Banks et al., 1999). There were sex- and concentration-dependent differences possibly reflecting distinctive life history strategies and cost–benefit trade-offs of male and female voles when exposed to varying levels of predation risk. In particular, reproductive success of females is strongly and positively associated with body mass (Myers and Master, 1983) but in males the effect is much less clear (Klemme et al., 2006; Bartmann and Gerlach, 2001). Hence, for females, the benefits of reducing mass in the face of elevated predation risk must be traded off against reproductive success. In males, the balance of this trade-off has a solution at a lower body mass because mass has a much smaller effect on reproductive output. These data are consistent with other work suggesting that an animal’s response to a specific situation may be determined by the its life-history stage (Wingfield, 2003). For example, an animal within the breeding stage of its life cycle may respond to a detrimental environmental event (stressor) in a different manner, either physiologically or behaviorally, than an animal in the non-breeding phase (Wingfield et al., 1998; Jessop et al., 2004). Small mammals that reduce body mass in winter may benefit from reduction in energy requirements and decreased predation risk at this time of the year (Peacock et al., 2004; Sundell and Norddahl, 2002; Sundell and Ylönen, 2004). However, the positive relationship between body mass and reproductive success (Schultz, 1991; Bartmann and Gerlach, 2001) suggests that the amount of mass gained in the spring may reflect a trade-off between reproductive success and predation risk.

When there was a slight increase in predation risk (LC), we found that male voles gained less weight than controls, a response we did not observe when the exposure to predator odor was further increased (HC). This reduction in body mass gain in LC voles was associated with a decrease in food intake, suggesting reduced foraging activity as seen in other studies (Calder and Gorman, 1991; Borowski, 1998b). The DEE increase we observed in all male groups over time most likely reflects higher metabolic expenditure associated with gain in body mass (Brodin, 2001). Interestingly, male LC voles exhibited an additional 27% rise. This may also reflect a stress response, indicated by the rise in fecal corticosterone, rather than an increase in physical activity (Boonstra et al., 1998), as bank voles reduce mobility in the presence of a weasel (Jędrzejewski et al., 1993). If possible, male voles will move to areas not utilized by a predator or escape by climbing twigs (Jędrzejewski and Jędrzejewska, 1990). Neither of these responses were possible in the present study – a fact which may have contributed to the stress hormone rise. In contrast, we found that female voles responded by reducing body mass only when risk of predation was perceived to be high (HC). Female HC voles increased both DEE and food intake over time; however, this was also seen in the LC and control groups, suggesting the response was to increased body mass rather than the level of predation risk. We are unable to determine the mechanisms involved in body mass regulation in HC female voles that led to reduced body mass gain in this group. However, differential regulation of individual components of DEE (metabolic rate, physical activity) may be important.

From our results, we hypothesize that when a male vole perceives a slight increase in predation risk (LC), he may be able to reduce this risk in the short term by reducing the amount of body mass gained in response to increased photoperiod, as seen in the present experiment. When the risk subsides, body mass may be regained without having a great effect on reproductive output for the season. Reducing the amount of body mass gained by a female vole in response to a slight increase in predation risk (LC) may have a profound effect on her productivity for the season (Dobson et al., 1999). The reason being that it may delay the onset of breeding (Hickling et al., 1991; Schultz, 1991) or affect the size or number of pups she gives birth to or weans (Singleton et al., 2001). In support, we found no difference in body mass gain between LC and control females.

When the risk of predation becomes much higher (HC), the benefit a male vole receives by gaining less weight may be negated, as the probability of death is increased. A better strategy may be to gain mass and maximize reproductive output (Bartmann and Gerlach, 2001) in the short time he may have left. In support, we found no difference in body mass between males in the high group and controls. In contrast, a female puts a lot of energetic investment into producing and maintaining her litter, if the risk of predation is very high it may be better for her to delay breeding and save the energy for a time when risk is lower (Oksanen and Lundberg, 1995; Norddahl and Korpimäki, 2000). Therefore she does not expend all her energy on a litter that has a lower chance of survival. In support, we found that HC females reduced body mass gain compared to controls. We acknowledge that further studies are required to test these hypotheses; however, it is important to remember that males and females have different life history strategies and priorities to ensure survival and maximum fitness. It should therefore not be surprising to find differing responses to changing environmental conditions, such as predation risk, between the sexes.

Table 1 summarizes the methods and results of six studies (including the present study) in which a stress response of a prey species was measured in response to “predation risk”. Of these six, only one (Ylönen et al., 2006) did not show a significant increase in stress hormone levels in animals exposed to a greater perceived risk of predation. The methods used in these six studies vary widely in duration (minutes to weeks), type of exposure (predator call, odors or presence), and type of control used (distilled water, non-predator odor). This is only a selection of possibly hundreds of studies in which “predation risk” has been manipulated to examine behavioral, physiological and ecological responses of prey to their predators. This small selection highlights differences in methodologies used in studies, the results of which are then compared. In our present study, the two methods used to expose voles to predator feces resulted in different behavioral and physiological responses, suggesting that the protocol used may be critical for obtaining easily comparable results between studies.

In conclusion, we found that bank voles reduced the extent of their body mass response to long photoperiod, in response to
increased perceived predation risk, in a manner similar to that exhibited by birds. The present results likely reflect sex-differences in life history strategies and priorities to ensure survival and maximum fitness before and during the reproductive period. Furthermore, in light of the concentration-related differences found in our study we suggest the need for further work and careful consideration of methodology when exposing rodents to predator odors in laboratory or semi-natural enclosure experiments (Apfelbach et al., 2005). In particular, it is difficult in the laboratory to accurately mimic the level and pattern of exposure to predator odors that is experienced by wild mammals. Including a variety of different exposure levels as we have in the current study may reveal how robust a response is to the details of the protocols being employed. Including a control exposure to non-predator feces (e.g., Monclús et al., 2005) is desirable to eliminate the possibility that any response is not just to a novel odor, and we note that this protocol has not always been employed in previous studies (e.g., Ylönén et al., 2006).

Acknowledgments

This work was carried out with the support of a BBSRC studentship. We would like to thank the animal house staff in the zoology department for their help with the care-taking of the studentship. We would like to thank David Tidhar and Jill Mateo for their helpful comments on earlier versions of the manuscript.

References


