



# Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*

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Food and predators are thought to have independent effects on avian reproductive success. Several studies have now shown that extra food can reduce nest predation rates. Most hypotheses suggest that this is due to changes in adult and/or nestling behaviour. A critical test as to whether behaviour is key, is to examine when predation events occur for birds with and without extra food. If behaviour is important, extra food should lead to fewer nest predation events during the day, when birds are active, but have no effect at night. We conducted a food supplementation experiment on song sparrows and tested for food effects on timing of nest predation events, adult antipredator behaviour and nestling begging behaviour. Food supplementation significantly reduced the relative frequency of daytime nest predation especially during incubation. During incubation, fed females had shorter foraging bouts and longer bouts on the nest, and these behaviours were associated with a reduced probability of being preyed upon. During brooding, we found trends ( $P < 0.1$ ) towards lower daytime predation and greater adult nest attendance for fed birds than for unfed birds, but nestling begging did not differ with food treatment. Our results show that food availability does influence nest predation through its effect on antipredator behaviour. We highlight the importance of examining adult behaviour and vulnerability to predation at both stages of the nesting period because behavioural changes with extra food were extreme at the egg stage and were more effective at reducing nest predation than were behavioural changes at the nestling stage.

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Food and predators are two of the most important factors limiting reproductive success in birds and mammals (reviewed in Boutin 1990; Newton 1998). In general, it is assumed that food availability affects reproduction (i.e. clutch/litter size, hatching success in birds, number of offspring fledged/weaned) and partial brood loss through starvation (Martin 1987; Boutin 1990), while the abundance of predators affects complete brood loss (Ricklefs 1969; Martin 1992, 1993). However, studies have now demonstrated that increased food availability can significantly reduce predation on avian nests (Yom-Tov 1974; Högstedt 1981; Ward & Kennedy 1996; Zanette et al. 2006). Most hypotheses suggest that increased food availability reduces nest predation through changes in adult (Yom-Tov 1974; Dewey & Kennedy 2001) or nestling (Högstedt 1981; Ward & Kennedy 1996) behaviour. A

critical test of whether changes in behaviour are in fact the mechanism responsible for food effects on nest predation is that extra food should lead to a reduction in predation events that happen during the day when birds are indeed behaving. By contrast, food availability should have little bearing on nest predation at night because, generally speaking, most birds are inactive at night. Therefore, when tallying up all predation events for birds with access to extra food, we should observe proportionately less predation during the day. No such pattern should exist for unsupplemented birds.

Increased food availability reduces foraging time and, in turn, allows more time for antipredator activities (Martin 1987; Lima 1998; Nagy & Holmes 2005), such as nest guarding, which can potentially deter predators (Arcese & Smith 1988; Martin 1992; Ward & Kennedy 1996). Also, high food supply may allow parents to provision their offspring more often, which can decrease the intensity of begging by nestlings (Smith & Montgomerie 1991; Price & Ydenberg 1995), thereby decreasing their conspicuousness to predators (Haskell 1994; Leech & Leonard 1997). Although it is clear that food availability can

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influence adult antipredator behaviour and nestling begging behaviour, in order to determine the effectiveness of these behaviours at reducing nest predation, we must investigate whether the behaviour affected by food availability influences the fate of the nest.

Most studies have examined the effects of food on adult behaviour at the nestling stage (Simons & Martin 1990; Ward & Kennedy 1996; Nagy & Holmes 2005), whereas behaviour during incubation and its effect on nest predation has largely been overlooked. Increases in food availability that increase time spent on the nest at the egg stage are likely to have positive consequences by concealing the nest and its contents (Weidinger 2002). At the nestling stage, however, increases in food availability could have positive effects by increasing time spent at the nest and decreasing begging behaviour, but it also may increase the number of parental feeding trips (Simons & Martin 1990) and the likelihood of the nest being discovered by a predator (Skutch 1949). Therefore, when examining the effects of food surplus on overall nest predation (i.e. during the egg and nestling stages combined), the reduced conspicuousness to diurnal predators at the egg stage might be counter-balanced by the increased conspicuousness at the nestling stage, thereby producing a null effect of food on nest predation. Distinguishing between effects during these two stages should help us better understand how food availability affects adult behaviour and vulnerability to diurnal nest predation.

Zanette et al. (2006) showed that experimental food supplementation significantly reduced nest predation in song sparrows. In the present study, we tested for effects of supplemental food on the timing of nest predation events, adult antipredator behaviour and nestling begging behaviour. We then tested whether the behaviour affected by food supplementation in turn was associated with whether or not a nest was preyed upon. We conclude that food availability does indeed affect nest predation through changes in adult behaviour, especially during incubation, and we suggest that future studies would benefit from considering food effects on both incubation and brood-rearing behaviour.

## METHODS

### General Field Methods

We studied song sparrows near Victoria, British Columbia, Canada in 2003. Song sparrows build open-cup nests on the ground or in bushes (e.g. *Rubus* sp.), and are multi-brooded with pairs rearing up to four broods of one to four young per year. Females alone incubate, but both parents care for the young. Song sparrows typically lay a clutch of three to four eggs, incubate for 13 days and fledge nestlings 10–12 days posthatch. We monitored 75 song sparrow territories at 14 study sites. Pairs of sites were selected that were matched for vegetation: one site was then provided with supplemental food (fed) and the other site remained an unsupplemented (unfed) control. Fed and unfed territories were separated by a minimum of 200 m (four territory lengths; Clinchy et al. 2004) and

a maximum of 1 km. Individuals were capable of moving between any two sites (Smith et al. 1996), but never did so following territorial establishment each spring.

Supplemental food was provided ad libitum from 1 March to 5 August 2003. The feed consisted of equal parts of white proso millet and high fat/high protein pellets (Purina Mills Aquamax Grower 400, St Louis, Missouri, U.S.A.), with approximately 2 g of oyster shell per kilogram of feed. Food was supplied in a gravity-fed feeder (41 × 41 × 30 cm) elevated 1 m above the ground at the centre of the territory. Feeder watches confirmed that each target pair used the feeder (Zanette et al. 2003). We also occasionally observed parents feeding the supplemental food to their nestlings. Nests were monitored every 3–4 days to determine their fate (preyed upon or fledged). We never observed entire broods dying from starvation, and nonpredator nest failures (e.g. floods) were rare and excluded from the analyses. Further details can be found in Zanette et al. (2003, 2006).

### Time of Predation

We quantified the time when predation events occurred using Onset Computer Corp. HOBO Temp/External temperature data loggers (Bourne, Massachusetts, U.S.A.). Sensor probes were inserted in the bottom of nests from as early as the fourth day of incubation up to day 5 of the nestling stage. Nest temperature was recorded once every 2 min. Data loggers remained at nests until a predation event occurred or the young fledged. Ambient temperature at each site was recorded every 30 min.

To assess the time of predation, we compared nest and ambient temperature patterns (see also Wiebe & Martin 1997). This methodology was calibrated using data from 13 miniature 24-h video cameras (Sandpiper Technologies Inc., Manteca, California, U.S.A.). Average nest temperature was 23.4°C. We identified nest predation times as a drop in nest temperature (average 18% drop) to ambient temperature (average 12.7°C). At temperatures below 24°C embryo development in the egg ceases (Haftorn 1988; Conway & Martin 2000) and nestlings become hypothermic (Chaplin et al. 2002), so nests that were continuously at ambient temperature were considered empty. Predation times were categorized as diurnal, nocturnal or crepuscular based on sunrise and sunset times. Crepuscular events occurred in the 1-h time period around sunrise and sunset. The time of predation was determined from 71 nests with data loggers.

### Behaviour of Adults

Temperature data loggers allowed us to sample a given female's behaviour at the nest continuously over several days during the egg and nestling stages. The loggers were effective at quantifying female incubation rhythms as the temperature in the nest increased and decreased with the arrival and departure of the female on the nest (see also Weathers & Sullivan 1989; Joyce et al. 2001). We used video recordings of 13 nests that also contained data

logger probes to confirm that the temperature patterns were reflective of female activity patterns.

We obtained data from 23 food-supplemented and 32 control females during the incubation stage, and 15 food-supplemented and 20 control females during the nestling stage. We calculated four female behaviour measurements during both incubation and brooding: total proportion of time spent on the nest (total time spent on nest/daytime activity period), average time spent incubating/brooding (on-nest bout), average time spent foraging (off-nest bout) and the number of departures from the nest per hour.

During the nestling stage, we conducted focal animal sampling at 14 food-supplemented and 19 control nests, for 1 h between 0700 and 1200 hours, on day 6 or 7 of the nestling stage, to complement the female behaviour information extracted from the thermal data. We observed the nest from approximately 15 m, and every 7 s we noted whether one or both parents were at or within 5 m of the nest to obtain a measure of total parental nest attendance. A distance of 5 m has been widely used in parental behaviour studies (e.g. Smith et al. 1984; Knight & Temple 1988). We also counted the number of provisioning trips and calculated the feeding rate per hour per nestling.

### Behaviour of Nestlings

To determine whether food supplementation affected begging behaviour, we simultaneously audio-recorded nestling begging behaviour while observing parental behaviour at 14 food-supplemented and 19 control nests. We used an Optimus 33-3003 lapel microphone attached 10 cm from the nest rim and connected to a Marantz PMD-222 audio-cassette recorder about 15 m away. After installing the audio recording equipment, we waited at least 20 min before starting the session to allow the adult sparrows to resume normal feeding behaviour. We calibrated our amplitude measurements in an anechoic chamber at the University of Western Ontario (Duncan Rastogi 2005). We measured begging bout duration (s) and call rate (number of calls/bout duration  $\times$  60 s). We also calculated relative amplitude as begging amplitude minus background amplitude (amplitude standard is root mean square sound pressure, in dB, re. 0.02 mPa). Data from all clear bouts throughout the hour were averaged.

### Statistical Analyses

As noted in the Introduction, Zanette et al. (2006) showed that the proportion of nests that were preyed upon, from among all nests, was lower among supplemented than unsupplemented birds (i.e. nest survival was higher among supplemented birds). Here we were interested only in nests that were preyed upon. Among those nests that were preyed upon, we compared the proportion that were preyed upon during the day versus the night between fed and unfed birds. We conducted a simple  $2 \times 2$  contingency table of these data. Such an analysis may be conservative given that there are almost twice as many exposure hours during the day (14.1 h on average) as there are during the night (7.8 h on average), so one

might expect there to be roughly twice as many diurnal predation events as there are nocturnal predation events. Consequently, we conducted a second analysis (i.e. goodness-of-fit test) comparing the observed predation events against the expected frequencies given the above ratio of exposure hours. We conducted each of the preceding analyses on data from the incubation and brood-rearing stages separately, and pooled data from both stages. Before conducting these analyses, we verified that there were no biases associated with season.

To test the effects of food availability on female behaviour, we conducted one-way ANOVAs or ANCOVAs comparing each of the four female behaviour variables between fed and unfed birds at the incubation and brood-rearing stages. We evaluated five potential covariates using simple linear regressions: clutch size, brood size, ambient temperature, incubation age and nestling age; there was no effect of clutch size, brood size or incubation age.

To test whether these behaviours were in turn associated with the probability of being preyed upon, we conducted a binomial logistic regression with occurrence of predation as the dependent variable (coded yes or no) and the four behaviour variables as continuous predictors. Separate regressions were conducted for the egg and nestling stages. We used a backwards-stepwise procedure to find the most parsimonious model following the procedures outlined in Hosmer & Lemeshow (2000).

To test whether food availability affected parental nest attendance and feeding visits, we conducted one-way ANOVAs comparing total parental nest attendance and the number of feeding visits per hour per nestling between fed and unfed territories. We evaluated four potential covariates using simple linear regressions: brood size, ambient temperature, Julian date and age of nestlings, none of which was significant.

Where we found significant food effects on behaviour at a particular stage (i.e. eggs or nestlings) and we found a significant association between behaviour and the probability of predation (logistic regression above), we conducted a second logistic regression to determine whether the relevant behaviour, for unfed birds only, was associated with the probability that the nest was preyed upon during that stage only. This procedure was designed to establish that: (1) adding food influenced behaviour; and (2) the behaviour in question (independent of feeding) influenced nest predation risk.

To test whether food affected nestling begging behaviour, we compared each of the three begging behaviour variables between fed and unfed birds using either one-way ANOVAs or ANCOVAs. We evaluated four potential covariates using simple linear regressions: brood size, nestling age, ambient temperature and Julian date. There was no effect of brood size, ambient temperature or Julian date.

Assumptions of normality and homogeneity of variances were met and all statistical analyses were performed in SPSS 12.0 (SPSS 12.0, Chicago, Illinois, U.S.A.) and Statistica 6.1 (StatSoft, Tulsa, Oklahoma, U.S.A.). We set  $\alpha$  at 0.05 and all statistical tests for adult and nestling behaviour were two tailed. Unless indicated, for ease of interpretation, figures show least-squared means  $\pm$  1 SE using the untransformed data.

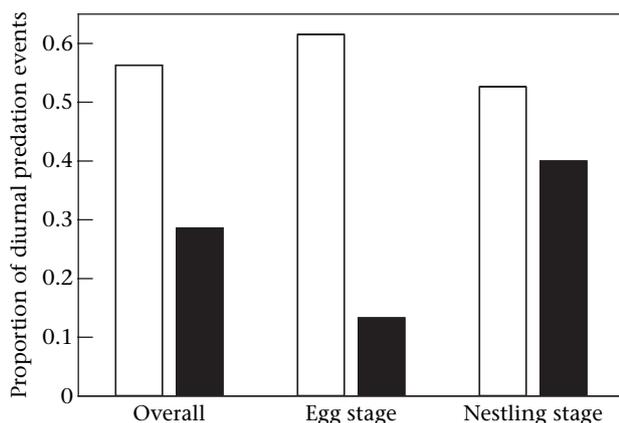
## RESULTS

### Time of Predation

Considering first the data uncorrected for daylength, fed birds experienced a significantly lower proportion of diurnal nest predation events than did unfed birds (29% of 35 predation events for fed birds were diurnal versus 56% of 32 for unfed birds; Fisher's exact one-tailed test:  $P = 0.020$ ; Fig. 1). Distinguishing between the incubation and brood-rearing periods, fed birds suffered a significantly lower proportion of diurnal nest predation events than did unfed birds during incubation (13% of 15 predation events for fed birds were diurnal versus 61% of 13 for unfed birds; Fisher's exact one-tailed test:  $P = 0.011$ ; Fig. 1), but there was no difference between fed and unfed birds during brood-rearing (40% of 20 predation events for fed birds were diurnal versus 53% of 19 for unfed birds; Fisher's exact one-tailed test:  $P = 0.320$ ; Fig. 1). When we corrected for daylength, the effects of food were clearer still: fed birds had significantly fewer diurnal nest predation events over both nesting stages combined (fed: 10 observed versus 23 expected; unfed: 18 observed versus 21 expected; goodness-of-fit test:  $\chi^2_3 = 22.7$ ,  $P < 0.0001$ ), and during the incubation stage (fed: 2 observed versus 10 expected; unfed: 8 observed versus 8 expected;  $\chi^2_3 = 19.2$ ,  $P = 0.0002$ ). Correcting for daylength highlighted a tendency towards food effects during the brood-rearing period (fed: 8 observed versus 13 expected; unfed: 10 observed versus 12 expected;  $\chi^2_3 = 6.4$ ,  $P = 0.094$ ).

### Behaviour of Adults

Ambient temperature and Julian date varied positively with all behaviour variables except for bout length off the nest (simple linear regression: ambient temperature: proportion of time on the nest:  $R^2_{300} = 0.07$ ,  $P = 0.0001$ ; bout length on the nest:  $R^2_{286} = 0.07$ ,  $P = 0.0001$ ; bout length off the nest:  $R^2_{286} = 0.01$ ,  $P = 0.866$ ; departures/h:  $R^2_{287} = 0.07$ ,  $P = 0.0001$ ; Julian date: proportion of time



**Figure 1.** Proportion of preyed upon song sparrow nests that were taken during the day (diurnal predation events/(diurnal + nocturnal predation events)). □: control (unfed); ■: food-supplemented (fed) song sparrow territories. 'Overall' results include all data, which were then subdivided into nests that were preyed upon during the 'egg stage' or the 'nestling stage'.

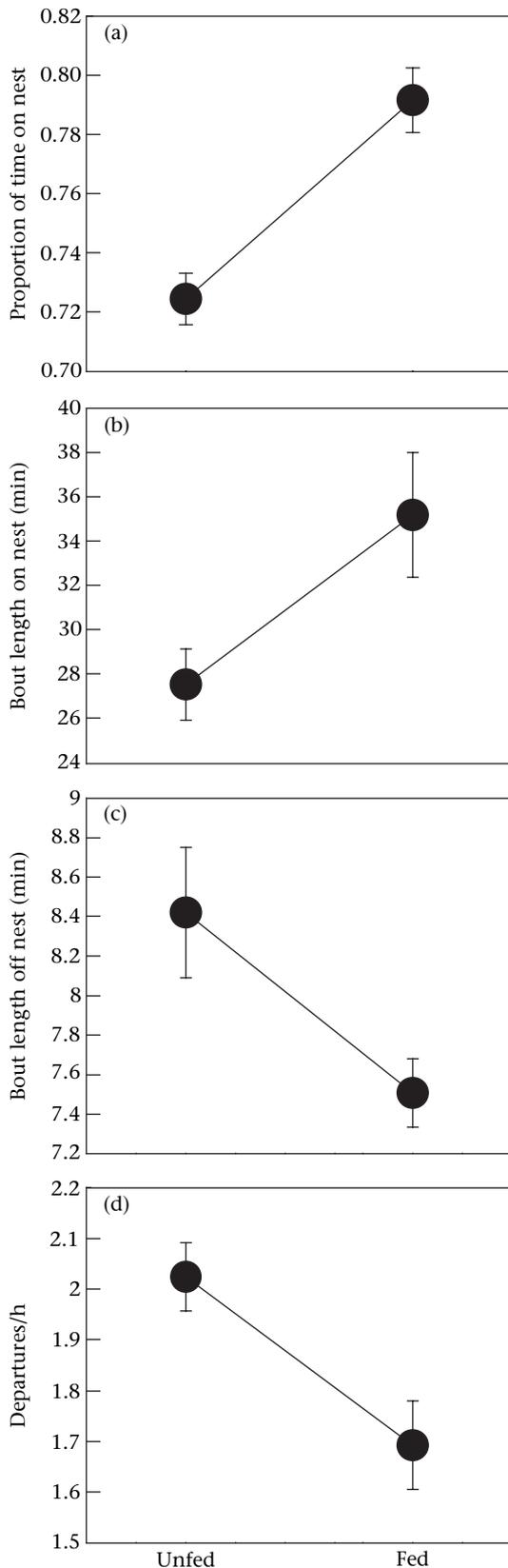
on the nest:  $R^2_{289} = 0.01$ ,  $P = 0.567$ ; bout length on the nest:  $R^2_{289} = 0.03$ ,  $P = 0.003$ ; bout length off the nest:  $R^2_{289} = 0.01$ ,  $P = 0.156$ ; departures/h:  $R^2_{289} = 0.02$ ,  $P = 0.016$ ). We included only ambient temperature as a covariate in our models because temperature and Julian date were highly correlated ( $R^2 = 0.65$ ,  $P < 0.0001$ ), and temperature explained more of the variation in the behaviour data ( $R^2$  values above).

During incubation, fed birds spent proportionately more time on the nest (ANCOVA:  $F_{1,53} = 23.6$ ,  $P = 0.001$ ; Fig. 2), had longer incubation bouts (ANCOVA:  $F_{1,53} = 7.2$ ,  $P = 0.01$ ; Fig. 2), made fewer departures/h (ANCOVA:  $F_{1,53} = 10.7$ ,  $P = 0.002$ ; Fig. 2) and had shorter foraging bouts (ANOVA:  $F_{1,53} = 4.1$ ,  $P = 0.047$ ; Fig. 2) than did unfed birds. The backwards-stepwise binomial logistic regression indicated that these behaviours were associated with the probability that a nest would be preyed upon (logistic regression:  $\chi^2_3 = 10.4$ ,  $P = 0.016$ ), with bout length off the nest (Wald statistic:  $W_1 = 6.8$ ,  $P = 0.009$ ) and bout length on the nest ( $W_1 = 3.8$ ,  $P = 0.052$ ) being particularly important. Since adult behaviour was significantly affected by food availability and these behaviours were associated with nest predation risk, we conducted a second logistic regression. In this case, we restricted the data to unfed birds and considered only nests that survived or failed the incubation stage. Again, we found that adult behaviour was significantly associated with whether or not a nest was preyed upon (backwards-stepwise logistic regression:  $\chi^2_2 = 7.1$ ,  $P = 0.028$ ), with female bout on the nest being especially important ( $W_1 = 4.1$ ,  $P = 0.042$ ). Thus, females given extra food showed behaviour at the nest that was beneficial in reducing predation risk.

During brood-rearing, nestling age affected the proportion of time that females were on the nest (one-way ANOVA:  $F_{4,140} = 8.4$ ,  $P = 0.001$ ) and was included as a covariate for this variable. There were no significant differences in the behaviours of fed and unfed females measured using data loggers (ANCOVA: proportion of time on the nest:  $F_{1,33} = 0.15$ ,  $P = 0.705$ ; ANOVAs: bout length on the nest:  $F_{1,33} = 0.04$ ,  $P = 0.834$ ; departures/h:  $F_{1,33} = 0.07$ ,  $P = 0.794$ ; bout length off the nest:  $F_{1,33} = 0.87$ ,  $P = 0.358$ ), and there was no significant association between a female's behaviour and whether or not the nest was preyed upon (backwards-stepwise logistic regression:  $\chi^2_4 = 2.5$ ,  $P = 0.638$ ). Our focal animal sampling of both parents showed that food-supplemented adults spent slightly more time attending the nest (i.e. proportion of time spent at or within 5 m of the nest) ( $\bar{X} \pm \text{SE} = 0.59 \pm 0.05$ ,  $N = 14$ ) than did unfed adults ( $0.45 \pm 0.05$ ,  $N = 19$ ; ANOVA:  $F_{1,31} = 3.9$ ,  $P = 0.057$ ), however, there was no effect of food supplementation on the number of feeding visits per hour per nestling (fed:  $\bar{X} \pm \text{SE} = 4.52 \pm 0.50$ ,  $N = 14$ ; unfed:  $4.40 \pm 0.46$ ,  $N = 19$ ; ANOVA:  $F_{1,31} = 0.6$ ,  $P = 0.445$ ). Neither nest attendance nor visits per hour were associated with whether or not a nest was preyed upon (backwards-stepwise logistic regression:  $\chi^2_2 = 0.14$ ,  $P = 0.921$ ).

### Behaviour of Nestlings

Nestling age affected the relative amplitude of begging calls (simple linear regression:  $R^2 = 0.19$ ,  $P = 0.009$ ) and



**Figure 2.** Female behaviour during incubation at control and food-supplemented territories. (a) Proportion of time on the nest. (b) Bout length on the nest. (c) Bout length off the nest. (d) Number of departures per hour. Values are least-square means  $\pm$  SE.

was included as a covariate for this variable. Nestlings in the food-supplemented treatment had begging bouts that were somewhat shorter (fed:  $\bar{X} \pm \text{SE} = 21.83 \pm 2.51$  s,  $N = 14$ ; unfed:  $22.23 \pm 2.16$  s,  $N = 19$ ) and lower in relative amplitude (fed:  $11.03 \pm 1.42$  dB,  $N = 14$ ; unfed:  $12.45 \pm 1.22$  dB,  $N = 19$ ), and they called at a lower rate (fed:  $110.70 \pm 11.95$  calls/min,  $N = 14$ ; unfed:  $122.82 \pm 10.26$  calls/min,  $N = 19$ ), but none of these differences were significant (ANOVA: duration:  $F_{1,30} = 0.01$ ,  $P = 0.911$ ; ANCOVA: relative amplitude:  $F_{1,29} = 0.08$ ,  $P = 0.780$ ; ANOVA: rate:  $F_{1,30} = 0.33$ ,  $P = 0.567$ ).

## DISCUSSION

Food availability was related to both parental behaviour and time of predation in song sparrows. Food-supplemented birds spent more time engaged in antipredator activities and suffered proportionately less diurnal nest predation than did control birds, particularly at the egg stage. Female sparrows with additional food had longer incubation bouts on the nest, shorter foraging bouts off the nest, fewer departures from the nest per hour and they spent a greater proportion of their time on the nest than did control females. The change in the behaviour of females given extra food was also an important predictor of the occurrence of nest predation. Females that had short foraging bouts and long incubation bouts were least likely to have their nests preyed upon. Food-supplemented parents had more time available for guarding and attending their nestlings than did their unfed counterparts, but this had no impact on the probability of nest predation. Additional food was not associated with more feeding visits to the nest, nor did it significantly alter begging activity of offspring.

Our results show that food supplementation was associated with both an increase in antipredator behaviour and a relative decrease in diurnal nest predation events in song sparrows, consistent with hypotheses proposed by Yom-Tov (1974), Högstedt (1981) and Martin (1992) that food supplementation indirectly reduces nest predation because it allows adult birds to spend less time away from the nest foraging for food and, consequently, to have more time available for guarding and defending the nest from predators. Establishing that diurnal nest predators were prevalent was the first step in evaluating this indirect behavioural mechanism. Those few studies that have simultaneously measured adult behaviour and nest predation have largely been correlative (Knight & Temple 1988; Olendorf & Robinson 2000) and have consistently looked at behaviour and overall nest predation rates (Cresswell 1997; Komdeur & Kats 1999). While these studies suggest that behaviour does affect predation, our results on adult behaviour and diurnal predation provide a more direct link, given that birds are only active in the daytime.

Adult antipredator behaviour is a function of food availability, and thus, more time should be allotted to antipredator behaviour when food is plentiful (Martin 1992). We observed strong food effects on female behaviour at the egg stage and more mild food effects on the

behaviour of both parents at the nestling stage. Taking advantage of a high-quality supplemental food source (e.g. with high fat and protein content) keeps adults in better physiological condition (Cucco et al. 2002; Clinchy et al. 2004) and consequently allows them to spend less time and energy foraging and more time nest guarding (Martin 1987; Dewey & Kennedy 2001). Our results on adult behaviour at the egg stage are consistent with several food supplementation experiments on incubating passerines (e.g. Arcese & Smith 1988; Eikenaar et al. 2003; Pearse et al. 2004). Increasing time spent sitting on the nest and reducing time away from the nest has been proposed as a passive nest defence strategy (Martin 1992; Martin et al. 2000) that may be effective at camouflaging the nest and its contents (Montgomerie & Weatherhead 1988; Martin 1992), while also potentially deterring predation (Schmidt et al. 2001; Weidinger 2002). In addition, prolonged absence from the nest increases the vulnerability of the nest to incidental predation (Cadiou & Monnat 1996; Samelius & Alisauskas 2001; Tewksbury et al. 2002). In our study, not only did female behaviour change with food supplementation, but also the changes in behaviour were effective at reducing the proportion of diurnal predation events and the probability of nest predation overall, because females that spent less time away and more time on the nest at the egg stage were less likely to suffer from nest predation. Therefore, food-supplemented song sparrows in our study showed behaviour that is consistent with a passive nest defence strategy.

As opposed to the egg stage, where female song sparrows divide their time between incubating and foraging, the nestling stage requires the parental care of both adults to share the duties of feeding, guarding and defending nestlings. We suggest that the weaker effect of food supplementation on adult nest attendance is due to the increased demand on parents' time to forage both for themselves and their nestlings. In a food addition experiment on northern goshawks, *Accipiter gentilis*, food-supplemented females significantly increased the time they spent nest guarding at the nestling stage (Ward & Kennedy 1996). However, the parenting strategy of northern goshawks may have allowed for this increase because males forage for themselves and the nestlings, whereas females forage only for themselves (Ward & Kennedy 1996).

Supplemental food led to large increases in antipredator behaviour, which strongly reduced vulnerability to diurnal predators at the egg stage but not at the nestling stage. We propose two reasons why increased nest attendance was not effective at reducing the relative frequency of diurnal nest predation events at the nestling stage, each depending on how nest defence is accomplished at each stage for song sparrows. First, small songbirds, including song sparrows, seem capable of deterring species that cause nest failure at the egg stage (Olendorf & Robinson 2000). If deterrence is an important defence tactic, then our results suggest that adult sparrows are less able to deter predators of nestlings than they are those of eggs, indicating that predators of nestlings may be relatively large and aggressive birds (e.g. raptors, McCallum & Hannon 2001), medium-sized mammals (Pietz & Granfors 2000) and/or snakes (reviewed in Weatherhead

& Blouin-Demers 2004). Second, the nestling stage is undoubtedly more conspicuous than the egg stage. Indeed, in our study, adult sparrows made 13.5 departures/h during the nestling stage and only 1.9 departures/h during incubation. Therefore, the moderate increase in nest attendance that we observed with food supplementation during chick rearing may not have been enough to offset the increased conspicuousness of nests containing young (see also Tewksbury et al. 2002).

Although begging behaviour has been well studied in the laboratory (Haskell 1994; Leech & Leonard 1997; Dearborn 1999; but see Redondo & Castro 1992; Halupka 1998), we are not aware of any prior study that has measured begging behaviour in relation to both food availability and nest predation in the field. Food deprivation experiments in the laboratory have found that nestling hunger levels are encoded in their begging calls (Smith & Montgomerie 1991; Price & Ydenberg 1995; Leonard & Horn 2001). Therefore, we expected the begging behaviour of nestlings on food-supplemented territories to be significantly less conspicuous than that of nestlings on control territories (Högstedt 1981; Ward & Kennedy 1996). However, our results suggest that all song sparrow nestlings were comparably hungry and conspicuous, regardless of food availability. Nestlings may require an extended period of starvation for begging behaviour to dramatically increase, and it is unlikely that nestlings in our control treatment showed the same level of food deprivation as that seen in the laboratory studies, because we have never observed entire broods of song sparrows dying of starvation. As the majority of studies exploring the predation cost of begging have used artificial nests broadcasting nestling begging calls (Haskell 2002), further work is needed on begging in natural nests to determine whether nestling begging behaviour really does increase vulnerability to nest predation.

Our results suggest that the diel periodicity of the main nest predators could help to explain discrepancies in the literature where food supplementation has reduced nest predation in some cases (Yom-Tov 1974; Högstedt 1981) but not in others (Hochachka & Boag 1987; Arcese & Smith 1988). If in some cases the predators were primarily diurnal, then the behaviour of parents or nestlings would have affected vulnerability to predation, but if the predators were primarily nocturnal, behaviour would have had little effect on vulnerability to predation. Similarly, supplemental food often leads to a strong reduction in nest predation in some years but not in others (Ward & Kennedy 1996; Zanette et al. 2006). In these cases, the relative abundance of diurnal to nocturnal predator species might change from year to year (Weidinger 2002; Schmidt & Ostfeld 2003), and the change in behaviour with food supplementation should be most effective in years where diurnal predators are most prevalent.

We show a clear link between food availability and vulnerability to nest predation via adult behaviour. During incubation, food-supplemented females showed more antipredator behaviour and, in turn, suffered a lower relative frequency of diurnal nest predation than did control birds. In contrast, during brood-rearing, there was a tendency for parental nest attendance to increase and vulnerability to diurnal nest predators to decrease with

food supplementation, but otherwise there was little evidence of food effects. The next step is to identify which particular species are the most important egg and nestling predators to understand in detail how changes in adult behaviour reduce vulnerability to certain types of diurnal nest predators.

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