



REASSESSING THE COWBIRD THREAT

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ABSTRACT.—The demographic significance of parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) has been debated for years, because manipulative studies are few and mathematical models of cowbird–host systems have not led to tests of their predictions. We combine results from a cowbird-removal experiment (Smith et al. 2002, 2003) with a stochastic simulation model that we developed, to reassess the effect of cowbirds on the annual reproductive success (ARS) and nesting success in Song Sparrows (*Melospiza melodia*). Our model followed the breeding success of individual Song Sparrow nests and extrapolated to output variables including ARS, nest survival, and parasitism rates. We parameterized the model with field data from cowbird control sites (i.e., cowbirds not manipulated) and found that output variables matched those observed. We used the reduced parasitism rates observed on cowbird-removal sites, reran the model, and compared output with observed values. On removal sites, ARS was greater than predicted by the model, which indicates that the model failed to account for some biological phenomenon that occurred when cowbirds were in the system. To assess what this phenomenon might be, we conducted further analyses that indicated that cowbirds may facilitate nest predation by “conventional” predators. Using elasticity analyses, we show that cowbirds have their largest effect on ARS through egg removal and that conventional predators are more important than cowbirds in directly affecting nest survival rates. We report that to assess the effect of cowbirds on nest survival, researchers must avoid using the common technique of comparing survival rates of parasitized and unparasitized nests within populations. *Received 16 February 2005, accepted 7 February 2006.*

Key words: annual reproductive success, Brown-headed Cowbird, cowbird parasitism, elasticity values, *Melospiza melodia*, *Molothrus ater*, nest predation, nest survival rates, simulation model, Song Sparrow.

Réévaluation de la Menace du Vacher

RÉSUMÉ.—L'importance démographique du parasitisme par le Vacher à tête brune (*Molothrus ater*, ci-après « vacher ») est une source de débat depuis plusieurs années, car les études comportant des manipulations sont peu nombreuses et les modèles mathématiques des systèmes vacher-hôte n'ont pas mené à des tests sur leurs prédictions. Nous avons combiné les résultats d'une expérience impliquant le retrait des vachers (Smith et al. 2002, 2003) avec un modèle de simulation stochastique que nous avons développé afin de réévaluer l'effet des vachers sur

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le succès de reproduction annuel (SRA) et le succès de nidification des Bruants chanteurs (*Melospiza melodia*). Notre modèle a suivi le succès de reproduction de nids individuels de Bruant chanteur et a extrapolé pour produire des variables dont le SRA, la survie du nid et le taux de parasitisme. Nous avons entré dans le modèle les données de terrain provenant de sites témoins (i.e. sans retrait des vachers) et nous avons trouvé que les variables produites correspondaient à celles observées. Nous avons utilisé le taux de parasitisme réduit observé sur les sites dont les vachers avaient été retirés, réexécuté le modèle et comparé les données de sortie avec celles observées. Sur les sites manipulés, le SRA était plus élevé que prévu par le modèle, ce qui indique que le modèle n'a pas tenu compte d'un phénomène biologique qui s'est produit lorsque les vachers étaient dans le système. Pour identifier ce phénomène, nous avons réalisé d'autres analyses qui suggèrent que les vachers peuvent favoriser la prédation des nids par des prédateurs « conventionnels ». À l'aide d'analyses d'élasticité, nous montrons que les vachers ont le plus d'influence sur le SRA en retirant les œufs de l'hôte et que les prédateurs conventionnels sont plus importants que les vachers en affectant directement le taux de survie des nids. Nous rapportons que pour évaluer l'effet des vachers sur la survie du nid, les chercheurs doivent éviter d'utiliser une technique ordinaire pour comparer les taux de survie des nids parasités avec ceux des nids non parasités.

THE DEMOGRAPHIC SIGNIFICANCE of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") has been debated for many years. Some have suggested that cowbird parasitism can explain the population declines of many forest songbirds (e.g., Brittingham and Temple 1983), but others have disagreed (Smith et al. 2000). This debate has persisted mainly because the data necessary to resolve it are lacking. Although many studies have shown that fewer host young fledge from parasitized than from unparasitized nests within a population, extrapolating these results to annual reproductive success (ARS) is problematic. Cowbirds can reduce fledgling production per nest by removing or puncturing host eggs in nests they parasitize (e.g., Smith 1981), thus reducing the clutch size at hatch. Cowbird nestlings can outcompete host young, which results in partial brood loss of host offspring during the nestling period (Smith et al. 2002). Many hosts, however, may be able to compensate for the negative effects of parasitism in any one nest by building more nests over the course of the breeding season (Pease and Grzybowski 1995, Schmidt and Whelan 1999, Grzybowski and Pease 2000). Thus, to assess the severity of cowbird parasitism on demography, it is essential to follow individual hosts throughout the entire breeding season rather than subsampling the nests of females. Then, the effect of cowbird parasitism

on the ARS of hosts can be assessed by comparing ARS in different populations subjected to varying levels of nest parasitism rather than comparing individual nests that had or had not been parasitized. The most direct way of establishing the degree to which cowbirds affect the ARS of their hosts is to manipulate cowbird parasitism. However, even though cowbird removal by trapping is frequently implemented in songbird conservation programs, only one spatially and temporally replicated, controlled cowbird-removal experiment has been conducted so far, and the results from this experiment were only recently published (Smith et al. 2002, 2003; see below).

Another difficulty in estimating the effect of cowbird parasitism on the ARS of hosts is that the effects of nest parasitism and nest predation may be hard to disentangle if they are inter-related. Nest predation is believed to be the most important cause of total nest failure in birds (Ricklefs 1969), and this could affect ARS, but some cowbird activities can mimic those of "conventional" nest predators. Cowbirds can remove enough host eggs that clutch size falls below a desertion threshold (Rothstein 1982), which leads to nest abandonment and total nest failure. Cowbirds also pull entire host broods out of nests and peck them to death (i.e., nestling destruction; Elliott 1999, Smith et al. 2003). Finally, there has been a suggestion that even if cowbirds themselves do not directly destroy

nests, their activities near nests may facilitate predation by other nest predators (Arcese et al. 1992). Cowbirds are not true predators because they do not commonly eat host eggs or nestlings, but these predator-like effects make it difficult to separate the independent effects of parasitism and conventional nest predation using observational results alone. Without this separation, it is impossible to assess either how important cowbirds are in causing total nest failure or the relative contributions of cowbirds and conventional nest predators on the ARS of songbirds. It is logistically challenging, however, to empirically manipulate brood parasitism and nest predation and to follow individual females in several populations over the entire breeding season.

A possible solution to these empirical difficulties was proposed by Pease and Grzybowski (1995) and Grzybowski and Pease (2000), who developed a deterministic mathematical model that was designed to use available data from observational studies to evaluate the relative effects of cowbird parasitism and nest predation by conventional predators. According to Pease and Grzybowski (1995), the demographic significance of cowbirds could be judged by varying the level of brood parasitism in the model and examining the effect on the projected ARS of the host. As the authors acknowledged, the pitfall in developing any model in the absence of experimental results is that the fit of the model to the data set for which it was developed is not a proper test of the model, because it is relatively easy to adjust the model to make the predicted and observed values match. Instead, predictions from models should be tested against independent, experimental evidence to ensure that all relevant biological phenomena are accounted for.

To avoid this problem and more fully evaluate the cowbird threat, we developed a stochastic simulation model parameterized using data from experimental control sites and tested it against results from our cowbird-removal experiment mentioned above (Smith et al. 2002, 2003). In the experiment, cowbird removal reduced parasitism by nearly 60%, increased daily nest survival rates by about one-third, and resulted in a doubling in the ARS of Song Sparrows (*Melospiza melodia*). We developed our stochastic simulation model to

evaluate the means by which cowbirds had this effect on their host and examined the relative contributions of cowbirds and conventional nest predators on nest survival and ARS. The basic structure of our model is similar to that of Pease and Grzybowski (1995) and Grzybowski and Pease (2000), except that we included separate parameters for egg removal by cowbirds (not inducing abandonment), cowbird-induced nest abandonment, nestling destruction, and partial brood loss. We parameterized our model with field data from the control sites. For our removal model, we reduced the parasitism rate to that observed on removal sites and compared the predicted ARS with the observed data. A match between the data and model predictions would suggest that the direct effects of cowbirds incorporated into the model would be sufficient by itself to predict the ARS of Song Sparrows. A mismatch between our model and experimental data would reveal that additional indirect effects of cowbird parasitism may be acting to influence Song Sparrow ARS. Here, we describe the structure of our model and its fit to the experimental field data.

Because the model failed to predict the full benefits to Song Sparrows of cowbird removal, it is likely that cowbirds indirectly influence ARS through facilitation of nest predation by conventional predators. We suggest that our experimental and simulation results together demonstrate that the cowbird threat to host reproductive success is real, and that the magnitude of that threat may be greater if cowbirds enhance the threat from conventional nest predators.

METHODS

COWBIRD REMOVAL EXPERIMENT

Details of this experiment can be found in Smith et al. (2002, 2003). Briefly, we worked at three riparian study sites in the Fraser River Delta, British Columbia, between 1995 and 1999. The sites were separated from one another by a minimum of 7 km. Song Sparrows are multibrooded, breeding from late March to late July each year. Cowbirds were trapped using portable house traps and removed to outdoor aviaries until the end of the breeding season, at which time they were released unharmed. We

removed cowbirds from one site in 1996 and 1997, with the remaining two sites acting as controls. In 1998, cowbird removal occurred at a different site, and the remaining two sites were controls. Song Sparrow nests were monitored regularly (every 3–4 days) and noted as active, fledged, or failed. We defined a parasitized nest as one that contained at least one cowbird egg or nestling. Smith et al. (2003) describe how causes of nest failure were categorized. We defined ARS as the average number of sparrow offspring produced per female per year. Nest success is the proportion of nests that escape total nest failure (from cowbirds or conventional nest predators).

THE MODEL

Model structure and parameters.—Details of the model's parameters can be found in Table 1. The model considers the breeding success of a female Song Sparrow over the course of a single breeding season. The season begins ($s_b + \epsilon_b$) and ends ($s_e + \epsilon_e$) on a randomly chosen date. We used the observed data to estimate the earliest (s_b) and latest (s_e) nesting date and then selected means and variances for random additions to these dates (ϵ_b, ϵ_e) to obtain a good fit to the observed number of nesting attempts per season.

Once the season has begun, it proceeds as a series of nest cycles, each lasting 28 days (3 days to build a nest, 1 day pre-incubation, 13 days incubation, 11 days brooding). Egg laying begins on day 4, with birds laying one egg a day thereafter until a clutch is complete. The size of the clutch is randomly chosen from a specified distribution that depends on the month as calculated from the observed data. Birds begin incubation on day 5. After a nest has failed or fledged, there is a resting stage (i.e., internest interval) of duration t_r days, which depends on the number of offspring fledged in the previous nest (i.e., 0 to 4 fledglings) as determined from observed values. Following the resting stage, birds begin a new nest cycle.

During each day of the egg stage, the nest may be destroyed by predators other than cowbirds with a fixed probability d_e , which we selected to fit observed proportions of nests preyed upon at this stage. The nest could also be parasitized with probability ρ_e , which was time-dependent (see Fig. 1) and

estimated from the observed data. A nest that is parasitized undergoes removal of i eggs with probability e_i , which we obtained by fitting the average observed productivity of parasitized nests. A nest that is parasitized more than once, or loses more than one egg to parasitism, is deserted with probability a_p , which was fitted to the observed abandonment frequency of parasitized nests.

On day 17 of the nest cycle, eggs hatch but i eggs may fail to hatch with probability h_i obtained from the observed data. During each day of the nestling stage, the nest may be destroyed by predators other than cowbirds with a fixed probability d_n , selected to fit observed proportions of nests preyed upon at this stage. The nest could also fail if a cowbird killed all nestlings, and we estimated the daily probability of nestling destruction by cowbirds (ρ_n) from the observed data. On day 23 of the nest cycle, the cumulative effects of partial brood loss are accounted for, with i nestlings lost with probability b_i , the value of which differs depending on parasitism status. All nestlings surviving to the end of day 28 of the nest cycle are assumed to have successfully fledged.

Nest cycles are all followed to completion unless the nest is destroyed or deserted, in which case the cycle skips directly to the rest stage. On completion of the nest cycle, another starts immediately, so long as the date is prior to the end of the breeding season. If the previous nest cycle yielded no fledglings, nesting attempts for a particular female may cease with probability c , which was estimated from the observed data.

Model output.—Smith et al. (2002) followed the success of 119 breeding females at control sites, and 49 breeding females at the cowbird-removal sites. We ran our model on the same number of breeding females over 2,000 breeding seasons. From this, we calculated population level means and 95% confidence intervals (CI) for 13 output variables (Table 2) and compared these values with averages obtained from the observed data as a way to test the accuracy of our model at predicting unmanipulated controls. Observed means falling outside of these 95% CI predicted by the model were judged to be inconsistent with model output (neglecting error in the observed mean makes it more likely that an observed value will be regarded

TABLE 1. Parameters, their notation, values, and source of data used in the simulation model.

Parameter	Purpose	Value	Source
s_b	Earliest nesting date	$s_b = 18$ th March	Determined from the control data
ϵ_b	Random addition to s_b	$\epsilon_b = N(24, 64)^a$	Fitted using observed distribution of nesting effort
t_r	Duration of resting stage	0 fledglings: $D(5, 6)^b$ 1 fledgling: $D(5, 6)$ 2 fledglings: $D(12, 13)$ 3 fledglings: $D(12, 13)$ 4 fledglings: $D(13, 14)$	Determined from the control data
	Clutch size	March–April 2 eggs: 0.08 3 eggs: 0.41 4 eggs: 0.51 May 2 eggs: 0.04 3 eggs: 0.58 4 eggs: 0.38	Determined from the control data
d_e	Daily probability of nest failure during egg stage by predators other than cowbirds	June–July 2 eggs: 0.24 3 eggs: 0.52 4 eggs: 0.24 $d_e = 0.028$	Fitted to egg-stage unparasitized nest survivorship (control data)
p_e	Daily probability of nest parasitism by cowbird	Time-dependent function	Determined from independent data (see Fig. 1)
e_i	Probability of removal of i eggs following parasitism	$e_0 = 0.15$ $e_1 = 0.65$ $e_2 = 0.20$	Fitted to the average productivity of parasitized nests (control data)
a_p	Probability of nest abandonment following multiple parasitism or loss of more than one egg to parasitism	$a_p = 0.60$	Fitted to the desertion frequency of parasitized nests (control data)
h_i	Probability that i eggs fail to hatch	$h_0 = 0.70$ $h_1 = 0.23$ $h_2 = 0.06$ $h_3 = 0.01$	Determined from the average productivity of unparasitized nests (control data)

TABLE 1. Continued.

Parameter	Purpose	Value	Source
d_n	Daily probability of nest failure during nestling stage by predators other than cowbirds	$d_n = 0.025$	Fitted to nestling-stage unparasitized nest survivorship (control data)
ρ_n	Daily probability of nest destruction during nestling stage by cowbirds	$\rho_n = 0.007$	Determined from independent data
b_i	Probability that i nestlings die on day 23 (i.e., partial brood loss)	$b_{0 unparasitized} = 0.78$ $b_{1 unparasitized} = 0.12$ $b_{2 unparasitized} = 0.10$ $b_{3 unparasitized} = 0.00$	Determined from independent data
s_e	Latest date at which a nest cycle may be started	$s_e = 19\text{th May}$	Determined from the control data
ϵ_e	Random addition to s_s	$\epsilon_e = N(24, 64)^a$	Fitted using observed distribution of nesting effort
c	Probability that nesting attempts are abandoned for the season (assuming the last nesting attempt to have failed)	$c = 0.02$	Determined from independent data

^a $N(\mu, \sigma^2)$ is the normal distribution with mean μ and variance σ^2 .

^b $D(x, y, \dots, z)$ is a discrete distribution containing the variates x, y, \dots, z , each chosen with equal probability.

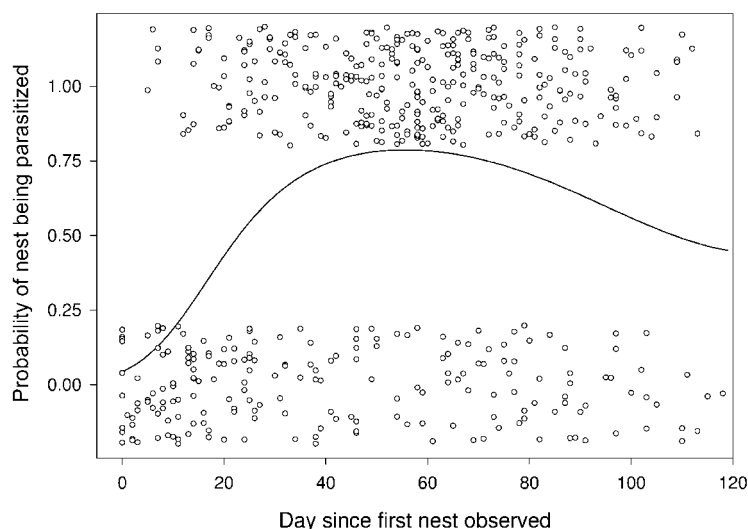


FIG. 1. Parasitism rates as a function of season (where day 0 is the day the first nest was observed). The line represents a logistic regression:

$$y = \frac{\exp(-3.089 + 0.185\text{day} - 0.002\text{day}^2 + 0.00001\text{day}^3)}{1 + \exp(-3.089 + 0.185\text{day} - 0.002\text{day}^2 + 0.00001\text{day}^3)}$$

The parameter p_c is obtained from the function $p_c = 1 - \exp \ln(1 - y)/14$, which converts the overall probability of parasitism measured over the 14-day egg stage to a daily probability. The y values are either 1 or 0, but random “jiggle” has been added to the values used in constructing the figure to avoid superimposition.

as deviating from the predictions of the model). For the removal model, we changed one parameter, parasitism rate (ρ_e), reducing it to 41% of controls. Thus, the parasitism rate for our removal model matched that found when we removed cowbirds in the field. Again, population-level means and 95% CI for the 13 output variables were calculated and compared with the field data obtained at the cowbird-removal sites. This allowed us to test whether the direct effects of parasitism alone, as represented in the model, were good predictors of ARS for Song Sparrows.

The effects of cowbird parasitism on Song Sparrow reproduction include egg removal (e_i), which can reduce fecundity per nest; nest abandonment at the egg stage (a_p); nestling destruction (ρ_n); and partial brood loss ($b_{i|p}$). Thus, manipulating parasitism rates for the removal model should affect several output parameters, including ARS and nest success. Because both the model and field study reduced parasitism by the same amount, we

expected to see an increase in ARS and nest survival rates in the removal model, which was comparable to that found in the field experiment. Conventional nest predators can affect reproduction through complete nest failure at either the egg (d_e) or nestling stage (d_n). Mortality also can come about through hatching failure (probability that i eggs fail to hatch, h_i) and partial brood loss (b_i , the probability that i nestlings die on day 23 of the nest cycle in unparasitized nests).

ELASTICITIES

Elasticities are defined as the proportional change in a response variable given a proportional change in a model parameter (Caswell 2001). For example, if our response variable was nest survival rate and our elasticity value for cowbird-induced nest abandonment was -0.53 , then a 10% increase in abandonment would cause a 5.3% decrease in nest survival (-0.53×10). We calculated elasticities to assess the

TABLE 2. Observed and model summary statistics on control and cowbird removal sites ("sparrow" = Song Sparrow). Ranges are 95% confidence intervals (CI) and are given in parentheses below the model means. Model values in bold were considered inconsistent with the observed data.

Summary statistics	Control sites		Removal sites		
	Observed	Model	Observed	Model	Model (adj. survival rates) ^a
Overall					
Annual reproductive success	1.65	1.83 (1.52–2.13)	3.31	2.61 (2.08–3.10)	2.83 (2.26–3.35)
Average number of sparrows fledged per nest attempt	0.53	0.58 (0.47–0.70)	1.05	0.92 (0.70–1.13)	1.03 (0.81–1.26)
Average number of nesting attempts per season	3.18	3.16 (3.00–3.28)	2.61	2.85 (2.61–3.08)	2.74 (2.53–2.98)
Fraction of nests attempted that were parasitized	0.62	0.58 (0.53–0.63)	0.30	0.31 (0.24–0.39)	0.33 (0.24–0.40)
Parasitized nests					
Average number of sparrow fledglings per successful parasitized nest	1.23	1.27 (1.04–1.49)	1.56	1.27 (0.82–1.74)	1.28 (0.87–1.71)
Survival rate of parasitized nests at egg stage	0.49	0.47 (0.40–0.54)	0.69	0.62 (0.47–0.76)	0.64 (0.50–0.79)
Survival rate of parasitized nests at nestling stage	0.68	0.70 (0.61–0.79)	0.75	0.73 (0.56–0.90)	0.76 (0.60–0.92)
Survival rate of parasitized nests overall	0.32	0.33 (0.26–0.39)	0.50	0.45 (0.31–0.60)	0.49 (0.34–0.65)
Proportion of successful parasitized nests that fledged only cowbirds	0.30	0.25 (0.15–0.35)	0.29	0.25 (0.06–0.47)	0.25 (0.07–0.44)
Unparasitized nests					
Average number of sparrow fledglings per successful unparasitized nest	2.45	2.6 (2.34–2.84)	2.73	2.62 (2.30–2.85)	2.63 (2.33–2.86)
Survival rate of unparasitized nests at egg stage	0.46	0.45 (0.38–0.53)	0.63	0.57 (0.48–0.68)	0.63 (0.53–0.73)
Survival rate of unparasitized nests at nestling stage	0.69	0.69 (0.58–0.79)	0.74	0.72 (0.59–0.83)	0.74 (0.62–0.86)
Survival rate of unparasitized nests overall	0.31	0.31 (0.24–0.38)	0.46	0.41 (0.32–0.51)	0.47 (0.36–0.57)

^a Daily nest predation rates at the egg stage down 18% (from 0.028 to 0.023), daily nest predation rates at the nestling stage down 12% (from 0.025 to 0.022).

relative importance of cowbirds as opposed to conventional nest predators in influencing our two response variables: ARS and nest survival rates. Elasticity values were calculated by examining the response of output variables (e.g., effects on ARS or nest survival rates) of a single female Song Sparrow averaged over 10,000 nesting seasons to decreasing and increasing input parameters by 20% of observed values. The input parameters we examined were egg removal by cowbirds, cowbird-induced nest abandonment at the egg stage, nestling destruction from cowbirds, and nest failure from conventional predators.

RESULTS

SIMULATION MODEL

The model closely approximated results from control sites (see Table 2). All observed summary statistics were well matched by the model. For the removal treatment, we reduced parasitism rates to 41% of those observed on the control sites to match our field data (Table 2). All but two summary statistics remained well matched. Our model underestimated ARS by 21% and overestimated the average number of nests built per season by 10%.

One variable that could affect both ARS and the number of nests built is nest survival rates, so we investigated this variable in more detail. Our model underestimated the overall survival rates of both parasitized (observed: 0.50 vs. predicted: 0.45) and unparasitized (observed: 0.46 vs. predicted: 0.41) nests in cowbird-removal areas. This is a small discrepancy, but our elasticity analyses (see below) indicated that ARS was most strongly influenced by nest failure caused by conventional predators, especially on the removal sites. Therefore, even small discrepancies in this parameter may be enough to account for the mismatch in ARS between our model predictions and the observed results. To check this, we reduced daily nest predation rates at both the egg (from 0.028 to 0.023; Table 2) and nestling (from 0.025 to 0.022; Table 2) stages, so that overall nest survival rates predicted by the model matched those observed on the removal sites (Table 2). Following this modification, the observed means for ARS and number of nests attempted per season fell within the 95% CI predicted by the model (Table 2).

ELASTICITY ANALYSES

Controls

Annual reproductive success.—Nest failure by conventional predators had a strong influence on ARS (−0.53). Cowbirds had their largest effect on the ARS of their hosts by reducing clutch sizes through egg removal (−0.50). Cowbird-induced nest failure had only a small effect on ARS (−0.14), with neither nest abandonment (−0.08) nor nestling destruction (−0.07) being important.

Nest survival rates.—Nest survival rates were substantially affected by both cowbird-induced nest failure and by conventional predators (elasticity values: −0.39 and −0.74, respectively), though the effect of conventional predators was ~2× greater than that of cowbirds. Cowbirds influenced nest survival mainly by causing nest abandonment at the egg stage (−0.31), with nestling destruction (−0.07) having a negligible effect. Conventional predators affected nest survival rates strongly at both the egg (−0.44) and nestling (−0.30) stages. Examining nest survival rates overall, we found that the elasticity values were ~2× greater at the egg (−0.76) than at the nestling

stage (−0.37), which corresponds with our finding that cowbirds and conventional predators both had large effects at the egg stage, whereas only conventional predators had an appreciable effect at the nestling stage.

Removals

Annual reproductive success.—Nest failure by conventional predators again strongly influenced ARS (−0.48). Cowbirds affected ARS mainly through egg removal (−0.32). Cowbird-induced nest failure had a small effect on ARS (−0.03), with neither nest abandonment (−0.001) nor nestling destruction (−0.03) playing a major role.

Nest survival rates.—Cowbirds had only one-third as much influence on nest survival rates at the removal as at the control sites (−0.13 vs. −0.39). Conventional predators, by contrast, continued to play a major role in affecting nest survival rates (−0.71). They were ~6× more important than cowbirds (−0.71 vs. −0.13) in affecting nest survival rates. Cowbird-induced nest abandonment (−0.09) and nestling destruction caused by cowbirds (−0.03) each had small effects on nest survival rates at the removal sites, but conventional predators continued to have strong influences at both the egg (−0.43) and nestling stages (−0.29). Combining all causes of nest failure, we found that the egg stage was still more important than the nestling stage (−0.54 vs. −0.32) but that their relative contributions were more similar than they had been on the controls (−0.76 vs. −0.37).

DISCUSSION

Our results indicate that the mere presence of cowbirds may have adverse effects on the ARS of hosts, above and beyond those attributable to the direct effects of brood parasitism. The most likely reason is that the presence of cowbirds facilitates nest predation by conventional predators. The relative effects of brood parasitism and nest predation were not independent and additive. This was revealed only when we compared our model's predictions against our independent experimental evidence; modeling alone was not sufficient.

Our elasticity analyses point to nest failure by conventional predators as a key parameter. Annual reproductive success was most sensitive

to changes in nest predation at the removal sites, and our simulation model somewhat underestimated nest survival rates there. When we adjusted the nest survival values so that they matched those observed, the differences between the model and observed values for ARS were also well matched. The relatively low nest-survival rates predicted by our model would also explain why it overestimated the number of nests built in a season on removal sites (Table 2). Renesting after a predation event commonly occurs in birds. Thus, when we increased nest survival rates, this reduced the model estimates for the number of nests built, such that they were no longer inconsistent with the observed values. Another parameter that had a large effect on Song Sparrow ARS was egg removal by cowbirds. An underestimation of ARS on the removal sites could have occurred if cowbirds removed or damaged fewer eggs than expected in every Song Sparrow nest when cowbird numbers were low. We believe this possibility unlikely. First, we know of no reason why egg-removal behavior would change in this fashion. Second, if cowbirds remove fewer eggs per nest than expected given the lower numbers of cowbirds, the number of host fledglings produced per successful nest should increase for parasitized but not for unparasitized nests when comparing removal with control sites. Examining the observed number of Song Sparrow fledglings produced per successful nest (Table 2), we find that both parasitized and unparasitized nests produced ~0.3 extra fledglings when cowbirds were removed.

Facilitation may be one way in which cowbirds could affect nest failures that were ultimately caused by conventional predators (e.g., Arcese et al. 1992). Cowbirds elicit defense behaviors from their hosts that may render the nest more conspicuous to conventional predators (Robertson and Norman 1977, Smith et al. 1984). These behaviors may occur when the nest is being parasitized or when cowbirds damage or remove host eggs. Also, the mere presence of a cowbird near the nest is often enough to elicit at least some of these responses (e.g., Ward and Smith 2000). Cowbird nestlings may increase the conspicuousness of a nest, because they often beg more loudly and persistently than host nestlings (Dearborn 1999). Cowbirds also increase the overall begging intensity in the nest, which stimulates the parents to bring more

food (Bengtsson and Rydén 1983, Kilner 2003), and more feeding trips may increase predation risk (Martin et al. 2000). Our model tells us that additional (non-cowbird) predation facilitated by the presence of cowbirds may be responsible for between 10% and 20% of the daily predation rate (Table 2). The reason this small number had an effect on our model results was because of the high sensitivity of ARS to conventional predators. We suggest, then, that cowbirds have a dual effect on nest survival rates: they cause nest failure directly (through nest abandonment and nestling destruction) and indirectly (through facilitation of predation by non-cowbird predators). A second explanation for our underestimation of nest survival rates is that we misidentified the process responsible for nest failure in some cases. For example, cowbirds may remove eggs, which leads to abandonment in nests that they do not parasitize (Arcese and Smith 1999). In the field, failure of an unparasitized nest would have been ascribed to a conventional predator rather than a cowbird. Although possible, we believe this unlikely because our cowbird-removal experiment (Smith et al. 2003) showed that the abandonment of unparasitized nests increased rather than decreased on removal sites, which suggests that cowbirds were not the cause.

Some have argued that cowbird-induced nest failure (i.e., nest abandonment and nestling destruction) itself may have an appreciable influence on the ARS of hosts (e.g., Smith and Arcese 1994, Arcese and Smith 1999), but we found little evidence for this. Our elasticity values for cowbird-induced nest failure on ARS were relatively small, even when cowbirds were abundant. Instead, egg removal by cowbirds greatly affected ARS on both control and removal sites (Trine 2000). Others have suggested that when cowbird numbers are low, egg removal by cowbirds may have little demographic effect on their host if nest predation is also important (e.g., Stutchbury 1997). The reasoning is that the benefit of having more host young per nest when cowbirds are reduced may be swamped by the effects of predators that would destroy most of these nests anyway. Our model shows that, on the contrary, nest predation (by other predators) and egg removal by cowbirds were both important factors affecting the ARS of Song Sparrows on control and removal sites.

The relative importance of cowbirds as opposed to conventional predators in affecting overall nesting success has been contentious, because the evidence has been conflicting. On the one hand, studies comparing individual nests find that for parasitized compared with unparasitized nests, nest survival rates can be lower (Payne and Payne 1998, McLaren and Sealy 2000), higher (Arcese et al. 1996), or the same (Rogers et al. 1997, Smith et al. 2002). On the other hand, cowbird-removal experiments have led to increases in overall nest-survival rates for populations (Whitfield et al. 1999, Smith et al. 2002; but see Stutchbury 1997) in addition to decreases in failures caused specifically by cowbirds either through nest abandonment or the death of nestlings from cowbird punctures (Smith et al. 2003). Other studies on entire populations typically show a positive correlation between parasitism and nest predation rates (Arcese et al. 1992, Arcese and Smith 1999, Clotfelter and Yasukawa 1999), which suggests a link between cowbirds and nest failure. Video-monitoring studies have recorded cowbirds causing losses of eggs and nestlings at host nests, but only at a low rate (Thompson et al. 1999, Granfors et al. 2001). Notably, these video studies were conducted at sites where cowbird parasitism was low.

The results from our experiment appeared to provide conflicting evidence regarding the importance of cowbirds in nesting success. On the one hand, the observed data showed little difference in survival rates for parasitized versus unparasitized nests on either the control (0.32 vs. 0.31) or removal sites (0.50 vs. 0.46) (Table 2), which suggests that cowbirds play no role in affecting nest survival rates. On the other hand, nest survival rates greatly improved on the removal sites compared with control sites both for parasitized (0.50 vs. 0.32) and unparasitized (0.46 vs. 0.31) nests, which suggests that cowbirds were the cause. Our simulation model yielded similar patterns (Table 2) that may provide a clue as to why these two types of results differ. The only parameter we varied for the removal model was nest parasitism rate. Here, an increase in survival rates of parasitized nests on the removal compared with control sites would be reasonably expected, given that reducing the parasitism rate should have led to fewer nest-abandonment and nestling-destruction events. Reducing the parasitism rate should have had no effect on the

nest survival rates of unparasitized nests, yet we saw a considerable increase in both the field data and the model predictions (Table 2). Because the model includes no biological mechanism for such an increase, this suggests that some sort of sampling artifact underlies this effect. We propose that this artifact is generated when nest survival rates are partitioned according to parasitism status. We found that the nest survival rates for unparasitized nests must necessarily increase as parasitism decreases, simply because of the way in which survival is calculated (see the Appendix for our mathematical explanation; Fig. A1). Survival values are essentially concerned with the proportions of individuals (e.g., nests) that survive out of a total population (though they can be calculated using many different estimators). As parasitism rates decrease, the total number of nests that are neither preyed on nor parasitized will increase. Therefore, the proportion of unparasitized nests that survive must necessarily increase, thereby inflating the survival rate for unparasitized nests. Simply comparing static nest-survival rates of parasitized with those of unparasitized nests within a population can provide misleading information as to the role of cowbirds in affecting nest success. Estimating nest survival rates within a dynamic framework avoids these pitfalls.

The results of our study are likely applicable to many cowbird hosts, especially those that abandon parasitized nests and suffer from clutch reduction because of egg removal by cowbirds. However, the relative importance of the parasites' activities may differ across species. For instance, like Song Sparrows, small hosts such as some warblers (Parulidae) and vireos (*Vireo* spp.) (e.g., Hayden et al. 2000, Whitfield 2000, Ortega and Ortega 2003) will abandon parasitized nests, but for those nests that remain active, small hosts rarely rear any of their own young because cowbird nestlings outcompete host young, who then starve to death. In this case, ARS would be affected not so much by egg removal, as it was for Song Sparrows, but by competition between host and parasite nestlings that would affect host brood losses.

We have shown that Song Sparrow ARS and their nest survival rates benefit from cowbird removal to an extent that could not be predicted from the independent actions of nest predation and cowbird parasitism. Our experimental data, combined with a closely

parameterized model, were critical in identifying the role of cowbirds in potentially facilitating additional predation activity that acts to suppress the ARS of the host. The synthesis of results from empirical data and model-testing can help us better understand complex systems such as the cowbird–host system. Indeed, without the combination of the two, the effects of important processes can easily be missed.

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APPENDIX

Suppose we have unparasitized and undepredated nests (S), parasitized nests (I), and depredated nests (R).

Suppose for simplicity that unparasitized and undepredated nests become parasitized at rate β , and that predation on both unparasitized and undepredated nests proceeds at rate γ . Suppose that depredated nests are abandoned and cannot be parasitized.

This gives

$$\frac{dS}{dt} = -\beta S - \gamma S \quad \frac{dI}{dt} = \beta S - \gamma I \quad \frac{dR}{dt} = \gamma S + \gamma I$$

where the initial conditions at time zero are S_0 , I_0 , and R_0 .

The survival rate of unparasitized and undepredated nests ($u_{S,t}$) after time t would be given by

$$u_{S,t} = \frac{S_t}{S_t + R_t}$$

whereas the survival rate of parasitized and undepredated nests ($u_{I,t}$) would be given by

$$u_{I,t} = \frac{I_t}{I_t + R_t}$$

Solving the differential equations directly, we obtain

$$S_t = S_0 \exp[-(\beta + \gamma)t], \quad I_t = \frac{S_0(1 - e^{-\beta t})}{e^{\gamma t}},$$

$$R_t = S_0(1 - e^{-\gamma t})$$

and substituting these expressions into

$$\frac{S_t}{S_t + R_t}$$

gives $u_{S,t} = \frac{e^{-(\beta+\gamma)t}}{e^{-(\beta+\gamma)t} + 1 - e^{-\gamma t}}$

Plotting $u_{S,t}$ over time for different values of β shows that as β decreases, $u_{S,t}$ increases (Fig. A1). The intuitive explanation for this is that S_t will inevitably remain larger when parasitism rates are low than when they are high and, consequently, that S_t is a larger proportion of the sum ($S_t + R_t$) when parasitism rates are low than when they are high. This sampling effect will lead to the impression that the survival rate of unparasitized nests is influenced directly by the parasitism rate.

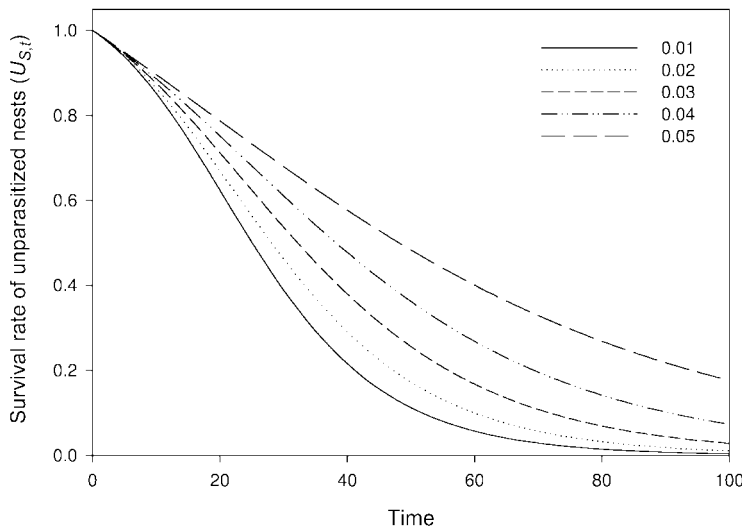


FIG. A1. The relationship between survival rate of unparasitized nests ($u_{S,t}$) over time, as a function of different rates of parasitism, according to the model described. Rates of parasitism (β) vary between 0.01 and 0.05 per day, and γ is set at 0.01. Note that apparently substantial changes in the survival rates of unparasitized nests are indicated, even though only the parasitism rate is changing.