

LETTER

Prey change behaviour with predation threat, but demographic effects vary with prey density: experiments with grasshoppers and birds

Gary E. Belovsky*, Angela Nardoni Laws[†] and Jennifer B. Slade

Environmental Research Center and Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

*Correspondence: E-mail: belovsky.1@nd.edu

[†]Present address: Division of Biology, Kansas State University, Manhattan, KS, USA

Abstract

Increasingly, ecologists emphasize that prey frequently change behaviour in the presence of predators and these behavioural changes can reduce prey survival and reproduction as much or more than predation itself. However, the effects of behavioural changes on survival and reproduction may vary with prey density due to intraspecific competition. In field experiments, we varied grasshopper density and threat of avian predation and measured grasshopper behaviour, survival and reproduction. Grasshopper behaviour changed with the threat of predation and these behavioural changes were invariant with grasshopper density. Behavioural changes with the threat of predation decreased *per capita* reproduction over all grasshopper densities; whereas the behavioural changes increased survival at low grasshopper densities and then decreased survival at high densities. At low grasshopper densities, the total reproductive output of the grasshopper population remained unchanged with predation threat, but declined at higher densities. The effects of behavioural changes with predation threat varied with grasshopper density because of a trade-off between survival and reproduction as intraspecific competition increased with density. Therefore, resource availability may need to be considered when assessing how prey behavioural changes with predation threat affect population and food web dynamics.

Keywords

Birds, grasshoppers, intraspecific competition, predation, prey behavioural changes, trophic cascades.

Ecology Letters (2011) 14: 335–340

INTRODUCTION

A central issue in ecology is the relative importance of top-down (predatory) and bottom-up (resource) control of populations and food webs (Hunter *et al.* 1997; Schmitz *et al.* 2000; Chase 2000, Borer *et al.* 2005). As part of top-down mechanisms, presence of predators sometimes causes prey to modify their behavioural and morphological traits to reduce predatory mortality. These prey trait changes may reduce prey survival and reproduction, irrespective of predatory killing, by reducing resource acquisition or increasing resource demand (i.e. physiological stresses) by the prey; thereby, affecting prey population and food web dynamics (e.g. Peacor & Werner 1997, 2001; Werner & Peacor 2003; Bolker *et al.* 2003; Preisser & Bolnick 2008a,b; Sheriff *et al.* 2009; Hawlena & Schmitz 2010).

This phenomenon has led some ecologists to propose that top-down controls of populations and food webs are enhanced by prey trait changes with predation and this effect may exceed predatory mortality itself (e.g. Schmitz *et al.* 1997; Nelson *et al.* 2004; Creel & Christianson 2007; Křivan 2007). Tempering this view, it has been suggested that the impacts of prey trait changes with predation may differentially affect prey survival and/or reproduction depending on biotic conditions such as prey density (Křivan & Schmitz 2004; Trussell *et al.* 2006; Preisser *et al.* 2005; Wojdak & Luttbeg 2005). This issue has been examined more extensively in aquatic than in terrestrial systems. It has been suggested that this issue is less important in terrestrial systems (Schmitz *et al.* 2000; Chase 2000).

In the above reviews, numerous examples are cited of prey changing traits in the presence of predators; fewer examples demonstrate that trait changes affect prey survival and/or reproduction and very few studies examine whether the survival and/or reproductive effects of

trait changes vary with conditions such as prey density. We experimentally examined how behavioural responses of grasshoppers to bird predation affected grasshopper survival and reproduction at the National Bison Range (MT, USA) at different grasshopper densities.

Studies indicate that grasshoppers modify their behaviour (activity and height in the vegetation) in the presence of predators (spiders: Schmitz *et al.* 1997, Schmitz 2005; birds and lizards: Pitt 1999). At some locations, predation lowers grasshopper survival or produces trophic cascades; at other sites, predators do not affect survival or produce trophic cascades, whereas some sites exhibit both depending on the year (spiders: Schmitz 1993; Chase 1996; Schmitz *et al.* 1997; Oedekoven & Joern 2000; Danner & Joern 2003; birds: Joern 1986, 1992; Fowler *et al.* 1991; Bock *et al.* 1992; Branson 2005; birds and spiders: Belovsky & Slade 1993; lizards: Chase 1998). Finally, Schmitz *et al.* (1997) observed that the behavioural changes, induced by spiders, reduce spider predation and grasshopper survival by the same proportion due to diminished food intake. As a result, there was no net change in survival whereby restricted-nutrition mortality is substituted with direct-predatory mortality.

Grasshopper densities naturally vary among years at our study site by more than an order of magnitude. When we experimentally examined this range of densities, we found that at all densities, grasshoppers exhibited behavioural changes in response to the threat of avian predation that affected their survival and/or reproduction, even though birds were prevented from killing the grasshoppers. While behavioural changes did not vary over this wide range of grasshopper densities, the impact on survival and reproduction did vary with density due to intraspecific competition for food and a subsequent trade-off between survival and reproduction. Therefore, the effects of prey behavioural changes on prey performance varied with *per capita* food

availability. This type of variable response is generally overlooked when prey behavioural changes with predation are considered in how predation affects prey populations.

METHODS

We conducted field experiments in Palouse prairie at the National Bison Range (MT, USA) where the most common (> 80% of individuals) grasshopper (Orthoptera, Acrididae: *Melanoplus sanguinipes* Fabricius) regularly exhibits density dependent survival and reproduction in response to intraspecific competition for food plants (Belovsky & Slade 1995; Belovsky & Joern 1995; Schmitz 1993; Chase 1996; Branson 2003). These grasslands are dominated by grasses (> 90% of biomass: *Pseudoroegneria spicata* Pursh, *Pascopyrum smithii* Rybd., *Festuca idahoensis* Elmer, *F. scabrella* Torr., *Poa pratensis* L., *P. compressa* L. and *Bromus* spp.) and include a wide variety of dicots (e.g. *Achillea millefolium* L., *Balsamorhiza sagittata* Pursh, *Symphoricarpos occidentalis* Hook. and *Artemisia frigida* Willd.) (Belovsky 1986; Belovsky & Slade 1995). Predation on grasshoppers is great with a loss of up to 2% day⁻¹ and birds account for c. 65% of predation (Belovsky *et al.* 1990; Belovsky & Slade 1993).

Following methods from previous studies at the National Bison Range (see Belovsky & Slade 1995), *M. sanguinipes* survival was studied in the field using cages. Grasshopper populations were established in cages made of aluminium window screen with a basal area of 0.36 m² and a height of 0.7 m. The base of each cage was made of aluminium garden edging, which was buried in the ground. Each cage was secured with stakes to minimize wind damage. Cage tops were closed with clips, which permitted easy access. Cages were placed in a grid of five rows, with each row containing seven cages. Each cage was placed c. 2 m from surrounding cages, but exact position was based on similarity of vegetation abundance for the dominant grasses (*P. smithii* and *P. pratensis*). One grid of cages was enclosed within a tent (16 m × 20 m × 2 m high) constructed of aviary net (5 cm mesh). The tent created a 'no avian threat' area as birds were prevented from approaching cages because tent sides were 2 m from the nearest cage or from sitting on cages because the tent roof was at least 1 m above the cages and was not rigid, discouraging birds from perching. A second grid of cages was located 20 m away and provided an 'avian threat' area because cages were not enclosed by a tent, which allowed birds to feed around cages and frequently perch on them while consuming grasshoppers (see Fig. S1).

Cages were stocked with 2nd–3rd instar nymphs captured with sweep nets at an adjacent site. Grasshoppers were kept in terraria for 2 days prior to stocking and provided with *ad libitum* food collected from the site twice a day. Holding grasshoppers for 2 days prior to stocking minimized the use of injured individuals. Seven grasshopper densities were employed in the study (4, 6, 8, 10, 16, 24 and 32 per cage), spanning the range of nymph densities observed in the field (Belovsky & Slade 1995). Each density level had five replicate cages in the 'avian threat' and 'no avian threat' (three replicates in 2001) areas for a total of 70 cages (56 in 2001). Density levels were assigned to cages at random.

Cages were stocked in late June (± 3 days) and censused every week thereafter for 9 weeks (early July to September) by two observers. The observers also recorded each grasshopper's developmental stage and the number of dead bodies. Body counts provide a check on the current census in comparison to the previous census. We measured

survival as the proportion of individuals surviving from the original stocking number.

After the 9th week (early September), we collected the surviving females from cages and froze them for later determination of reproductive output using microscopic analysis of reproductive tissues (Bellinger & Pienkowski 1985; Sundberg *et al.* 2001). A female's reproductive tract consists of ovarioles that produce eggs. The number of ovarioles that are currently forming an egg (functional ovarioles) reflects current reproductive activity (Branson 2003). When an egg is produced, a white or yellowish ring known as a follicle resorption body remains at the base of the ovariole (Bellinger & Pienkowski 1985; Sundberg *et al.* 2001). The sum of follicle resorption bodies and functional ovarioles is a measure of a female's annual reproduction.

The study was repeated over 3 years (1999–2001). Each year within the same cages in the two 'threat' areas, cages were stocked anew with grasshoppers with a randomly assigned density as described above. Before stocking cages with grasshoppers, all cages were checked twice for other grasshoppers or invertebrates, which were removed from the cages. The 3-year data set were analysed using ANCOVA: where year (1999, 2000, 2001) and 'avian threat'/'no avian threat' were treated as blocks (see Fig. S1), density was treated as a covariate and the 9 weekly measures of survival constituted repeated measures, but reproduction had a single annual measure made after the 9th week.

Behavioural observations were made in 2001. An observer slowly approached each cage and then sat still beside the cage for 5 min before making observations. Based on preliminary observations, grasshoppers did not hop away upon the observer's slow approach, but either sat still or moved to the other side of the plant that they were perched upon. Furthermore, these grasshoppers appeared to recover if they were disturbed, because they generally resumed their previous activity within 5 min (Belovsky & Slade 1986), a common observation for grasshoppers (Uvarov 1977). During the 5 minutes of sitting still, the observer attempted to locate all of the grasshoppers known to be in the cage (previous cage count, see above), so that at the end of the 5 min, all individuals were scanned and their behaviour was instantaneously recorded (active = feeding or walking vs. resting = not feeding or moving). By using a set time period and protocol, any disturbance and observations among cages were standardized. The important measurement was not the absolute proportion of time active and height above ground-level, but whether there existed a difference between the 'threat' areas; this difference would include any difference in their 'willingness' to resume feeding or walking. Heights above ground-level (in vegetation or on cage) of grasshoppers were measured with a metre stick outside the cage after the behavioural scan sample was conducted.

Behavioural observations were made three times during 2001 (weeks 2, 4 and 6) for all 21 'no avian threat' cages and 21 of the 35 'avian threat' cages, where three of the five cages for each density level were randomly selected at the start of summer. Each cage was observed in the morning (09:00–12:00 h) and afternoon (12:00–15:00 h) over 2–4 days during the week by the same observer. Combining morning and afternoon observations, behaviour in each cage for each week was summarized as the average proportion of all individuals active and the average height above ground-level for all individuals. Repeated measure ANCOVA with 'threat' area as a block and inverse of density as a covariate was employed. Three of the initial 'avian threat' cages were lost during the summer and were replaced by randomly selecting from the remaining two unused cages of the same density for continued observation; however, because these three cages

were not observed over the entire summer, they were dropped from the repeated measure ANCOVA.

Long-term monitoring of plant biomass and grasshopper densities with and without avian predators (three 100 m² areas enclosed and unenclosed by avian net) has been conducted since 1985 at the site (Belovsky & Slade 1993). These data were used to assess whether avian predation controlled grasshopper populations or produced trophic cascades in the years studied.

Survival and activity data were logit transformed and height above ground-level was log transformed to normalize values. Inverse of cage density was employed to linearize ANCOVA relationships. Statistical analyses were conducted using SYSTAT 13.0 (Systat Software, Inc., Chicago, IL, USA).

RESULTS

The repeated measure ANCOVAs for grasshopper behaviour (average activity and average height above ground-level) did not indicate any density effect (for activity, $P < 0.60$ and for height, $P < 0.20$). Therefore, data were pooled across densities and repeated measure ANOVAs were employed. Grasshopper activity tended to increase over the summer (Fig. 1a) ($F = 5.17$; d.f. = 2,74; $P < 0.008$). Activity tended to be lower in the 'avian threat' area ($F = 5.69$; d.f. = 1,37; $P < 0.02$); however, this pattern tended to vary over the summer ($F = 2.41$; d.f. = 2,74; $P < 0.097$), where activity was greater in the 'no threat' area in weeks 2 and 6, but not 4. Grasshopper average height above ground-level (Fig. 1b) tended to increase over the summer in both 'threat' areas ($F = 2.52$; d.f. = 2,74; $P < 0.08$) and was always lower in the 'avian threat' area ($F = 6.07$; d.f. = 1,37; $P < 0.018$). Therefore, grasshopper behaviour changed similarly with the threat of avian predation irrespective of grasshopper density.

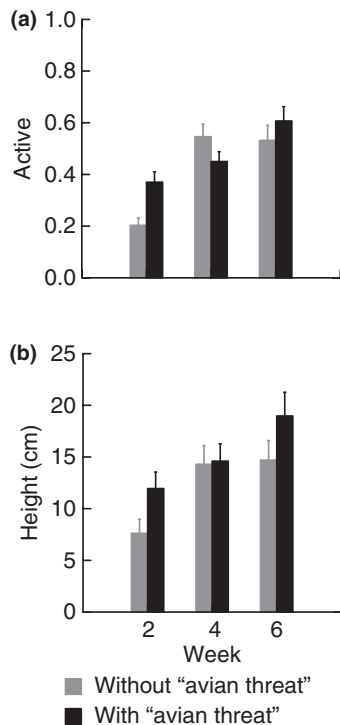


Figure 1 (a) Grasshopper activity (\pm SE) and (b) grasshopper height in the vegetation (\pm SE) with and without 'avian threat' in relation to week during the summer.

Survival averaged over the 3 years appeared to respond differently to 'threat' at low (4–8 per cage: Fig. 2a), intermediate (10 per cage: Fig. 2b) and high (16–32 per cage: Fig. 2c) density levels. Therefore, repeated measure ANCOVAs (inverse of density as covariate, year and 'threat' as blocks) were conducted separately for density levels. For each density level, homogeneity of slope was indicated (insignificant inverse of density \times year and inverse of density \times 'threat'). At all density levels, year and year \times 'threat' effects were not significant (low density: $P < 0.28$ and $P < 0.67$, respectively; intermediate density: $P < 0.91$ and $P < 0.60$, respectively; high density: $P < 0.46$ and $P < 0.39$, respectively), so data across all years were pooled.

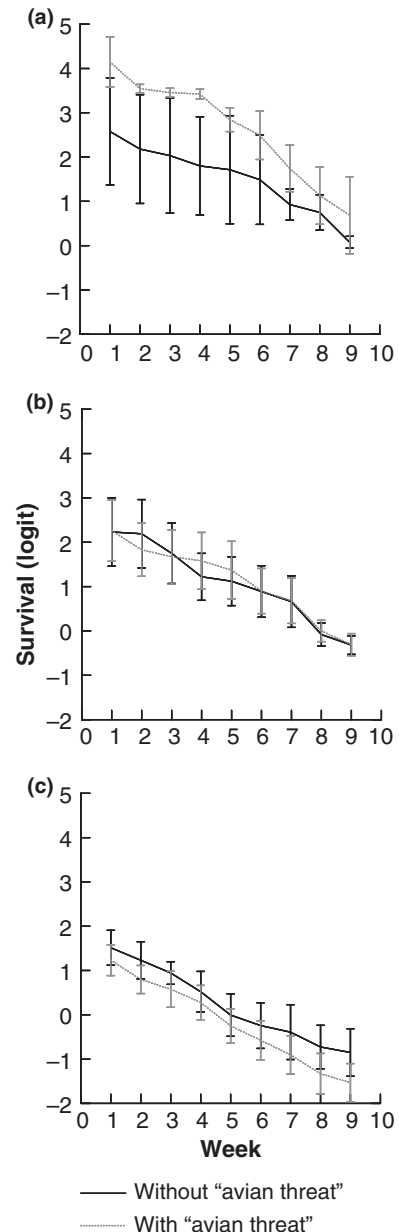


Figure 2 Logit transform of the proportion of grasshoppers surviving (\pm SE) measured with and without 'avian threat' in relation to week during the summer for all 3 years of the study. Data are presented separately for (a) lower densities (4, 6 or 8 per cage), (b) the intermediate density (10 per cage) and (c) the highest densities (16, 24 and 32 per cage).

At low densities, survival was greater with 'avian threat' ($F = 4.09$; d.f. = 1,79; $P < 0.04$) and decreased with density ($F = 6.72$; d.f. = 1,79; $P < 0.01$) and over the summer ($F = 1.43$; d.f. = 8,632; $P < 0.18$). At the intermediate density, survival did not differ with 'threat' ($F = 0.003$; d.f. = 1,25; $P < 0.96$), but did decrease over the summer ($F = 16.03$; d.f. = 8,200; $P < 0.00001$). At high densities, survival was lower with 'avian threat' ($F = 6.89$; d.f. = 1,79; $P < 0.01$) and decreased with density ($F = 32.52$; d.f. = 1,79; $P < 0.000001$) and over the summer ($F = 17.22$; d.f. = 8,632; $P < 0.00001$). As expected, survival was density dependent decreasing with density (Belovsky & Slade 1995) in both 'threat' areas, but the effect of 'threat' on survival differed with density. Grasshopper survival was greater with 'threat' at low densities and lower with 'threat' at high densities (Fig. 2).

Per capita reproduction (Fig. 3a) did not appear to respond differently to 'threat' at different density levels as observed with survival, so that a single repeated measure ANCOVA (inverse of density as covariate, year and 'threat' as blocks) was conducted and homogeneity of slopes was indicated (insignificant inverse of density \times year and inverse of density \times 'threat'). *Per capita* reproduction (Fig. 3a) was less in the 'avian threat' area ($F = 9.38$; d.f. = 1,173; $P < 0.002$), decreased with density ($F = 83.63$; d.f. = 1,173; $P < 0.000001$) and unlike survival, varied among years ($F = 12.41$; d.f. = 2,173; $P < 0.000009$). The block design should have no interaction between year \times 'threat' and none was observed ($P < 0.53$).

Total reproduction (adult females \times *per capita* reproduction: Fig. 3b) should respond differently to 'threat' at different density levels as observed for survival, because adult female numbers depend on

survival. Therefore, ANCOVAs (inverse of density as covariate, year and 'threat' as blocks) were conducted at various density 'breakpoints' to determine if total reproduction responded to 'threat' differently with density level. For all density ranges, homogeneity of slope was indicated (insignificant inverse of density \times year and inverse of density \times 'threat'). A significant 'threat' effect did not emerge until densities exceeded 10 per cage ($F = 4.20$; d.f. = 1,76; $P < 0.04$), the 'breakpoint' where survival also shifted. Total reproduction declined with density ($F = 6.73$; d.f. = 1,76; $P < 0.01$), as expected (Belovsky & Slade 1995). At densities ≤ 10 , there were no significant response to 'threat' ($F = 1.18$; d.f. = 1,91; $P < 0.48$) and no significant effect of density ($F = 1.29$; d.f. = 1,91; $P < 0.30$). Total reproduction at both density levels varied with year, as expected with *per capita* reproduction (≤ 10 : $F = 8.86$; d.f. = 2,91; $P < 0.0003$; > 10 : $F = 15.82$; d.f. = 2,76; $P < 0.000002$) and the block design should have no interaction between year \times 'threat' and none was observed (respectively, $P < 0.22$ and $P < 0.49$).

From long-term monitoring of areas with and without bird exclosures at our site, plant biomass did not differ between areas with and without birds from 1999 to 2001 (paired *t*-test: $t = 0.12$, d.f. = 8, $P_{\text{one-sided}} < 0.46$), indicating an absence of a trophic cascade. Grasshopper densities differed counter-intuitively between areas, as densities were greater with birds (paired *t*-test: $t = 1.98$, d.f. = 8, $P_{\text{one-sided}} < 0.04$). Paired *t*-tests were used because areas with and without birds were matched and one-sided tests were employed because *a priori* expectation was for plant biomass to be greater and grasshopper density to be less with birds (Belovsky & Slade 1993).

DISCUSSION

The potential for prey to change their traits in the presence of predators may diminish prey survival and reproduction, irrespective of predatory killing, by reducing resource acquisition and/or increasing demand (physiological stress), thereby enhancing top-down control of populations and food webs (Peacor & Werner 1997, 2001; Werner & Peacor 2003; Schmitz *et al.* 1997, 2000; Chase 2000; Nelson *et al.* 2004; Křivan & Schmitz 2004; Preisser *et al.* 2005; Wojdak & Luttbeg 2005; Trussell *et al.* 2006; Creel & Christianson 2007; Křivan 2007; Preisser & Bolnick 2008a,b; Sheriff *et al.* 2009; Walzer & Schausberger 2009; Hawlena & Schmitz 2010). Our experiment with grasshoppers and the 'threat' of avian predation illustrates this potential. However, while grasshopper behavioural responses to predation 'threat' were invariant with density, the effect of this behavioural response on their survival and reproduction did vary: enhancing survival and maintaining reproduction at low densities, whereas decreasing survival and reproduction at high densities. These contextual responses with prey density and resource availability have only recently been considered (e.g. Barton & Schmitz 2009; Dupuch *et al.* 2009; Ferrari *et al.* 2009; Hebblewhite & Merrill 2009; Preisser *et al.* 2009). We believe that contextual responses in our system arise from intraspecific competition for food.

Behavioural responses by grasshoppers were only due to predation 'threat', because grasshoppers could not be killed by birds, but were aware of bird presence in the 'avian threat' area, as birds sat on cages while consuming grasshoppers caught outside cages (43 avian faeces containing grasshoppers found on 'avian threat' cages vs. 2 on 'no threat' cages: $\chi^2 = 36.1$, d.f. = 1, $P < 0.0001$). Avian predation is greater on grasshoppers that are more active or located higher in vegetation (Belovsky *et al.* 1990), and hence, grasshoppers should

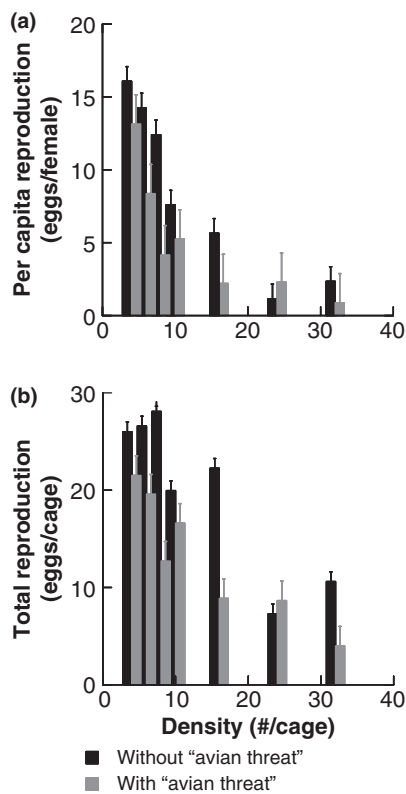


Figure 3 (a) *per capita* reproduction (\pm SE) and (b) total reproduction (product of surviving adult females and *per capita* reproduction) (\pm SE) are presented with grasshopper density and with and without 'avian threat' for all 3 years of the study.

reduce activity and remain low in vegetation with avian predation 'threat', as observed except for activity in week 4.

The behavioural responses in week 4 that were opposite or reduced from expectation may have arisen due to the high proportion of grasshoppers moulting into adults at this time in cages in the absence of avian 'threat', because prior to moulting, individuals strongly curtail activity. Between week 4 and 5, 60% of the nymphs moulted into adults in cages in the absence of avian 'threat', whereas 44% moulted in cages with avian 'threat' ($\chi^2 = 21.52$, d.f. = 1, $P < 0.000003$); while the proportion moulting was comparable between the two 'threat' areas prior to this (21% for both). Moulting in the absence of avian 'threat' should occur faster, as the grasshoppers are feeding more and consequently, growing faster.

Grasshopper activity in the 'avian threat' cages from 09:00 h to 15:00 h was 42.5% (SE = 3.37%) of individuals; this activity compares favourably with 39.6% observed for 'free-roaming' individuals with birds at our site (Belovsky & Slade 1986), so that behaviour did not appear to be affected by cages. Furthermore, behavioural responses to predation 'threat' should diminish over the summer as food becomes scarce due to drought and consumption and as individuals become larger requiring more food. Under these conditions, grasshoppers can nutritionally less afford to reduce activity or hide, but must spend more time feeding to meet nutritional requirements.

As grasshopper populations at our site are food-limited (Belovsky & Slade 1995), *per capita* reproduction and survival should decline with density, as observed. In addition, reduced activity and restricted use of higher vegetation with predation 'threat' should exacerbate food-limitation. While *per capita* reproduction differed among years as food availability varied and always was less in the 'threat' area, survival did not vary with year and responded differently with 'threat': increasing at low density levels and decreasing at high density levels. This finding suggests a trade-off where *per capita* reproduction is reduced to maintain survival.

At low densities, as activity and use of higher vegetation are reduced with predation 'threat', grasshoppers maintain high survival by trading-off reproduction for survival, which can occur because competition for food is not great. Competition may be further reduced as lower activity with predation 'threat' reduces consumption and thereby, food depletion. Consequently, total reproduction (adult females \times *per capita* reproduction), the foundation for next year's population in this univoltine grasshopper, is unchanged with predation 'threat' as reduced *per capita* reproduction is compensated for by more adult females due to better survival, as observed.

At high densities, food competition is greater, so a trade-off between survival and reproduction cannot compensate for reduced activity and use of higher vegetation with predation 'threat'. Now survival and *per capita* reproduction both decline. Consequently, total reproduction (adult females \times *per capita* reproduction), the foundation for next year's population in this univoltine grasshopper, must decline, as observed.

The above trade-off creates the density dependent context for the different responses in survival and total reproduction despite invariant behavioural responses to predation 'threat'. This concept also explains why we did not observe field grasshopper populations declining or exhibiting a trophic cascade with predation at our study site. In all 3 years of our study, grasshopper densities were low ($c.$ 6–8 per cage), within the density range where behavioural changes with predation 'threat' increased survival and have no effect on total reproduction.

At observed field densities (see above), our experimental results indicated that survival increased by 13%, which was consistent with the observed 17.6% (SE \pm 2.8) increase with predators observed in our monitoring of field populations with and without avian predators.

We find that behavioural responses to predation risk do not always enhance top-down control of populations or food webs, including trophic cascades. Instead, behavioural responses to predation 'threat' may or may not enhance top-down control of a population depending upon biotic factors such as prey density or *per capita* food availability (Preisser *et al.* 2009). The potential for this type of contextual response to trait changes with predation have been reported elsewhere (Borer *et al.* 2005; Wojdak & Luttbeg 2005; Barton & Schmitz 2009; Dupuch *et al.* 2009; Ferrari *et al.* 2009; Hebblewhite & Merrill 2009; Sheriff *et al.* 2009) and led some (Křivan 2007; Okuyama & Bolker 2007) to caution against inferring a general increase in top-down controls when traits are observed to change with predation. Our study experimentally supports these cautions.

ACKNOWLEDGEMENTS

We thank the National Bison Range for permitting this study and financial support provided by the National Science Foundation, the United States Department of Agriculture and the Utah State University Ecology Center. Under supervision of D. Shetrone, E. Bartner, R. Rosa Garcia, E. Laws, C. Shetrone and T. Wright assisted.

REFERENCES

- Barton, B.T. & Schmitz, O.J. (2009). Experimental warming transforms multiple predator effects in a grassland food web. *Ecol. Lett.*, 12, 1317–1325.
- Bellinger, R.G. & Pienkowski, R.L. (1985). Non-random resorption of oocytes in grasshoppers (Orthoptera: Acrididae). *Can. Ent.*, 117, 1067–1069.
- Belovsky, G.E. (1986). Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia*, 70, 35–52.
- Belovsky, G.E. & Joern, A. (1995). The dominance of different regulating factors for rangeland grasshoppers. In: *Population Dynamics: New Approaches and Synthesis* (eds Cappuccino, N. & Price, P.). Academic Press, New York, pp. 359–386.
- Belovsky, G.E. & Slade, J.B. (1986). Time budgets of grassland herbivores: body size similarities. *Oecologia*, 70, 53–62.
- Belovsky, G.E. & Slade, J.B. (1993). The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos*, 68, 193–201.
- Belovsky, G.E. & Slade, J.B. (1995). Dynamics of some Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. *Oecologia*, 101, 383–396.
- Belovsky, G.E., Slade, J.B. & Stockhoff, B. (1990). Susceptibility to predation for different grasshoppers: an experimental study. *Ecology*, 71, 624–634.
- Bock, C.E., Bock, J.H. & Grant, M.C. (1992). Effects of bird predation for different grasshoppers: an experimental study. *Ecology*, 73, 1706–1717.
- Bolker, B., Holyoak, M., Křivan, V., Rowe, L. & Schmitz, O. (2003). Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, 84, 1101–1114.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B. *et al.* (2005). What determines the strength of a trophic cascade? *Ecology*, 86, 528–537.
- Branson, D. (2003). Effects of a parasitic mite on life-history variation in two grasshopper species. *Evol. Ecol. Res.*, 5, 397–409.
- Branson, D. (2005). Direct and indirect effects of avian predation on grasshopper communities in northern mixed grass prairie. *Env. Ent.*, 34, 1114–1121.
- Chase, J.M. (1996). Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos*, 77, 495–506.
- Chase, J.M. (1998). Central-place forager effects on food web dynamics and spatial pattern in northern California meadows. *Ecology*, 79, 1236–1245.

- Chase, J.M. (2000). Are there real differences among aquatic and terrestrial food webs? *Trends Ecol. Evol.*, 15, 408–412.
- Creel, S. & Christianson, D. (2007). Relationships between direct predation and risk effects. *TREE*, 23, 194–201.
- Danner, B.J. & Joern, A. (2003). Resource mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia*, 137, 352–359.
- Dupuch, A., Dill, L.M. & Magnan, P. (2009). Testing the effects of resource distribution and inherent habitat riskiness on simultaneous habitat selection by predators and prey. *Anim. Beh.*, 78, 705–713.
- Ferrari, M.C.O., Sih, A. & Chivers, D.P. (2009). The paradox of risk allocation: a review and prospectus. *Anim. Beh.*, 78, 579–585.
- Fowler, A.C., Knight, R.L., George, T.L. & McEwen, L.C. (1991). Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology*, 72, 1775–1781.
- Hawlena, D. & Schmitz, O.J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am. Nat.*, 176, 537–556.
- Hebblewhite, M. & Merrill, E.H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, 90, 3445–3454.
- Hunter, M.D., Varley, G.C. & Gradwell, G.R. (1997). Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proc. Natl. Acad. Sci. USA*, 94, 9176–9181.
- Joern, A. (1986). Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos*, 46, 243–249.
- Joern, A. (1992). Variable impact of avian predation on grasshopper assemblages in sandhills. *Oikos*, 64, 458–463.
- Kiivan, V. (2007). The Lotka-Volterra predator-prey model with foraging-predation risk trade-offs. *Am. Nat.*, 170, 771–782.
- Kiivan, V. & Schmitz, O.J. (2004). Trait and density mediated indirect interactions in simple food webs. *Oikos*, 107, 239–250.
- Nelson, E.H., Matthews, C.E. & Rosenheim, J.A. (2004). Predators reduce prey population growth by inducing changes in prey behavior. *Ecology*, 85, 1853–1858.
- Oedekoven, M.A. & Joern, A. (2000). Plant quality and spider predation affects grasshoppers (Acrididae): food-quality-dependent compensatory mortality. *Ecology*, 81, 66–77.
- Okuyama, T. & Bolker, B.M. (2007). On quantitative measures of indirect interactions. *Ecol. Lett.*, 10, 264–271.
- Peacor, S.D. & Werner, E.E. (1997). Trait-mediated indirect interactions in a simple aquatic food web. *Ecology*, 78, 1146–1156.
- Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA*, 98, 3904–3908.
- Pitt, W.C. (1999). Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation. *Evol. Ecol.*, 13, 499–515.
- Preisser, E.L. & Bolnick, D.I. (2008a). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE*, 3, e2465.
- Preisser, E.L. & Bolnick, D.I. (2008b). When predators don't eat their prey: non-consumptive predator effects on prey dynamics. *Ecology*, 89, 2414–2415.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.
- Preisser, E.L., Bolnick, D.I. & Grabowski, J.H. (2009). Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecol. Lett.*, 12, 315–323.
- Schmitz, O.J. (1993). Trophic exploitation in grassland food chains: simple models and a field experiment. *Oecologia*, 93, 327–335.
- Schmitz, O.J. (2005). Behavior of predators and prey and links with population level processes. In: *Ecology of Predator-Prey Interactions* (eds Barbosa, P. & Castellanos, I.). Oxford University Press, Oxford, pp. 256–278.
- Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, 78, 1388–1399.
- Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.*, 155, 141–153.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009). The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hare. *J. Anim. Ecol.*, 78, 1249–1258.
- Sundberg, S.V., Luong-Skovmand, M.H. & Whitman, D.W. (2001). Morphology and development of oocyte and follicle resorption bodies in the lubber grasshopper, *Romalea microptera* (Beauvois). *J. Orthop. Res.*, 10, 39–51.
- Trussell, G.C., Ewanchuk, P.J. & Matassa, C.M. (2006). Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecol. Lett.*, 9, 1245–1252.
- Uvarov, B.P. (1977). *Grasshoppers and Locusts: A Handbook of General Acridology. Volume 2: Behavior, Ecology, Biogeography, Population Dynamics*. Centre for Overseas Pest Research, London, 613 pp.
- Walzer, A. & Schausberger, P. (2009). Non-consumptive effects of predatory mites on thrips and its host plant. *Oikos*, 118, 934–940.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Wojdak, J.M. & Luttbeg, B. (2005). Relative strengths of trait-mediated and density-mediated indirect effects of a predator vary with resource levels in a freshwater food chain. *Oikos*, 111, 592–598.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Field experimental design along with sampling protocol.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Tim Benton

Manuscript received 20 December 2010

Manuscript accepted 22 December 2010