

Food supplementation leads to bottom-up and top-down food–host–parasite interactions

Liana Zanette^{1*} and Michael Clinchy²

¹Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada; and ²Department of Biology, University of Victoria, Victoria, BC V8W 3N5, Canada

Summary

1. Food–prey–predator interactions may involve both ‘bottom-up’ and ‘top-down’ processes. Conventionally, food–host–parasite interactions have been seen as governed solely from the ‘bottom-up’, i.e. well-fed hosts can better resist parasites and so suffer less parasitism. Recent studies on diverse endo- and ecto-parasites increasingly highlight that well-fed hosts provide parasites with a better resource base, and so may be more likely to be parasitized.
2. Brood parasites exploit host parental behaviour by laying their eggs in others’ nests. The brown-headed cowbird (*Molothrus ater*) is a North American brood parasite that exploits over 100 host species.
3. We conducted a food addition experiment on song sparrows (*Melospiza melodia*), a frequently parasitized cowbird host, near Victoria, BC, Canada. We expected results consistent with conventional ‘bottom-up’ effects because we previously found that food supplemented sparrows better eluded nest predation, and we thus also expected them to be better at eluding cowbird parasitism.
4. Here, we report results to the contrary. Food supplemented sparrows were parasitized as often as non-food supplemented sparrows, were multiply parasitized significantly more often, and suffered significantly more parasitism-induced egg loss. Our results suggest cowbirds preferentially parasitized better fed hosts and cowbirds benefited from doing so as food supplemented sparrows fledged significantly more cowbird young per multiply parasitized nest. The pattern of egg loss also accorded with recent evidence indicating that cowbirds may remove just the right number of host eggs to maximize provisioning of the cowbird nestling.
5. Our work suggests that brood parasitism in vertebrates involves both ‘top-down’ and ‘bottom-up’ processes consistent with the growing number of studies showing that food–host–parasite interactions are more complex than previously thought. One of the conservation implications of our results is that greater food availability may not provide hosts a respite from brood parasitism, but is, nonetheless, beneficial overall.

Key-words: brood parasitism, brown-headed cowbird, *Melospiza melodia*, *Molothrus ater*, multi-scale effects, song sparrow

Introduction

Food–prey–predator interactions are one of the cornerstones of community ecology with recent calls to view food–host–parasite interactions in a similar fashion (Hall *et al.* 2007; Pedersen & Fenton 2007; Raffel, Martin & Rohr 2008). Hosts with access to high quality food (hereafter ‘well-fed’ hosts) should be better at resisting parasites via behavioural and/or physiological mechanisms, and have conventionally been assumed to suffer less from parasitism (Pulkinen & Ebert 2004). However, well-fed hosts also provide the parasite with

a better resource base. A growing number of studies, on endo- and ecto-parasites of both vertebrates and invertebrates, that have experimentally manipulated the host’s diet, confirm that well-fed hosts often may be more, rather than less heavily parasitized (Krasnov *et al.* 2005; Kolluru *et al.* 2006; Hall *et al.* 2007; Tschirren *et al.* 2007; Carvell *et al.* 2008). The net effect of increased food availability on host–parasite interactions is therefore not as predictable as once presumed.

Interspecific brood parasitism has evolved repeatedly in birds and afflicts hundreds of host species (Davies 2000). Brood parasites lay their eggs in other birds’ nests, burdening hosts with the costs of provisioning the brood parasite’s

*Correspondence author. E-mail: lzanette@uwo.ca

nestlings. The brown-headed cowbird (*Molothrus ater*) is a North American brood parasite that successfully exploits more than 100 host species (Kilner, Madden & Hauber 2004). Cowbirds appear less virulent than other brood parasites, like cuckoos, because cowbirds generally do not kill all of the host's young in nests they parasitize though they usually do cause some host offspring mortality (Smith, Taitt & Zanette 2002; Kilner 2005; Zanette *et al.* 2007). Female cowbirds, for example, frequently return to a nest after parasitizing it (i.e. adding their egg) to remove some of the host's eggs (Tewksbury *et al.* 2002). Kilner, Madden & Hauber (2004) presented evidence that removing just the right number of eggs may be part of a strategy aimed at ensuring two host young remain, as this maximizes the host parents' provisioning of the cowbird nestling. Assuming cowbirds are capable of employing a sophisticated strategy to maximize food provisioning of parasitic young, it would be perplexing if they did not preferentially parasitize well-fed hosts that can be better providers of food (Parejo & Avilés 2007).

One of the cornerstones of behavioural ecology is that well-fed prey devote more time to anti-predator behaviour (Caro 2005) and there are compelling reasons to expect that increased anti-predator behaviour may be effective against brood parasites (Raffel, Martin & Rohr 2008). Food supplemented songbird parents typically behave elusively (e.g. reduce the number of visits made to the nest), and also spend more time attending their nest, and these behavioural changes are shown to be effective in reducing nest predation rates (Yom-Tov 1974; Högstedt 1981; Rastogi, Zanette & Clinchy 2006; Zanette, Clinchy & Smith 2006a). Being better at eluding detection by nest predators and thus suffering less nest predation, well-fed parents also may be better at eluding detection by cowbirds and so be less likely to be parasitized (Arcese & Smith 1988). Well-fed parents may further be expected to suffer less egg loss because increased nest attentiveness has been shown to reduce egg removal following parasitism (Tewksbury *et al.* 2002).

Consistent with the growing number of studies highlighting the complexity of food effects on host–parasite interactions, increased anti-predator behaviour could conceivably increase the likelihood of being parasitized. From a cowbird's perspective, lower nest predation rates could provide an added reason for preferring to parasitize well-fed hosts (Krüger 2007; Pöysä & Pesonen 2007) in addition to their increased ability at provisioning the cowbird's young. Surprisingly, given the large literature on brood parasitism, only one previous experimental study (Arcese & Smith 1988) has addressed how increased food availability may affect brood parasitism, and this study examined only the incidence of parasitism (i.e. the presence of at least one cowbird egg in a nest).

In this article, we address whether well-fed hosts suffer less brood parasitism, suffer less when parasitized, and whether cowbirds that parasitize well-fed hosts fare better, in the context of a food addition experiment we conducted on song sparrows (*Melospiza melodia*), a frequently parasitized cowbird host. We previously reported that food supplemented

sparrows fledged significantly more of their own young over the season partly because they produced more eggs (Zanette, Clinchy & Smith 2006b) and also because they suffered significantly less nest predation (Zanette, Clinchy & Smith 2006a). We showed that a reduction in nest predation was associated with food supplemented parents being more elusive (i.e. fewer visits to the nest), and spending more time attending the nest (Rastogi, Zanette & Clinchy 2006). Here, we report that, contrary to the expectation that well-fed hosts can better resist parasitism, food supplemented sparrows actually suffered more brood parasitism, and suffered more, in some respects, when parasitized. The purpose of our article is to establish the consequences of host–parasite behavioural interactions in terms of how cowbirds affect host reproduction especially when the host is well fed. From there, we then infer the nature of these behaviours. We suggest that our results are consistent with cowbirds preferentially parasitizing well-fed hosts, and we present direct evidence that well-fed hosts clearly provide the cowbird with a better resource base. We suggest our findings add to the growing number of studies demonstrating that food–host–parasite systems often are not uni-directional, wherein food affects the host which then affects the parasite, but rather show more complex interactions.

Materials and methods

FIELD PROCEDURES AND FOOD SUPPLEMENTATION

Our study was conducted as part of an experiment described in full by Zanette, Clinchy & Smith (2006a,b). We monitored song sparrow populations resident in Victoria, BC, Canada, over three consecutive breeding seasons. Song sparrows are multi-brooded and in this region can fledge 3–4 broods of 1–5 young per year. On monitored territories, we recorded each female's breeding activities over the entire March–August breeding season (Grzybowski & Pease 2005).

We erected a gravity fed feeder (41 × 41 × 30 cm) elevated 1 m above-ground near the centre of a total of 45 territories over the 3-year study. A total of 65 non-food supplemented territories were monitored over the same period. Territories within six study plots (three with and three without food supplementation) were located over an area of c. 500 ha. Territories with and without supplemental food were separated by at least four intervening territories and non-food supplemented birds were never seen at the feeders (Zanette, Clinchy & Smith 2006b). Feed consisting of equal proportions of white proso millet, similarly sized high fat/high protein (45%) pellets, and about 2 g of oyster shell per kg of feed, was provided *ad libitum* throughout all breeding seasons.

MEASURES OF BROOD PARASITISM

We tested for food effects on nine measures of brood parasitism. To aid in interpretation, we contrast our observed effects with those that may be expected under a generalized 'bottom-up' scenario whereby, based on convention, well-fed hosts are assumed to be better able to resist parasites and so suffer less from parasitism (Table 1). Results from our previous studies (Rastogi, Zanette & Clinchy 2006; Zanette, Clinchy & Smith 2006a) demonstrated that food supplemented sparrows behave less conspicuously at their nests and that by doing so, sparrows elude detection of their nests by natural enemies. The

Table 1. Nine measures of brood parasitism evaluated. Our observed results are compared to those expected from a ‘bottom-up’ scenario where, by convention, well-fed hosts are assumed to be better at avoiding being parasitized, and suffer less when parasitism occurs. Observed results in bold indicate those that matched the expected

Measures of brood parasitism	Bottom-up expectations	Observed results
Presence of cowbird eggs		
Parasitism rate (> 0 cowbird eggs/nest)	Fed < Unfed	Fed = Unfed
Multiple-parasitism rate (> 1 cowbird eggs/nest)	Fed < Unfed	Fed > Unfed
Parasitism-induced sparrow losses		
Egg loss	Fed < Unfed	Fed > Unfed
Egg loss due to multiple parasitism	Fed < Unfed	Fed = Unfed
Nest desertion	Fed < Unfed	Fed = Unfed
Nestling loss	Fed < Unfed	Fed < Unfed
Relative number of sparrows fledging		
Per parasitized nest fledging young	Fed > Unfed	Fed = Unfed
Per territory, when parasitism rate is high	Fed > Unfed	Fed = Unfed
Number of cowbirds fledging		
Per multiply parasitized nest	Fed ≤ Unfed	Fed > Unfed

fact that food enhances anti-predator behaviour is one of the most well established principles in behavioural ecology (Lima 1998; Caro 2005) and it is quite clear that such behavioural changes can have an impressive effect on the reproduction of prey (Preisser, Bolnick & Benard 2005; Creel & Christianson 2008). Thus, based on first principles, we anticipated that by behaving less conspicuously, food supplemented sparrows would be parasitized less often than non-food supplemented birds (Table 1), which is the result Arcese & Smith (1988) reported in their food addition experiment on song sparrows. Multiple parasitism (> 1 cowbird egg/nest) may result from either different cowbird females laying in the same nest or a single cowbird female returning to lay again (Hahn *et al.* 1999; McLaren *et al.* 2003; Ellison, Sealy & Gibbs 2006). If several cowbirds are involved, each laying female must find the nest. In this case, the greater elusiveness of food supplemented birds should lower the rate of multiple parasitism (Table 1). If multiple parasitism primarily involves a single cowbird female returning to lay in a nest she has already found, then food supplemented sparrows should still suffer less multiple parasitism because they spend more time attending their nest (Tewksbury *et al.* 2002; Rastogi, Zanette & Clinchy 2006).

Spending more time attending their nest, food supplemented sparrows may be expected to suffer less egg removal when parasitized (Table 1; Tewksbury *et al.* 2002). Egg removal may be greater when different cowbirds multiply parasitize the same nest if each returns to remove an egg (Hahn *et al.* 1999; McLaren *et al.* 2003; Ellison, Sealy & Gibbs 2006). If most multiple parasitism is of this type, food supplemented sparrows may experience less egg removal because they are more elusive which, as explained above, should help in avoiding multiple parasitism by different cowbirds (Table 1). For the same reason, food supplemented sparrows should suffer less parasitism-induced nest desertion (Table 1) caused by the removal of multiple eggs (Kosciuch, Parker & Sandercock 2006).

We previously reported that food supplemented sparrows lost a significantly lower proportion of their nestlings to starvation compared to non-food supplemented sparrows where cowbirds are rare (Zanette, Clinchy & Smith 2006a). Food supplemented sparrows may similarly be expected to lose fewer of their own nestlings when

burdened with the added demand of provisioning a cowbird nestling as compared to non-food supplemented sparrows (Table 1).

If food supplementation allows birds to better resist brood parasites (i.e. fewer host egg and nestling losses) once they have discovered a nest, then the net result may be more sparrow offspring produced per parasitized nest for food compared with non-food supplemented birds (Table 1). As noted above, we previously reported that food supplemented sparrows fledged more of their own young partly because they lay more eggs (Zanette, Clinchy & Smith 2006a,b). Here, we are interested in the effects of parasitism on the relative number of host offspring fledging per nest, i.e. whether food supplemented sparrows fledge relatively more young than expected from their simply laying a larger clutch. Furthermore, if sparrows given extra food fledge relatively more young in each parasitized nest (Table 1) then this benefit should accumulate over the season. In this case, the number of sparrows fledging over the season in each food vs. non-food supplemented territory may be expected to differ most dramatically on territories that experience relatively high parasitism rates (Table 1), with smaller differences between food treatments evident on territories where little parasitism occurs.

Better resistance by food supplemented sparrows may lessen losses of their own young while lowering cowbird fledging production. Multiple parasitism has been reported to sometimes reduce cowbird productivity (Rothstein & Robinson 1998; Trine 2000) at least partly because subsequent cowbird eggs tend to be laid out of synchrony with the rest of the nest compared with the first laid cowbird egg, in cases where different cowbirds multiply parasitize the same nest (McLaren *et al.* 2003). Being more elusive, food supplemented sparrows may be expected to increase the interval between the first and subsequent cowbird eggs laid, and so decrease cowbird productivity in multiply parasitized nests (Table 1). Any decrease in cowbird productivity during the egg stage may, however, be counterbalanced by the likely better survival of cowbird nestlings in the nests of food supplemented sparrows, with no resulting difference between treatment groups in the number of cowbirds fledging per multiply parasitized nest (Table 1). The expectation of higher cowbird nestling survival in the nests of food supplemented sparrows follows from the facts that, food supplemented sparrows better provision their broods (Zanette, Clinchy & Smith 2006a), and cowbird nestlings generally get the majority of parental provisioning (Kilner, Madden & Hauber 2004).

STATISTICAL ANALYSES

We conducted separate tests for food effects on the incidence of parasitism and multiple parasitism (Table 1), using a generalized linear model with a logit-link function and binomial errors (StatSoft 2000). Multiple parasitism was collapsed into a binomial variable (i.e. singly vs. multiply parasitized nests) because almost all cases of multiple parasitism involved two cowbird eggs (i.e. 32/39 multiply parasitized nests contained two cowbird eggs, the remainder contained three; of the latter, four nests were on food supplemented and three on non-food supplemented territories). However, to ensure no information was lost by collapsing this variable, we also counted the number of cowbird eggs per parasitized nest and compared food treatments with a Mann–Whitney *U*-test. The *ad libitum* feed provided to sparrows could conceivably attract either large numbers of female cowbirds or encourage individual cowbirds to remain on food supplemented territories longer than those on non-food supplemented territories thereby increasing the chances of finding sparrow nests. Higher rates of parasitism and multiple parasitism for food supplemented sparrows could occur for these reasons, contrary to ‘bottom-up’ expectations. Consequently, we conducted incidental observations on

sparrow territories during fieldwork as outlined in Zanette, Clinchy & Smith 2006a. Briefly, we obtained cowbird encounter rates (i.e. female cowbirds observed per hour) by recording the number of female cowbirds seen on sparrow territories and compared this to the number of hours spent on territories in the two treatment groups using a chi-square goodness-of-fit test.

To test for food effects on parasitism-induced sparrow egg losses (Table 1), we conducted two separate two-way ANOVAS. To maximize our sample size, we first examined inferred egg losses by counting the number of sparrow eggs remaining in nests found during incubation, and comparing this egg count between the parasitized vs. unparasitized nests of food vs. non-food supplemented parents. Next, using a smaller data set of nests found during egg-laying, we compared the number of directly quantified egg losses in the singly vs. multiply parasitized nests of food vs. non-food supplemented parents. This second analysis tests whether food affects parasitism-induced egg loss (Table 1) and also whether egg loss is greater in multiply parasitized nests (Table 1). To test if food affects parasitism-induced nest desertion (Table 1), we compared the proportion of nest desertions associated with parasitism between food treatments using a Fisher's exact test. To test for food effects on parasitism-induced sparrow nestling losses (Table 1), we conducted a two-way ANOVA comparing the number of directly quantified nestling losses in the parasitized vs. unparasitized nests of food vs. non-food supplemented parents. We calculated nestling loss per nest by subtracting the number of sparrow eggs present immediately prior to hatch from the number of sparrows that fledged. A value of 1.0, for example, indicates there was one less fledgling than the number of eggs present at hatch.

To test for food effects on the number of sparrows fledging per successful parasitized nest (Table 1), we conducted a two-way ANOVA comparing the number of sparrows fledged according to parasitism status (parasitized vs. unparasitized), food treatment and the interaction. Knowing that food supplemented parents fledge more of their own young (Zanette, Clinchy & Smith 2006a), our interest lay in the interaction term. We expected to see a significant interaction indicating that food supplemented parents fledge relatively more sparrow nestlings than non-food supplemented parents especially when nests are parasitized. To test for a cumulative food effect on the number of sparrows fledging per territory in relation to parasitism rates (Table 1), we conducted a one-way ANCOVA with food treatment as the fixed effect and parasitism rate (the proportion of a territory's nests that were parasitized) as the covariate. Once again our interest lay in the interaction term. If food supplemented parents can better resist cowbirds, then the difference in annual reproductive success (ARS) for food vs. non-food supplemented parents should become increasingly more pronounced as the parasitism rate increases. For example, imagine that food and non-food supplemented hosts each fledged three nests. If food supplemented parents are better at resisting parasites, they may fledge four young per nest whether or not parasitism has occurred. Hosts on non-food supplemented territories, however, may fledge three young per nest when unparasitized and only two young when parasitized. Thus, if no parasitism has occurred, food vs. non-food supplemented hosts will show an ARS of 12 vs. 9 offspring; a difference of 3. If one nest is parasitized, ARS will be 12 vs. 8; a difference of 4 young. If two nests are parasitized, the difference will be five young, and so on. Hence, we should see a food treatment \times parasitism rate interaction. If, on the other hand, food supplementation confers no advantage in resisting cowbirds, then no such cumulative effect would be apparent and the food treatment \times parasitism rate interaction term would not be significant.

To test for food effects on the number of cowbirds fledging per multiply parasitized nest (Table 1), we conducted a two-way ANOVA

comparing the number of cowbirds fledging from the singly vs. multiply parasitized nests of food vs. non-food supplemented parents.

All data were tested for normality and homogeneity of variances prior to conducting parametric tests. We initially included female identity as a random effect in every analysis incorporating data from more than one nest per female, and then removed this variable from the reported analyses, as it was never significant. We included year as a random variable in every analysis, but then removed it from the reported analyses because parasitism rate did not vary significantly across years and there were no significant food \times parasitism \times year interactions. In the Results, we only report *F*-values for those terms that were significant or where non-significant terms are relevant to the Discussion. The descriptive statistics reported are means \pm SE.

Results

FOOD EFFECTS ON THE INCIDENCE OF PARASITISM

Contrary to the 'bottom-up' expectation that well-fed hosts can better resist parasitism, food supplemented sparrows were parasitized as often as non-food supplemented birds and were, moreover, multiply parasitized significantly more often. Fifty-eight per cent of 95 nests initiated by food supplemented sparrows were parasitized compared with 57% of 108 nests initiated by non-food supplemented sparrows ($\chi^2_1 = 0.0$, $P = 0.98$). Food supplemented sparrows were multiply parasitized in 43% of 55 parasitized nests, compared with 26% of 61 parasitized nests for non-food supplemented birds ($\chi^2_1 = 4.7$, $P = 0.03$). Similarly, we counted significantly more cowbird eggs in the parasitized nests of food compared with non-food supplemented sparrows (1.52 ± 0.08 vs. 1.29 ± 0.08 , respectively; Mann–Whitney U , $Z = -2.1$, $P = 0.036$). We encountered female cowbirds at similar rates on the food and non-food supplemented territories (0.34 and 0.27 h^{-1} , respectively; $\chi^2_1 = 0.4$, $P = 0.54$), indicating that our results are not likely attributable to there being more female cowbirds spending more time on food supplemented territories.

FOOD EFFECTS ON PARASITISM-INDUCED SPARROW LOSSES

Contrary to the 'bottom-up' expectation that well-fed hosts suffer less when parasitized, food supplemented sparrows suffered significantly more parasitism-induced egg loss than non-food supplemented sparrows. This result was apparent in our analyses of both inferred and directly quantified egg losses. In unparasitized nests, clutch sizes were larger when sparrows were food supplemented, containing about one more sparrow egg than their non-food supplemented counterparts (Fig. 1a). Regarding inferred losses, when parasitized, food supplemented sparrows lost this extra egg, whereas non-food supplemented sparrows maintained their clutch sizes (Food \times Parasitism $F_{1,188} = 13.7$, $P < 0.001$). The net result was that when parasitized, sparrows ended up having roughly the same number of host eggs in their nests regardless of food treatment (Fig. 1a). Considering directly quantified egg losses, significantly more eggs were lost from

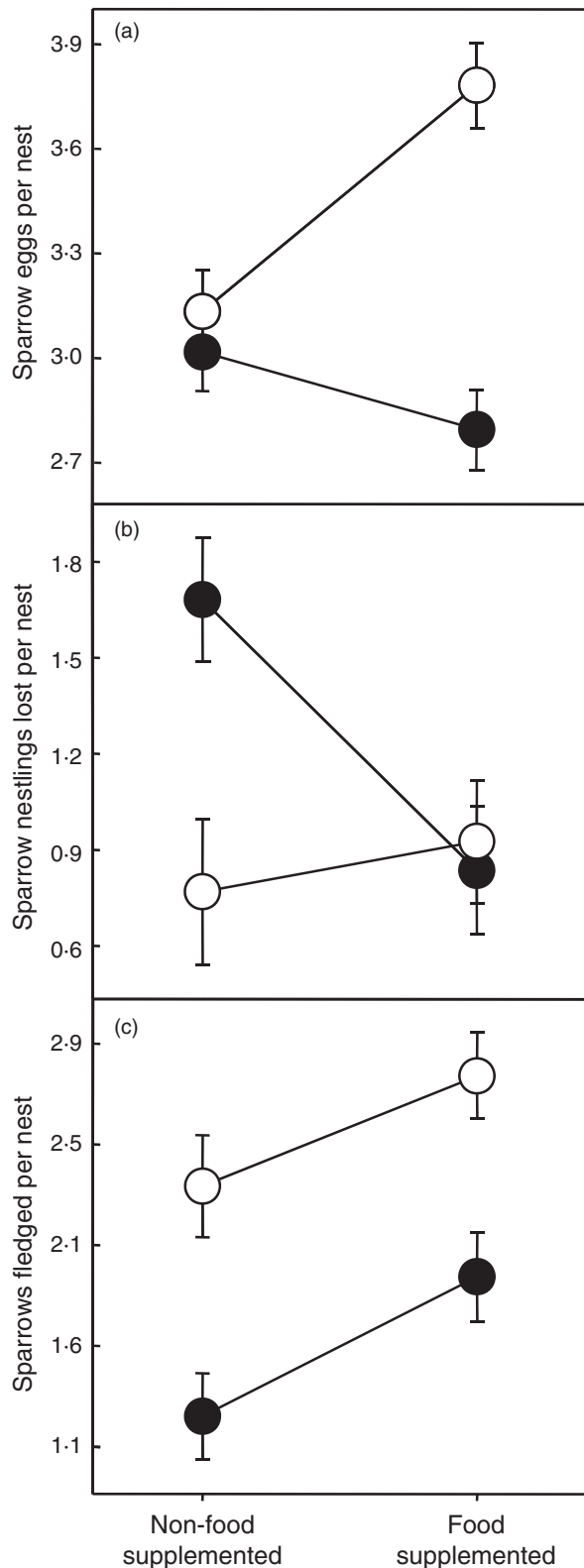


Fig. 1. Effects of food addition and cowbird parasitism on the number of (a) sparrow eggs in nests during incubation; (b) sparrow nestlings lost between hatch and fledging, and; (c) sparrows fledged per nest fledging young. Food supplemented refers to sparrow territories provided with added food, as compared to non-food supplemented territories. Open symbols = unparasitized nests, filled symbols = cowbird parasitized nests. Values are means \pm SE.

parasitized food supplemented sparrow nests (0.9 eggs lost ± 0.20) than from parasitized non-food supplemented nests (0.32 eggs lost ± 0.19 ; Food $F_{1,42} = 4.4$, $P = 0.04$) indicating that cowbird females were indeed more likely to remove eggs from the larger-sized clutches laid by food supplemented sparrows.

If most multiple parasitism involves different cowbird females laying in the same nest, the 'bottom-up' expectations were that food supplemented sparrows should suffer less egg loss from multiply parasitized nests and less parasitism-induced nest desertion than non-food supplemented sparrows. However, this was not the case. Egg losses were similar in singly vs. multiply parasitized nests (0.7 ± 0.13 vs. 0.5 ± 0.24 ; Parasitism Level, $F_{1,42} = 0.7$, $P = 0.42$) regardless of food treatment (Food \times Parasitism Level, $F_{1,42} = 0.3$, $P = 0.62$). The rate of parasitism-induced nest desertion was also similar between treatment groups (53% of 19 nests deserted by food supplemented sparrows were parasitized, compared with 54% of 28 nests deserted by non-food supplemented sparrows; Fisher's exact $P = 1.0$).

Although food supplemented sparrows lost eggs when parasitized it was the non-food supplemented sparrows that lost nestlings, such that the pattern of nestling loss (Fig. 1b) was virtually the inverse of egg loss (Fig. 1a). When unparasitized, sparrows in both food treatments lost about one nestling per nest (Fig. 1b). When parasitized, non-food supplemented sparrows lost one extra nestling (Fig. 1b; Food \times Parasitism $F_{1,98} = 6.1$, $P = 0.015$). This result is the only one consistent with the 'bottom-up' expectation that food supplemented sparrows can better resist brood parasites.

FOOD EFFECTS ON THE RELATIVE NUMBER OF SPARROWS FLEDGING

The net result of food supplemented sparrows losing eggs when parasitized (Fig. 1a) and non-food supplemented sparrows losing nestlings (Fig. 1b) was that sparrows in each treatment suffered equally when parasitized (in terms of the relative reduction in the number of their own young fledged), whether examined on a per nest (Fig. 1c) or on a per territory basis. Unparasitized food supplemented sparrows fledged more of their own young per nest than unparasitized non-food supplemented sparrows (Fig. 1c) because the nests of food supplemented sparrows contained more eggs. When parasitized, all birds fledged about one young less per nest, relative to unparasitized nests, because food supplemented parents lost about one egg and non-food supplemented parents one nestling when parasitism occurred (Fig. 1c; Food \times Parasitism $F_{1,98} = 0.1$, $P = 0.75$). The evident equivalence of the loss suffered per parasitized nest (Fig. 1c) was confirmed by our examination of cumulative differences. Here, we analysed host offspring fledged per territory in relation to the parasitism rate observed on each territory and found that the interaction term was not significant (Food treatment \times Parasitism rate $F_{1,105} = 1.9$, $P = 0.18$). Thus, while food supplemented sparrows produced nearly two

times more offspring per territory (4.0 ± 0.33) than non-food supplemented sparrows (2.3 ± 0.29 ; Food treatment, $F_{1,106} = 12.8$, $P = 0.0005$), the difference in per capita offspring production was consistent regardless of the parasitism rate. The apparent inability of sparrows to resist parasitism was clearly costly, as parasitism significantly reduced the number of sparrows fledged per nest (Fig. 1c; Parasitism $F_{1,98} = 22.4$, $P < 0.001$) independent of food treatment, and because the parasitism rate was negatively related to the number of host offspring fledged per territory (Parasitism rate $F_{1,106} = 9.1$, $P < 0.003$; β coefficient, -0.3), regardless of food.

FOOD EFFECTS ON THE NUMBER OF COWBIRDS FLEDGING

Cowbird females clearly benefited from multiply parasitizing food supplemented sparrows as significantly more cowbird nestlings fledged from these nests compared with the multiply parasitized nests of non-food supplemented birds (Fig. 2; Food \times Parasitism $F_{1,45} = 4.5$, $P = 0.039$). This result is contrary to the ‘bottom-up’ expectation that better resistance by food supplemented hosts may reduce or limit cowbird productivity in multiply parasitized nests.

Discussion

Eight of the nine measures of brood parasitism, we evaluated demonstrated a different or opposite pattern to that expected from the ‘bottom-up’ scenario that well-fed hosts are better

at eluding and resisting parasites and so suffer less from parasitism (Table 1). Rather than being parasitized less, food supplemented hosts were parasitized as often, and multiply parasitized more often, than non-food supplemented hosts (Table 1). Rather than suffering less when parasitized, food supplemented hosts suffered more parasitism-induced egg loss (Fig. 1a), and were as likely as non-food supplemented hosts to lose eggs from multiply parasitized nests, and to suffer parasitism-induced nest desertion (Table 1). Most importantly as regards conservation implications, rather than fledging relatively more of their own young, food supplemented sparrows fledged the same proportion per parasitized nest (Fig. 1c) and per territory regardless of the parasitism rate. The only result consistent with ‘bottom-up’ effects was that food supplemented sparrows lost fewer of their own nestlings when burdened with a cowbird nestling than did non-food supplemented birds (Fig. 1b; Table 1). Food supplemented sparrows were evidently better able to provision not just their own but all of the young in their nest (cowbird and sparrow alike) and thus clearly represented a better resource base from the cowbird’s perspective, as demonstrated by the significantly greater number of cowbirds fledging from the multiply parasitized nests of food supplemented sparrows (Fig. 2).

Nest predation and cowbird parasitism are the two principal determinants of ARS in song sparrows in the region where we worked (Zanette, Clinchy & Smith 2006a; Zanette *et al.* 2007). Food supplemented sparrows better eluded detection by nest predators (Rastogi, Zanette & Clinchy 2006) and thereby increased their nest survival by 37%, resulting in a 53% increase in ARS (Zanette, Clinchy & Smith 2006a). Our results (Fig. 1c) show that sparrows that eluded being parasitized (i.e. those remaining unparasitized) fledged over 50% more young per nest, in correspondence with a 50% increase in ARS that we found in response to a previous cowbird removal experiment (Smith, Taitt & Zanette 2002; Zanette *et al.* 2007). Given the comparable benefits of eluding nest predation and cowbird parasitism, and that food supplemented sparrows were successful at eluding nest predators, there was every reason to expect results consistent with ‘bottom-up’ expectations (Table 1), making the numerous contrasts between these expectations and our results are all the more surprising.

Having established the consequences of host–parasite interactions and how these consequences vary with food supplementation, we next provide possibilities as to the mechanisms that could have generated these results.

Viewing food–prey–predator and food–host–brood parasite interactions from the perspective of the nest predator and brood parasite, rather than that of the prey/host, suggests why food supplemented sparrows could avoid nest predators better than cowbirds. Nest predators would receive no greater benefit from consuming the clutch or brood of a food supplemented sparrow, even though they produce more eggs and nestlings, because there was no difference between fed and unfed sparrows in the total mass of their clutches or broods (Zanette, Clinchy & Sung 2009). In contrast, we

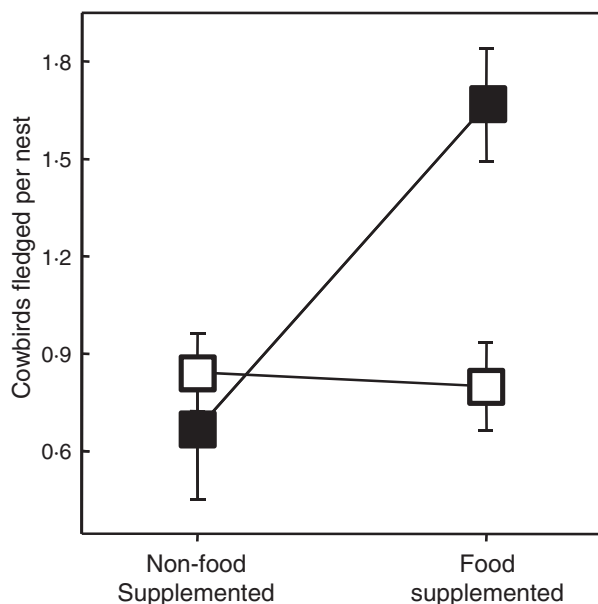


Fig. 2. Effects of food addition and multiple cowbird parasitism on the number of cowbirds fledged per nest fledging young. Food supplemented refers to sparrow territories provided with added food, as compared to non-food supplemented territories. Open symbols = singly parasitized nests (i.e. containing just one cowbird egg), filled symbols = multiply parasitized nests (i.e. containing two or more cowbird eggs). Values are means \pm SE.

demonstrate that cowbirds directly benefited from multiply parasitizing the nests of food supplemented sparrows (Fig. 2). Moreover, parasitizing well-fed hosts would provide the further benefit that nest survival was 37% better. Preferentially parasitizing well-fed sparrows would thus be advantageous, and the fact that cowbirds more often multiply parasitized nests of food supplemented sparrows, where the direct benefit of doing so was greater (Fig. 2), is clearly congruent with them actively choosing to do so. This is the first experimental study to provide evidence consistent with cowbirds preferentially parasitizing better quality hosts (Grant & Sealy 2002; Parejo & Avilés 2007).

Viewing matters from the cowbird's perspective also provides an explanation for the observed pattern of parasitism-induced egg loss (Table 1), as it accords with the evidence Kilner, Madden & Hauber (2004) that cowbirds optimize the rearing environment for parasitic young. Kilner, Madden & Hauber (2004) showed that cowbird nestlings reared with more than three host young do less well than those reared with fewer. Food supplemented sparrows laid around four eggs on average, whereas non-food supplemented sparrows laid about three (Fig. 1a, unparasitized nests). A cowbird attempting to optimize circumstances for its young would thus be expected to remove at least one egg from each food supplemented sparrow nest to reduce the host's brood size, whereas no egg removal would be necessary in the case of non-food supplemented sparrows, which is the pattern we observed (Fig. 1a). Food supplemented sparrows did not lose more of their own nestlings when parasitized but they typically did experience some brood loss (Fig. 1b), with the result being that in parasitized nests, at fledging, there were generally two host young in the nest together with the cowbird nestling (Fig. 1c), as predicted by Kilner, Madden & Hauber (2004).

Multiple parasitism by different cowbird females could disrupt any attempt by each of them to optimize the number of host young in the nest because multiple eggs are often removed, thus inducing nest desertion (Hahn *et al.* 1999; McLaren *et al.* 2003; Ellison, Sealy & Gibbs 2006; Kosciuch, Parker & Sandercock 2006). The pattern of egg loss that we observed in our study (Fig. 1a) is consistent with individual cowbird females successfully optimizing the number of host young in the nest (Kilner, Madden & Hauber 2004) and constitutes one of several lines of evidence suggesting that most multiple parasitism of food supplemented sparrows likely involved the same cowbird female choosing to return and lay again in a nest she had already found. Other evidence is that the higher rate of multiple parasitism suffered by food supplemented sparrows was not associated either with greater egg loss or increased nest desertion (Table 1), nor was there any decrease in cowbird productivity (Fig. 2), as would be expected if multiple parasitism largely involved different cowbird females laying in the same nest (Rothstein & Robinson 1998; Trine 2000). Finally, as multiple parasitism by different females entails each individual finding the nest, then the higher rate of multiple parasitism (> 1 cowbird eggs/nest) suffered by food supplemented sparrows would suggest that

finding their nests was easier, which should then have been reflected in food supplemented sparrows suffering a higher incidence of parasitism *per se* (> 0 cowbird eggs/nest), which was not the case.

If individual cowbird females were choosing to preferentially parasitize food supplemented sparrows why was this not reflected in a higher incidence of parasitism (> 0 cowbird eggs/nest)? Considering the net effect of the food–host–brood parasite interaction suggests an answer. Food supplemented sparrows clearly represented a better resource base from the cowbird's perspective (Fig. 2). However, being more elusive, well-fed sparrows may have counterbalanced efforts by the cowbird to preferentially parasitize them (Parejo & Avilés 2007), with the net result conceivably being that sparrows end up parasitized equally often regardless of treatment, as we observed (Table 1). As for multiple parasitism, elusiveness is not relevant if it mainly involves the same cowbird returning to nests they have already found. To defend against a returning cowbird female, it is nest attendance that may prove effective (Tewksbury *et al.* 2002). Even though food supplemented song sparrows spend more time attending their nests than non-food supplemented birds, it would appear that this behaviour is not completely effective against cowbirds (see also Ellison & Sealy 2007) because food supplemented hosts lost more eggs to cowbirds and were multiply parasitized more often than non-food supplemented hosts. Indeed, we have filmed nine cowbird attacks on sparrow nests when one or both parents were present (i.e. in attendance at the nest), and in every case but one the cowbird succeeded in inflicting some damage to the nest contents despite the parent's invariably violent defense. Consequently, although song sparrows mount an enhanced behavioural response when food supplemented by increasing nest attendance, it would appear that cowbirds can counteract this defense (also see Tewksbury *et al.* 2002). It has been suggested that brood parasites will show preferences for hosts that offer high reproductive success to the parasite (e.g. De Mársico & Reboreda 2008) as long as host defenses are not insurmountable (e.g. Briskie, Sealy & Hobson 1990). Food supplemented sparrows in our study appear to fit both criteria.

Arcese & Smith (1988) previously showed that food supplemented sparrows are capable of better eluding being parasitized. Feeders were erected on the territories of 16 of 72 song sparrow pairs resident on a 6-ha island (Mandarte Island), located 18 km from our study sites in Victoria. Just one cowbird female was resident on the island in the year of study, and food supplemented sparrows were parasitized by this lone cowbird female significantly less often than non-food supplemented birds. Although this result could be due to an idiosyncrasy of the cowbird, it does make biological sense if it is the net effect of the food–host–brood parasite interaction that governs observed parasitism rates. The cowbird never multiply parasitized any nest (Smith & Arcese 1994) and food addition did not affect nest predation (Arcese & Smith 1988; in accord with there being few nest predators on the island, Wilson & Arcese 2006), so there was no apparent reason for

the cowbird to preferentially parasitize these food supplemented sparrows. In this case, greater elusiveness of food supplemented sparrows would not be counteracted by any greater effort by the cowbird to preferentially parasitize them, allowing food supplemented sparrows to avoid being parasitized. If so, then the food–host–parasite interactions that we have described would further suggest that in systems with low numbers of cowbirds (and hence, low multiple parasitism rates) and low predation rates of host nests (as in Arcese & Smith 1988), any pattern of preference for well-fed, high quality hosts could effectively be reduced, while higher cowbird numbers and nest predation rates (this study; also see Jewell, Arcese & Gergel 2007) would strengthen it.

Recent aviary trials demonstrate that female cowbirds are capable of discriminating among nests differing in egg number and appearance (White *et al.* 2007). Consequently, cowbirds could use clutch size as a cue for preferentially parasitizing well-fed hosts that lay more eggs. This explanation also is consistent with the idea that cowbirds can count the number of host eggs in a nest and remove the right number to help optimize conditions for her young (Kilner, Madden & Hauber 2004). Alternatively, cowbirds could assess the quality of the host's territory rather than the host itself. In our case, the presence of a feeder presented a very salient cue as to food availability on a territory. The presence of a feeder, however, is not a sufficient explanation of our results because we used a virtually identical protocol to Arcese & Smith (1988) who obtained a different result (i.e. less parasitism for food supplemented birds).

Cowbirds are considered an invasive species throughout much of their current range, and have been implicated in the declines of several threatened or endangered songbirds (Jewell, Arcese & Gergel 2007; Kosciuch & Sandercock 2008). We suggest one of the conservation implications of our work is that where cowbird (and/or nest predator) numbers are relatively high (e.g. our sites), management actions designed to provide better habitat for hosts that increases food availability may not provide a respite from cowbird parasitism because, under these circumstances, preferentially parasitizing well-fed hosts provides the cowbird with clear benefits. Nonetheless, increased food availability did increase overall sparrow productivity, despite cowbird parasitism (Fig. 1c). Consequently, while not providing a respite from parasitism, increasing food availability would still benefit sparrows, and presumably other similar hosts. However, the best strategy to use in landscapes where cowbirds are abundant may be to simultaneously increase food availability while reducing cowbird (and/or nest predator) numbers, as this could provide more than additive (or 'synergistic') benefits with respect to host reproduction (Clotfelter, Yasukawa & Newsome 1999; also see Zanette *et al.* 2003; Zanette, Clinchy & Smith 2006a), given the available evidence that increased food availability can help hosts elude cowbirds when cowbird numbers are low (Arcese & Smith 1988; Smith & Arcese 1994).

The preceding assessment may be overly conservative since increasing food availability without reducing cowbird numbers could have a more beneficial effect on the host popula-

tion than our results indicate, even where cowbirds are abundant. Working with non-food supplemented sparrows at our sites, Zanette *et al.* (2005) found that the proportion of female sparrows fledging from parasitized nests (0.27 ± 0.06) was roughly half that fledging from unparasitized nests (0.52 ± 0.11), and a subsequent experiment (L. Zanette & M. Clinchy, unpublished data) provided support that this was due to increased female mortality during the nestling stage. Recent modelling (Engen, Lande & Sæther 2003; Rankin & Kokko 2007) suggests deviations from a 1 : 1 sex ratio could dramatically reduce the population growth rate in species, like many cowbird hosts, that typically require bi-parental care to successfully rear young. Conservation actions aimed at increasing food availability could provide a respite from this demographically significant secondary effect of cowbird parasitism, as food supplemented sparrows did not lose nestlings (Fig. 1b), but instead lost eggs (Fig. 1a), when parasitized and so most likely fledged a roughly equal proportion of male and female young (i.e. 0.50 : 0.50).

Avian host–brood parasite interactions have long served as textbook examples of evolutionary 'arms races' (e.g. Alcock 2005; Krebs 2009). In just the past few years, there have been a spate of experimental studies published demonstrating a surprisingly greater complexity to host–brood parasite interactions than previously suspected (e.g. Kilner, Madden & Hauber 2004; Hoover & Robinson 2007; Pagnucco *et al.* 2008; reviewed in Krüger 2007). Our results (Table 1) add a third dimension (food–host–brood parasite) to these interactions, and point to a probable fourth dimension (food–host/prey–nest predator–brood parasite), wherein brood parasites prefer to parasitize well-fed hosts because they suffer less nest predation (Zanette, Clinchy & Smith 2006a; Krüger 2007). Parallel to our findings, Pöysä & Pesonen (2007) presented evidence from a series of experiments showing that conspecific brood parasites preferentially parasitize hosts that suffer less nest predation. We suggest there are almost certainly many more such insights to be gained by approaching brood parasitism from a community ecology perspective, in accord with the recent calls for a community ecology approach to parasitism in general whereby 'top-down', 'bottom-up', and other multiple-scale processes are considered at the same time.

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