Synergistic effects of food and predators on annual reproductive success in song sparrows

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The behaviour literature is full of studies showing that animals in every taxon balance the probability of acquiring food with the risk of being preyed upon. While interactions between food and predators clearly operate at an individual scale, population-scale studies have tended to focus on only one factor at a time. Consequently, interactive (or 'synergistic') effects of food and predators on whole populations have only twice before been experimentally demonstrated in mammals. We conducted a 2×2 experiment to examine the joint effects of food supply and predator pressure on the annual reproductive success of song sparrows (*Melospiza melodia*). Our results show that these two factors do not operate in an additive way, but instead have a synergistic effect on reproduction. Relative to controls, sparrows reared 1.1 more young when food was added and 1.3 more when predator pressure was low. When these treatments were combined 4.0 extra young were produced, almost twice as many as expected from an additive model. These results are a cause for optimism for avian conservation because they demonstrate that remedial actions, aimed at simultaneously augmenting food and reducing predators, can produce dramatic increases in reproductive success.

Keywords: food supplementation; predator pressure; synergistic effects; annual reproductive success; *Melospiza melodia*

1. INTRODUCTION

Hundreds of behavioural studies have shown that animals balance the probability of acquiring food with the risk of being preyed upon (reviewed in Lima 1998). While interactions between food and predators are known to influence the behaviour of individuals, interactive (or 'synergistic') effects of food and predators on the demography of populations have been less well studied (Anholt & Werner 1995; Korpimäki & Krebs 1996; Newton 1998). The first published reports of synergistic effects of food and predators on the demography of terrestrial vertebrates came from a large-scale field experiment conducted on small-mammal populations. Krebs *et al.* (1995) reported that snowshoe hares (*Lepus americanus*) increased threefold in numbers when food was added, twofold when predators were removed, and 11-fold when food was added and predators were removed. The response of arctic ground squirrels (*Spermophilus parryii*) to these same experimental treatments was even more extreme (Karels *et al.* 2000).

Single factor experiments conducted on avian populations have demonstrated that increases in food supply (Martin 1987; Boutin 1990; Newton 1998) and decreases in predator pressure (McCleery *et al.* 1996) can each have an independent, positive influence on annual reproductive success. How these factors operate in conjunction with one another in affecting reproductive success is not known (Newton 1998). We conducted a large-scale, spatially rep-

licated, 2×2 experiment to explicitly examine the effects of food supply and predator pressure on the annual reproductive success of song sparrows. If either food supply or predators were dominant, we expected to see a strong response to that factor alone. If food addition and predator pressure interacted, then we expected the benefits of adding food to be strong only in situations where predator pressure was low and not where predator pressure was high.

2. METHODS

(a) *Study species*

We studied song sparrow populations near Victoria, British Columbia, Canada. Song sparrows in this area are resident and multi-brooded. Breeding typically begins in late March or early April and ends in July or August. Individuals can rear up to four broods of 1–4 young per year. In February 2000, we located 3–11 sparrow territories at each of 14 study sites (total number of territories, 76) using playbacks and behavioural cues. Adults were captured in mist nets or treadle-operated box traps and colour ringed for individual recognition.

(b) *Food supplementation*

We provided supplementary food *ad libitum* to all of the territories at 7 of the 14 sites from 4 March to 15 August 2000. We reduced variation between sites by selecting pairs of sites in the same area that were matched for vegetation. We then randomly assigned one of these sites as fed, the other as unfed. In all cases, unfed sites within an area were separated from fed sites by a minimum of two intervening territories.

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Proc. R. Soc. Lond. B (2003) **270**, 799–803
DOI 10.1098/rspb.2002.2311

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The supplementary food consisted of equal proportions of white proso millet and similarly sized (1.8 mm) high-fat and high-protein (45%) pellets (Aquamax Grower 400), together with *ca*. 2 g of oyster shell per kg of feed. Feed was provided from a single, gravity-fed feeder (41 cm × 41 cm × 30 cm), elevated 1 m above the ground, and placed near the singing post of the male territory owner. We conducted feeder watches 3–7 days after the feeders went up to ensure that both members of the territorial pair used the feeder. In all cases, the target pair was observed.

(c) *Predator pressure*

Sites were selected that were likely to differ in predator pressure given previous research in the region (Smith *et al.* 1996; Rogers *et al.* 1997). High predator pressure sites (three fed plus three unfed) were located just outside Victoria on Vancouver Island (31 284 km²), while low predator pressure sites (four fed plus four unfed) were on several small (less than 200 ha), coastal islands less than 20 km northeast of Victoria. High predator pressure sites supported a diverse community of potential predators including the highest density of Cooper's hawks (*Accipiter cooperii*) in Canada, brown-headed cowbirds (*Molothrus ater*), northwestern crows (*Corvus caurinus*), deer mice (*Peromyscus maniculatus*), domestic cats (*Felis domesticus*), mink (*Mustela vison*), raccoon (*Procyon lotor*), rats (*Rattus* spp.) and three species of garter snake (*Thamnophis* spp.). Low predator pressure sites lacked cats, rats and two of the three species of garter snake. Cooper's hawks and cowbirds were both uncommon.

(d) *Assessment of annual reproductive success, predator abundance and nest predation*

We monitored each sparrow territory for the entire breeding season. Most nests (88.5% of 256) were located during nest building, egg laying or incubation. The nests were monitored regularly (usually every 3–4 days) and noted as active, failed or fledged. Fledging was confirmed when we heard begging calls by fledglings and observed parents with food.

We analysed reproductive data using the methods recommended by Krebs *et al.* (1995). We used mixed-model nested ANOVAs where each site (the random variable) was nested in its designated treatment (the fixed variable). The four treatments were: (i) controls (high predator and unfed); (ii) added food (high predator and fed); (iii) low predator (low predator and unfed); and (iv) combined (low predator and fed). Relative to the controls, we expected to see small increases in reproductive success in response to the added food and low predator treatments, and a more than additive response to the combined treatment. Subsequently, we conducted three planned, orthogonal linear contrasts, comparing the combined treatment with each of the others.

To assess the relative abundances of predators at our sites we conducted incidental observations during the fieldwork (Hochachka *et al.* 2000). Every day, we logged in the number of hours spent in the field and recorded the number of potential predators observed on the study sites. We conducted goodness-of-fit tests to determine whether predators were observed more often than expected at the high versus low predator pressure sites. We calculated daily survival rates of nests and their standard errors (s.e.) using the maximum-likelihood estimator (Bart & Robson 1982; program in Krebs 1999). Total nest survival was estimated using a 25-day nest period. Four per cent of nests failed as a result of rainstorms or because the entire clutch was infertile and were excluded from analyses. We com-
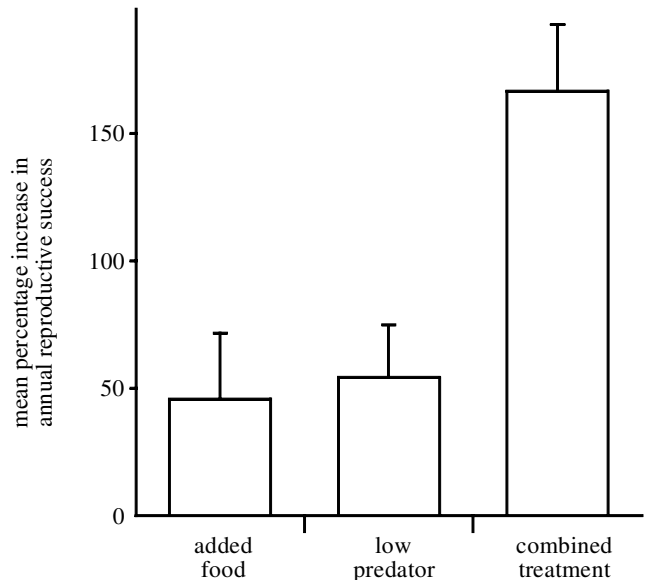
Figure 1. Mean (± s.e.) percentage increase in annual reproductive success in each treatment relative to the control (high predator and unfed) treatment.

pared daily nest survival rates among sites and treatments using CONTRAST (Sauer & Williams 1989).

3. RESULTS

### (a) *Annual reproductive success*

Adding food had a strong effect on annual reproductive success only when predator pressure was low (figure 1). Annual reproductive success differed significantly across the experimental treatments (one-way nested ANOVA, main effect $F_{3,62} = 10.06$, $p < 0.001$; nested term $F_{10,62} = 2.96$, $p = 0.005$; table 1). Sparrows subject to the combined treatment produced significantly more offspring than those in the low predator treatment ($t_{62} = 3.5$, $p = 0.001$), the added food treatment ($t_{62} = 3.5$, $p = 0.001$) and the control ($t_{62} = 5.5$, $p < 0.001$). Relative to the high predator and unfed controls, adding food increased the number of offspring produced by 1.1, and lower predator pressure resulted in an increase of 1.3 young (table 1). If independent and additive, the combined treatment should have produced an increase of 2.4 offspring, whereas 4.0 more young were fledged at the combined treatment sites (table 1). Thus, territories subject to the combined food supplementation × low predator treatment fledged almost twice as many young as would be expected if the effects of food supplementation and lower predator pressure were independent and additive (figure 1).

(b) *Nest predation*

Incidental observations taken throughout the breeding season showed that significantly more potential predators were observed per hour at the high (0.96) than low (0.42) predator pressure sites ($\chi_1^2 = 115.0$, $p < 0.001$). Daily survival rates of sparrow nests differed significantly across treatments ($\chi_1^2 = 15.13$, $p = 0.002$). In accordance with our experimental design, nest survival (figure 2) was significantly greater ($\chi_1^2 = 11.02$, $p = 0.001$) at the low predator pressure sites (60 ± 5%) than at the high predator pressure sites (39 ± 9%). While daily nest survival rates increased

Table 1. Mean number of song sparrow fledglings produced per territory over the entire breeding season in each of the four treatments.

	control (high predator and unfed)			added food (high predator and fed)			low predator (low predator and unfed)			combined (low predator and fed)		
	mean	s.e.	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.	n
by site	1.9	0.7	10	2.2	0.9	5	2.8	1.0	4	5.3	1.2	3
	1.4	0.9	5	3.0	0.9	6	3.0	0.8	7	5.7	1.2	3
	3.9	0.8	7	5.8	0.9	6	3.7	0.9	6	5.2	0.9	5
							5.8	1.0	4	8.8	0.9	5
overall	2.4	0.5	22	3.5	0.6	17	3.7	0.5	21	6.4	0.6	16
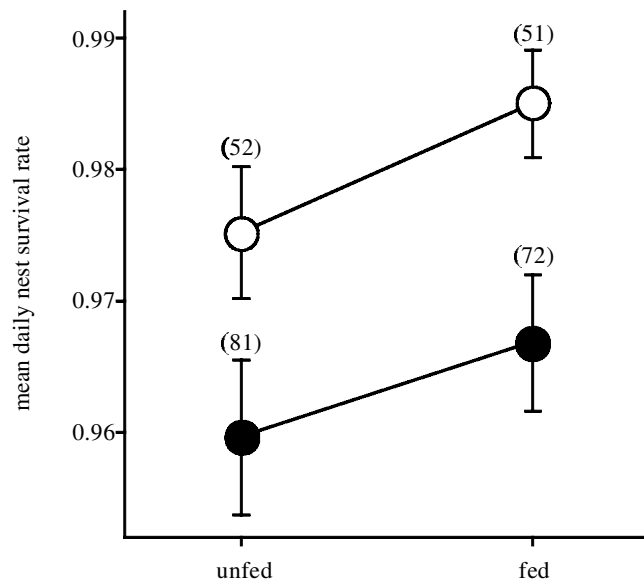
Figure 2. Mean (± s.e.) daily nest survival rates at low (open circles) and high (filled circles) predator pressure sites for unfed and fed sparrows. Values in parentheses denote sample sizes.

with food addition (figure 2), the effect was not significant at either the low predator ($\chi_1^2 = 2.30$, $p = 0.13$) or high predator sites ($\chi_1^2 = 0.84$, $p = 0.34$).

4. DISCUSSION

Our results demonstrate that the effects of food and predators may interact in determining the demography of avian populations. The correspondence between our findings and those of recent mammal studies (Krebs *et al.* 1995; Karels *et al.* 2000) suggest that synergistic effects of food and predators on terrestrial vertebrate populations may commonly occur in nature.

The rates of nest predation we found in our study are similar to those reported for other song sparrow populations in this region (Smith *et al.* 1996, 2002; Rogers *et al.* 1997). Nonetheless, because our predator reduction treatment was mensurative rather than manipulative, factors that covary with predator pressure might explain the effects on reproduction that we observed (Krebs *et al.* 1995). To assess this possibility, we compared our results with those of Smith *et al.* (2002) who directly manipulated predator pressure on song sparrow nests near Vancouver, British Columbia, by removing brown-headed cowbirds. The manipulation resulted in an almost 50% decrease in

nest failure and an increase in reproductive success, with females producing an extra 1.4 young in manipulated areas. Our mensurative predator reduction treatment produced effects that closely parallel those of Smith *et al.* Nest predation was 50% lower at our low predator treatment sites than at control sites, and sparrows at the low predator treatment sites produced 1.3 more young compared with controls (table 1).

A greater relative response to food supplementation at one site than another might arise because of differences in the levels of natural food abundance (Boutin 1990; Dewey & Kennedy 2001). However, differences in natural food abundance cannot explain differences in reproductive success between food-supplemented sites. When given *ad libitum* food, song sparrows in the combined treatment fledged six young on average while those in the added-food treatment fledged only three (table 1). This significant difference in the absolute number of young produced demonstrates that variation in natural food levels among sites cannot explain our results. Instead, some factor other than natural food abundance must be involved that attenuates the animal's ability to exploit the *ad libitum* food source.

Our results indicate that predator pressure is the factor which mediates the response to food addition. High predator pressure could reduce foraging efficiency (Hik 1995; Anholt & Werner 1998; Lima 1998; Sih & McCarthy 2002; also see Hake 1996) or induce chronic physiological stress (Sapolsky 1992; Boonstra *et al.* 1998; Scheuerlein *et al.* 2001), both of which could impair reproduction even when food is plentiful. Thus, predator pressure may define a limit to nutrition independent of absolute food supply (Krebs *et al.* 1995). By the same token, absolute food supply could mediate nest predation rates. Supplementary food may allow parents to decrease foraging time and increase time spent guarding nests from predators thereby reducing nest predation rates (Arcese & Smith 1988; Richner 1992; Komdeur 1996; Ward & Kennedy 1996). Our results provide some support for this suggestion as nest survival rates did improve with food addition at both the high and low predator pressure sites (figure 2).

David Lack (1954) was one of the strongest advocates of the idea that food abundance is the single most important influence on avian reproduction and many subsequent studies have supported this idea (reviews in Martin 1987; Boutin 1990; Newton 1998). However, our results indicate that prior food addition experiments should be re-examined with interactions between food and predators in mind. Specifically, most food supplementa-

tion experiments have been conducted on species that experience relatively low levels of nest predation, such as cavity nesters (Newton 1993, 1998), while open-nesting species, which are typically subject to much greater rates of nest predation (Martin 1995; Matthysen & Adrianensen 1998), are underrepresented. In a recent review (Newton 1998) of studies showing dramatic increases in annual reproductive success in response to experimental food addition, only 4 of the 10 species investigated were songbirds that build open nests. Of these, one was a Hawaiian endemic (*Hemignathus virens*) that remains extant only where predators are rare, and two were corvids, who themselves are predators of nests. The only study involving a songbird (*Melospiza melodia*) normally subject to high rates of nest predation was conducted on a small coastal island with few predators, very near to where our study was conducted (Arcese & Smith 1988). These studies accord with our results showing that large increases in reproductive success can result when food is added in environments, or under circumstances, where predator pressure is low. Our study further shows, however, that such food effects may be restricted to these environments or circumstances. We suggest that previous food addition experiments have been telling us not only about the effects of food on reproductive success, but about how food supply influences birds exposed to low levels of predator pressure. Thus, while we agree with Lack's hypothesis that food is important in avian reproduction, we do not agree with its emphasis on food alone.

If food and predators do commonly interact to influence reproductive success, then our results have definite implications for songbird conservation. In fragmented landscapes, two of the principal factors thought to be having a negative influence on the reproduction of some songbird populations are high nest predation rates (Donovan *et al.* 1995; Zanette 2000; Zanette & Jenkins 2000) and low food supply (Zanette *et al.* 2000). The implication here is that less disturbed landscapes contain both more food and fewer predators, and are thus akin to our combined added food × low predator treatment. Songbirds in less fragmented landscapes ought then to have high rates of reproductive success similar to birds in the combined treatment. Our results suggest that in fragmented systems, *either* a reduction in food supply, *or* an increase in nest predation rates, may produce greater than expected declines in reproductive success. At the same time, our results are also a cause for optimism with respect to the recovery of avian populations. If songbird numbers are low in fragmented systems because of poor reproduction owing to a shortage of food and abundant predators, then remedial actions aimed at simultaneously augmenting food and reducing predation should produce dramatic increases in reproductive success.

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