

High offspring survival of the brown-headed cowbird in an invaded habitat

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Abstract

The brood parasitic brown-headed cowbird (*Molothrus ater*) is considered an important threat to bird conservation in North America because it reduces the reproduction of its numerous host species. Prior to the colonisation of America by Europeans, the cowbird was largely confined to the North American prairie region, but it has since invaded forests and other habitats and is now one of the continent's most abundant breeding passerines. The objective of this study was to examine cowbird reproduction with different host communities to determine whether habitat-specific reproduction might contribute to the cowbird's population expansion. Cowbird offspring survival was estimated with hosts breeding in fragmented deciduous forest (a newly invaded habitat) and old fields (a habitat more similar to the cowbird's original range). Offspring survival was 1.8–3.1 times higher in forest compared to old fields and was high enough to cause the cowbird population to increase with most forest hosts. The results suggest that increased offspring survival in an invaded habitat facilitates cowbird population growth. Land management for extensive, continuous forests, which cowbirds are known to avoid, could help control the cowbird population and reduce parasitism levels for the >140 species of cowbird hosts.

INTRODUCTION

The spread of species outside their native range is a serious conservation problem worldwide (Williamson, 1996; Mooney & Hobbs, 2000), and in the United States of America invasive species are second only to habitat destruction as a factor contributing to species endangerment (Wilcove *et al.*, 1998). The present understanding is limited, however, as to why certain species become invasive and what can be done to control them (Kolar & Lodge, 2001; Allendorf & Lundquist, 2003). This study of the brown-headed cowbird (*Molothrus ater*) investigated a potential mechanism of invasion, high offspring survival in an invaded habitat. The cowbird is an obligatory brood parasite that can only reproduce via its host species. Although native to North America, the cowbird was originally a prairie-breeding bird and, until the 18th century, was largely absent from the deciduous forest that covered the eastern part of the continent (Mayfield, 1965). As humans fragmented the eastern forest, however, the cowbird moved into this region and began parasitising the hosts breeding there. The cowbird is, therefore, an invasive species (*sensu* Davis & Thompson, 2000) because it has greatly expanded its geographical range and habitat use, even though it did so by diffusion rather than saltation.

Today the cowbird is abundant throughout the continent and is found in a variety of habitats (Fig. 1). It heavily parasitises forest-breeding hosts, as long as the forests are sufficiently fragmented for cowbirds to gain access (e.g. Robinson *et al.*, 1995). The cowbird is considered one of the most important threats to North American bird conservation because it is so widespread and abundant and because it reduces the reproduction of its >140 host species, in some cases to below sustainable levels (Friedmann & Kiff, 1985; Trine, Robinson & Robinson, 1998; Lorenzana & Sealy, 1999).

In this study the possible effects of the invaded habitat and its naïve host bird community on cowbird population growth were investigated. The focus was on the survival of cowbird offspring from the egg to the fledgling stage because this is the only life history transition that can be attributed to a single habitat. In contrast, both juvenile and adult survival are integrated over a large variety of habitats because cowbirds are highly mobile on both a daily and yearly basis, moving several km per day during the breeding season (Thompson & Dijak, 2000) and migrating to the southern USA and Mexico during the non-breeding season. Specifically, the hypothesis tested was that cowbird offspring would survive better with the host species found in deciduous forest, an invaded habitat, than with the host species breeding in old fields, a habitat more similar to the cowbird's original range. However, the observed transition success was also compared to what would be required for stable population size, i.e. for

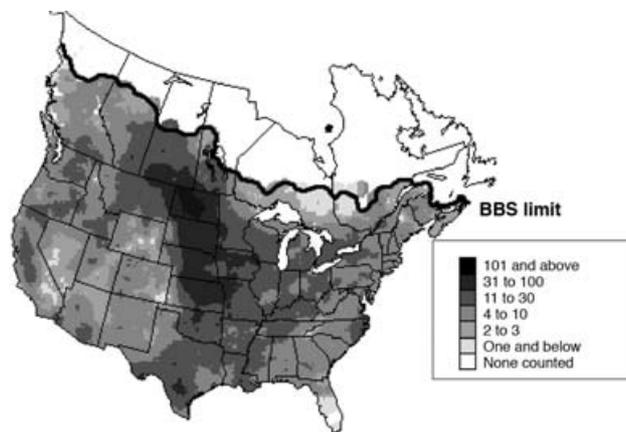


Fig. 1. Current breeding range of the brown-headed cowbird, based on Breeding Bird Survey data (Sauer, Hines & Fallon, 2001). Values are number of cowbirds detected per survey route.

breeding females to exactly replace themselves in each generation ('replacement').

Several factors might influence cowbird offspring survival, including differences between habitats or host species in nest mortality rates and differences between host species in their response to parasitism, or in their ability to raise cowbirds. At the start of this study, it was expected that cowbirds would reproduce well in the forest due to high acceptance of cowbird eggs by naïve forest-breeding host species. Bird species that nest in open habitats, such as prairies, old fields and other grasslands, have probably interacted with the cowbird for much of its 0.5 million-year history in North America (Lowther, 1993), and they are known to have anti-parasite behaviours such as removing cowbird eggs from the nest (Rothstein, 1975; Grzybowski & Pease, 1999; Winfree, 1999; Peer, Robinson & Herkert, 2000). In contrast, forest-breeding species have interacted with cowbirds on a large scale for less than 300 years (Mayfield, 1965) and no true forest interior species is known to remove cowbird eggs from its nests, although the red-eyed vireo (*Vireo olivaceus*), which breeds in both forest interiors and edges, may preferentially abandon parasitised nests (Graham, 1988). To determine the relative importance to overall cowbird reproduction of host responses to cowbird eggs, host nest survival and cowbird offspring survival within surviving host nests, the contribution of each of these factors was examined separately.

METHODS AND MATERIALS

Study sites and data collection

The study was carried out in and around the Shawnee National Forest in southern Illinois, USA. This region was chosen because of its high cowbird density, which increased sample sizes, and because it is representative of originally continuous eastern deciduous forest that is now highly fragmented (Iverson, 1989).

The study was replicated at a large geographical scale with $n = 2$ study areas roughly 34 km apart. These areas

are referred to hereafter as 'replicate one' and 'replicate two.' Large-scale replication was necessary due to the high mobility of cowbirds, which can range over 15 km in one day (Curson, Goguen & Mathews, 2000), although distances of 1–4 km are more typical (Thompson, 1994). Within each replicate, data were collected in two habitat types (Fig. 2). 'Forest' consisted of mature deciduous forest, dominated by maple-beech in lowland areas and oak-hickory in upland areas ($n = 3$ sites in replicate one, $n = 5$ sites in replicate two: Fig. 3(a)). 'Old field' consisted of early to mid-successional old fields dominated by grasses and herbs, or in places by shrubs ($n = 3$ sites in replicate one, $n = 3$ sites in replicate two: Fig. 3(b)). Data were combined by habitat type within each replicate because sites were not far enough apart to be considered independent, given the cowbird's mobility.

Data on nest mortality rate and cowbird egg and nestling survival within active host nests were collected by monitoring nests (Martin & Geupel, 1993). In replicate one, data were collected between 1998–2000 for all cowbird host species and the data for the 15 species with the largest sample sizes were analysed. In replicate two data were collected between 1993–1995 and the analysis focused on only nine of the more important cowbird host species (in the sense that these species produce many cowbirds per capita and/or are highly abundant: unpublished results), but larger sample sizes were available for each species. It was particularly difficult to obtain nest data for canopy-nesting species, whose nests can be 25 m off the ground. However, the most abundant canopy species were studied, notably red-eyed vireos and scarlet/summer tanagers (*Piranga olivacea* and *P. rubra*). The tanager species are morphologically and ecologically similar and were analysed as one species since they could not always be reliably separated. Due to small sample sizes, data were combined for canopy-nesting species to estimate one 'canopy' nest mortality rate. In addition, in estimating canopy nest mortality rate for replicate one, additional data on the same species collected between 1989 and 1993 in other parts of Shawnee National Forest were used. Total sample sizes were 380 nests for replicate one and 260 nests for replicate two (Table 1).

Numerical methods

Cowbird egg-to-fledgling transition success (T_i) was calculated for each host species (i) as:

$$T_i = U_i V_i W_i \quad (1)$$

where U_i = the probability that the cowbird egg will be accepted by the host, V_i = the probability that the host nest will survive long enough to fledge a cowbird and W_i = the probability that the cowbird will survive to fledging within the nest, given that the nest itself survives. To calculate the fraction of cowbird eggs accepted (U_i) and its associated error, species-specific values from large data sets were used (Best, 1978; Nolan, 1978; Graham, 1988). Daily nest and cowbird survival rates were calculated using the Mayfield method (Mayfield, 1975), which provides the

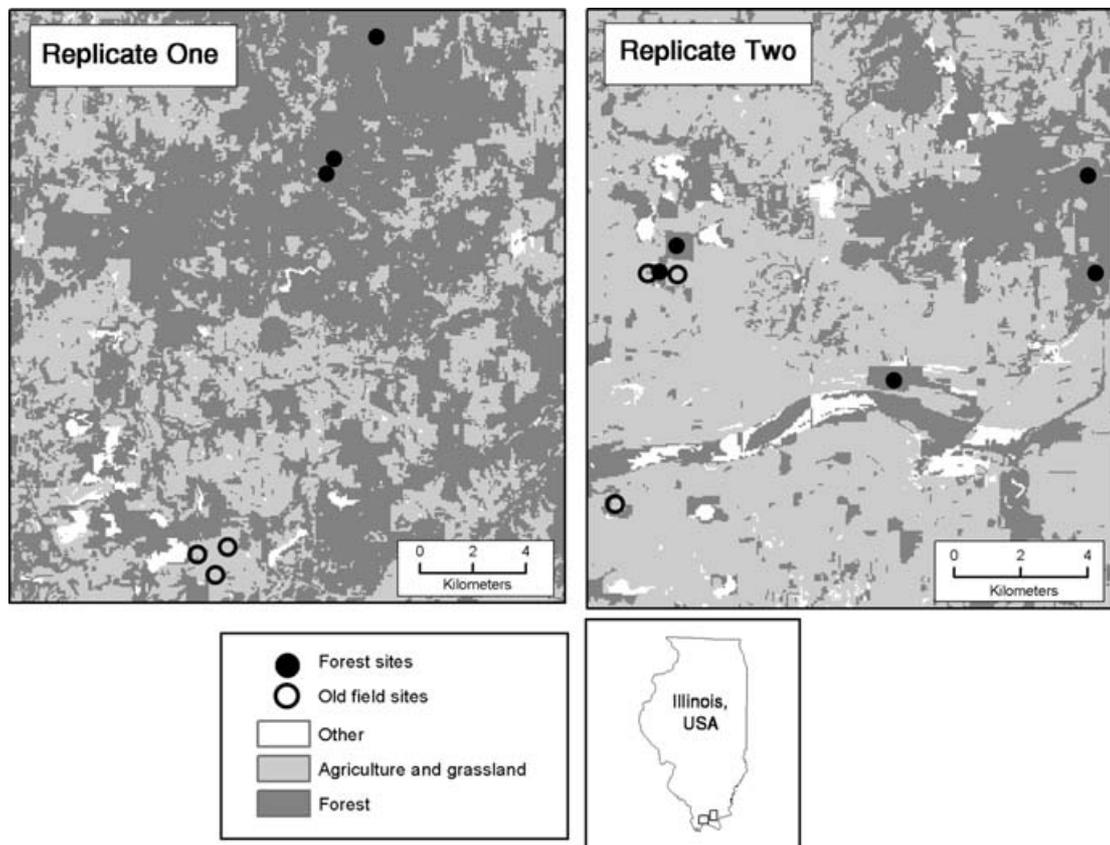


Fig. 2. Map of the two replicate study areas, with the centres of the forest (●) and old field (○) study plots indicated.

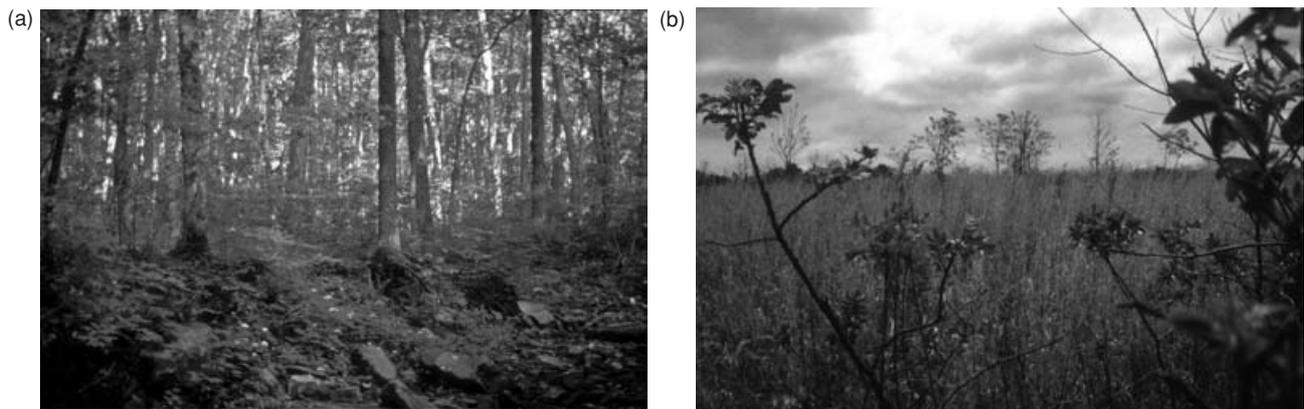


Fig. 3. The habitat types studied. (a) Eastern deciduous forest site in replicate one. (b) Old field site in replicate one.

maximum likelihood estimate (Bart & Robson, 1982). To calculate nest survival (V_i), the data for a given host species within a replicate across years and sites were combined to generate one mean value and its associated error, for each species in each replicate. The data were combined in this way because sites within a replicate were too close together to be considered independent and because sample sizes for many species within a site and a year were too small to generate reliable estimates of mortality rate.

To calculate cowbird survival within surviving nests (W_i), data across all host species within a replicate and habitat type were combined. No significant differences were found in cowbird survival between host species, although small sample sizes limited the statistical power for many species. In contrast, daily cowbird survival did differ significantly by stage of the nest cycle (incubation, hatching and nestling), so these rates were calculated separately for each stage and overall survival was derived as the product of the probability of surviving each nest

Table 1. Total sample sizes for nest data

	Species with nest data	Nests	Nest exposure days	Cowbird eggs and young	Cowbird exposure days
Replicate one					
Forest sites	8	133	1537	75	636
Additional canopy data	2	24	213	Not used	Not used
Old field sites	7	223	1920	72	321
Total	15	380	3669	147	957
Replicate two					
Forest sites	5	190	2782	247	1350
Old field sites	4	70	653	38	160
Total	9	260	3435	285	1510

An exposure day is a 24-h interval during which a nest or cowbird was under observation; this is the sample size unit for calculating survival rates.

stage. Cowbird survival also varied according to the number of cowbird offspring in the nest, so W_i was calculated using data for cowbirds that shared the nest with host offspring only. This was done to remove any density-dependent effects from the estimated transition success.

All of the variables in Equation 1 are sample means and all errors reported are standard errors of the mean. Observation error was propagated through all of the calculations using an equation derived from a Taylor expansion, which sums the fractional errors associated with each term in a product (Roe, 1992). For example, error was propagated through Equation 1 as:

$$\frac{\sigma_{T_i}^2}{T_i^2} = \frac{\sigma_{U_i}^2}{U_i^2} + \frac{\sigma_{V_i}^2}{V_i^2} + \frac{\sigma_{W_i}^2}{W_i^2} \quad (2)$$

To examine the sensitivity of cowbird egg-to-fledgling success to each of the three parameters in Equation 1, for each host species in each replicate each parameter was varied by $\pm 10\%$ and $\pm 20\%$ and the resulting change in egg-to-fledgling success was recorded.

Estimating replacement values for the egg-to-fledgling life-history transition

To calculate the egg-to-fledgling success that would be required for a stable population size ('replacement'), a source-sink equation was used:

$$\lambda = S_A + S_J P \quad (3)$$

where λ = the discrete-time population growth rate (which is 1 at steady state), S_A = the annual adult female survival probability, S_J = the annual juvenile female survival probability (defined here as from fledging to age at first breeding) and P = the number of female offspring produced each year by one breeding female (Pulliam, 1988). P can be broken down as:

$$p = \frac{FT}{2} \quad (4)$$

where F = the annual fecundity (the number of eggs laid per female per year; a 50–50 sex ratio is assumed for

eggs, based on Weatherhead, 1989) and T = the transition success from egg to fledgling. Published information on S_A , S_J and F was compiled and fitted to $\lambda = 1$ to estimate the critical value of T required for replacement (T_{crit}). The existing data on cowbird demography are insufficient to estimate T_{crit} precisely. Instead, a range of published values were used for S_A , S_J and F in order to generate a conservatively broad range of possible replacement values for T_{crit} . The existing data were also insufficient to estimate habitat-specific values for annual survival and fecundity. The breeding habitat probably has a minimal effect on these parameters, however: first, because cowbirds spend only part of each day in their egg-laying area (e.g. Thompson & Dijak, 2000) and second, because they spend only a few months each year in their breeding range.

Woolfenden, Gibbs & Sealy (2001) estimated the annual survival for female cowbirds (S_A) using a capture-recapture statistical model and they obtained values of 0.65 ± 0.08 SE to 0.70 ± 0.08 SE. Annual juvenile survival (S_J) has only been measured for a few migratory bird species and it has not been measured for cowbirds. The limited data available suggest that S_J for migratory passerines is $1/4$ to $1/2$ of S_A and this ratio is generally used in bird population studies (Ricklefs, 1973; Greenberg, 1980; Smith, Taitt & Zanette, 2002). Values for S_J were estimated on the basis of adult male rather than female survival, because female cowbirds have lower survival than males once they reach reproductive age (Woolfenden, *et al.*, 2001). This reduced survival is probably due to the females' high fecundity (Saether, 1988) and should not apply to juveniles. Annual survival for adult males is 0.75 ± 0.05 SE to 0.90 ± 0.04 SE (Woolfenden, *et al.*, 2001). The low estimate of S_J was therefore 0.19 ($= 0.25 \times 0.75$) and the high estimate was 0.45 ($= 0.50 \times 0.90$). The high estimate is probably too high, given that survival during the first few weeks after leaving the nest is probably $< 50\%$ (Woodward & Woodward, 1979; Scott & Ankney, 1980). Nevertheless, it is used here for the purposes of establishing upper and lower bounds on T_{crit} . For female cowbird fecundity, values were used from studies that assessed the presence/absence of oviductal eggs in a sample from a wild population and these values were then multiplied by the length of the breeding season, in order to estimate the number of eggs laid female⁻¹

Table 2. Estimates of the T_{crit} values required to reach replacement population growth

	Adult annual survival probability (S_A)	Juvenile annual survival probability (S_J)	Fecundity (female eggs laid year ⁻¹)	T_{crit}
Upper bound for T_{crit}	0.65	0.19	8.5	0.22
Lower bound for T_{crit}	0.70	0.45	20	0.03

Estimates of the critical egg-to-fledgling transition success (T_{crit}) required in order for the cowbird population to achieve replacement population growth ($\lambda = 1 = S_A + S_J P$; see Equations 3 & 4). All values are in terms of females only.

year⁻¹. Values ranged from a low of 17 eggs (Woolfenden *et al.*, 2003) to a high of 40 eggs (Scott & Ankney, 1980).

The upper and lower bounds for T_{crit} were found by using the extreme values reported in the published literature for other life-history parameters and assuming correlated errors (e.g. pairing low adult survival with low juvenile survival and low fecundity). These methods result in the broad, i.e. conservative, range of replacement values reported in Table 2.

RESULTS

In replicate one, all forest host species provided higher egg-to-fledgling success for cowbirds than did any field host (Fig. 4(a), Table 3). Even when a very broad range of replacement values was used (Table 2), all but one of the forest hosts were above replacement and none was below replacement, whereas none of the field hosts was above replacement and most were near the lower bound on replacement values. A similar pattern was found in replicate two (Fig. 4(b), Table 4), with the exception of one old field species, the common yellowthroat (*Geothlypis trichas*). In replicate one, cowbird egg-to-fledgling survival with forest hosts was, on average, 3.1 times higher than with field hosts and the difference was highly significant ($p < 0.001$, Mann–Whitney U -test). In replicate two, cowbird offspring survival with forests hosts was, on average, 1.8 times higher, but the difference was not significant ($p > 0.20$, Mann–Whitney U -test).

The most important factor for causing higher cowbird survival in the forest was host nest survival. On average, nest survival was 2.2 times higher for forest than for old field hosts in replicate one and 2.4 times higher in replicate two. This difference was significant in replicate one ($p = 0.02$, Mann–Whitney U -test), although it was not significant with the smaller sample size of species in replicate two ($p = 0.20$, Mann–Whitney U -test). In contrast to the starting expectations, the fraction of cowbird eggs accepted by hosts made a smaller contribution than did host nest survival to the observed difference between habitats. On average, acceptance was 1.2 times higher with the forest as opposed to the old field hosts and the difference was not significant ($p > 0.20$, Mann–Whitney U -test). Lastly, cowbird eggs and young did not survive consistently better with either host community. In replicate one, cowbird survival given nest survival was 1.1 times higher in the forest (not significant). In replicate two, it was only 0.8 times as high in the forest (significant at $p < 0.05$, based on

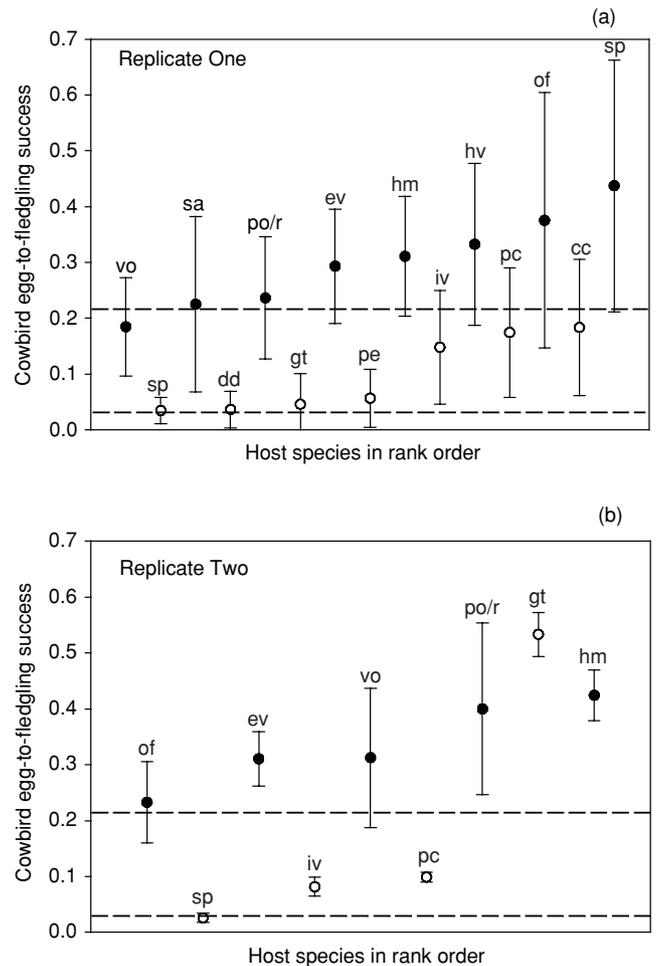


Fig. 4. Estimated cowbird egg-to-fledgling success (mean \pm standard error of the mean (SE)) with host species from forest (●) and old field (○) habitats in (a) replicate one and (b) replicate two. The broken lines represent the upper and lower bounds on the egg-to-fledgling success required for zero population growth. Above both broken lines cowbird population growth is positive, while below both broken lines cowbird population growth is negative, even when extreme values are assumed for all other life history parameters. Host species are identified by the first letter of the genus and species: ev, Acadian flycatcher (*Empidonax virescens*); gt, common yellowthroat (*Geothlypis trichas*); sp, Eastern phoebe (*Sayornis phoebe*); pe, Eastern towhee (*Pipilo erythrophthalmus*); sp, Field sparrow (*Spizella pusilla*); pc, Indigo bunting (*Passerina cyanea*); of, Kentucky warbler (*Oporornis formosus*); cc, Northern Cardinal (*Cardinalis cardinalis*); sa, Ovenbird (*Seiurus aurocapillus*); dd, Prairie warbler (*Dendroica discolor*); vo, Red-eyed vireo (*Vireo olivaceus*); po/r, Scarlet/summer tanager (*Piranga olivacea* and *P. rubra*); hm, Wood thrush (*Hylocichla mustelina*); hv, Worm-eating warbler (*Helminthos vermivorus*); iv, Yellow-breasted chat (*Icteria virens*).

Table 3. Parameter values used in Equation 1 for host species in replicate one

Host species	Proportion of cowbird eggs accepted (U_i)	24-day nest survival probability (V_i)	24-day cowbird offspring survival probability, given nest survival (W_i)
Acadian flycatcher (<i>Empidonax virescens</i>)	1.00 ^a	0.36 (± 0.08)	0.81 (± 0.22)
Common yellowthroat (<i>Geothlypis trichas</i>)	1.00	0.06 (± 0.06)	0.77 (± 0.44)
Eastern phoebe (<i>Sayornis phoebe</i>)	1.00	0.54 (± 0.24)	0.81 (± 0.22)
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	1.00	0.07 (± 0.05)	0.77 (± 0.44)
Field sparrow (<i>Spizella pusilla</i>)	0.45 (± 0.12)	0.10 (± 0.03)	0.77 (± 0.44)
Indigo bunting (<i>Passerina cyanea</i>)	1.00	0.23 (± 0.08)	0.77 (± 0.44)
Kentucky warbler (<i>Oporornis formosus</i>)	1.00	0.46 (± 0.25)	0.81 (± 0.22)
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0.52 (± 0.10)	0.45 (± 0.14)	0.77 (± 0.44)
Ovenbird (<i>Seiurus aurocapillus</i>)	1.00	0.28 (± 0.18)	0.81 (± 0.22)
Prairie warbler (<i>Dendroica discolor</i>)	0.59 (± 0.05)	0.08 (± 0.06)	0.77 (± 0.44)
Red-eyed vireo (<i>Vireo olivaceus</i>)	0.78 (± 0.09)	0.29 (± 0.11)	0.81 (± 0.22)
Scarlet/summer tanager (<i>Piranga olivacea</i> and <i>P. rubra</i>)	1.00	0.29 (± 0.11)	0.81 (± 0.22)
Wood thrush (<i>Hylocichla mustelina</i>)	1.00	0.38 (± 0.14)	0.81 (± 0.22)
Worm-eating warbler (<i>Helmitheros vermivorus</i>)	1.00	0.41 (± 0.14)	0.81 (± 0.22)
Yellow-breasted chat (<i>Icteria virens</i>)	1.00	0.19 (± 0.07)	0.77 (± 0.44)

All values are means ± SE.

^aHost species with 100% acceptance are not known to reject cowbird eggs at all.

Table 4. Parameter values used in Equation 1 for host species in replicate two

Host species	Proportion of cowbird eggs accepted (U_i)	24-day nest survival probability (V_i)	24-day cowbird offspring survival probability, given nest survival (W_i)
Acadian flycatcher	1.00	0.40 (± 0.06)	0.77 (± 0.03)
Common yellowthroat	1.00	0.53 (± 0.19)	1.00 ^a
Field sparrow	0.45 (± 0.12)	0.06 (± 0.04)	1.00
Indigo bunting	1.00	0.10 (± 0.04)	1.00
Kentucky warbler	1.00	0.30 (± 0.09)	0.77 (± 0.03)
Red-eyed vireo	0.78 (± 0.09)	0.52 (± 0.20)	0.77 (± 0.03)
Scarlet/summer tanager	1.00	0.52 (± 0.20)	0.77 (± 0.03)
Wood thrush	1.00	0.55 (± 0.06)	0.77 (± 0.03)
Yellow-breasted chat	1.00	0.08 (± 0.08)	1.00

All values are means ± SE.

^aNo cowbird mortality events within surviving nests were observed in the old field host community in replicate two ($n = 123$ observation days).

non-overlapping 95% confidence intervals for the mean); however, no cowbird mortality events with old field hosts were observed, so the confidence intervals are probably underestimated.

Sensitivity analysis indicated that cowbird egg-to-fledgling success was most strongly affected by changes in host nest mortality rate and secondarily by decreases in host acceptance of cowbird eggs. In contrast, changes in

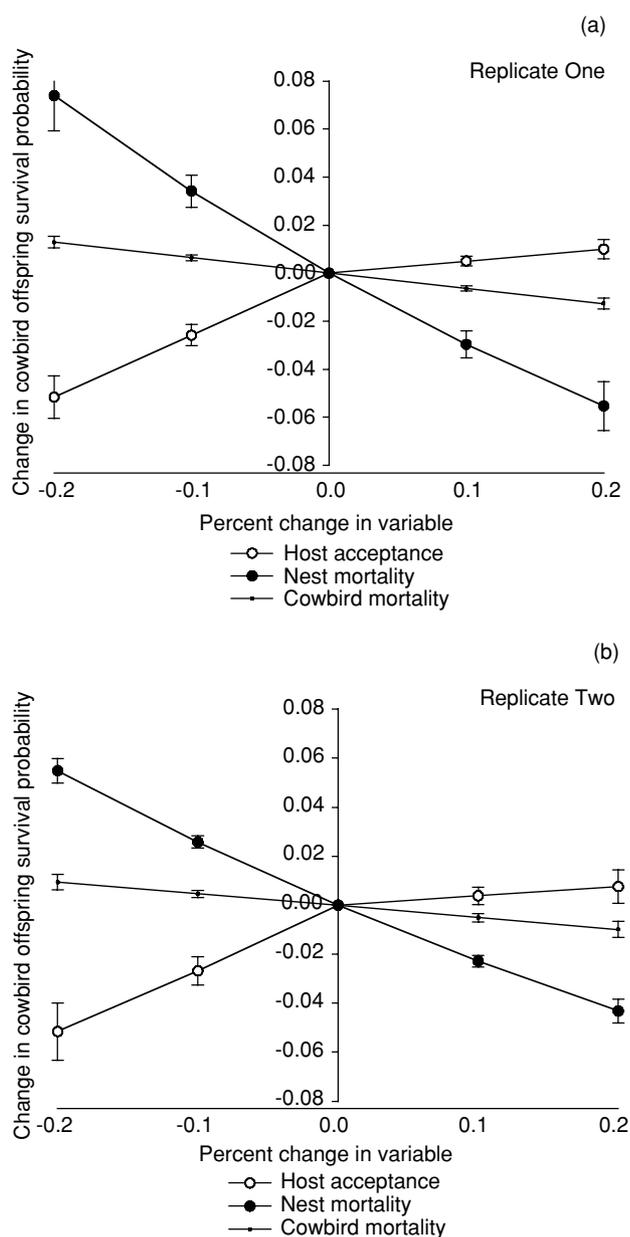


Fig. 5. Results of sensitivity analysis for (a) replicate one and (b) replicate two. The following parameters were varied from -20% to $+20\%$: fraction of cowbird eggs accepted by the host (○), daily mortality of host nests (●) and daily mortality of cowbird eggs and young within the host nest (■). The dependent variable (y -axis) is the mean \pm SE change in the cowbird's probability of egg-to-fledgling success, calculated over $n = 15$ host species in replicate one and $n = 9$ host species in replicate two.

the cowbird survival given nest survival had little effect on overall success. The results of sensitivity analysis were similar across replicates (Fig. 5).

DISCUSSION AND CONCLUSIONS

This study found that the cowbird's egg-to-fledgling success was several times higher with the host community

breeding in an invaded habitat, deciduous forest, than with hosts breeding in old fields, a habitat more similar to the cowbird's original range. This result suggests that high offspring survival in an invaded habitat, together with the cowbird's pre-existing exceptionally high fecundity (Table 4), has furthered the cowbird's population growth.

The most important cause of high cowbird reproduction in the forest was a low mortality rate for host nests in that habitat. Sensitivity analysis indicates that nest mortality rate is also the factor to which cowbird reproduction responds most strongly. In this study the general term 'nest mortality' has been used because often it is not possible to infer the cause of mortality from the appearance of the inactive nest. However, avian ecologists have long believed that for open-cup nesting passerines such as those studied here, most nest mortality events are attributable to nest predation (Lack, 1954). A review of studies using traditional observation methods found that nest predation accounted for 3–5 times more nest mortality events than did any other cause of mortality (abandonment, cowbird parasitism, weather, etc: Ricklefs, 1969). More recently, remote video camera filming has also found nest predation to be the primary cause of mortality, although video results can be difficult to interpret due to a bias in favour of abandonment (birds often abandon their nests in response to camera set-up, whereas cameras do not appear to affect nest predation rates; Pietz & Granfors, 2000; Williams & Wood, 2002; Thompson & Burhans, 2003). That nest predation accounted for most nest mortality in this study is further supported by > 1000 h of video filming in which 5 predation events, but no other causes of nest failure, were captured (unpublished results).

As predicted, the study also found that the forest contained fewer host species known to reject cowbird eggs from their nests, but this factor was of secondary importance in determining cowbird offspring survival. Sensitivity analysis indicated that increases in host rejection behaviour could have a large effect on cowbird reproduction, however, if hosts evolved such behaviour.

The third factor examined, the survival of cowbirds within surviving host nests, was not important in either explaining the difference between habitats, or in the sensitivity analysis. This is probably because survival rates were high with both host communities. This result confirms the fact that the cowbird is a successful host generalist and can take advantage of new hosts.

The main finding of this study, that cowbird offspring survival is higher in forests, should have wide generality. Forests as fragmented as those in this study (Fig. 2) typically have higher nest mortality rates than do more intact forests (Wilcove, 1985; Robinson, *et al.*, 1995; Donovan, Thompson & Faaborg, 2000; Chalfoun, Thompson III & Ratnaswamy, 2002). Therefore, the cowbird's egg-to-fledgling success is likely to be higher in other, less fragmented forests. Note that this conclusion applies to a *per capita* measure, i.e. the egg-to-fledgling success. Absolute measures, such as the total number of juvenile cowbirds produced, will vary with the local density of breeding females and could either increase or

decrease with forest size, depending on the rates of change in both *per capita* reproduction and breeding cowbird density.

It is more difficult to generalise about cowbird offspring survival in old fields, since the literature on old field nest mortality rates is small and reaches little consensus. Similarly, cowbird reproduction in its original prairie habitat has never been measured and certainly was not measured when cowbirds began invading forests in the 18th century. However, it seems probable that reproduction in prairies is lower than in forests for two reasons. First, cowbird host density is much lower in mixed-grass prairie as compared to eastern deciduous forests: U.S. Breeding Bird Census data for mixed grass prairies average 36 ± 18 (SD) territories of cowbird host species per 40 ha, whereas forests average 126 ± 44 (SD) territories per 40 ha (Anonymous, 1993, 1994). Second, many prairie-breeding species reject cowbird eggs from their nests (Peer *et al.*, 2000).

The findings of this study have practical applications for bird conservation. Cowbird parasitism can reduce or eliminate host reproduction and some host species are so heavily parasitised that across large parts of their range, a third or more of all nests contain cowbird eggs (Trine *et al.*, 1998). The cowbird constitutes a greater threat to its hosts than does the European nest parasite, the common cuckoo (*Cuculus canorus*), because the cowbird is an abundant host generalist (Friedmann & Kiff, 1985), whereas the cuckoo is relatively rare and, to some degree, a host specialist (Davies, 2000). This means that unlike the cuckoo, the cowbird can depress the population size of particular host species without necessarily depressing its own reproduction (for reviews, see Winfree, 1999; Davies, 2000). The cowbird's behavioural pattern, however, offers encouraging points for land management. Cowbirds are rarely found in extensive forests (Smith *et al.*, 2000), presumably due to the high energetic costs of travelling between forest breeding habitat and the open areas where cowbirds feed. Similarly, both cowbird density and parasitism rates decrease with increasing distance from cowbird feeding areas (for a review, see Chace *et al.*, 2004). A strategy of reducing forest fragmentation and eliminating cowbird feeding habitats, such as livestock enclosures and mown lawns, in otherwise forested areas, could reduce the population growth rate of this highly detrimental species.

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