

Observations on non-additive predation: birds and grasshoppers

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ABSTRACT

Background: Classic predator–prey theory assumes that predatory mortality is additive with other sources of mortality, but predatory mortality can be non-additive. If predators preferentially kill individuals already ‘doomed’ from other mortality causes, then predation can be less than additive. If predators preferentially kill individuals more likely to survive, then predation can be greater than additive. In either case, to be non-additive, predation must modify other causes of mortality such as intraspecific competition, decreasing it in the former case and increasing it in the latter. Non-additive predation also can modify selective pressures of predation and is seldom considered except when prey are much larger than their predators.

Question: Can non-additive predation be observed in the most common type of predator–prey system (prey much smaller than their predators) where this is considered very unlikely?

Organisms: Two sympatric grasshoppers and their avian predators.

Field site: National Bison Range, Montana, USA.

Methods: Field experiments to determine: (1) whether better foraging individuals survive longer in the absence of predators or if they die from non-predatory causes in the presence of predators; (2) whether predators preferentially kill better or poorer foragers; and (3) how predators affect prey populations.

Conclusions: Both grasshoppers exhibit intraspecific competition with better foragers surviving longer. Both experience high predation rates, but their populations respond differently to predation. One increased with predation, due to the non-additive effect of the predators preferentially killing poor foragers, and thereby diminishing intraspecific competition, which counters predatory mortality. The other population declined more than expected with predation due to the non-additive effect of the predators preferentially killing good foragers, and thereby intensifying intraspecific competition.

Keywords: birds, compensatory mortality, foraging, grasshoppers, non-additive mortality, predation.

INTRODUCTION

A common assumption in classic predator–prey ecology is that predation always reduces prey populations and the underlying mathematical theory, such as the Lotka–Volterra model and its variants, assumes that predation mortality is additive with other sources of mortality (e.g. Taylor, 1984; Stiling, 1992; Getz, 1998; Case, 2000). This assumption not only is the foundation for much of predator–prey theory, but also the theory behind classic consumer–resource and food web dynamics (e.g. Hairston *et al.*, 1960; Slobodkin *et al.*, 1967; Pimm, 1982). However, predation often produces unanticipated effects on prey populations; for example, the prey population is increased, unchanged or even affected more than expected by predators (Sih *et al.*, 1985).

Unanticipated effects might emerge if predation mortality is non-additive. Non-additive effects can emerge if predation modifies other forms of mortality, for example decreases or increases intraspecific competition (Errington, 1946a, 1946b, 1956; Osenberg and Mittlebach, 1996). Non-additive effects have been discussed using graphical predator–prey models (Rosenzweig and MacArthur, 1963), and in models where prey biomass, rather than prey numbers, and categories of prey individuals that differ in behaviour, etc., are examined (Getz, 1993, 1998). The non-additive effects referred to here are the combination of predatory and other forms of mortality, not how predatory mortality changes with single predators versus multiple predators (Crowder *et al.*, 1997; Pitt, 1999; Schmitz, 2007).

Predator and prey behaviours may influence non-additive predation mortality in two ways. First, predators may preferentially kill already ‘doomed’ individuals, that is less fit individuals that would inevitably die from other causes (e.g. starvation, disease, etc.) are selectively killed by predators. Errington (1946a, 1946b, 1956) first argued this when working with wildlife species where the predator is of comparable or smaller body size than its prey. His rationale was that these predators must attack weaker (young, old, sick or infirm) individuals to be able to subdue them. On the other hand, in the absence of predation, individuals who are more fit because they forage or mate more may be preferentially killed in the presence of predators. In this case, greater prey activity may increase exposure to predation and the ability of predators to kill prey is not inhibited by prey vigour, as might be expected if prey are easily subdued because they are smaller than their predators. Obviously, these individual-level (behavioural) mechanisms can produce very different selection pressures on prey: potentially removing less fit individuals in the former case and otherwise more fit individuals in the latter case.

For the above mechanisms to produce non-additive predation, other forms of mortality must also be modified as a result of predation. For example, a reduction of current prey numbers by predation may reduce intraspecific competition, which can lead to better survival and reproduction of remaining individuals (Errington, 1946a, 1946b, 1956; Osenberg and Mittlebach, 1996). This is especially possible if predators preferentially kill already ‘doomed’ individuals. In this case, future prey numbers with predators might remain unchanged or even increase compared with numbers in the absence of predation. Another possibility for non-additive predation emerges if predation increases intraspecific competition. This might occur if predators selectively remove individuals that are better competitors so that the poorer competitors survive longer, thus increasing intraspecific competition. In this case, future prey numbers with predators might decrease more than expected when compared with numbers in the absence of predation.

Non-additive predatory mortality has rarely been investigated. When examined, emphasis has been on larger-bodied prey and predators. In part this arises because

Errington (1946a, 1946b, 1956), who identified the potential for non-additive predatory mortality, was a wildlife biologist, which created a tradition in this field. But also, the 'health' of large-bodied prey is easier to study than that of small-bodied prey. Therefore, evidence of non-additive predatory mortality being compensatory with other mortality exists for larger-bodied prey when young, old or malnourished individuals are preferentially killed (e.g. McCullough, 1979; Taylor, 1984; Mech and DelGiudice, 1985; Shaw, 1985; Cook *et al.*, 2001a, 2001b; Husseman *et al.*, 2003). However, most studies assume additive predatory mortality, especially for small prey that have larger predators (e.g. insects with insectivorous birds or zooplankton with fish), because large predators can easily capture even the 'healthiest' small prey. One exception is small prey that modify their morphology when predators are present [e.g. spined vs. unspined zooplankton morphs (Harvell, 1990)].

We examined the potential for non-additive predatory mortality in a system where prey (grasshoppers: Orthoptera, Acrididae) are very small relative to their predators (birds and rodents). We studied two grasshopper species (*Melanoplus sanguinipes* and *Arphia pseudonietana*) at the National Bison Range, Montana. We suspected the potential for non-additive predatory mortality in this system, because while both species exhibit high mortality due to avian predation [birds account for >65% of predation (Belovsky *et al.*, 1990)], one species (*M. sanguinipes*) actually increases in abundance with avian predators, while *A. pseudonietana* decreases in abundance (Belovsky and Slade, 1993). We conducted a series of field experiments to examine how non-additive predatory mortality might occur in this system.

First, because we know that survival of both species in the absence of predators is density dependent due to intraspecific competition for food (Belovsky and Slade, 1995, unpublished data; Chase 1996), we hypothesized that better foraging individuals might survive better in the absence of avian predators or survive longer if they are not killed by predators. Second, we hypothesized that avian predators might produce non-additive effects if they preferentially kill better or poorer foraging individuals. Third, we hypothesized that the two grasshopper populations would continue to exhibit the previously observed different responses to predation.

We found that better foraging *M. sanguinipes* individuals survive better with or without predators present; predators selectively killed poor foraging individuals; and this species' densities increased with predators present. On the other hand, we found that better foraging *A. pseudonietana* individuals that die from causes other than predation survive longer, but overall better foragers survive less well with predators present. This is because predators selectively killed better foraging individuals, and this species' densities decreased with predators more than expected from the predation rate alone. Therefore, contrary to the expectation of a large part of classic predator-prey theory that assumes that predatory mortality is additive with other sources of mortality, the two grasshoppers exhibited opposite non-additive predatory effects. We suggest that the potential for non-additive effects on predatory mortality might perhaps be more common than frequently considered.

METHODS

We conducted the study at the National Bison Range (Lake County, Montana, USA). Experiments were conducted on 4 ha at ~800 m elevation, where the vegetation was dominated (>85% of biomass) by two grasses, *Poa pratensis* and *Pascopyrum smithii*. *Melanoplus sanguinipes* is a medium-sized grasshopper (391 mg adults) and the most

common species (>80% by numbers). *Arphia pseudonietana* is the most common (~5% by numbers) large-sized grasshopper (555 mg adults). More experiments could be conducted with *M. sanguinipes* because of its abundance and smaller body size.

Two experiments that we conducted required *a priori* knowledge of each individual grasshopper's feeding performance. We measured feeding by individuals of each grasshopper species under similar outdoor conditions during August 1990 and 1991 (air temperature 24–27°C and diffuse sunlight) (see Belovsky *et al.*, 1996). Adults caught at the study site were starved for 3 h, weighed, and used in feeding trials. We placed each adult in a 0.5-litre jar covered with screen and containing four pieces (each 125 mm²) of readily eaten and measurable (large leaf area) plants (two of grass, *Dactylis glomerata*, and two of forb, *Taraxacum officinale*). Each plant piece was suspended on a pin with the four pieces forming a square (8 × 8 cm), where pieces from the same species were on the diagonal. More food was presented than could be consumed by an adult in the 20-min trial. At the end of a trial, we measured the plant area consumed by an adult. We converted area consumed (mm²) to mass (mg dry mass) using a mass-to-area constant measured for each plant species. To standardize consumption among individuals that differed in body size, we divided mass consumed by the adult's body mass (g). Foraging performances were repeatable among the same individuals in several trials [$r = 0.87$ (Belovsky *et al.*, 1996)].

The experiments requiring knowledge of each individual's foraging performance were as follows:

Experiment 1: Survival of individuals of known foraging performance

(a) Without predators

In August 1990, we measured the survival of *M. sanguinipes* individuals of known foraging performance in field cages, which eliminated predation. In total, 150 *M. sanguinipes* adults (75 males, 75 females) of known foraging performance (see above) were stocked at two densities (10 and 5 per cage). Twenty cages (0.1 m² area: 0.32 × 0.32 × 0.90 m) constructed of aluminium window screen and garden edging were buried in the ground and supported with two wooden stakes. Cages were placed 2 m apart in a 4 × 5 grid and density treatments (10 cages each) were randomly assigned. These methods are described in Belovsky and Slade (1995), and have been used by others (e.g. Joern and Klucas 1993; Schmitz, 1993; Chase, 1996). We identified individuals in each cage by placing dots of fingernail polish on the pronotum of each grasshopper, and we censused them every 2 days for 50 days. The rank number of days that an individual survived was related to its known rank foraging performance among all individuals in the cage using Spearman rank correlation. *Arphia pseudonietana* individuals were not used because sufficient numbers could not be caught.

(b) With predators

We measured survival in August 1991, using 50 adults (25 males, 25 females) of each grasshopper species whose foraging performance was known. We held adults in captivity no more than 3 days to conduct the feeding trials, during which time they were fed an *ad libitum* mix of plants from the study area when not in their feeding trial. When we completed feeding trials for all adults, we placed each adult randomly at the site on a 0.5-m tether of monofilament. We examined adults every 6 h during daylight to determine whether they had been killed by a predator, died from other causes or survived (see Belovsky *et al.*, 1990). We

monitored tethered adults for 5 days at a location and then we moved them to a new location if they were still alive. This prevented depletion of available food that was within reach of the tether (Belovsky and Slade, 1995). We previously demonstrated that tethering does not impact grasshopper behaviour, other than to reduce their ability to move long distances and we independently assessed escape success from avian predators using captive birds in field aviaries (Belovsky *et al.*, 1990). Days-surviving for each grasshopper was related to their foraging ability (continuous variable) using analysis of covariance (ANCOVA), where sex, species, and mortality agent (predation vs. other) were categorical variables.

Experiment 2: Preferential killing by avian predators

We measured preferential killing by predators using the individuals in Experiment 1b. Individuals of each species were designated as poor (lowest 50%) or good (highest 50%) foragers based upon their performance in the feeding trials. The proportion of individuals killed by predators could be determined and compared between foraging categories using χ^2 contingency tables.

Experiment 3: Grasshopper field densities with and without predation

Using methods developed by Joern (1986), we compared three 100-m² areas that excluded birds using aviary netting with three matched 100-m² control areas that allowed birds access. We erected exclosures in early June 1991. During a mid-September day, we censused grasshoppers in all controls and exclosures by surrounding each area with nylon screen to prevent grasshoppers from escaping or to force them to fly over the screen so we could count them and identify them to species. We then caught all grasshoppers in each area during four periods of 15 min, which provided two estimates of grasshopper numbers – total caught and catch-effort (Southwood and Henderson, 2000). We identified the captured grasshoppers to species, sex, and developmental stage. Because the expectation was that predation reduces grasshopper numbers (i.e. number in exclosure greater than matched control), we used one-sided paired *t*-tests.

RESULTS

Experiment 1: Survival of individuals of known foraging performance

(a) Without predators

Melanoplus sanguinipes individuals survive longer the better that they forage. With 10 adults per cage, rank foraging performance was positively correlated with rank time to death (Spearman rank correlation = 0.54, $N = 56$, $P < 0.000026$), whereas with 5 adults per cage, a weaker positive correlation emerged (Spearman rank correlation = 0.32, $N = 34$, $P < 0.14$). Therefore, *M. sanguinipes* individuals survived longer if they foraged relatively better than other population members, and this relationship was stronger as density increased.

(b) With predators

An individual's survival time was also related to its foraging performance, but there were differences with mortality cause between the two species and sexes. Since slopes differed

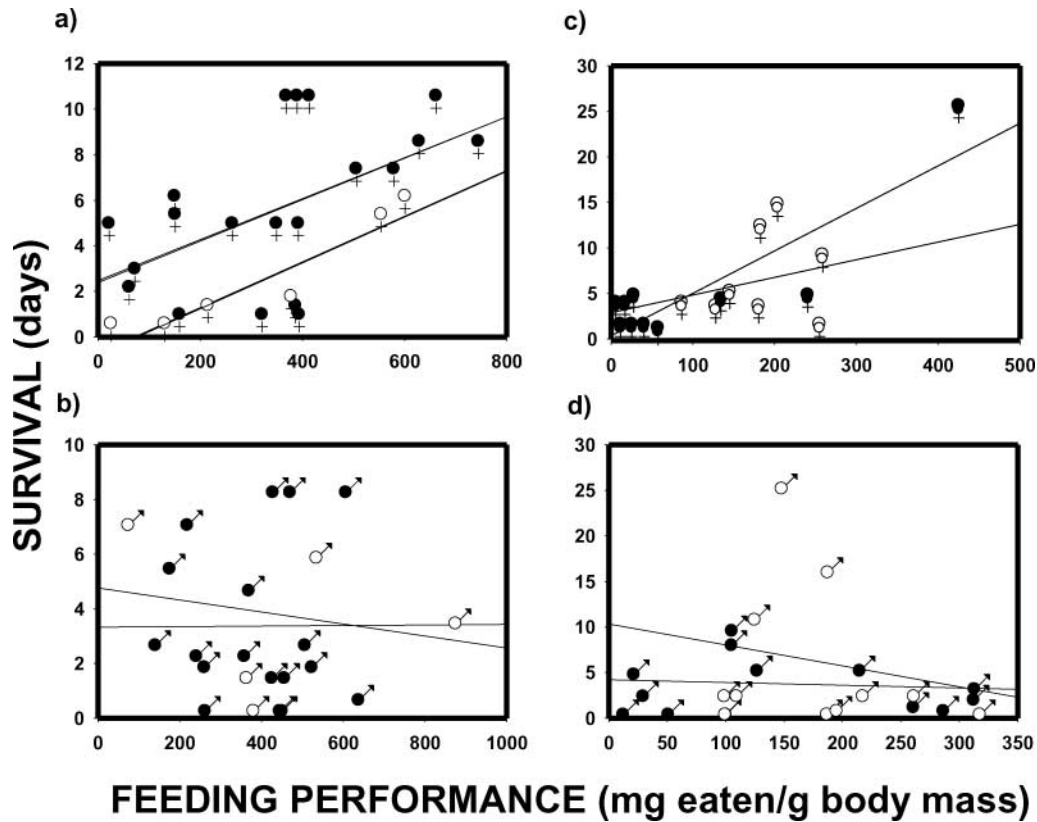


Fig. 1. Survival times measured for *M. sanguinipes* (a, females; b, males) and *A. pseudonietana* (c, females; d, males) individuals of known feeding performance that died from other causes (solid symbols) and predation (open symbols) in Experiment 1b.

between the sexes (homogeneity of slopes in ANCOVA: $F_{1,84} = 5.18$, $P < 0.03$) and tended to differ between species (homogeneity of slopes in ANCOVA: $F_{1,84} = 1.89$, $P < 0.17$), we conducted separate regression analyses by species and sex. Females of both species dying from non-predatory causes exhibited a positive relationship between survival time and foraging performance (*M. sanguinipes*: $r = 0.55$, $N = 20$, $P < 0.001$; *A. pseudonietana*: $r = 0.87$, $N = 10$, $P < 0.001$; Fig. 1a,c). A positive relationship was also observed for *M. sanguinipes* females killed by predators ($r = 0.94$, $N = 6$, $P < 0.005$; Fig. 1a), but not for *A. pseudonietana* females ($r = 0.24$, $N = 8$, $P < 0.56$; Fig. 1c). Males of both species exhibited no relationship between survival and foraging performance regardless of cause of death (*M. sanguinipes*: other, $r = 0.005$, $N = 19$, $P < 0.98$; predation, $r = 0.22$, $N = 5$, $P < 0.72$; *A. pseudonietana*: other, $r = 0.11$, $N = 13$, $P < 0.71$; predation, $r = 0.20$, $N = 11$, $P < 0.56$; Fig. 1b,d). Consequently, *M. sanguinipes* females with better foraging performance survived longer, regardless of cause of death, but for *A. pseudonietana* females this was true only for non-predatory mortality. Male survival of either species, regardless of mortality cause, was unrelated to foraging performance.

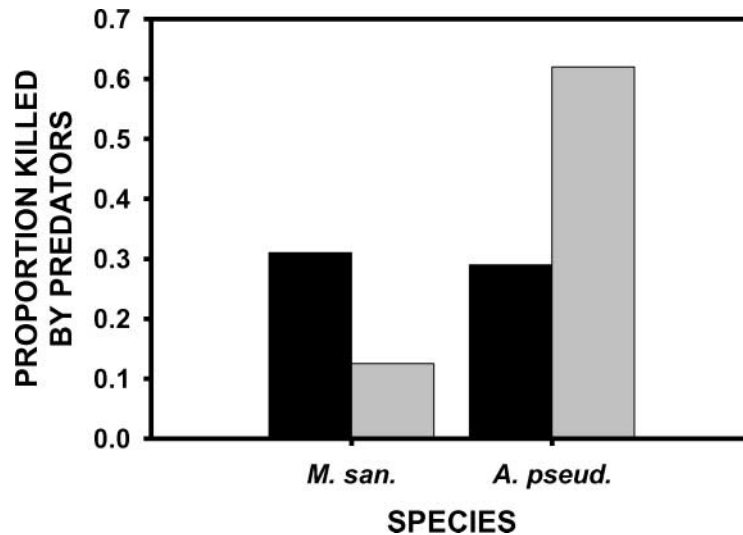


Fig. 2. Proportion of individuals killed by predators based on feeding performance (black = poorer half and grey = better half) in Experiment 2.

Experiment 2: Preferential killing by avian predators

Preferential killing by predators was observed to differ between species. Avian predators tended to preferentially kill poor foraging *M. sanguinipes* individuals ($\chi^2 = 2.42$, d.f. = 1, $P_{\text{one-sided}} < 0.06$; Fig. 2). In contrast, good foraging *A. pseudonietana* individuals were preferentially killed by predators ($\chi^2 = 4.71$, d.f. = 1, $P_{\text{one-sided}} < 0.01$; Fig. 2). Therefore, predators appeared to select individuals of different foraging performance (good vs. poor) between the two grasshopper species.

Experiment 3: Grasshopper field densities with and without predation

Grasshopper field densities of the two species in 1991 responded differently with and without predation. *Melanoplus sanguinipes* was not predator-limited, because its numbers with avian predators (47.67, s.d. = 13.80, $N = 3$) were not less than without avian predators (41.67, s.d. = 12.86, $N = 3$); in fact, its numbers were significantly greater with predators (paired t -test: $t_2 = 10.39$, $P_{\text{one-sided}} < 0.004$). Predator limitation was indicated for larger-bodied grasshoppers like *A. pseudonietana*, because large-bodied species with avian predators (2.33, s.d. = 2.08, $N = 3$) tend to be less abundant than without avian predators (5.00, s.d. = 3.61, $N = 3$) (paired t -test: $t_2 = -2.22$, $P_{\text{one-sided}} < 0.08$). This same pattern was observed from 1985 to 1990 at this site (Belovsky and Slade, 1993). Therefore, the two species' populations appear to be affected differently by predation.

DISCUSSION

At the same location and time, two grasshopper species exhibited density-dependent survival in the absence of predation due to intraspecific competition for food (Fig. 3) (Belovsky

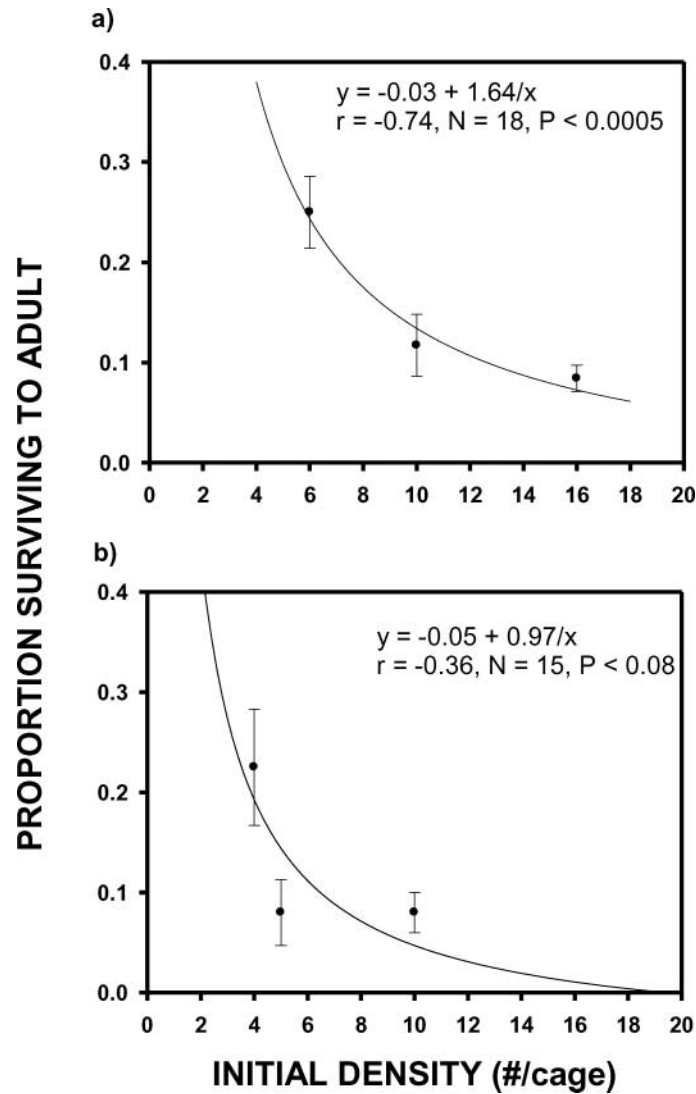


Fig. 3. Examples of density dependence from previous studies (Belovsky and Slade, 1995, unpublished data; Chase, 1996) for (a) *M. sanguinipes* and (b) *A. pseudonietana* demonstrated as the proportion of early instar nymphs surviving to become adults at different initial densities. Best fit regressions are presented.

and Slade, 1995, unpublished data; Chase, 1996). Also, both grasshoppers exhibited similar losses of tethered individuals to predators over the same five 2-day periods [data from Experiment 1b following Zens and Peart's (2003) protocols – *M. sanguinipes*: $1.5\% \cdot \text{day}^{-1}$, s.D. = 0.2, $N = 5$; *A. pseudonietana*: $1.7\% \cdot \text{day}^{-1}$, s.D. = 1.2, $N = 5$; paired t -test: $t_4 = 0.48$, $P < 0.67$). However, the two grasshopper populations responded differently to avian predation: *M. sanguinipes* densities were not reduced and even increased with predation, while *A. pseudonietana* densities were reduced. The key difference is the preferential killing behaviour of the avian

predators, which kill poor foraging *M. sanguinipes* but kill good foraging *A. pseudonietana*. This creates very different selective pressures and population dynamics.

For *M. sanguinipes*, the selective advantage of good foraging in the face of intraspecific competition for food is maintained and enhanced by the predator. Poor foraging individuals that would linger in the population and consume food are preferentially removed by the predator (poor foragers died 32% faster in Experiment 1b than in Experiment 1a), which makes more food available to those individuals who would tend to ultimately survive. Consequently, the intensity of intraspecific competition is diminished by predation and the *M. sanguinipes* population attained a 14% higher density in Experiment 3. This is the original premise of non-additive predation being compensatory or even increasing prey populations with the preferential removal of already 'doomed' individuals (Errington, 1946a, 1946b, 1956).

For *A. pseudonietana*, the selective advantage of good foraging in the face of intraspecific competition for food is lost as the predators preferentially kill good foragers. Now, good foragers are removed more quickly from the population and poor foragers survive 43% longer (Experiment 1b). If the net effect is simply that survival of good foragers is substituted for survival of poor foragers, then predation would be additive – predation only reduces the population by the numbers killed. However, if the removal of good foragers allows poor foragers to linger longer in the population as observed, then the intensity of intraspecific competition may increase – non-additive effects decrease the population more than the numbers killed by predators. This may be why the *A. pseudonietana* population declined 53% with predation, while an upper estimate of predation was 40% [$1 - e^{-0.0173(30)}$], i.e. 30 days in Experiment 3 when *A. pseudonietana* individuals were larger than third instar, which made them vulnerable to avian predators (Belovsky *et al.*, 1990), and a $1.7\% \cdot \text{day}^{-1}$ predation rate for tethered individuals that could not escape in Experiment 1b].

We do not know why avian predators preferentially kill different individuals in the two grasshopper species. One might suspect that good foraging individuals move more and this increases exposure to predators, but this only applies to *A. pseudonietana*, not *M. sanguinipes*. However, we know that large-bodied grasshoppers, like *A. pseudonietana*, are less concealed by sparse grassland vegetation when moving about feeding, mating, etc., and when this grasshopper flies in its escape response, its red wings may attract avian predators (Belovsky *et al.*, 1990). On the other hand, *M. sanguinipes*' smaller body may allow it to be concealed while active, even in sparse vegetation, and when it flies, its clear wings may be less attractive to avian predators.

Sexual differences also emerged in the present study. Females of both grasshoppers that died from non-predatory causes in the field survived longer if they were good foragers, and good foraging *M. sanguinipes* females survived longer even when eventually killed by predators in the tethering experiment (Experiment 1b). Furthermore, the survival advantage of better foraging for female *M. sanguinipes* increased as population density increased in Experiment 1a. However, males of neither species exhibited a relationship with foraging performance regardless of how they died. We know that female grasshoppers in the laboratory have greater nutritional demands than males due to egg production. Consequently, their survival is more sensitive to nutrition (Belovsky *et al.*, 1996), which may explain the observed differences between females and males in the field. Furthermore, with predators, we know that males are highly vulnerable as they move about looking for and displaying to females (Belovsky *et al.*, 1990).

CONCLUSION

The species and sex differences observed in our study suggest that the natural selection and population dynamic effects of predation may be much more complicated than often thought. Our study questions the classic predator–prey theory assumption that predatory mortality is additive with other forms of mortality, because the presence of predators in one case reduced prey numbers less than expected and in the other more than expected. The non-additive predation observed in our study system is intriguing because our system has the characteristic (predator > 100 times larger than prey) that is thought to lead to additive predatory mortality, when predators much larger than their prey easily subdue ‘healthy’ individuals that would otherwise survive. Therefore, it is no wonder that a meta-analysis of predation studies found that predators in ~40% of cases affected prey, counter to expectation (Sih *et al.*, 1985).

We suggest that ecologists need to be cautious in attributing selective and population limiting effects of predation based on the assumption that predation is additive with other forms of mortality. Getz (1993, 1998) stressed that the types of behavioural differences observed in our study need to be incorporated into predator–prey models, because they can dramatically change population responses from classic expectation, as we observed. Our cautionary statement does not depend on the relative body sizes of predator and prey or how great the predation rate is. Therefore, the selective or population effects of predation are neither as simple nor as easy to study, as expected from classic predator–prey theory.

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