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Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment

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Abstract Food and predators have traditionally been viewed as mutually exclusive alternatives when considering factors affecting animal populations. This has led to long controversies such as whether annual reproductive success in songbirds is primarily a function of food-restricted production or predator-induced loss. Recent studies on both birds and mammals suggest many of these controversies may be resolved by considering the combined effects of food and predators. We conducted a 2×2 manipulative food addition plus natural predator reduction experiment on song sparrows (*Melospiza melodia*) over three consecutive breeding seasons. Food and predators together affected partial clutch or brood loss, nest survival (total clutch or brood loss) and annual reproductive success. When combined, our two treatments reduced partial losses by more than expected if the effects of food and predators were independent and additive. Food and predators also interacted in their effects on nest survival since food addition significantly reduced the rate of nest predation. While annual reproductive success was highly correlated with nest predation ($r^2 = 0.71$) the strength of this relationship was reinforced by the indirect effects of food addition on nest predation. A stepwise multiple regression showed that the residual variation in annual reproductive success was explained by food effects on the total number of eggs laid over the season and the combined effects of food and predators on partial losses noted above. We conclude that annual reproductive success in song sparrows is a function of both food-restricted production and predator-induced loss and indirect food and predator effects on both clutch and brood loss. We highlight the parallels between our results and those from a comparable bi-factorial experiment on mammals because we suspect combined food and predator effects are likely the norm in both birds and mammals.

Keywords Food supplementation · Nest predation · Predator pressure · Song sparrows

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Introduction

Bi-factorial experiments on mammals, and more recently on birds as well, have shown that food and predators together can have combined effects on everything from individual physiology (Boonstra et al. 1998; Clinchy et al. 2004) to population dynamics (Krebs et al. 1995; Karels et al. 2000). Zanette et al. (2003) provided the first experimental evidence of such interactive (or 'synergistic') food and predator effects on demography in birds. They showed that the combined effect of added food and lower predator pressure produced an increase in the annual reproductive success of song sparrows (*Melospiza melodia*) almost twice that expected if the effects of food and predators were independent and additive. The recentness and rarity of such results is attributable to the rarity of such bi-factorial experiments, as most population-scale experiments on terrestrial vertebrates to date have been focused on one limiting factor at a time.

Annual reproductive success in songbirds is a function of how many eggs are laid over the course of the breeding season and how many of those eggs produce young that survive to fledging. The general consensus in the literature has been that food and predators independently govern the number of eggs laid (Lack 1947; Martin 1987; Newton 1998), and the number of eggs or young lost (Skutch 1949; Martin 1995; Newton 1993), respectively. Which process limits annual reproductive success, food-restricted production or predator-induced loss, has in turn been debated in the literature for decades (Lack 1954; Martin 1987; Boutin 1990; Newton 1998; Nagy and Holmes 2004). Zanette et al.'s (2003) results suggest instead that food and predators may regularly have inseparable effects on annual reproductive success.

Once a clutch is laid, all of the eggs, or the young that hatch from them, may be lost (total clutch/brood loss); only some may be lost (partial clutch/brood loss); or all may produce young that survive to fledging. Following conventional usage in the avian literature, a 'successful nest' denotes a nest in which at least one young survived to fledging. The number of young fledging from a successful nest is therefore a function of how many eggs were laid in it and whether and how much partial clutch/brood loss there was subsequently. 'Nest survival' refers to the proportion of successful nests from among the total number initiated, and is therefore the inverse of the proportion suffering total clutch/brood loss.

Both food and predators may directly or indirectly affect both nest survival (total clutch/brood loss) and partial clutch/brood loss. We define indirect effects as those involving combined food and predator effects mediated by anti-predator behaviour. The less time an animal spends foraging the more time it can devote to anti-predator behaviour (Lima 1998). Greater food availability may indirectly reduce partial, or total, clutch or brood loss from predation (Yom-Tov 1974; Högstedt 1981) by reducing the time parents require for foraging and so increasing the time available for anti-predator behaviour. Conversely, greater predator pressure may reduce nest survival (and increase partial losses) both directly, by increasing losses due to predation; as well as indirectly, by increasing the probability of nestling deaths from starvation, as parents devote more time to anti-predator activities and less time to foraging.

We conducted a 2×2 manipulative food addition plus natural predator reduction experiment on song sparrows over three consecutive breeding seasons. Zanette et al. (2003) reported results regarding nest survival and annual reproductive success from the first year of this 3-year experiment and Zanette et al. (2006) reported results regarding egg production in all 3 years. In this paper, we report the effects of our food and predator treatments on partial clutch/brood loss, nest survival and annual reproductive success in all 3 years of the study; together with evidence of significant inter-annual variability due largely to inter-annual variability in the indirect effect of food addition on nest predation. We conclude that annual reproductive success in song sparrows is a function of both food-restricted production and predator-induced loss and indirect food and predator effects on both clutch and brood loss. We suggest our results should help lay to rest the long controversy over whether food or predators limit annual reproductive success and we propose that future demographic studies should begin by assuming that food and predator effects are largely inseparable.

Materials and methods

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 and ends in late July. Individuals can successfully rear up to 4 broods of 1–4 young per year.

Field procedures

We located 3–11 sparrow territories at each of 14 study sites in 2000, and 2 more sites (16 in total) in 2001 and 2002, using playbacks and behavioural cues. Sites were separated by a minimum of 200 m (four territory lengths; Clinchy et al. 2004) and a maximum of <20 km. Individuals were capable of moving between any two sites (Smith et al. 1996), but never did so following territorial establishment each spring. We recorded all the breeding activities of each territorial female for the entire breeding season (Grzybowski and Pease 2005). Breeding adults were captured in mist nets or treadle-operated box traps and colour ringed for individual recognition. Nests were found mainly using behavioural cues from the parents. Nests were monitored regularly (usually every 3–4 days) and noted as active, failed, or fledged. Predation was inferred to be the source of total clutch/brood loss when: (1) the entire contents of the nest disappeared before the earliest possible fledging date (day 8 of the nestling stage); (2) all the eggs were smashed; or (3) all the nestlings were wounded and dead. Fledging was confirmed when we heard begging calls by fledglings and observed parents with food. The relative abundance of diurnal predators was assessed from incidental observations during fieldwork (Hochachka et al. 2000). We logged the number of hours spent in the field and the number of potential predators observed on the study sites every day.

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) and the general observation that predators are less abundant on islands (Palkovacs 2003). Half the sites selected were high predator pressure (HPP) sites located just outside of Victoria on the Vancouver Island 'mainland' (31,284 km^2; in the Island View, Rithet's Bog and Swan

Lake Conservation Areas), while the other half were low predator pressure (LPP) sites situated on several small (< 200 ha), coastal islands < 2 km offshore (Brackman, Domville, Portland, Rum, Russell and Tortoise islands). HPP sites supported a greater diversity of potential predators (cats, rats, cooper's hawks, cowbirds, crows, raccoons, mink and garter snakes were present at the HPP sites; whereas cats and rats were absent, and cooper's hawks and cowbirds were both rare at the LPP sites; Zanette et al. 2003) and differences in the relative abundance of potential predators are documented below. There were no significant differences between HPP and LPP sites in nesting density, extra-pair paternity rates at fed sites (Clinchy et al. 2004), or overstorey or understorey vegetation.

Food supplementation

We provided supplementary food ad libitum to all territories at 7 (3 HPP + 4 LPP) of 14 sites from 4 March to 15 August 2000; 8 (4 HPP + 4 LPP) of 16 sites from 28 February to 15 August 2001; and 8 (4 HPP + 4 LPP) of 16 sites from 26 February to 15 August 2002. Within both the HPP and LPP areas, we selected pairs of sites that were matched for vegetation: one site was then provided with supplemental food with the other remaining as an unfed control. Unfed sites were separated from fed sites by a minimum of two intervening territories. We assigned feeding treatments at random between pairs of sites in 2000. We then switched feeding treatments between pairs of sites in 2001 and did so again in 2002 to ensure that any effects we observed were due to food and predators and not the site itself.

The supplemental feed consisted of equal proportions of white proso millet and similarly sized (1.8 mm) high fat/high protein (45%) pellets (Purina Mills Aquamax Grower 400), together with roughly 2 g of oyster shell per kilogram of feed. Feed was provided from a single, gravity fed feeder (41×41×30 cm), elevated 1 m above 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. In no case did we ever observe an 'unfed' bird at a feeder.

Statistical analyses

We used goodness-of-fit tests to determine whether predators were observed more often than expected by chance at the HPP than LPP sites. Following the methods recommended by Krebs et al. (1995) and Karels et al. (2000), we tested for effects on partial clutch/brood loss and annual reproductive success using two-factor mixed model ANOVAs, where treatment ('control' = unfed/HPP; 'added food' = fed/HPP; 'low predator' = unfed/LPP; and 'combined' = fed/LPP) and year (2000–2002) were the fixed factors and study site was nested within each. We tested for normality and homogeneity of variances prior to conducting any analysis involving general linear models. All post hoc tests for ANOVAs were Newman–Keuls.

To test for treatment effects on partial clutch/brood loss we began by calculating the average number of young hatched and fledged per successful nest per pair per year. We conducted preliminary analyses with site nested within each of the two fixed factors (see above) and then removed the nested terms when it was found none were significant. We report the results of four analyses regarding successful nests. To test whether our treatments affected the absolute number of young fledging from successful nests we conducted a two-way ANOVA with treatment and year as fixed factors and number of fledglings as the dependent variable. As noted in the Introduction, differences in the absolute number of young fledging from successful nests could reflect treatment effects on either the number of eggs laid or partial clutch/brood loss. To control for effects on the number of eggs and test for effects on partial clutch/brood loss per se, we re-ran the above analysis as a two-way ANCOVA using number of eggs as a covariate: the greater the number of 'egg-corrected' young fledging the lower the level of partial clutch/brood loss. We then conducted comparable analyses on number of young at hatch corrected for eggs laid, and number of young at fledging corrected for number at hatch: the greater the number of 'egg-corrected' young at hatch the lower the level of partial clutch loss during the egg stage, and the greater the number of 'hatchling-corrected' young at fledging the lower the level of partial brood loss during the nestling stage.

To test for treatment effects on nest survival we calculated daily survival rates and their standard errors using the maximum likelihood estimator (Bart and Robson 1982; Program in Krebs 1999) and compared them using CONTRAST (Sauer and Williams 1989). Total nest survival was estimated using a 25-day nest period.

Annual reproductive success was calculated as the total number of fledglings produced per pair per year. To evaluate the relationships between annual reproductive success and nest survival (total clutch brood/loss), partial clutch/brood loss and the total number eggs laid over the season (data from Zanette et al. 2006), we compared the average annual reproductive success per treatment per year (total $n = 12$: four treatments × 3 years) against the corresponding values for the other three variables. For nest survival, we first tested for homogeneity of slopes between fed and unfed treatments and then conducted a simple linear regression on all 12 data points. We then conducted a stepwise multiple regression with annual reproductive success as the dependent variable and nest survival, partial clutch/brood loss and the total number of eggs laid over the season included as independent variables.

Results

Relative predator abundance

Consistent with our a priori selection of sites likely to differ in predator pressure we observed roughly twice as many diurnal predators at the HPP than the LPP sites on average over all 3 years ($\chi^2_1 = 331.4$, $P < 0.001$; Table 1) and in each year separately ($P < 0.001$ in each year). We recorded 2.5 times more predators at the HPP sites in 2000, 3 times more in 2001, and 1.5 times more in 2002 (Table 1).

Partial clutch/brood loss

Food and predators together affected the absolute number of young fledging from successful nests. Parents in the 'combined' treatment consistently fledged significantly more young per successful nest than parents in any other treatment (two-way ANOVA: treatment, $F_{3,243} = 7.1$, $P < 0.001$; year, $F_{2,243} = 0.04$, $P = 0.96$; treatment × year, $F_{6,243} = 0.9$, $P = 0.50$; ranking from post hoc tests on overall results from all 3 years: 'combined' > 'low predator' = 'added food' = 'control'; means ± SE: 3.02 ± 0.10; 2.62 ± 0.13; 2.46 ± 0.12; 2.31 ± 0.14).

Parents in the 'combined' treatment fledged a greater absolute number of young per successful nest in part because food and predators together affected partial clutch/brood loss (Fig. 1a). Compared to parents in the other three treatments parents in the 'combined' treatment demonstrated significantly lower partial clutch/brood loss (two-way ANCOVA on 'egg-corrected' fledglings: treatment, $F_{3,242} = 5.9$, $P = 0.001$; year, $F_{2,242} = 0.3$, $P = 0.72$; treatment × year, $F_{6,242} = 1.5$, $P = 0.17$; covariate, $F_{1,242} = 38.6$, $P < 0.001$; ranking from post hoc tests on overall results from all 3 years: 'combined' > 'low predator' = 'added food' = 'control'; means ± SE: 2.95 ± 0.10; 2.70 ± 0.12; 2.44 ± 0.11; 2.37 ± 0.13).

Parents in the 'combined' treatment suffered fewer partial losses over the entire egg-laying to fledging period because food and predators together affected both partial clutch loss during the egg stage and partial brood loss during the nestling stage. Compared to parents in the other three treatments, parents in the 'combined' treatment demonstrated both significantly lower partial clutch loss and significantly lower partial brood loss [(two-way ANCOVA on 'egg-corrected' hatchlings: treatment, $F_{3,241} = 3.5$, $P = 0.017$; year $F_{2,241} = 0.4$, $P = 0.69$; treatment × year, $F_{6,241} = 1.6$, $P = 0.14$; covariate, $F_{1,241} = 197.5$, $P < 0.001$; ranking from post hoc tests on overall results from all 3 years: 'combined' > 'added food' = 'low predator' = 'control'; means ± SE: 3.32 ± 0.07; 3.16 ± 0.08; 3.13 ± 0.08; 2.96 ± 0.09), (two-way ANCOVA on 'hatchling-corrected' fledglings: treatment, $F_{3,241} = 3.9$, $P = 0.009$; year, $F_{2,241} = 0.2$, $P = 0.83$; treatment × year, $F_{6,241} = 1.2$, $P = 0.33$; covariate, $F_{1,241} = 137.1$, $P < 0.001$; ranking from post hoc tests on overall results from all 3 years: 'combined' > 'low predator' = 'control' = 'added food'; means ± SE: 2.85 ± 0.08; 2.74 ± 0.10; 2.53 ± 0.11; 2.46 ± 0.10)].

Nest survival (total clutch/brood loss)

Because we observed no instances of total brood loss attributable to starvation (i.e. no nests in which all the nestlings were dead but otherwise intact), and total clutch loss attributable to nest abandonment was extremely rare (< 4%), we treat nest predation and nest survival as (inversely) synonymous (Fig. 1b). As outlined in the Introduction, any food effects on nest survival must therefore represent indirect effects of food on nest predation.

Both food and predators significantly affected daily nest survival rates. Overall, over the three years of the study combined, there were significant differences among the four treatments ($\chi^2_3 = 12.6$, $P = 0.006$; Table 1). Post hoc contrasts on the overall data from all 3 years showed that, consistent with our a priori selection of sites likely to differ in predator pressure, nest predation was significantly lower (and nest survival was therefore higher) at the LPP than HPP sites ($\chi^2_1 = 5.6$, $P = 0.018$). Nest predation was also significantly lower (and nest survival was therefore higher) at fed sites than unfed sites ($\chi^2_1 = 7.6$, $P = 0.006$).

Table 1 Relative predator abundance (number of potential predators observed per hour in the field) and nest survival rates (proportion of nests surviving over 25 days) of song sparrows (*Melospiza melodia*) at the HPP and LPP sites, and in each treatment separately, overall and in each year

	Relative predator abundance				Nest survival [1−nest predation]			
	2000	2001	2002	Overall	2000	2001	2002	Overall
HPP sites	0.96	1.52	1.15	1.21	0.39	0.44	0.39	0.41
Controls	0.99	1.32	1.03	1.12	0.36	0.31	0.37	0.35
Added food	0.92	1.74	1.28	1.33	0.42	0.60	0.43	0.48
LPP sites	0.42	0.53	0.70	0.57	0.61	0.52	0.36	0.50
Low predator	0.41	0.37	0.62	0.49	0.54	0.52	0.31	0.47
Combined	0.42	0.65	0.77	0.63	0.69	0.52	0.40	0.52

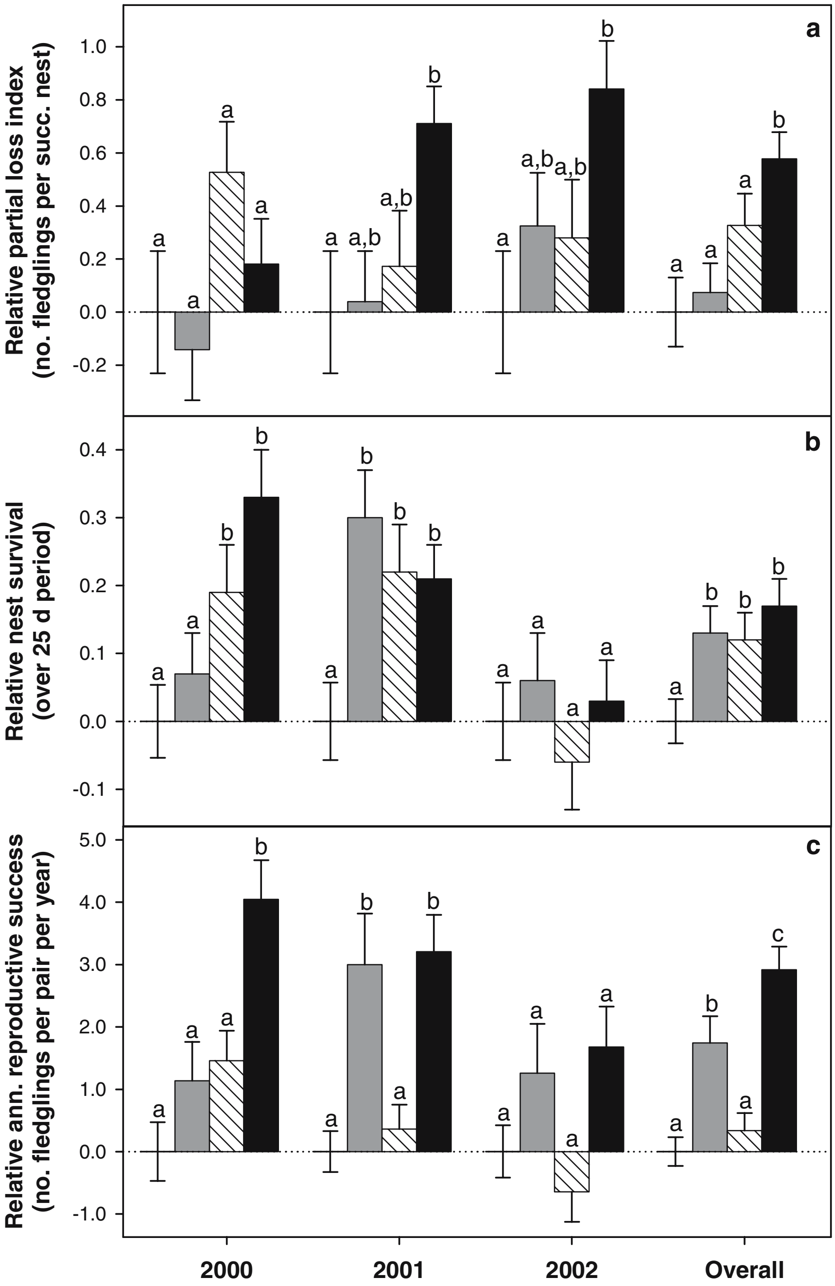

Fig. 1 Effects in song sparrows (*Melospiza melodia*) of the added food (*grey*), low predator (*cross-hatched*) or combined (*black*) treatments relative to controls (*zero line*) on **a** our partial clutch/brood loss index (the number of 'egg-corrected' fledglings per successful nest), **b** nest survival [(1−nest predation) the proportion of nests surviving 25 days] and **c** annual reproductive success (the number of fledglings per pair per year), in 2000, 2001, 2002 and overall. *Values* are the difference (±SE) between results in a given treatment and those at control sites in the same year, or overall control results in the case of overall comparisons. *Letters* show the results from post hoc tests (Newman–Keuls for fledgling numbers, Sauer–Williams for survival) comparing treatments in the same timeframe (*year or overall*). Treatments sharing the same letter were not significantly different from one another ($P > 0.05$)

Considering each year separately, there was also evidence of inter-annual variability in the effects of our treatments on daily nest survival (Table 1; Fig. 1b). In 2000, daily nest survival differed across the four treatments ($\chi^2_3 = 15.8$, $P = 0.001$) and post hoc contrasts showed that nest survival was significantly greater at the LPP than HPP sites ($\chi^2_1 = 11.5$, $P < 0.001$), but it was not significantly greater for fed birds than unfed birds overall ($\chi^2_1 = 2.22$, $P = 0.14$), or at either the LPP ($\chi^2_1 = 2.30$, $P = 0.13$) or HPP sites ($\chi^2_1 = 0.84$, $P = 0.36$), though there was an obvious trend towards food effects (Fig. 1b). In 2001, while daily nest survival again varied significantly across the four treatments ($\chi^2_3 = 9.9$, $P = 0.020$) and was significantly greater ($\chi^2_1 = 6.7$, $P = 0.010$) at the LPP ('low predator' and 'combined') than the unfed, HPP ('control') sites (Fig. 1b); food addition had no effect on nest survival at the LPP sites ($\chi^2_1 < 0.1$, $P = 0.95$; 'low predator' vs 'combined', Fig. 1b) at the same time as having such a spectacular effect on nest survival at the HPP sites ($\chi^2_1 = 9.8$, $P = 0.002$; 'control' vs 'added food'; Fig. 1b) that nest survival at the 'added food' sites was the same as at the LPP sites ($\chi^2_1 = 1.2$, $P = 0.27$; Fig. 1b). In 2002, nest survival was uniformly low (Table 1) and there was no significant difference across the treatments ($\chi^2_3 = 1.4$, $P = 0.70$) though again there was a trend towards food effects (Fig. 1b).

Annual reproductive success

Food and predators together affected annual reproductive success (Fig. 1c). Considering the overall results from all 3 years the effect of treatment was strongly significant (two-way nested ANOVA: treatment, $F_{3,191} = 16.0$, $P < 0.001$). Parents in the 'combined' treatment had significantly better annual reproductive success than parents in any other treatment (Newman–Keuls $P = 0.006$, Fig. 1c) while parents in the 'added food' treatment had significantly better annual reproductive success than parents in the 'low predator' and 'control' treatments (Newman–Keuls $P = 0.001$; Fig. 1c). Compared to 'controls' (mean ± SE total fledglings per pair per year = 2.3 ± 0.23) birds in the 'low predator' treatment fledged 16% more young (2.6 ± 0.28), those in the 'added food' treatment fledged 76 % more (4.0 ± 0.43), while those in the 'combined' treatment fledged 127 % more (5.2 ± 0.37), 1.4 times more than expected if the effects of food and predators were independent and additive.

Just as with nest survival (Fig. 1b), there was significant inter-annual variability in the effects of food and predators on annual reproductive success (two-way nested ANOVA: treatment × year, $F_{6,191} = 2.6$, $P = 0.018$). In 2000, there was an obvious synergism between the effects of food and predators, as reported by Zanette et al. (2003). Parents in the 'combined' treatment had significantly better annual reproductive success than parents in any other treatment (Newman–Keuls $P = 0.001$), fledging almost twice (1.8 times) as many young as expected if the effects of food and predators were independent and additive (Fig. 1c). This was because fed birds laid more eggs over the season than unfed birds (Zanette et al. 2006), LPP birds suffered less partial clutch/brood loss than HPP birds (Fig. 1a) and birds in the 'combined' treatment had higher nest survival (and therefore suffered lower nest predation) than birds in any other treatment (Fig. 1b).

In 2001, birds in the 'combined', 'low predator' and 'control' treatments all did poorer than they had in 2000, but all by about the same proportion (roughly 25%: 2001 vs 2000 mean ± SE; 5.3 ± 0.59 vs 6.4 ± 0.63; 2.4 ± 0.39 vs 3.9 ± 0.48; 2.1 ± 0.33 vs 2.4 ± 0.47; respectively). In contrast, birds in the 'added food' treatment did 44% better than they had in 2000 (5.1 ± 0.82 vs 3.5 ± 0.62). As a consequence, the annual reproductive success of 'added food' birds was only marginally less than that of 'combined' treatment birds (Fig. 1c). By itself, this result would suggest a 'pure' food effect on annual reproductive success. However, the greatly increased success of 'added food' birds was largely due to indirect food effects on nest predation (Fig. 1b): 'added food' birds fledged three more young than 'controls' (Fig. 1c), yet they only laid one more egg over the season than 'controls' (mean ± SE, 12.3 ± 0.97 vs 11.3 ± 0.93; Zanette et al. 2006) and there was no 'added food' effect on partial clutch/brood loss (Fig. 1a). The 'added food' results in 2001 demonstrate that food addition by itself can produce dramatic increases in annual reproductive success, through indirect effects on nest predation. At the same time, the 'low predator' results in 2001 (Fig. 1c) show that low nest predation (Fig. 1b) by itself is not sufficient to produce dramatic increases in annual reproductive success.

In 2002, birds in the 'added food' and 'control' treatments fledged almost exactly the same number of young as they had in 2000 (2002 vs 2000 mean ± SE; 3.7 ± 0.79 vs 3.5 ± 0.62; 2.4 ± 0.42 vs 2.4 ± 0.47, respectively). Parents in the 'combined' treatment again fledged more young than parents in any other treatment (Fig. 1c), but unlike in 2000 they did not fledge significantly more young than parents in the 'added food' and 'control' treatments, largely because nest survival at the LPP sites was not significantly better than at the HPP sites, as had been the case in 2000 (Fig. 1b). There were clearly predator effects on partial clutch/brood loss in 2002 (Fig. 1a), and our index continued to indicate lower predator abundances at the LPP sites (Table 1), but these differences, in the absence of corresponding effects on nest survival (Fig. 1b), were not sufficient to significantly affect annual reproductive success (Fig. 1c). Comparing the 'added food' results in 2001 and the 'combined' treatment results in 2002 (Fig. 1c), the latter show that food addition in the absence of low nest predation (Table 1 and Fig. 1b), is not sufficient to produce dramatic increases in annual reproductive success.

From the preceding, annual reproductive success (Fig. 1c) and nest survival (Fig. 1b) were associated in each year. Considering the mean per treatment in all three years ($n = 12$), annual reproductive success was highly correlated with nest survival ($r^2 = 0.71$, $t_{10} = 4.9$, $P < 0.001$; Fig. 2). There was no difference between fed and unfed birds in the slope of the correlation between annual reproductive success and nest survival ($F_{1,8} = 1.6$, $P = 0.24$). Food addition strengthened the relationship between annual reproductive success and nest survival by 'moving' results up along the same slope (Fig. 2) since food addition simultaneously increased annual reproductive success for a given level of nest survival (e.g. 'low predator' vs 'combined' treatments in 2001, Fig. 1b, c), while it also increased average nest survival (Fig. 1c). When the total number of eggs laid over the season and partial clutch/brood loss were included with nest survival in a stepwise multiple regression all three loaded significantly on annual reproductive success (multiple $r^2 = 0.84$, $F_{3,8} = 19.5$, $P < 0.001$; nest survival, $t_8 = 4.34$, $P = 0.002$; total eggs, $t_8 = 2.99$, $P = 0.017$; partial clutch/brood loss, $t_8 = 2.46$, $P = 0.040$).

Discussion

Food and predators together affected partial clutch/brood loss, nest survival and annual reproductive success. Food and predators interacted in their effects on partial clutch/brood loss as shown by the fact that birds in the 'combined' treatment did 1.5 times better than would be expected if the effects of food and predators were independent and additive ('Overall' results in Fig. 1a). Food and predators also interacted in their effects on nest survival (total clutch/brood loss). As noted, total brood loss attributable to starvation was never observed and total clutch loss due to abandonment was negligible, so the significant food effects on nest survival we recorded (Fig. 1b) represent indirect effects of food on nest predation (Yom-Tov 1974; Högstedt 1981). Zanette et al. (2006), reporting results from the same experiment described here, showed that while food and predators together affected both the number of clutches laid per season and average clutch size, food alone affected the total number of eggs laid per season and egg production was consequently food-restricted. The multiple regression results reported here demonstrate that annual reproductive success in song sparrows is therefore a function of both food-restricted production (given the significant loading of 'total eggs') and predator-induced loss (given the significant loading of both partial clutch/brood loss and nest survival) and indirect food and predator effects on both clutch and brood loss (given the interactive food and predator effects described above; Fig. 1a, b).

The significant inter-annual variability in the effects of our treatments on annual reproductive success (Fig. 1c) appeared to stem largely from the significant inter-annual variability in nest survival (Fig. 1b) for two reasons. Firstly, there was no significant inter-annual variability in the other two parameters that affected annual reproductive success according to our multiple regression results. While there was considerable inter-annual variability in both the total number of eggs laid per season (Zanette et al. 2006) and partial clutch/brood loss (Fig. 1a), the variability was not statistically significant in either case. Secondly, variation in nest survival accounted for the greatest proportion (>70%) of the variation in annual reproductive success (Fig. 2).

The inter-annual variability in the effects of our treatments appeared to be the result of interactions between our treatments and inter-annual variability in specific elements in the environment, since there was very little inter-annual variability in either nest survival or annual reproductive success at the 'control' sites (open squares in Fig. 2; note that these results are not from the same physical locations in each year because treatments were switched between years). Relative to 'controls' there was considerable variation at the 'low predator' sites and as much or more at the fed sites (Fig. 2). We suggest these differences likely reflect changes in the relative abundance of different predators over the years (Schmidt and Ostfeld 2003). Where predators are abundant (e.g. at 'control' sites) your fate will probably be the same regardless of the culprit whereas, where predators are less abundant (e.g. at 'low predator' sites), the increase or decline of a more efficient predator may have more of an effect. Similarly, since food effects on anti-predator behaviour are irrelevant at night, because the birds are asleep, changes in the relative abundance of nocturnal and diurnal predators should affect the strength of indirect food effects on nest predation (Fig. 1b). We are now employing a large number of nest cameras to identify the principal nest predators and how food addition affects vulnerability to specific predators.

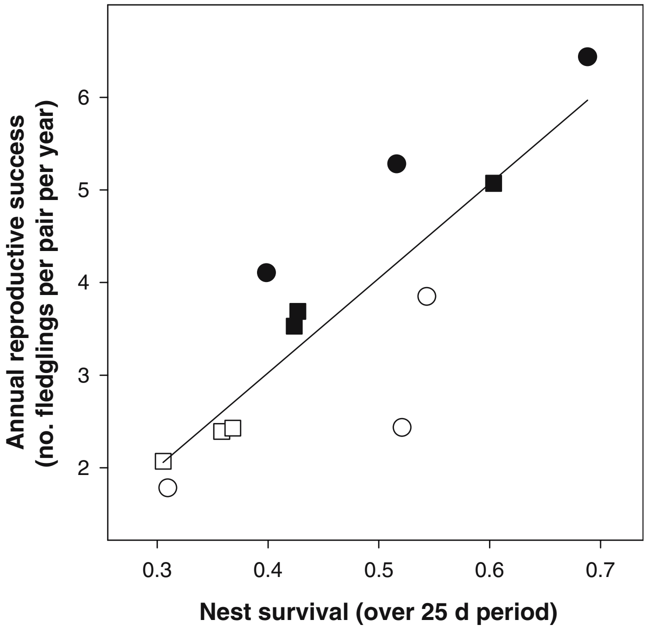

Fig. 2 Correlation between nest survival [(1−nest predation) the proportion of nests surviving 25 days] and annual reproductive success (the number of fledglings per pair per year) based on the mean per treatment per year for each variable. *Open squares* control, *open circles* low predator, *filled squares* added food and *filled circles* combined treatment results. The *line* shows the slope from a simple linear regression ($r^2 = 0.71$, $P < 0.001$)

The results from our bi-factorial experiment on song sparrows in many ways parallel the results from the bi-factorial experiment on snowshoe hares and arctic ground squirrels described by Krebs et al. (1995) and Karels et al. (2000). Like the song sparrows ('Overall' results in Fig. 1c), the hares and squirrels showed modest responses to predator reduction, stronger responses to food addition, and more than additive responses to the combined treatment. The pattern of inter-annual variability we observed also parallels the pattern seen in the hares. Our results indicate that food addition can lead to dramatic increases in annual reproductive success (e.g. 'added food' sites in 2001 and 'combined' sites in 2000 and 2001; Fig. 1c), but only when nest predation is low (regardless of whether it is low because of indirect food effects, e.g. 'added food' sites in 2001; or because there are fewer predators, e.g. 'combined' sites in 2000 and 2001; Fig. 1b). Krebs et al. (1995: their Fig. 1) reported that hare densities at their added food and combined treatment sites were comparable during the 'increase' phase of the 10-year snowshoe hare cycle when predation was low everywhere (Hodges et al. 2001: their Fig. 8.6). The more than additive contrast among the treatments only emerged during the 'decline' phase (Hodges et al. 2001: their Fig. 8.3) when the increase in predation at the added food sites (Hodges et al. 2001: their Fig. 8.6) caused a precipitous drop in hare densities, while numbers remained high at the combined site where hares were protected from predation (Hodges et al. 2001: their Fig. 8.6).

While we found strong evidence of indirect food effects on nest predation (Fig. 1b), our 'added food' treatment had very little effect, direct or indirect, on partial clutch/brood loss ('Overall' results in Fig. 1a). We have observed predators directly remove only part of a clutch or brood, so direct predator effects could explain the partial clutch/brood loss results at the 'low predator' sites ('Overall' results in Fig. 1a), but direct predator effects alone are insufficient to explain the more than additive results at the 'combined' treatment sites ('Overall' results in Fig. 1a). We suggest this more than additive result most likely stems from indirect predator effects: lower predator abundance means parents can spend more time foraging, taking full advantage of the added food and thereby substantially reducing partial clutch/brood loss. This again parallels results from the bi-factorial experiment on hares and squirrels mentioned above, because Karels et al. (2000) documented indirect predator effects on several demographic parameters in arctic ground squirrels. Sparrows were clearly affected by the greater abundance of predators at the HPP sites since they showed many signs of 'chronic stress' (elevated plasma corticosterone and free fatty acid levels, anaemia and developmental anomalies) compared to birds at the LPP sites (Clinchy et al. 2004), consistent with predictions derived from the snowshoe hare study (Boonstra et al. 1998), and parents at the HPP sites did spend more time engaged in anti-predator activities (Budden et al., unpublished manuscript).

The contrast between the pattern of partial clutch/brood loss (Fig. 1a) and nest survival (Fig. 1b) shows that total loss is not simply partial loss writ large, or vice versa, and therefore these two parameters must be affected by different processes. If nest predation affected how birds 'perceive' the risk of predation and thereby affected their anti-predator behaviour, there should have been a closer correspondence between nest predation (Fig. 1b) and partial clutch/brood loss (Fig. 1a). Instead, partial clutch/brood loss appears to be affected more by predator abundance (Table 1). This was most clearly illustrated in 2002: the more than additive effects on partial clutch/brood loss at the 'combined' sites in 2002 (Fig. 1a) are indicative of indirect predator effects in response to the lower diurnal predator abundance at LPP sites (Table 1), yet there were no notable differences in nest survival (Fig. 1b). There are at least two reasons why predator pressure may affect partial clutch/brood loss while nest predation rates may not. Firstly, our index of predator abundance (Table 1) includes predators of both adults and young. Suffering a nest predation event may only convey information on the risk to one's future young and not to oneself. If parents are primarily concerned with their own survival then nest predation rates may be an unsuitable index for evaluating indirect predator effects. Secondly, our index of predator abundance is an index of predators seen during the day. Nocturnal predators should be literally 'invisible' to diurnally active birds and so may not affect the parent bird's 'perception' of risk even when nocturnal predators are the primary nest predators, leading to a disconnect between indirect predator effects (Fig. 1a) and nest predation rates (Fig. 1b).

We suggest the long controversy (Lack 1954; Martin 1987; Boutin 1990; Newton 1998; Nagy and Holmes 2004) over whether annual reproductive success is a function of food-restricted production or predator-induced loss stems from a false dichotomy. Several of our results, taken in isolation, might be interpreted as evidence of either a 'pure' food-restricted production effect on annual reproductive success or a 'pure' predator-induced loss effect. The 2001 results (Fig. 1c), taken in isolation, are superficially consistent with a 'pure' food-restricted production effect, but are in fact due primarily to indirect food effects on nest predation (Fig. 1b). Figure 2 graphically illustrates this point even more clearly: ignoring the regression line, the mean annual reproductive success at fed sites was clearly greater, pointing to a 'pure' food effect; ignoring the distinction between fed (filled symbols) and unfed (open symbols) sites, the regression results point to a 'pure' predator effect, as already noted. In truth, the strength of the regression was a joint function of both food and predator effects and the residuals from the regression were explained by combined food (total eggs) and predator (partial clutch/brood loss) effects on annual reproductive success. Nagy and Holmes (2004) used data from a long-term observational study on warblers to show that a strong correlation between nest predation and annual reproductive success is not sufficient evidence of a predominant effect of predators, because food availability, which is rarely measured, could be even more strongly correlated. We suggest our experiment shows that assessing both food and predator effects is indeed essential, as Nagy and Holmes (2004) argue, but not because these are mutually exclusive alternatives, but rather because food and predators are so likely to have combined effects.

Our results demonstrate that combined food and predator effects were always present (Fig. 2) whether or not these had synergistic consequences in a given year (Fig. 1c). We have highlighted the parallels between the results of our bi-factorial experiment and that on the hares (Krebs et al. 1995) and squirrels (Karels et al. 2000) because we suspect combined food and predator effects are not just the norm for songbirds but other birds and mammals as well (Clinchy et al. 2004). We propose that future demographic studies should begin by assuming that food and predator effects are largely inseparable.

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