FOOD AND PREDATORS AFFECT EGG PRODUCTION IN SONG SPARROWS

Liana Zanette,[1,4] Michael Clinchy,[2] and James N. M. Smith[3,5]

[1]*Department of Biology, University of Western Ontario, London, Ontario N6A 5B7 Canada*
[2]*Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5 Canada*
[3]*Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada*

Abstract. Although the possibility that food and predators may interact in limiting avian populations has long been recognized, there have been few attempts to test this experimentally in the field. We conducted a manipulative food addition experiment on the demography of Song Sparrows (*Melospiza melodia*) across sites that varied in predator abundance, near Victoria, British Columbia, Canada, over three consecutive breeding seasons. We previously showed that food and predators had interactive effects on annual reproductive success (young fledged per female). Here, we report the effects on egg production. Our results show that food limits the total number of eggs laid over the breeding season ("total egg production") and that interactive food and predator effects, including food effects on nest predation, determine how those eggs are "parceled out" into different nests. Food addition alone significantly affected total egg production, and there was no significant interannual variability in this result. At the same time, both food and predators affected the two determinants of total egg production: "clutch number" (total number of clutches laid) and average clutch size. Both clutch number and size were affected by a food × predator × year interaction. Clutch number was lower at low-predator locations because there was less nest predation and thus less renesting. Food addition also significantly reduced nest predation, but there was significant interannual variation in this effect. This interannual variation was responsible for the food × predator × year interactions because the larger the effect of food on nest predation in a given year, the smaller was the effect of food on clutch number; and the smaller the effect of food on clutch number, the larger was the effect of food on clutch size. Potential predator and year effects on total egg production were thus cancelled out by an inverse relationship between clutch number and clutch size. We suggest that combined food and predator effects on demography could be the norm in both birds and mammals.

Key words: egg production; food supplementation; Melospiza melodia; *nest predation; predator pressure; Song Sparrow; synergistic effects.*

INTRODUCTION

Bi-factorial experiments on mammals, and more recently on birds as well, have shown that food and predators 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 due to the rarity of such bi-factorial analyses, as most

demographic experiments on terrestrial vertebrates to date have focused on one limiting factor at a time.

The manipulative food addition experiment across areas that differed in predator pressure described by Zanette et al. (2003) was repeated over three consecutive breeding seasons. Zanette et al. (2003) documented the effects on annual reproductive success in the first year and Zanette et al. (2006) reported the results in all three years. Zanette et al. (2006) also showed that food and predators interacted in their effects on both nest predation (total clutch or brood loss) and partial clutch or brood loss. Working in the context of the same study, Clinchy et al. (2004) showed that food and predators had combined effects on the stress physiology of parents, consistent with predictions from an earlier bi-factorial food and predator experiment on snowshoe hares (*Lepus americanus*; Boonstra et al. 1998).

The number of young fledged per female over a breeding season (annual reproductive success) is necessarily some function of the number of "births" (total number of eggs laid) and "deaths" (eggs that fail to hatch and hatchlings that fail to fledge). In this paper we

report the effects of food and predators on "total egg production" over the breeding season (i.e., the number of "births") in the context of the same study described by Zanette et al. (2003, 2006); the effects on the number of "deaths" having been described in Zanette et al. (2006). Our focus is on the proximate effects of food and predators on egg production, within a particular group of individuals at a particular time; as opposed to food and predators as ultimate, selective factors affecting evolutionary adaptations over a number of generations (see Krebs [2001:22–23] for an excellent discussion of this distinction regarding the determinants of clutch size in birds).

"Total egg production" (total number of eggs laid over the breeding season) in multi-brooded species such as the Song Sparrow is a function of the number of clutches laid over the breeding season ("clutch number") multiplied by the number of eggs per clutch (clutch size) (Grzybowski and Pease 2005). Food and predators may affect total egg production through their effects on clutch number or clutch size or both. Our experiment was designed to test the effects of food and predators on these demographic parameters. The physiological and behavioral mechanisms responsible for the demographic patterns that we report are best tested by physiological and behavioral experiments. Nonetheless, to understand why the combined effects of food and predators on demography are likely to be complicated, and even counterintuitive, it is helpful to review some of the theoretical and empirical evidence regarding the potential physiological and behavioral mechanisms responsible.

Nagy and Holmes (2005) recently argued that, in multi-brooded species, variation in total egg production may be better explained by the variation in clutch number rather than clutch size. Despite this, few songbird studies directly measure clutch number (Grzybowski and Pease 2005). Renesting after losing a nest to predators is almost certain to be a common cause of variation in clutch number; with higher rates of nest predation causing an increase in average clutch number (Martin 1992, Newton 1998, Nagy and Holmes 2004). If clutch size is constant, nest predation will thus determine total egg production. Food addition may increase clutch number (Arcese and Smith 1988, Rodenhouse and Holmes 1992, Nagy and Holmes 2005) by increasing the probability of laying a subsequent clutch or decreasing the interval (hereafter the "inter-nest interval") between clutches (Martin 1987, Arcese and Smith 1988, Simons and Martin 1990) or both. A greater abundance of predators in the vicinity may have the opposite effect. Scheuerlein et al. (2001) showed that tropical Stonechats (*Saxicola torquata axillaris*) with predatory Fiscal Shrikes (*Lanius collaris*) in their territories were significantly less likely to lay a second clutch, and took significantly more time to do so, than those without shrikes in their territories. Finally, because food addition may reduce nest predation

(Yom-Tov 1974, Högstedt 1981, Zanette et al. 2006), adding food could conceivably result in a reduction in clutch number (Martin 1992).

The effect of food addition on clutch size in songbirds has been shown to be highly variable. Even where experiments have been conducted on the same species, increases are often found in one study but not another, or in one year but not another (reviews in Nager et al. 1997, Newton 1998). Only two studies have shown proximate effects of predators on clutch size in song-birds (Julliard et al. 1997, Doligez and Clobert 2003). Both studies were on single-brooded species and both tested the effects of nest predation in one year on the size of clutches laid in the following year. In both cases there was a significant negative correlation between nest predation and clutch size that the authors concluded was mostly phenotypic, although the proximate mechanism was not definitively identified. The corresponding pattern in a multi-brooded species would consist of a negative correlation between nest predation and clutch size in the same year. Martin (1992: Fig. 1) proposed one possible proximate pathway that could explain this pattern wherein nest predation affects "perching time" (i.e., vigilance), which affects "foraging time," which thus affects the size of subsequent clutches. A different proximate pathway is that nest predation causes renesting, the physiological "cost" of renesting affects the "body condition of parents" and this, in turn, affects the size of subsequent clutches (Williams 2005). This second pathway may also be inferred from Martin's (1992) model, although he did not make an explicit connection between renesting and the physiological cost to parents. In this latter case, one would expect to see a significant negative correlation between clutch number and clutch size in addition to a negative correlation between nest predation and clutch size.

A recent meta-analysis by Preisser et al. (2005) suggests that "intimidation" by predators may often have as significant an effect on prey demography as direct consumption. The study of Scheuerlein et al. (2001) shows that the mere presence of a predator (i.e., intimidation), independent of nest predation, can affect egg production. Our experiment tested whether birds responded equally to food addition in high and low predator pressure areas. Both predator abundance and nest predation rates differed significantly between these areas (Zanette et al. 2006: Table 1). However, while predator abundance differed consistently, there was significant interannual variability in the difference in nest predation rates due to interannual variation in the extent to which food addition reduced the rate of nest predation. The difference in predator abundance, rather than nest predation, was more relevant to the effects of our experiment on parental stress physiology (Clinchy et al. 2004) and partial clutch or brood loss (Zanette et al. 2006). As outlined in the previous two paragraphs, differences in egg production between the high and low predator pressure areas could arise from the differences

in predator abundance or nest predation or both. In our analyses, we first test for treatment effects (fed vs. unfed in high and low predator pressure areas) on egg production, and then test whether the differences in egg production between the treatments are correlated with the differences in nest predation between the treatments (reported in Zanette et al. 2006). This helps to differentiate between effects potentially due to predator abundance and effects probably due to nest predation.

We expected to find both significant food and predator effects on total egg production, as well as significant interannual variability in these effects. We expected there to be a significant food effect, based on an earlier food addition experiment on Song Sparrows by Arcese and Smith (1988). We expected there to be a significant predator effect because we expected that the higher rate of nest predation in our high predator pressure treatment (Zanette et al. 2006) would cause more renesting (i.e., a larger clutch number) and thus an increase in total egg production. We expected significant interannual variability, given: (1) the significant inter-annual variability in the effect of food addition on nest predation (Zanette et al. 2006); and (2) the fact that interannual variability in food effects on clutch size would seem to be the norm (Nager et al. 1997, Newton 1998). To help interpret the effects of our experiment on total egg production, we also report the effects of our food and predator treatments on inter-nest intervals, clutch number, and clutch size, together with results regarding the effects of food on the relationship between nest predation and clutch number, and between clutch number and clutch size.

METHODS

Study species

We studied Song Sparrows (*Melospiza melodia*) 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. We recorded individuals laying up to eight clutches in a season; the maximum clutch size seen was five eggs, and the maximum total egg production for an individual was 28 eggs.

Field procedures

We monitored 89, 95, and 91 Song Sparrow territories in 2000, 2001, and 2002, respectively. Breeding adults were captured in mist nets or treadle-operated box traps and were color-banded for individual recognition. We recorded all of the breeding activities of each territorial female (Grzybowski and Pease 2005). Nests were found mainly by using behavioral cues from the parents. All eggs were marked with a nontoxic, odor-free pen. Song Sparrows lay one egg a day, so a clutch was considered complete if no new eggs were observed after >24 hours. If a nest was preyed upon, abandoned, or parasitized in the interim, the clutch size was designated "unknown."

Nests were monitored regularly (every 3–4 days) thereafter and were noted as active, failed, or fledged. Predation was inferred to be the source of total clutch or 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 of the eggs were smashed; or (3) all of the nestlings were wounded and dead. Hereafter, we treat nest predation and nest survival as (inversely) synonymous (Zanette et al. 2006) because there were no instances of total brood loss attributable to starvation (i.e., no nests in which all of the nestlings were dead but otherwise intact), and total clutch loss attributable to nest abandonment was extremely rare (<4%). Fledging was confirmed when we heard begging calls by fledglings and observed parents with food. Inter-nest intervals refer to the time (in days) between the fail or fledge date for a given nest and the start of incubation of the following nest.

Food supplementation

We positioned a feeder at the center of the territory, in roughly half of the territories, in a given year. Because it was physically demanding to haul the hundreds of kilograms of feed provided every year on foot, we fed only those territories near vehicular access points (3–11 per access point). As a result, the monitored territories were distributed across 14 (2000) to 16 (2001, 2002) different locations. To reduce statistical error variation due to spatial location, we treated adjacent locations in the same area as a pair and then (in 2000) randomly assigned one as "fed" and the other as "unfed" (Zanette et al. 2003). Again, for logistical reasons, we fed all of the territories at "fed" locations. Interspersing fed and unfed territories at the same location is not practical because unfed birds too readily raid the feeders at fed territories (Arcese and Smith 1988). Paired fed and unfed locations were separated by 200–800 m (4–16 territory lengths; Clinchy et al. 2004). The maximum distance between any two locations was <20 km. Individuals were capable of moving between any two locations (Smith et al. 1996) but were never observed to do so following territorial establishment each spring. Thus, unfed birds were never seen at feeders at fed locations. In 2001 we switched the feeding treatment between the paired locations (i.e., fed became unfed and vice versa), and did so again in 2002.

Supplemental feed was provided ad libitum throughout the breeding season (4 March on). The 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, Purina Mills, St. Louis, Missouri, USA), and ~2 g of oyster shell per kilogram of feed. The 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. Feeder watches conducted 3–7 days after the feeders went up confirmed that both members of the territorial pair used the feeder.

Predator pressure

Based on 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), we were able to contrast birds living in close proximity that were nonetheless subject to different levels of predator pressure. Roughly half of the territories that we monitored each year were at high predator pressure (HPP) locations (three or four fed and three or four unfed) just outside of Victoria on the Vancouver Island "mainland" (31 284 km^2), whereas the other half were at low predator pressure (LPP) locations (four fed and four unfed) situated on several small (<200 ha) coastal islands <2 km offshore (see Zanette et al. [2006] for specific locations). There were no significant differences between HPP and LPP locations in nesting density, extra-pair paternity rates, or over-story or understory vegetation (Clinchy et al. 2004, Zanette et al. 2006). Consistent with our a priori selection of areas likely to differ in predator pressure, HPP locations supported a greater diversity (listed in Zanette et al. [2003]) and abundance (Zanette et al. 2006: Table 1) of potential predators, and birds at the HPP locations suffered significantly higher nest predation (65% vs. 53%, HPP vs. LPP) and brood parasitism (40% vs. 9%) and had lower survival from fledging to independence (53% vs. 82%) and lower adult breeding season survival (84% vs. 92%; Clinchy et al. 2004, Zanette et al. 2006).

Statistical analyses

We report the results from three sets of analyses. In the first set we evaluate treatment ("control," unfed/HPP; "added food," fed/HPP; "low predator," unfed/LPP; and "combined," fed/LPP) and year effects on the four egg production parameters identified in the *Introduction*: total egg production, inter-nest interval, clutch number, and clutch size. We report the results from AN(C)OVAs of the total (total egg production and clutch number) or average (inter-nest interval and clutch size) for a given female in a given year.

In the second set of analyses we evaluate the relationships between nest predation and each of the four egg production parameters. As part of this set, we also evaluate the relationship between clutch number and clutch size because, as noted in the *Introduction*, it is necessary to know the nature of this relationship to evaluate that between nest predation and clutch size. We calculated the average nest survival rate per treatment per year using the maximum likelihood estimator (Bart and Robson 1982; program in Krebs [1999]), giving us a total of 12 average nest survival rates (reported in Zanette et al. [2006: Table 1]), each based on at least 50 known-fate nests. We then used the Spearman rank correlation method to test the relationships between average nest survival per treatment per year and the average per treatment per year of each of the four egg production parameters; and average clutch number and

average clutch size per treatment per year. As noted in the *Introduction*, Zanette et al. (2006) showed that food addition significantly affected nest predation. Because we were interested in nest predation effects per se, independent of food effects, in this set of analyses, we corrected for food effects by subtracting the difference between the mean for the fed locations and the mean for the unfed locations from each of the values for the fed locations prior to testing each correlation.

In the third set of analyses, we evaluate the relationships between the magnitude of food effects on nest predation (shown in Zanette et al. 2006) and the magnitude of food effects on clutch number and clutch size. The difference between fed and unfed locations is the focus of these analyses, rather than something to be corrected for, as in the previous set. Starting with the 12 non-food-corrected averages per treatment per year for each parameter described in the previous set of analyses, we calculated the difference between fed and unfed locations subject to the same predator pressure in the same year, giving us six difference scores reflecting the magnitude of food effects. We again used the Spearman rank correlation method to test the relationship between the magnitude of food effects on one parameter and the magnitude of food effects on another.

Prior to performing the AN(C)OVAs, the data were Box-Cox-transformed (Krebs 1999) and tested for normality and homogeneity of variances. We conducted three-way AN(C)OVAs of each of the egg production parameters to test for food (fed vs. unfed), predator (HPP vs. LPP), and year effects, and all possible interactions. In the *Results*, we report *F* values only for those terms that were significant. We conducted preliminary analyses with location nested within treatment and then removed the nested terms when it was found that none were significant. Food addition may increase clutch number, and thus total egg production, merely by lengthening the breeding season rather than increasing or accelerating breeding effort in a given block of time (Nagy and Holmes 2005). Because our focus in the present paper is on the latter, we included season length as a covariate when analyzing both clutch number and total egg production. Consequently, our results are directly comparable to those of Nagy and Holmes (2005). We conducted separate analyses of the intervals following successful nests (in which at least one young survived to fledging) and unsuccessful nests. Brood size is known to affect inter-nest intervals following successful nests in Song Sparrows (Smith and Roff 1980) and was included as a covariate when analyzing this parameter. Clutch size in multi-brooded species typically peaks mid-season (Crick et al. 1993). To correct for this, we first modeled the effect of date on clutch size for each treatment in each year and then, to each observed clutch size, we added the difference (e.g., 0.1) between the overall mean for that treatment in that year (e.g., 3.6) and the predicted value for the date (e.g., 3.5 for 15 April) on which the clutch in question was

initiated, to give us the seasonally adjusted size of that clutch (e.g., 4.0 observed + 0.1 = 4.1 adjusted).

RESULTS

Data set

Over the three years of the study we found 769 nests, 527 (68.5%) of which were found early enough in the nesting cycle for us to accurately identify the clutch size. We were able to calculate the renesting interval following a successful nest in 120 cases and the interval following an unsuccessful nest in 219 cases. We identified every nest initiated by a given female in 55 cases in 2000, 59 cases in 2001, and 49 cases in 2002; and were able to calculate total egg production for a given female in 48 cases in 2000, 49 cases in 2001, and 47 cases in 2002.

Treatment and year effects

Food addition alone affected total egg production and there was no significant interannual variability in this result (Fig. 1A; food $F_{1,132} = 12.9$, $P < 0.001$; all other $P > 0.2$). Fed birds laid ~20% more eggs over the course of the breeding season (12.5 ± 0.40 eggs, mean ± SE) than did unfed birds (10.5 ± 0.35 eggs). Similarly, food addition alone affected inter-nest intervals and there was no significant interannual variability in this result (all other $P > 0.2$). Fed birds renested almost four days faster following a successful nest (fed, 11.4 ± 0.54 d; unfed, 15.0 ± 1.03 d; food $F_{1,107} = 12.7$, $P < 0.001$) and two days faster after an unsuccessful nest (fed, 7.3 ± 0.34 d; unfed, 9.0 ± 0.39 d; food $F_{1,207} = 12.2$, $P = 0.001$).

Both food addition (food $F_{1,150} = 4.2$, $P = 0.041$) and predator pressure (predator $F_{1,150} = 7.2$, $P = 0.008$) affected clutch number (Fig. 1B) and there was a significant food × predator × year interaction ($F_{2,150} = 6.9$, $P = 0.003$; all other $P > 0.10$). Fed birds laid ~9% more clutches (3.5 ± 0.10 clutches) than unfed birds (3.2 ± 0.10 clutches) and birds at HPP locations laid ~13% more clutches (3.6 ± 0.10) than birds at LPP locations (3.2 ± 0.09). Both food addition (food $F_{1,222} = 7.3$, $P = 0.007$) and predator pressure (predator $F_{1,222} = 4.7$, $P = 0.032$) also affected clutch size (Fig. 1C) and there was an almost significant food × predator × year interaction ($F_{2,222} = 2.8$, $P = 0.065$; all other $P > 0.10$). On average, fed birds laid ~5% more eggs per clutch (3.52 ± 0.05) than unfed birds (3.36 ± 0.05) and birds at HPP locations laid about 4% fewer eggs per clutch (3.36 ± 0.05) than birds at LPP locations (3.51 ± 0.04).

Nest predation effects

There was no significant correlation between nest survival (=1 − nest predation; see *Methods*) and total egg production or the inter-nest intervals following either successful or unsuccessful nests ($P > 0.80$ in all cases). Nest survival and clutch number were significantly negatively correlated (Spearman $r_S = -0.69$, $t_{10} = 3.0$,
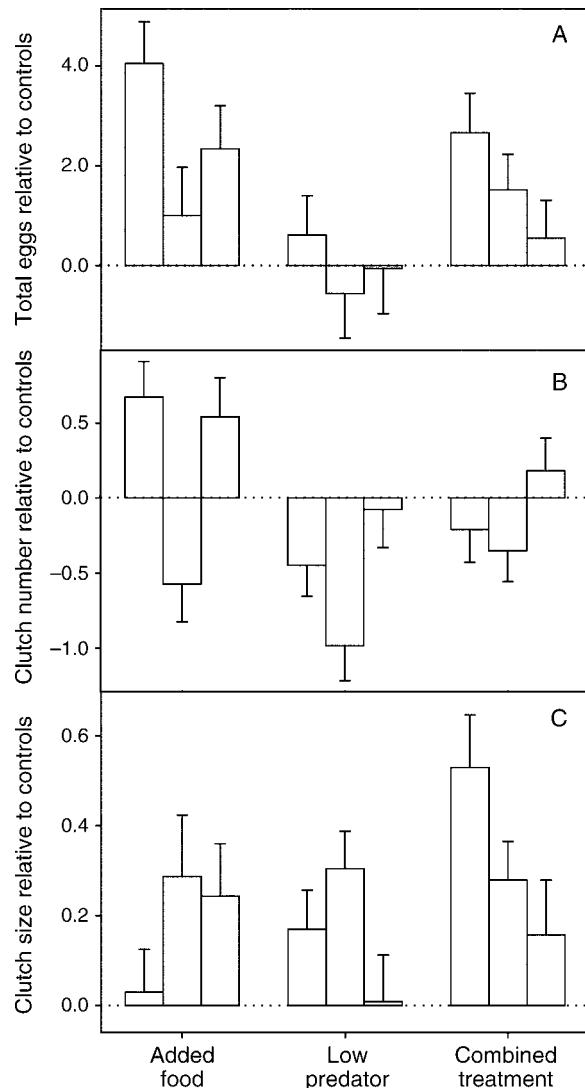

FIG. 1. Effects of the "added food" (fed/high predator pressure [HPP] locations), "low predator" (unfed/low predator pressure [LPP]locations), and "combined" (fed/LPP) treatments, relative to "controls" (unfed/HPP), on (A) total egg production, (B) clutch number, and (C) clutch size. Values are the mean difference (and SE) between results in a given treatment and those at controls (zero line) in the same year. The three bars shown for each treatment represent the results in each of the three years of the study (from left to right: 2000, 2001, and 2002). Observed means ± SE for controls in each year were: (A) 10.1 ± 1.2, 11.5 ± 0.9, 9.9 ± 1.0 eggs; (B) 3.2 ± 0.3, 3.7 ± 0.2, 3.0 ± 0.3 clutches; and (C) 3.2 ± 0.1, 3.1 ± 0.1, 3.3 ± 0.1 eggs per clutch.

$P = 0.013$), consistent with there being more renesting (a higher clutch number) when more nests are lost to predators (lower nest survival). Clutch number and clutch size were also significantly negatively correlated (Fig. 2; $r_S = -0.73$, $t_{10} = 3.4$, $P = 0.007$). Nest survival and clutch size were significantly positively correlated ($r_S = 0.66$, $t_{10} = 2.8$, $P = 0.02$), consistent with a negative correlation between nest predation and clutch size.
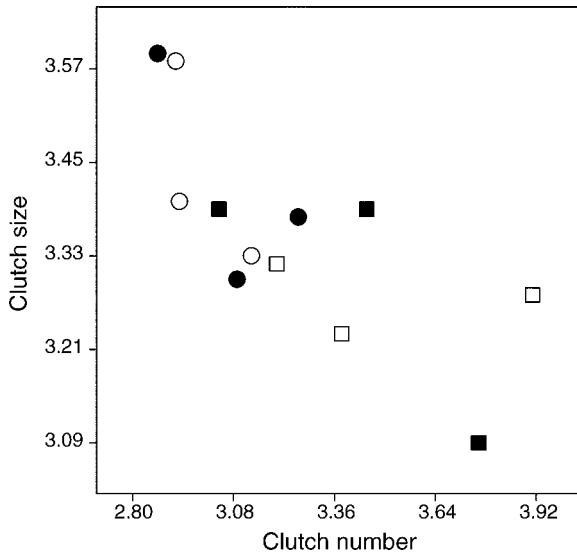
FIG. 2. Correlation between average clutch size and clutch number per treatment per year. Open symbols represent unfed treatments; solid symbols represent fed treatments. Squares represent high predator pressure locations; circles represent low predator pressure locations.

Effects of food effects on nest predation

Considering the magnitude of food effects on nest predation in relation to food effects on clutch number and clutch size, the larger the effect of food addition on nest survival (1 − nest predation) the smaller the effect of food addition on clutch number (Fig. 3; Spearman $r_S = -0.83$, $t_4 = 3.0$, $P = 0.04$). The smaller the effect of food on clutch number, the larger the effect of food on clutch
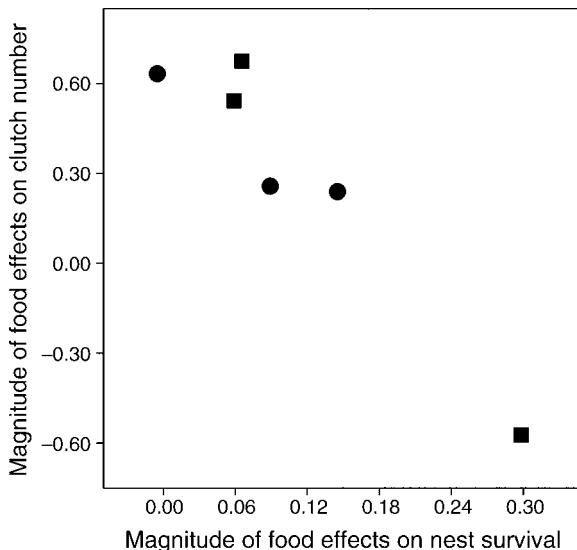

FIG. 3. Correlation between the magnitude of food effects on clutch number and the magnitude of food effects on nest survival (= 1 − nest predation). Squares represent high predator pressure locations; circles represent low predator pressure locations.
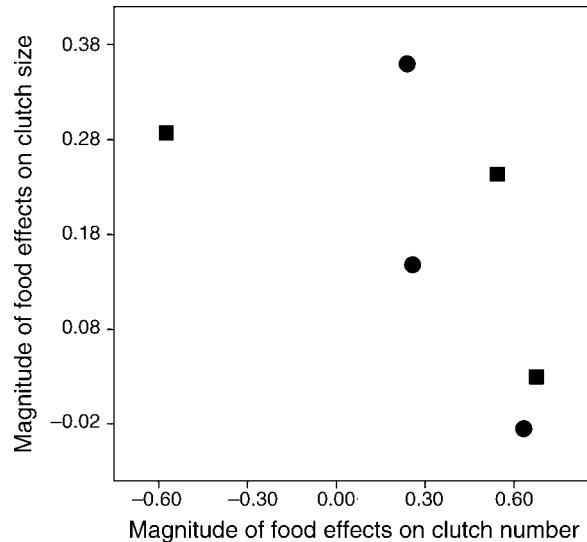

FIG. 4. Correlation between the magnitude of food effects on clutch size and the magnitude of food effects on clutch number. Squares represent high predator pressure locations; circles represent low predator pressure locations.

size (Fig. 4; $r_S = -0.83$, $t_4 = 3.0$, $P = 0.04$). The magnitude of food effects on nest survival was positively, but not significantly, correlated with the magnitude of food effects on clutch size ($r_S = 0.66$, $t_4 = 1.7$, $P = 0.16$).

DISCUSSION

Food set the limit to the total number of eggs laid over the course of the breeding season (Fig. 1A). Interactive food and predator effects (Fig. 1B, C), including food effects on nest predation (Figs. 3 and 4), determined how those eggs were parceled out. Given that predator pressure significantly affected both clutch number (Fig. 1B) and clutch size (Fig. 1C), the two determinants of total egg production, the absence of predator effects on total egg production is at first glance perplexing. The explanation appears to lie in the negative relationship between clutch number and clutch size (Fig. 2) and the absence of changes in egg production attributable to "intimidation" by predators. Predator effects on clutch number and clutch size generally cancelled each other out, as we will discuss. Unlike Scheuerlein et al. (2001), we found no evidence that predator intimidation affected the speed of renesting (as measured by the inter-nest intervals). Similarly, although the negative correlation between nest predation and clutch size that we observed could be the result of intimidation (via Martin's first proximate pathway as described in the *Introduction*), then there should have been a resulting predator effect on total egg production, but there was not (Fig. 1A).

Although food alone affected total egg production (Fig. 1A), Zanette et al. (2006) showed that annual reproductive success over the three years of this study

was a function of both food-restricted egg production (Fig. 1A) and predator-induced loss (Zanette et al. 2006: Fig. 2) and interactive food and predator effects on both clutch and brood loss (Zanette et al. 2006: Figs. 1A and B). Nest survival, total egg production, and partial clutch or brood loss all loaded significantly in a stepwise multiple regression with annual reproductive success as the dependent variable (Zanette et al. 2006). Superficially, predator effects appeared predominant because variation in nest predation accounted for 71% of the variation in annual reproductive success. However, much of the strength of this relationship was due to the significant effect of food addition in reducing nest predation (Zanette et al. 2006).

Our analyses of both clutch number (Fig. 1B) and clutch size (Fig. 1C) revealed a food × predator × year interaction, which we suggest is due in part to the interannual variation in food effects on nest predation reported by Zanette et al. (2006). The effects on clutch number in the "added food" and "low predator" treatments help to illustrate this (Fig. 1B). In every year, "low predator" birds laid fewer clutches than control birds because lower nest predation means less renesting. In two of three years, "added food" birds laid more clutches than "control" birds, as one would expect given that food addition accelerated renesting by reducing inter-nest intervals. In the middle year of the study, however, "added food" birds laid fewer clutches than control birds. In this year, food addition at the "added food" locations reduced nest predation to a level (40%) below that at the "low predator" locations (53%, 25-day nesting period; Zanette et al. 2006: Table 1). As noted, lower nest predation means less renesting. Less renesting means fewer inter-nest intervals and thus less scope for food to affect clutch number by accelerating renesting. Consequently, the magnitude of food effects on clutch number was, in part, determined by the magnitude of food effects on nest predation (Fig. 3). Our data show that the magnitude of food effects on clutch size was, in turn, associated with the magnitude of food effects on clutch number (Fig. 4). As a result, interannual variability in the effects of food on clutch size was associated with interannual variability in the effects of food on nest predation.

The effect of food addition on clutch size has generally been found to be highly variable; when no increase is observed, this is typically attributed to either the quality of the food provided or interannual variability in natural food abundance (Nager et al. 1997, Visser and Lessells 2001). Neither explanation can account for our results because we found strong and consistent food effects on total egg production (Fig. 1A). Instead, our data (Figs. 3 and 4) suggest that the often-observed variability in food effects on clutch size may, in some species, be due to variability in the effects of food on nest predation.

Nagy and Holmes (2005) recently showed that food addition significantly increased clutch number in Black-throated Blue Warblers (*Dendroica caerulescens*); they suggested that food effects on clutch number may be more important than effects on clutch size in determining annual reproductive success in multi-brooded species of songbirds. Our results showing a significant ($P = 0.041$) food effect on clutch number reinforce those of Nagy and Holmes (2005) and we strongly agree (as do Grzybowski and Pease 2005) that more attention should be paid to effects on clutch number. However, in our case, looking at clutch number alone, independent of clutch size, would have led to the erroneous conclusion that egg production in Song Sparrows was primarily determined by predators ($P = 0.008$) given that the more nests were preyed upon, the more sparrows renested. Instead, because clutch number and clutch size were strongly negatively correlated (Fig. 2), predator effects on one were cancelled out by effects on the other, with the result that there were no significant predator effects on total egg production. This canceling out is most clearly illustrated by the results from the "low predator" treatment (Fig. 1). "Low predator" birds laid markedly fewer clutches than controls (Fig. 1B), each with markedly more eggs (Fig. 1C); the net result being that the difference between the low predator and control locations in mean total egg production per year over the three years of the study was <0.01 eggs (Fig. 1A). This example equally well illustrates that looking at clutch size alone, independent of clutch number, also would have led to erroneous conclusions.

Martin (1995), in an interspecific comparison among the passerines, showed that clutch number and clutch size were strongly negatively correlated. As Martin (1995, 2004) has repeatedly emphasized, the mechanisms underlying inter- and intraspecific variation need not, and, in some respects cannot, be the same. The strongly negative correlation between clutch number and clutch size that we report (Fig. 2) is therefore novel because it is an intraspecific phenomenon and so is distinct from the interspecific pattern shown by Martin (1995).

No doubt because of the paucity of studies addressing proximate effects on clutch number (Grzybowski and Pease 2005, Nagy and Holmes 2005), there is little theory on the potential mechanism(s) underlying an intraspecific, negative correlation between clutch number and clutch size, such as we have shown (Fig. 2). We suggest that the most parsimonious hypothesis is that there is a cumulative energetic, nutrient, or physiological cost to laying ever more clutches, resulting in a successive decline in clutch size. Energy and/or nutrients clearly limit total egg production, as we have shown (Fig. 1A). On the other hand, our provision of an ad libitum, high-fat, high-protein, and high-calcium supplemental feed did not affect the negative relationship between clutch number and clutch size because both fed (Fig. 2, solid circles) and unfed (Fig. 2, open circles) birds showed the same pattern. It is the cumulative, rather than the instantaneous, cost of egg production (Monaghan and Nager 1997, Veasey et al. 2001, Williams 2005), there-

fore, that appears to be the key to understanding this phenomenon. Experimentally inducing renesting by removing successive clutches and testing effects on egg quality and indices of female condition (such as pectoral muscle mass; Veasey et al. 2001) would seem to be the most expedient means of addressing the proximate mechanism(s) responsible for this phenomenon.

Zanette et al. (2003, 2006) and Clinchy et al. (2004) discussed the many parallels between the results from our experiment and those from a bi-factorial food and predator experiment on snowshoe hares (Krebs et al. 1995) and arctic ground squirrels (Karels et al. 2000). In light of these parallel demographic results and the many hundreds of studies on both birds and mammals showing interactive food and predator effects on behavior (reviewed in Lima 1998), we suggest that future demographic studies on both birds and mammals should begin by assuming (i.e., should take as their null hypothesis) that food and predator effects are intimately linked.

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