

# Parental care of a cowbird host: caught between the costs of egg-removal and nest predation

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Avian brood parasites reduce host fitness through the addition of parasitic eggs and the removal of host eggs. Both parasitic egg-addition and host egg-removal may be important sources of selection on host behaviour, creating fitness trade-offs with selection imposed by nest predation. However, the relative costs hosts suffer from egg-addition and host egg-removal and the responses to these costs are largely unstudied. Through experimental manipulations and observations, we demonstrate that increased nest attentiveness by female yellow warblers (*Dendroica petechia*) reduces the cost of brood parasitism by reducing egg-removal by brown-headed cowbirds (*Molothrus ater*). However, female attentiveness does not reduce the addition of parasitic eggs. Experimentally parasitized females respond to the threat of egg-removal by increasing nest attentiveness. Increased attentiveness, however, reduces time for females to gather food and requires males to visit the nest more often to feed incubating females. This increased activity in turn increases the risk of nest predation. Thus, brood parasitism (specifically egg-removal) and nest predation produce conflicting selection on incubation strategies, as parasitized hosts are caught between the costs of egg-removal by brood parasites, and the costs of increased nest predation if the female spends more time on the nest to reduce egg-removal.

**Keywords:** brood parasitism; host egg-removal; nest predation; incubation

## 1. INTRODUCTION

Nest predation and brood parasitism are often primary constraints on reproductive success in passerine birds (Nolan 1978; Martin 1992; Robinson *et al.* 1995a,b) and can thereby exert strong selection on phenotypic traits (Martin 1996; Martin & Ghalambor 1999; Robert & Sorci 1999). Recent work has shown that nest predation can have large effects on parental care strategies during incubation (Martin & Ghalambor 1999; Conway & Martin 2000; Ghalambor & Martin 2000), but the influence of brood parasitism on incubation behaviour has not been assessed. Brood parasites typically reduce the reproductive success of hosts in two ways: by laying a parasitic egg (egg-addition) and by removing one or more host eggs (egg-removal) (Payne 1977; Lowther 1993; Robinson *et al.* 1995a). Egg-addition is the act of parasitism, and is thus essential for obligate brood parasites. Egg-removal is often not essential, but may benefit the brood parasite through increased hatching efficiency (Davies & Brooke 1988; Sealy 1992; Peer & Bollinger 1997), improved nutrition (Scott *et al.* 1992), or enhanced competitive ability with host nestlings (Sealy 1992). From the host's perspective, both parasitic egg-addition and host egg-removal may

impose fitness costs (Robinson *et al.* 1995a), but the cost of each may vary as a function of host life history, and behaviour that reduces parasitic egg-addition or host egg-removal may be favoured independently. Because both egg-addition and host egg-removal take cowbirds only seconds to complete (Nolan 1978; Sealy *et al.* 1995; Burhans 2000), effective nest protection may require increased nest attentiveness (per cent of time the female spends on the nest). However, changes in parental care strategies may also influence the ability of predators to detect and depredate nests (Martin *et al.* 2000a). Therefore, the effectiveness of changes in behaviour can only be assessed by considering the dual effects on brood parasitism and nest predation. This possible conflict—or synergism—between parasitism and predation costs on incubation behaviour has, to our knowledge, not been studied.

We assess the fitness costs of parasitic egg-addition and host egg-removal in a common cowbird host, the yellow warbler (*Dendroica petechia*), and determine the effect of female nest attentiveness on the success of cowbirds laying eggs in and removing host eggs from yellow warbler nests. Based on these results, we test the assumption that cowbird egg-addition is a reliable indicator of increased risk of egg-removal. If egg-removal is a predictable fitness cost that is preventable by increases in nest attentiveness, we may expect yellow warblers to adjust incubation behaviour. However, nest attentiveness is typically constrained by the rate at which males feed incubating females on the nest (incubation feeding) (Lyon & Montgomerie 1985; Martin & Ghalambor 1999; Conway & Martin 2000), and

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increased incubation feeding can in turn increase the risk of nest predation (Martin *et al.* 2000*a,b*). We experimentally examine these constraints on incubation behaviour through experimental parasitism, video observation, and comparison of nest predation rates between experimentally parasitized and control nests. Our results link changes in incubation behaviour to fitness benefits and costs manifested through different selective pressures: brood parasitism and nest predation.

## 2. METHODS

### (a) *Frequency of cowbird egg-addition and host egg-removal*

We established 16 study sites in deciduous habitats in the Bitterroot Valley of Western Montana and monitored nests at all sites from 1995 to 1999 (Tewksbury *et al.* 1998). A total of 466 yellow warbler nests were used in these analyses. Clutch sizes, brood parasitism frequencies (percentage of nests receiving a cowbird egg), nest fate, and the number of young fledged, were determined through frequent nest checks throughout building, egg-laying, incubation and nestling phases. We tested for seasonal changes in parasitism by calculating parasitism rates for nests initiated in 5 day intervals throughout the season (nine intervals). After transforming all rate data, we regressed parasitism rate at each interval against the median nest-initiation date for each interval. Results from logistic regression of nest-initiation date on the chance of parasitism produced similar results. To determine rates of egg-removal, we first compared clutch sizes between parasitized and unparasitized nests, using ANCOVA with the nest-initiation date as a covariate. To ensure that differences in clutch size were due to egg-removal, we intensively monitored a subset of parasitized and unparasitized yellow warbler nests to determine directly the frequency of host egg-removal by cowbirds in both groups ( $n = 63$  nests).

### (b) *Fitness costs and timing of parasitism and egg-removal*

The fitness costs of parasitic egg-addition ( $A_c$ ) and host egg-removal ( $R_c$ ) can be separated and compared by representing each as the reduction in potential fledglings from a successful nest, and recognizing that both costs are dependent on the host clutch size. For a species such as the yellow warbler, which commonly accepts cowbird eggs (Tewksbury *et al.* 1998) and is able to successfully raise mixed broods (one or more host young with a cowbird) (Weatherhead 1989), the average individual cost of cowbird egg-addition ( $A_c$ ) can be represented as

$$A_c = \sum_{i=1}^m (f_{iN} - f_{iP})n_{iP} \quad (2.1)$$

where  $i$  is the observed clutch size after egg-removal ( $i$  varies from 1 to the maximum clutch size ( $m$ )),  $f_{iN}$  is the average number of fledglings per unparasitized nest of clutch size  $i$ ,  $f_{iP}$  is the average number of fledglings from parasitized nests of clutch size  $i$ , and  $n_{iP}$  is the proportion of parasitized nests with clutch size  $i$ . An estimation of the observed cost of host egg-removal in parasitized nests ( $R_c$ ) can be calculated as:

$$R_c = \sum_{i=1}^m (f_{iP-er})n_{iN} \quad (2.2)$$

where  $n_{iN}$  is the proportion of unparasitized nests with clutch size  $i$  and  $Pi-er$  is the clutch size  $i$  minus the number of host

eggs per parasitized nest removed by cowbirds ( $er$ ). To calculate the expected number fledged ( $f_{iP-er}$ ) from fractional clutch sizes, we interpolated from empirical data, relating clutch size to the number fledged in parasitized nests. These representations of cost consider only the reduction in the number of young fledged, and represent minimum costs of parasitism and egg-removal.

The predictable timing of host egg-removal after parasitic egg-addition (Sealy 1992) may allow the addition of the cowbird egg itself to serve as a cue to yellow warblers that the danger of egg-removal has increased. To determine the predictability of this cue, we calculated the daily likelihood of host egg-removal in relation to the date of egg-addition. We used parasitized nests where the day of parasitic egg-addition and the day of host egg-removal were both known to determine the timing of egg-removal ( $n = 47$  nests) and the subset of nests monitored intensively ( $n = 63$  nests) to determine the total number of host eggs removed per parasitized nest. We multiplied the percentage of removal events that occurred over a given 24 h period before or after parasitism by the mean number of eggs removed per parasitized nest to determine the daily likelihood of egg-removal.

### (c) *Female attentiveness and cowbird-host interactions*

To document interactions between cowbirds and yellow warblers and determine the effects of cowbird egg-addition and host egg-removal on parental behaviour, we used HI-8 video cameras to videotape 132 nests, recording an average of 18 h of video per nest during building, laying, and incubation. Video cameras were placed a minimum of 5 m from the nest, covered with camouflage hoods, and operated for a minimum of 6 h, starting before 05.00 Mountain Daylight Time (MDT) during building and laying and before 06.00 MDT during incubation. Cowbird egg-addition (egg-laying) happens exclusively in the very early morning in all populations studied (Scott 1991; Neudorf & Sealy 1994), and we captured 10 cowbird laying events on video, all occurring before 05.30 MDT. Thus, we considered cowbird visits to previously parasitized nests occurring after 06.00 MDT as attempted host egg-removal ( $n = 30$ ). We examined the effectiveness of female presence on the nest in deterring egg-addition and in deterring egg-removal using binomial tests.

### (d) *Attentiveness, incubation feeding and parasitism*

To determine if brood parasitism affected incubation behaviour, we examined nest attentiveness and incubation feeding rates at naturally parasitized and unparasitized nests. We videotaped all nests from 06.00 until 11.00 MDT on the fourth or fifth full day of incubation.

To eliminate any possibility that differences in incubation behaviour between parasitized and unparasitized nests reflected non-random nest choices by cowbirds, or site-to-site differences in temperature or in predation risk, we experimentally tested host responses to parasitism. We paired naturally unparasitized nests and videotaped both nests on the first full day of incubation. We then experimentally parasitized one nest and videotaped the pair 3 days later. We paired nests by initiation date (within one week), height (within 5 m), and location (within 600 m and always on the same study plot), to eliminate potential effects of seasonality, microclimate, and predation pressure differences between nests. All nests were videotaped from 06.00 until 11.00 MDT on the first full day of incubation (pretreatment) and on the fourth day of incubation (post-treatment), the same period used for non-experimental nests.

We conducted the treatment itself (either experimental parasitism or control) on the day after the pretreatment video. We conducted treatments on 26 pairs; in 17 of these, all videos were completed on both nests, allowing behavioural analysis. In 13 of the 17 pairs, both nests had the same clutch size before treatment; the other four pairs differed in clutch size by one egg. For experimental parasitism, we played 10 min of cowbird vocalizations within 1 m of the nest to simulate a high risk of parasitism. Cowbird vocalizations frequently brought cowbirds to the nest area, but cowbirds did not remove host eggs. Later in the same day, when the female was off the nest, we replaced one host egg with a warmed, non-viable cowbird egg to simulate parasitic egg-addition and control for egg number. Our protocol thus presents two potential cues to yellow warblers that the risk of egg-removal has suddenly increased—the presence of the cowbirds and cowbird vocalizations at the nest—and the appearance of a cowbird egg. For our unparasitized control treatment, we played 10 min of grey catbird (*Dumetella carolinensis*) song and picked up and replaced one host egg to control for disturbance at the nest. We chose grey catbird vocalizations because catbirds are common and similar in size and call volume to cowbirds, but do not represent a threat to yellow warblers. We used paired *t*-tests to examine changes in behaviour from pre- to post-treatment videos and to examine behavioural differences between experimentally parasitized and control nests. Because we blocked all nest pairs by initiation date, height, location and clutch size, any differences in behaviour cannot be attributed to these factors.

#### (e) Parasitism, incubation feeding and nest predation

To examine the link between incubation feeding and nest predation, we compared incubation feeding rates (videotaped at day 4 or 5 of incubation) between nests that were successful through the second day after the first egg hatched, and nests that were depredated during that period. We used this period because hatching is often asynchronous and females may incubate eggs together with young nestlings for several days; thus, female attentiveness remains dependent on male incubation feeding. To determine explicitly the effect of parasitism on predation rates, we compared daily nest predation rates (the chance that a nest will be depredated over a 24 h period) between experimentally parasitized and control nests for the period from the day of the experimental treatment through the second day after the first egg hatched, as above (Mayfield 1961, 1975). The sample size for daily nest predation rates ( $n = 26$  pairs) was higher than for measures of attentiveness and incubation feeding ( $n = 17$  pairs) because video malfunctions and nest failures before the post-treatment video precluded the use of some pairs in comparison of pre- to post-treatment behaviour.

### 3. RESULTS

Parasitism on yellow warblers was high (58% of nests parasitized,  $n = 466$  nests) and did not vary throughout the season ( $r^2 = 0.19$ , d.f. = 1,8,  $p = 0.25$ ). Parasitized yellow warbler nests had clutch sizes 0.91 eggs smaller than those of unparasitized nests ( $F = 48$ , d.f. = 1,176,  $p < 0.0005$ ) and this difference was not attributable to differences in clutch initiation date (date by parasitism interaction  $F = 0.001$ , d.f. = 1,176  $p = 0.98$ ). Instead, this difference in clutch size appears completely attributable to egg-removal by cowbirds; in the subset of nests where the

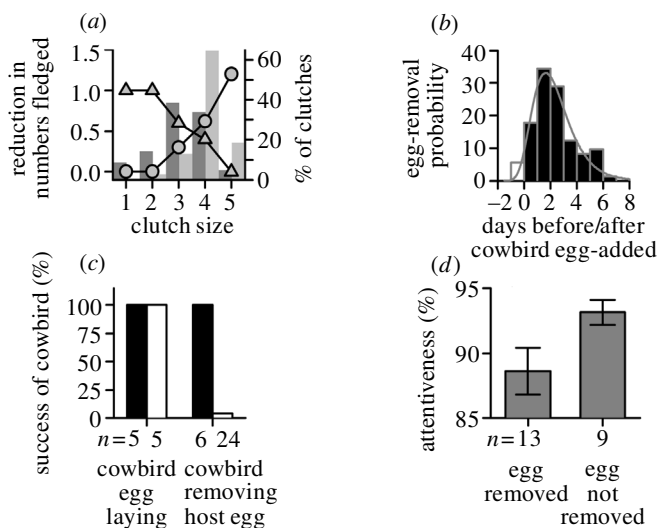


Figure 1. Costs, predictability, and effects of yellow warbler nest attentiveness on parasitic egg-addition (parasitism) and host egg-removal. (a) Reductions in the number of host young fledged due to cowbird egg-addition (circles) and host egg-removal (triangles) as a function of host clutch size ( $n = 44$  parasitized nests and 66 unparasitized nests where clutch size and the exact number fledged were known), and the frequency distribution of parasitized (dark bars) and unparasitized (light bars) clutch sizes (histogram, right y-axis:  $n = 127$  parasitized nests and 140 unparasitized nests with clutch size observed during early incubation). See equations (2.1) and (2.2) for calculations of costs of egg-addition ( $A_c$ ) and egg-removal ( $R_c$ ). (b) Daily chance of egg-removal (chance that a host egg will be removed over a 24 h period) for parasitized nests in relation to the time in which the cowbird egg was laid (represented by zero on the x-axis). The daily chance of host egg-removal increased dramatically immediately after the nest was parasitized (colour shift from white bar to black bars) and closely followed a log normal distribution ( $n = 47$  removal events; curve = 3 parameter log-normal regression,  $r^2 = 0.94$ ,  $F = 77$ ,  $p < 0.0001$ ). (c) Cowbirds successfully laid their eggs (parasitic egg-addition) in yellow warblers' nests whether the female warbler was away from the nest (black) or on the nest (white) when the cowbird approached. However, during host egg-removal events, cowbirds always removed a host egg when the female was absent (black), but rarely removed an egg if the female was on the nest (white) when the cowbird approached. Thus, the effectiveness of host female presence in preventing cowbirds from gaining access to the nest differed greatly between these two types of cowbird visits (likelihood ratio test  $G = 171$ ,  $p < 0.0005$ ). (d) Nest attentiveness (mean  $\pm 1$  s.e.) in naturally parasitized nests was significantly lower in nests where host eggs were removed than it was in nests where host eggs were not removed ( $F_{1,21} = 5.36$ ,  $p = 0.018$ ).

occurrence and timing of egg-removal was directly observed, parasitized nests ( $n = 37$ ) lost 1.32 ( $\pm 0.13$  s.e.) eggs per nest while unparasitized nests ( $n = 26$ ) lost 0.31 ( $\pm 0.12$  s.e.) eggs per nest, resulting in a 1.01 egg-decrease in clutch size in parasitized nests. Because our aim was to determine the costs and response of egg-removal in parasitized nests, we set 'er' equal to 1 for analysis of egg-removal costs.

Both cowbird egg-addition and removal impose substantial fitness costs (figure 1a). Yellow warblers often

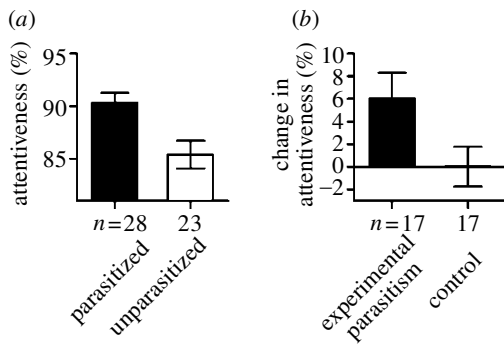


Figure 2. Effects of parasitism on nest attentiveness. (a) Naturally parasitized nests had significantly higher attentiveness than unparasitized nests ( $F_{1,50} = 9.7$ ,  $p = 0.002$ ). (b) Attentiveness increased significantly after experimental parasitism (paired  $t_{16} = 2.6$ ,  $p = 0.01$ ), but remained unchanged in control nests (paired  $t_{16} = 0.2$ ,  $p = 0.98$ ). Thus, yellow warblers increased attentiveness after parasitism.

raise one to three of their own young along with a cowbird nestling, so egg-addition had no effect on fitness for very small clutches, but a large effect on nests with large clutch sizes. Because egg-addition truncates the number of host fledglings possible from a parasitized nest, egg-removal costs show the opposite relationship, decreasing to near zero in the largest clutch size (figure 1a). When we summed over the frequency distribution of clutch sizes, egg-removal accounted for 49% of the total cost of parasitism in our population, reducing the number of young fledged from a successful parasitized nest by 0.37 fledglings.

The probability of a parasitized nest having an egg removed was predictable as well, being highest soon after parasitic egg-addition. In the first 72 h after egg-addition, the probability of egg-removal was higher than 80% (figure 1b), a large increase over the risk to these same nests before parasitic egg-addition.

Video observation revealed that the presence of the yellow warbler on the nest had no effect on the likelihood of parasitic egg-addition (figure 1c). Each time a cowbird approached to lay an egg in a nest attended by a female yellow warbler, the cowbird physically pulled the yellow warbler off the nest and laid her egg ( $n = 5$ ). By contrast, when cowbirds encountered a female on the nest during attempted egg-removal, physical interactions were rare (4 of 24 cases;  $G = 172$ ,  $p < 0.0005$ ), and cowbirds were successful in removing an egg in only 1 of 24 cases (figure 1c), while they always removed a host egg when they approached unattended nests ( $n = 6$ ). Moreover, females of naturally parasitized yellow warbler nests that did not have any eggs removed from their nest during incubation had significantly higher attentiveness than females of naturally parasitized nests that did suffer egg-removal (figure 1d). This difference cannot be attributed to differences in nest height ( $F = 0.01$ , d.f. = 1,21,  $p = 0.92$ ), or differences between study sites ( $F = 1.08$ , d.f. = 1,21,  $p = 0.42$ ). Thus host egg-removal poses a significant fitness cost to yellow warblers, is predictable, and is reduced through increased nest attentiveness. These results suggest yellow warblers should increase nest attentiveness once they detect that they have been parasitized.

Video observation of naturally parasitized and unparasi-

tized nests revealed that female attentiveness was significantly higher in parasitized nests (figure 2a) as predicted. In our experimental test of the effects of parasitism on incubation behaviour, treatment and control nests did not differ in attentiveness before treatment (paired  $t_{16} = 0.27$ ,  $p = 0.78$ ), but experimentally parasitized nests had significantly higher attentiveness than control nests after treatment (paired  $t_{16} = 2.2$ ,  $p = 0.023$ ). Consequently, attentiveness increased significantly following experimental parasitism, but did not change at control nests over the same period (figure 2b). This increase in attentiveness cannot be explained by disturbance at the nest because we controlled for disturbance. It is also unlikely to be a function of the change in clutch volume caused by replacing the host egg with the larger cowbird egg, because attentiveness in unparasitized nests tended to be negatively, rather than positively, related to clutch size ( $r = -0.31$ ,  $n = 31$ ,  $p = 0.089$ ). On average, attentiveness increased by 6%, decreasing the time nests were left unoccupied and vulnerable to egg-removal by 43% and, potentially, reducing egg-removal rates by a similar amount (figure 1d). While this behaviour could clearly increase fitness, such gains must be balanced against any costs of increasing attentiveness.

Increases in attentiveness were strongly associated with increased incubation feeding by males (figure 3a). Incubation feeding increased significantly in naturally parasitized nests (figure 3b) and in experimentally parasitized nests (figure 3c), where attentiveness also increased (figure 2b), and incubation feeding rates did not change in control nests (figure 3c), where attentiveness did not change (figure 2b). This result is directly attributable to parasitism: incubation feeding did not differ between treatments before manipulations (paired  $t_{16} = 1.3$ ,  $p = 0.19$ ), but was more than twice as high in experimentally parasitized nests compared with control nests after experimental manipulations (paired  $t_{16} = 2.7$ ,  $p = 0.008$ ). These increases in incubation feeding (to facilitate greater attentiveness) led directly to higher nest predation rates. Incubation feeding rates were higher at nests that were lost to predators than at nests that escaped predation during the incubation and early nestling phase (figure 3d). More directly, post-treatment daily nest predation was significantly higher on experimentally parasitized nests (figure 3e), which had higher rates of activity (figure 3c), than on post-treatment control nests (Mayfield  $\chi^2 = 5.0$ ,  $p = 0.025$ ). Because these nests were paired by location, height and initiation date, and one nest randomly parasitized, higher predation cannot be attributed to differences in nest location, concealment, or non-random choice of nests by cowbirds. These results clearly indicate that egg-removal and nest predation produce opposing selection pressures on incubation behaviour: the first selects for increased nest attentiveness and the second for low incubation feeding, which can only be achieved by reducing nest attentiveness.

#### 4. DISCUSSION

Yellow warblers are faced with a trade-off between increasing activity at the nest to defend against cowbird egg-removal versus reducing activity to minimize the risk of nest predation. This is the first evidence, to our knowledge, showing that egg-removal by cowbirds can cause

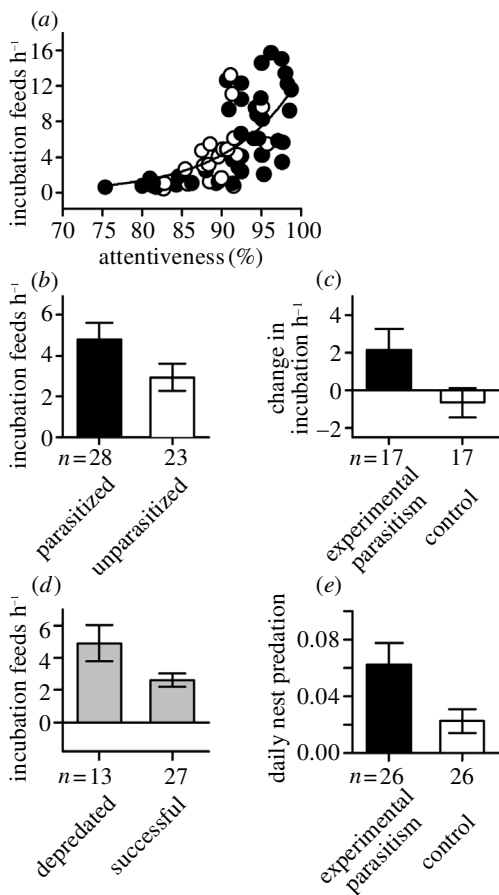


Figure 3. Effects of parasitism on incubation feeding and nest predation. (a) Incubation feeding (white, unparasitized nests; black, parasitized nests) was highly correlated with attentiveness ( $y = ae^{bx}$ ,  $F = 47$  d.f. = 62,  $r^2 = 0.44$ ,  $p < 0.0001$ ; all filmed from day three to five of incubation), thus (b) naturally parasitized nests had higher incubation feeding than unparasitized nests ( $F = 2.6$ , d.f. = 50,  $p = 0.048$ ), and (c) incubation feeding increased significantly after experimental parasitism (paired  $t_{16} = 1.9$ ,  $p = 0.03$ ), but remained unchanged in paired control nests (paired  $t_{16} = 0.84$ ,  $p = 0.415$ ) in the same experiment as figure 2b. Change in attentiveness and incubation feeding rates are differences between pretreatment and post-treatment measurements. Increased activity led directly to increases in nest predation as (d) nests that were lost to predators had significantly higher incubation feeding rates than nests that escaped predation ( $t_{38} = 2.2$ ,  $p = 0.02$ ) and (e) the daily nest predation rate was significantly higher for experimentally parasitized nests, which had higher activity (c), than for unparasitized control nests, which had lower activity.

shifts in host incubation behaviour, and in turn, that these shifts cause changes in nest predation. However, the conflicting selection pressures of parasitism and predation on host behaviour appear to be widespread because both parasitism costs from egg-removal and nest predation costs from parental activity have been documented for a variety of species and locations (Nolan 1978; Smith 1981; Sealy 1992; Massoni & Reboreda 1998; Martin *et al.* 2000a).

Parasitic egg-addition and host egg-removal both clearly represent fitness costs to yellow warblers. Our observed cost of egg-removal ( $R_c$ ), suggests that egg-removal is responsible for at least half of the total cost of parasitism.

Further, while increased attentiveness does deter removal (figure 1d), the shape of the relationship between the time the nest is unoccupied and the probability of cowbirds removing eggs is unknown, so our observed cost of egg-removal does not account for the effects of increased attentiveness on egg-removal. If the likelihood of egg-removal is proportional to the amount of time the nest is left unoccupied, yellow warblers are reducing egg-removal from a theoretical level of 1.76 eggs removed per nest ( $1.76 - 43\% = 1$  egg per nest, our observed 'er'). The task of estimating the total cost of parasitic egg-addition and removal is further complicated by the potential effects of cowbird nestling behaviour on predation rates during nestling development (Dearborn 1999), and the fact that both egg-addition and removal can increase the probability of outright nest-abandonment, which is frequently followed by re-nesting. Costs associated with these actions will clearly vary throughout the nesting season, as the potential for successful re-nesting changes.

The clear fitness costs of both parasitic egg-addition and host egg-removal suggest that responses need not be effective against both actions to be maintained. The large differences in levels of cowbird aggression between egg-laying and egg-removal events might be explained as follows: female cowbirds come directly from night-time roosts to lay their egg (Rothstein *et al.* 1984) and thus must remember the location of a nest found on a previous day (Sherry *et al.* 1993). Because cowbirds are selective in their choice of host nests and the stage in which to lay their eggs (Nolan 1978), they may only know the location of a single nest suitable for parasitism on a given morning. This would create strong selection for gaining access to that nest, as the only other option would involve wasting the day's egg. By contrast, while removal of host eggs from nests previously parasitized may benefit the cowbird, it is not necessary for the survival of parasitic eggs or young, and physically attacking a sitting host may increase the risk of nest abandonment or damage to the egg the cowbird has already laid (Sealy 1992; Rohwer & Spaw 1988). This should select against aggressive behaviour during egg-removal attempts.

Small hosts exhibit various forms of nest defence when cowbirds approach their nests (Robertson & Norman 1976; Smith *et al.* 1984). Yellow warblers in particular show a wide array of specialized nest defence strategies, such as sitting tightly on the nest, that appear to be directed only at cowbirds (Hobson & Sealy 1989; Briskie *et al.* 1990, 1992; Gill & Sealy 1996). These behaviours have been examined only in the context of their potential function in reducing the frequency of parasitism (parasitic egg-addition), yet there is no direct evidence that these nest defence behaviours deter cowbirds from laying their eggs (Sealy *et al.* 2000; Burhans 2000; figure 1c). By decoupling the effects of cowbird egg-laying and cowbird egg-removal, our results suggest a new interpretation for these specialized nest defence behaviours: they benefit hosts primarily by reducing egg-removal, not by reducing parasitism frequency. This may explain the existence of aggressive, potentially costly defence behaviour by some small hosts: even if they are ineffective at stopping cowbird egg-laying, they may be maintained due to their effectiveness in reducing egg-removal. The benefit of reducing egg-removal for hosts that typically are unable to raise their

own young with a cowbird will be confined to instances when the cowbird egg fails to hatch or hatches late enough to allow their own nestlings a competitive advantage. However, the benefits of reducing egg-removal may be large for hosts that do raise mixed broods, and hosts that remove cowbird eggs (rejecter species).

Protection of the nest from egg-removal can only be achieved if the female is present at the nest when the cowbird approaches. Cowbirds spent less than 5 s removing eggs from unattended nests (mean = 2.6 s,  $n = 5$ ); thus, effective defence depends on female attentiveness. However, increases in attentiveness depend on increased incubation feeding by males. To compensate, males must make more trips to the nest, causing increases in activity at the nest (Martin *et al.* 2000*a,b*) and, ultimately, a higher risk of nest predation. Given the predation costs of increasing incubation feeding and attentiveness, such behaviour is expected only where the probability of egg-removal is predictably high. Parasitic egg-addition may serve as a predictable cue of increased risk, but the presence of a cowbird at the nest, or even the abundance of cowbirds in the territory may also serve as cues. Such alternative cues may be particularly important for species unable to differentiate cowbird eggs from their own eggs (Rothstein 1982).

Whether the gains from reducing egg-removal offset the costs of increased nest predation depends on the relative cost of reduction in the number fledged from successful parasitized nests versus the cost of increased nest predation in parasitized nests. In our population, yellow warblers frequently re-nest following nest predation (86% of first nesting attempts that fail due to predation re-nest after failure), but they terminate nesting after successfully fledging either cowbird or host young. Thus, the costs of nest predation may be partially offset through re-nesting (Pease & Grzybowski 1995; Schmidt & Whelan 1999; Grzybowski & Pease 2000), while the costs of egg-removal may be more difficult to recoup. In addition, because parasitized nests essentially have a truncated maximum fledgling number, the seasonal fecundity that can be realized from a parasitized nest is substantially less than that which can be realized from an unparasitized nest. By increasing attentiveness, yellow warblers increase the potential seasonal fecundity of the parasitized nest, and because the potential of the parasitized nest is relatively low, the risk from increased predation is less costly and must be weighed against the opportunity for re-nesting and potentially avoiding parasitism in the subsequent attempt. This balance between costs and benefits surrounding behavioural responses to egg-removal will vary temporally, as a function of host life histories and as a function of parasitism frequency. Finally, the energetic costs of increasing attentiveness must also be considered, to determine the full balance between costs and benefits. Clearly, this antagonistic interaction between nest predation and brood parasitism costs deserves greater theoretical and empirical study, given its unappreciated consequences for both host fitness and parental care decisions.

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