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A Monte Carlo model for estimating the productivity of a generalist brood parasite across multiple host species

Rachael Winfree,[1]* Jonathan Dushoff,[1] Scott K. Robinson[2]‡
and David Bengali[3]§

[1]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544,*
[2]*Department of Animal Biology, University of Illinois, Champaign-Urbana, IL 61820 and*
[3]*Department of Computer Science, Princeton University, Princeton, NJ 08544, USA*

ABSTRACT

Questions: How can the productivity of a generalist brood parasite be estimated? Does an invasive brood parasite have greater productivity (defined as fledglings/egg and fledglings/area) in a recently invaded habitat than in a habitat similar to its original range?

Features of model: We developed a simulation model that uses Bayesian and Monte Carlo methods to integrate brood parasite productivity across multiple host species over the entire breeding season.

Organisms: We use the model to estimate the productivity of the brown-headed cowbird (*Molothrus ater*) in two host communities, one breeding in deciduous forests (a recently invaded habitat) and one in old fields (a grassland habitat more similar to the cowbird's original range). We parameterize the model with data from 616 nests of 14 cowbird host species, containing 428 cowbird eggs and young.

Results and conclusions: We developed methods for estimating the productivity of a brood parasite with an entire community of host species. We found that cowbirds have higher productivity in the recently invaded habitat, deciduous forest. Our findings are consistent with the rapid spread of the cowbird once it invaded the forested eastern United States

Keywords: Bayesian, bird conservation, brood parasite, demographic model, generalist parasite, habitat-specific reproduction, invasive species, *Molothrus ater*.

INTRODUCTION

Interspecific brood parasitism, the practice of abandoning one's offspring to the care of another species, is widespread in nature. Many species of bees are brood parasites (Michener,

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* Author to whom all correspondence should be addressed. e-mail: rwinfree@princeton.edu

‡ *Present address*: Florida Museum of Natural History, University of Florida, PO Box 117800, Gainesville, FL 32611-7800, USA.

§ *Present address*: Saint Ann's School, 129 Pierrepont Street, Brooklyn, NY 11201, USA.

2000), as are some fish (Wisenden, 1999), but brood parasitism is best known from birds, of which roughly 100 species are obligatory parasites (Payne, 1997). Brood parasitic birds such as the common cuckoo (*Cuculus canorus*) in Europe and the brown-headed cowbird (*Molothrus ater*) in North America have generated a large ecological literature demonstrating the detrimental effects of brood parasitism on host species (Rothstein and Robinson, 1998). However, to our knowledge no study has examined differences in reproductive success of a generalist brood parasite in different host communities. This gap is likely due to (1) the difficulty of collecting data on the success of parasitic offspring across an entire community of host species, and (2) the lack of analytical methods to integrate parasite productivity across multiple hosts.

It is relatively straightforward to estimate productivity for non-parasitic birds because each nest for which productivity data are collected is clearly related to one breeding female. In contrast, an individual female brood parasite distributes her eggs across multiple nests of multiple host species over the course of her breeding season. A method for estimating brood parasite productivity therefore needs to accomplish several objectives. First, it needs to sum parasite productivity, and propagate sampling error, across multiple host species. The sum is straightforward, but the error propagation is more challenging, given a large number of parameters related to data on the various host species. Second, it needs to sum parasite productivity over the parasite's entire breeding season, by including only that part of each host species' breeding season that overlaps with the breeding season of the parasite. Third, it needs to account for multiple nest attempts each breeding season by the host birds, because most host species will re-nest after nest failure if there is enough time left in their breeding season.

Our study focused on the brown-headed cowbird, which, in addition to being a brood parasite, is an important conservation threat to many North American birds (Trine *et al.*, 1998; Lorenzana and Sealy, 1999). Cowbirds are generalist parasites whose eggs have been found in the nests of over 140 host species (Friedmann and Kiff, 1985). This lack of specificity allows the cowbird to depress the population of particular hosts without suffering a concomitant decrease in its own population (May and Robinson, 1985). At the continental scale, the cowbird is more abundant than most of its host species (Sauer *et al.*, 2001), and in areas of high cowbird density, host nests can contain up to 12 cowbird eggs (Brawn and Robinson, 1996; Lorenzana and Sealy, 1999). For many host species, cowbird parasitism results in the loss of their own brood due to competition or smothering by the larger cowbird chick, and even host species that are able to raise some of their own young along with a cowbird produce fewer offspring from parasitized nests (Trine *et al.*, 1998; Lorenzana and Sealy, 1999). Some host species exhibit defences against parasitism, such as rejecting cowbird eggs from their nests, or abandoning parasitized nests (Winfree, 1999; Davies, 2000). However, many host species appear not to recognize that they have been parasitized, and continue to care for the cowbird chick even after the loss of their own young.

We studied cowbird productivity in old field and deciduous forest host communities because cowbirds have contrasting evolutionary histories in these communities. Cowbirds are native to the grassland regions of North America. They feed in areas of short grass or bare ground and originally fed in association with bison (*Bison bison*). When Europeans first arrived in North America, cowbirds were rare or absent in the extensively forested east (Mayfield, 1965). As humans created more open habitats, and as cattle and other livestock provided new feeding associates, the cowbird's range expanded to include most of North America (Mayfield, 1965; Sauer *et al.*, 2001). Widespread cowbird parasitism of hosts breeding in eastern deciduous forests is therefore a recent (last 200–300 years) phenomenon. Today cowbirds heavily parasitize birds breeding in fragmented forests (Robinson *et al.*, 1995; Chace *et al.*, 2005), although they are still rare in extensively forested areas.

Our first objective in this study was to develop methods for estimating the productivity of a generalist brood parasite. Our second objective was to gain insight into the role of habitat and host community composition in causing the spread of an invasive brood parasite. We used a combination of field data and modelling to estimate host- and habitat-specific productivity for the brown-headed cowbird. We collected data from cowbird hosts breeding in old fields and in deciduous forests in Illinois, USA. We expected that cowbirds would reproduce well in the forest habitat, which would be consistent with the cowbird's rapid spread throughout the eastern Unites States. We further expected that cowbird productivity would be reduced in old fields because of higher losses to nest predation, and more effective host defences against parasitism (Hosoi and Rothstein, 2000; Peer *et al.*, 2000), despite the fact that old field communities have high host densities (Robinson, 1999).

METHODS

Simulation model

We constructed a simulation model by using Bayesian methods to estimate posterior distributions of key parameters (distributions) from the data, and then using Monte Carlo methods to simulate the processes of parasitism, host nesting and cowbird offspring mortality in order to estimate annual cowbird productivity (fledglings/egg and fledglings/area) with each host species. This approach allowed us to include and propagate the error associated with each of ~50 parameters relating to the various host species, and to estimate the confidence limits associated with our results. Cowbird productivity with each host species results from several rates, such as host parasitism rate, host nest failure rate, cowbird egg and nestling mortality within host nests. To estimate cowbird productivity with entire host communities (i.e. per unit area), we also included the density of each host species. We parameterized the model by using a Bayesian approach to estimate posterior distributions for each of the host-specific rates, given the observed data (Gelman *et al.*, 1998). We assumed that parasitism, nest failure, and cowbird egg and nestling mortality rates were Poisson processes, each with a constant rate λ. We used a Poisson distribution for parasitism because the distribution of cowbird eggs in host nests was a good fit to the Poisson (R. Winfree, unpublished data), and for nest failure and cowbird mortality because both represented counts of rare events. For the Poisson rates, we observed n events in time T, so our estimate of the rate λ is n/T. To evaluate the effects of measurement uncertainty in our results, we calculated a Bayesian posterior distribution for each rate, based on our observations, and carried out repeated simulations, with rates drawn randomly from these posterior distributions.

For our prior distribution we chose a flat distribution on $\log\lambda$, equivalent to assuming a prior probability of $\pi(\lambda) = 1/\lambda$. This is an 'improper' distribution – meaning that it cannot be integrated – but this causes no difficulty in this case, as long as we observe at least one event. Using a flat distribution on $\log \lambda$, rather than on λ, has several advantages. First, because λ is a rate, differences in λ are most sensibly thought of in a proportional manner (e.g. the difference between a rate if 1/day and 2/day is similar to the difference between 1/week and 2/week, not 1/week and 8/week), and this is consistent with using the log.

Second, the posterior mean matches the observed mean n/T; and the posterior variance matches the classical (Fisher information) estimate of the variance.

For a Poisson process with mean λT, the probability of observing exactly n events is

$$L(\lambda) = \lambda^n T^n e^{-\lambda T}/n! \tag{1}$$

Thus the posterior probability of λ is

$$\frac{\pi(\lambda)L(\lambda)}{\int \pi(k)L(k)dk} = \frac{\lambda^{n-1}e^{-\lambda T}}{\int k^{n-1}e^{-kT}dk} = \lambda^{n-1}e^{-\lambda T}/(n-1)! \tag{2}$$

which is a gamma distribution with shape parameter n and scale parameter T. Thus the mean of the posterior distribution is our observed mean, n/T, and the variance is n/T^2.

We modelled the host nest parasitism rate, host nest abandonment rate (for parasitized nests), host nest failure rate, and cowbird egg and nestling mortality rate within host nests with gamma distributions. For host density, we had data from two years, which is not enough to parameterize a distribution. Instead, the simulation randomly drew one of the two yearly values for each host species' density at each repetition of the simulation. We had density data from replicate one only (see below), and we used these values for both replicates.

We wrote the simulation code in Matlab (MatLab 6.5, The MathWorks, Inc., 2002). Program input consists of the species-specific parameters further discussed below (Tables 2, 3 and 4). The primary program output consists of: (1) the proportion of cowbird eggs laid with each host species, and per unit area in each habitat type, that result in fledglings; and (2) the number of cowbird fledglings produced per year by each host species, and per unit area in each habitat type.

Each repetition of the simulation represents one breeding season, and we drew a new rate from each distribution for each breeding season. Within a breeding season, whether an event occurs on a given day is determined by randomly drawing from a uniform distribution, and having the event occur if the drawn value is less than the mean rate drawn for that breeding season. We ran the simulation using 500 pairs of nesting birds of each host species. Sampling error for the rate data is incorporated into the gamma distributions from which rates are drawn, and is therefore propagated through the simulation. Sampling error for host density was propagated by randomly drawing a density value for each host species in each repetition, as described above. We ran the simulation for 500 breeding seasons. Program output consists of the mean and variance of the per-breeding-season values across the 500 breeding seasons. We ran the simulation both without host density (to estimate cowbird productivity per breeding pair of the various host species) and with host density (to estimate cowbird productivity by the entire host community, per unit area of each habitat type).

The steps taken by the simulation are as follows. The simulation begins with a pair of host birds having completed a nest that is now available for parasitism. Parasitism occurs during the host's laying period (Friedmann, 1929). For the three host species known to preferentially abandon parasitized nests, abandonment occurs (with the appropriate probability; see below) within a few days of cowbird laying (Rothstein, 1975). If a nest is abandoned, all the cowbird eggs in that nest die. The pair of host birds then enters the re-nesting pool, where it waits for the appropriate interval before starting a new nest.

From the time that the first egg is laid, a nest is subject to a daily nest failure rate. If nest failure occurs, all cowbirds in the nest die, and the host pair enters the re-nesting pool.

Cowbirds within a surviving host nest are also subject to a separate, within-nest daily mortality rate. Whether or not this mortality occurs each day is determined individually and stochastically for each cowbird in the nest. When a cowbird dies within a host nest, its death is recorded as such, but the host pair and their nest continue through the nest cycle.

If a cowbird survives until it is mature (10 days post-hatching), it fledges. If the host species' nest cycle is longer than that of the cowbird, as is usually the case, the host pair continues with its nest until it either experiences nest failure or survives long enough to fledge the host young. Once a host pair has successfully fledged a cowbird and/or its own young, it either quits nesting (for host species that raise only one brood per year) or enters the re-brooding pool (for species that can raise multiple broods). In the re-brooding pool the host pair waits the appropriate interval while caring for its fledged offspring before beginning a new nest. A host pair will also quit nesting at any time during the breeding season after making seven nest attempts, all of which fail (Nolan, 1978). A simplified flow chart illustrating what the program does is shown in Fig. 1.

Field data collection

To parameterize the model, we used data collected in and around the 108,000-ha Shawnee National Forest in southern Illinois. This region is thought to have been almost entirely forested before the late eighteenth century, but today forest cover is approximately 50% (Iverson, 1989), with few forest fragments of larger than 2000 ha (Trine *et al.*, 1998). As such, it is representative of the patchy habitats made available to the cowbird over the past three centuries. Due to the high mobility of the cowbird, we replicated the study at the landscape scale, with replicate 1 being in the eastern Shawnee National Forest (three forest plots and

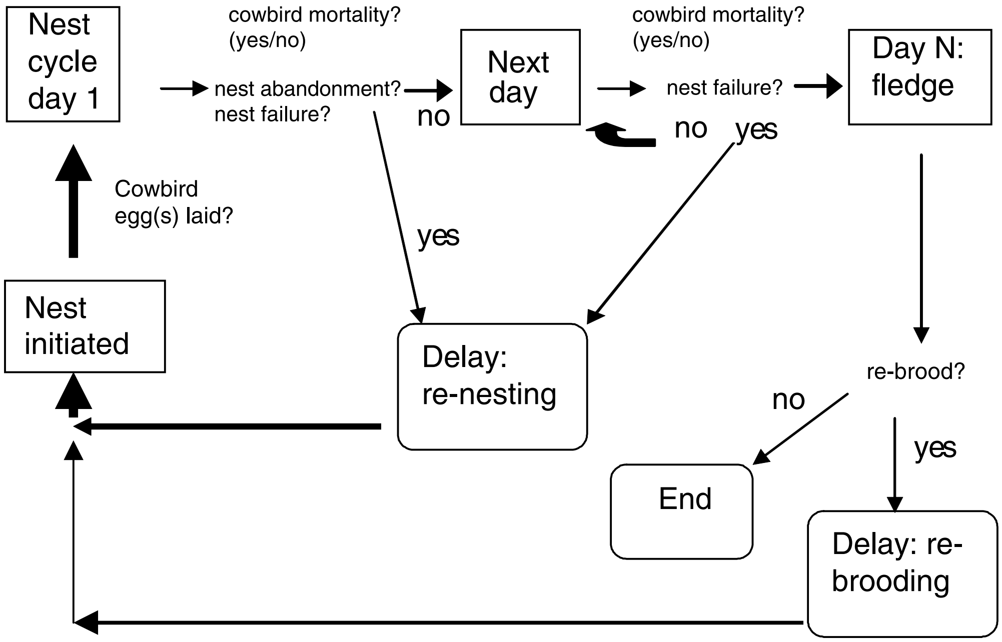

Fig. 1. A simplified flow chart to illustrate the simulation of the cowbird-host breeding season.

three old field plots), and replicate 2 in the Cache River watershed (five forest plots and three old field plots). Replicates were ~34 km apart, which is roughly 10 times the typical daily movement distance for female cowbirds in Midwestern landscapes (Thompson and Dijak, 2000). In both replicates, forest habitat was characterized by steep ravines and was dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.) along ridgetops and in lower areas by maples (*Acer rubrum* and *A. saccharum*) and beech (*Fagus americana*). Habitat in the old field areas was a mix of grassy areas dominated by *Festuca ovina*, *Andropogon virginicus* or *Lespediza* sp., and shrubby growth including *Juniperus virginiana*, *Rosa multiflora*, *Rubus* sp., *Eleaegnus sp.*, and saplings of early successional trees such as *Ulmus alata*, *Sassafras albidum* and *Acer rubrum*.

We collected data on four variables: host density, host nest failure rate, cowbird eggs per host nest, and cowbird mortality (egg and nestling) within host nests. We measured the density of all cowbird host species in replicate 1 only in 1999 and 2000 by using standard spot mapping methods (Verner, 1985), as follows. In one study plot of each habitat type, we established 25 census points on a 100-m grid and equalized plot area at 19 ha using a GPS (Trimble GeoExplorer; base station corrections USFS, Bedford, IN) and Arcview 3.0. From April to July of each year, we made eight repeat visits to each plot. During each visit we censused each of the 25 points for 6 min between 05:00 and 11:00 h, for a total of 800 point counts over the two years. During each point count, the radial direction and distance to all birds seen or heard was recorded on a map. We assigned territories on the basis of repeated localizations and counter-singing between males.

To obtain the nesting data, we searched for host nests and monitored them approximately every 3 days using standard methods (Martin and Geupel, 1993). We used the nest data to estimate cowbird eggs per nest and mortality rates, based on the assumption that we found a random sample of nests for each host species. We did not use nest data to estimate host density, because it is not possible to find all the nests in a given area, and because the nests of different species are not equally easy to find. A total of 356 nests provided data for replicate 1, and 260 nests provided data for replicate 2 (Table 1). In replicate 1, we collected nest data from 1998 to 2000, and had sufficient data to include all cowbird host species with densities ≥4 territories per 19 ha plot, for a total of seven forest and seven old field species (see Table 2 for species names). In replicate 2, we used nest data collected from 1993 to 1995 for a

Table 1. Total sample sizes for nest data

	Host species with nest data (*n*)	Host nests (*n*)	Host nest exposure days (*n*)	Cowbird eggs and young (*n*)	Cowbird exposure days (*n*)
Replicate 1					
Forest sites	7	129	1700	80	456
Additional canopy data	2	17	189	Not used	Not used
Old field sites	7	210	1734	59	362
Total	14	356	3623	139	818
Replicate 2					
Forest sites	4	190	2827	252	1348
Old field sites	4	70	653	37	160
Total	8	260	3480	289	1508

subset of the most important cowbird hosts [those that fledge the most cowbirds per capita and/or are highly abundant (R. Winfree, unpublished data)], for a total of four forest and four old field host species. The rare host species that we excluded from the study due to insufficient data were the blue-grey gnatcatcher (*Polioptila caerulea*), Louisiana waterthrush (*Seiurus motacilla*), eastern phoebe (*Sayornis phoebe*) and yellow-throated vireo (*Vireo flavifrons*) in the forest habitat, and the blue grosbeak (*Guiraca caerulea*) and northern cardinal (*Cardinalis cardinalis*) from the old field habitat. These excluded species were present at low enough densities (0.25–2.75 pairs per plot) that we expect they would have a minimal influence on the number of cowbirds produced at the community scale. In the forest, we also had insufficient nesting data to include two canopy-nesting species with higher densities (5–7 territories per plot; eastern wood-pewee, *Contopus virens*, and northern parula, *Parula americana*). This means that our estimates of cowbird productivity in the forest are biased low, which is a bias against our expectation that cowbird productivity is highest in forests.

A source of uncertainty for all studies of bird nests is that the act of visiting nests may attract or deter nest predators, thereby biasing the estimate of nest failure rates. The evidence on this point so far has been mixed (Willis, 1973; Westmoreland and Best, 1985; Ortega *et al.*, 1997; Sockman, 1997). Similarly, the estimates of parasitism could be too high, if researchers and cowbirds were likely to find the same nests. Because this is a comparative study, however, and the same methods were used in both habitats studied, our results should be reasonably robust to such biases.

Determining parameter values from field data

We calculated daily nest failure rate for each host species as the total number of nest failure events divided by the total number of nest exposure days (the number of days over which the nest was observed), which provides the maximum likelihood estimate (Mayfield, 1975; Bart and Robson, 1982). We defined nest failure to include any event that caused a nest to become inactive before the stage at which young were old enough to fledge. However, most nest failure events were probably attributable to nest predation, which avian biologists have long believed accounts for most nest failures for passerine birds (Ricklefs, 1969). This conclusion is also supported by >1000 h of video we filmed at nests, during which we captured five predation events and no other causes of nest failure. More extensive video studies done in similar habitats (e.g. Thompson and Burhans, 2003) have reported similar results. Our simulation assumes a constant mean nest failure rate for each host species, because daily nest failure rates were not significantly different within species for nests with and without cowbirds ($P \geq 0.2$ for the 6 host species with the largest sample sizes, Fisher's exact tests), or for nests in the incubation versus nestling stages [$P > 0.05$ for 21 host species, Fisher's exact tests; for one species $P < 0.05$, but this is not significant when the experiment-wise critical P-value is used (Sokal and Rohlf, 1995, p. 239)].

We calculated parasitism of each host species as total cowbird eggs/total nests. For replicate 1, where we had few data on canopy nests, we included observations of fledged families in our estimates for cowbird eggs per nest for canopy-nesting species. If we observed the adult bird feeding a cowbird, we counted the nest as parasitized; if we did not observe a cowbird, we counted the nest as unparasitized. This means that our canopy parasitism estimates are biased low (a bias against our hypothesis) because we could have missed cowbirds that were present. Parameter values for nest failure rate and cowbird eggs per nest for all host species are given in Table 2.

Table 2. Simulation parameter values for all host species

Host species	No. of cowbird eggs/no. of nests	No. of nest failure events/no. of nest exposure days	Re-nest interval (days)[a]	Brood number[a]	Re-brood interval (days)[a]	Nest cycle duration (days)[a]	Cowbird-host breeding season (days)	Density (territories per plot ± SE)[b]
Acadian flycatcher (*Empidonax virescens*); acfl	16/35 27/58	23/555.5 35/942	8	1	NA	27	44	11.0 ± 0.5
Common yellowthroat (*Geothlypis trichas*); coye	3/10 6/7	7/63 3/116	8	2	20	22	63	24.5 ± 4.5
Eastern towhee (*Pipilo erythrophthalmus*); eato	9/10	13/126	9	2	21	22	73	7.3 ± 0.3
Field sparrow (*Spizella pusilla*); fisp	13/84 3/20	72/807 18/160.5	9	3	21	18	74	52.0 ± 8.0
Indigo bunting (*Passerina cyanea*); inbu	16/31 24/31	18/300 29/315.5	7	3	12	24	58	28.8 ± 5.8
Kentucky warbler (*Oporornis formosus*); kewa	1/7 21/26	2/63.5 15/308	10	1	NA	22	59	4.0 ± 0.5

Ovenbird (*Seiurus aurocapillus*); oven	4/9	4/77	10	1	NA	22	43	12.3 ± 0.3
Prairie warbler (*Dendroica discolor*); prwa	5/14	13/130	9	2	16	22	67	22.0 ± 0.5
Red-eyed vireo (*Vireo olivaceus*); revi	9/10	11/218.5	9	1	NA	25	62	24.0 ± 0.0
Scarlet/summer tanager (*Piranga olivacea*/*P. rubra*); scta/suta	9/10 8/5	11/218.5 3/88.5	8	1	NA	29	67	7.8 ± 1.3
White-eyed vireo (*Vireo griseus*); wevi	1/3	1/36.5	9	2	21	24	62	4.5 ± 1.0
Wood thrush (*Hylocichla mustelina*); woth	33/35 182/84	22/563 35/1488.5	9	2	14	26	68	7.5 ± 1.0
Worm-eating warbler (*Helmitheros vermivorus*); wewa	8/19	7/192.5	8	1	NA	24	48	8.0 ± 0.5
Yellow-breasted chat (*Icteria virens*); ybch	10/22 3/5	18/271 6/60.5	8	2	20	21	66	21.3 ± 1.3

Note: For species studied in both replicates, values for replicate 1 are on the first line and values for replicate 2 on the second line. Parameters relating to the nest cycle (columns 3–7) are the same for both replicates as they are properties of the species, not the population.

[a] Values obtained from the published literature; see Appendix 1. [b] Density was measured in replicate 1 only.

To measure cowbird egg and nestling mortality rates within host nests, we recorded a mortality event if a cowbird egg or nestling present at one visit was dead or absent at a subsequent visit, while the nest and the rest of its contents remained active. We calculated cowbird mortality rates using the same methods as for nest failure rates. The simulation used different cowbird mortality rates according to the stage of the nest cycle (incubation, hatching, nestling) and/or the number of cowbirds in the nest, where there were significant differences in the data, as follows. First, cowbird daily mortality rates were significantly higher during the hatch interval than during the incubation or nestling stages. Second, cowbirds that shared the nest with other cowbirds had significantly higher mortality during hatching, for all comparisons with reasonably large sample sizes (≥29 hatch events observed). Third, in replicate 2 only, daily mortality rate for cowbird nestlings was significantly higher than daily mortality rate for cowbird eggs. In contrast, we found no significant differences in cowbird mortality by host species ($P > 0.18$, Fisher's exact tests), although small sample sizes may have precluded detecting such differences. Therefore, we combined data on cowbird mortality across all host species within a habitat type to generate four parameter values: forest hosts replicate 1, forest hosts replicate 2, old field hosts replicate 1 and old field hosts replicate 2 (Table 3). To simulate cowbird productivity in the absence of density dependence, we calculated cowbird mortality rates as described above, but using only the data from nests parasitized by a single cowbird.

For both nest failure rate and cowbird eggs per nest, one mean value was calculated for each host species in each replicate, by combining data across years and across sites within a given habitat type. We did this for two reasons. First, sites of given habitat type within a replicate were not always far enough apart to be considered independent, given the mobility of the cowbird and some nest predators (up to several kilometres per day). Second, given the community-scale questions we are asking, we would need a prodigious number of nests to analyse our data by site or year. For example, even a modest sample size of 15 nests per species per site per year would require a total of 3330 nests. Third, rates were not significantly different within species by site or year, although these comparisons had limited power due to small sample sizes. We compared nest failure rates and cowbird eggs per nest across

Table 3. Simulation parameter values for cowbird offspring mortality within active host nests

	1 cowbird per nest[a]			>1 cowbird per nest		
	Mortality events/ exposure days, incubation	Mortality events/ eggs observed, hatching	Mortality events/ exposure days, nestling	Mortality events/ exposure days, incubation	Mortality events/ eggs observed, hatching	Mortality events/ exposure days, nestling
Forest, replicate 1	2.5[b]/456.0	1.0/14.0	2.5/456.0	2.5/456.0	3.5/9.0	2.5/456.0
Old field, replicate 1	1.5/361.8	3.0/13.0	1.5/361.8	1.5/361.8	1.33/6.0	1.5/361.8
Forest, replicate 2	5.0/837.2	3.0/29.0	6.0/347.0	5.0/837.2	17.6/54.0	5.7/164.2
Old field, replicate 2	0.3/159.7	0.0/5.0	0.3/159.7	0.3/159.7	0.5/3.0	0.3/159.7

[a] Data for the incubation and nestling stages, and for 1 and >1 cowbird per nest, were combined within a replicate and habitat when daily mortality rates were not significantly different.

[b] Mortality events are not always whole numbers because cowbird eggs within the same nest were not considered to be independent, which resulted in fractional mortality events in some cases.

sites and years using the host species with the most data, and found two $P \leq 0.05$ in 12 comparisons, which is not significant after adjusting for multiple comparisons [experiment-wise critical $P = 0.004$; nest failure rates were compared with the Fisher-Freeman-Halton exact test, and cowbird eggs/nests was compared with an exact test for homogeneity of Poisson rates (Cytel, 2003)].

In replicate 1 we calculated parasitism and nest failure rates for the canopy-nesting species (red-eyed vireos and scarlet/summer tanagers) combined; we had limited data on these species because their nests are up to 30 m high. To calculate nest failure rates, we also included data for these species from additional sites in the Shawnee National Forest (S.K. Robinson, unpublished data). Nest failure rates were not significantly different between our study sites and the additional sites, for either canopy species or another species for which we had large sample sizes (the wood thrush, *Hylocichla mustelina*; $P > 0.80$, Fisher's exact test; $n = 563$ and $n = 2801$ nest exposure days). We consider our data on canopy nesters to be of lower quality than that of other species; this is a general problem for these species, whose nesting biology is poorly understood.

The length of the host breeding season was determined for each species by using the earliest and latest nests in the data set. To approximate the population mean start date, we added 7 days to the earliest empirical nest start date, based on the assumption that females in our study area arrive and begin nesting over a 2 week period (Pease and Grzybowski, 1995). For the end of the breeding season we used the empirical extreme value, because the program uses this as the extreme date on which a host pair would begin a new nest, had all their previous nests failed. We adjusted values for some host species by up to 7 days based on extensive field experience in this study system (S.K. Robinson, unpublished data). We defined the cowbird breeding season as the period between the laying of the first cowbird egg on 28 April to the laying of the last on 11 July. We calculated the length of the cowbird–host breeding season overlap, as used in the simulation, as the number of days that nests of a given host species would be available for cowbird parasitism. There were also several parameters that we were not able to measure in our study, and we obtained these from the published literature (Appendix 1).

Statistical analyses

Simulation results

Since our estimates of cowbird productivity with each host community were averaged over hundreds of simulations, we expected this output to be well approximated by a normal distribution. Therefore, to compare the total number (and proportion) of cowbirds fledged per unit area, we used z-tests on the estimated mean and variance of the difference between forest and old field distributions. Tests were one-tailed since we expected cowbird productivity to be higher in the forest.

We also compared cowbird productivity per host pair between the two sets of host species, those breeding in old fields and those breeding in forests, using Wilcoxon tests. We used rank correlation (Spearman's rho) to determine whether cowbird production by the various host species was similar between replicate 1 and replicate 2.

Empirical patterns

We compared host density (the number of pairs of cowbird hosts per unit area) between old field and forest habitats using a *G*-test. We used Wilcoxon tests to compare the distributions of species-specific parasitism and nest failure rates between habitats. To compare cowbird offspring mortality rates between the old field and forest communities, we used Fisher's exact tests.

RESULTS

Simulation results

Most measures indicated that cowbird productivity was higher with the host community breeding in the forest than with the host community breeding in the old field. When cowbird productivity was compared per unit area, a significantly higher proportion of cowbird offspring survived to fledging in the forest in both replicate 1 ($t = 2.38$, $P < 0.009$) and replicate 2 ($t = 1.69$, $P < 0.05$; Fig. 2a,b). The number of cowbirds fledged per unit area, however, did

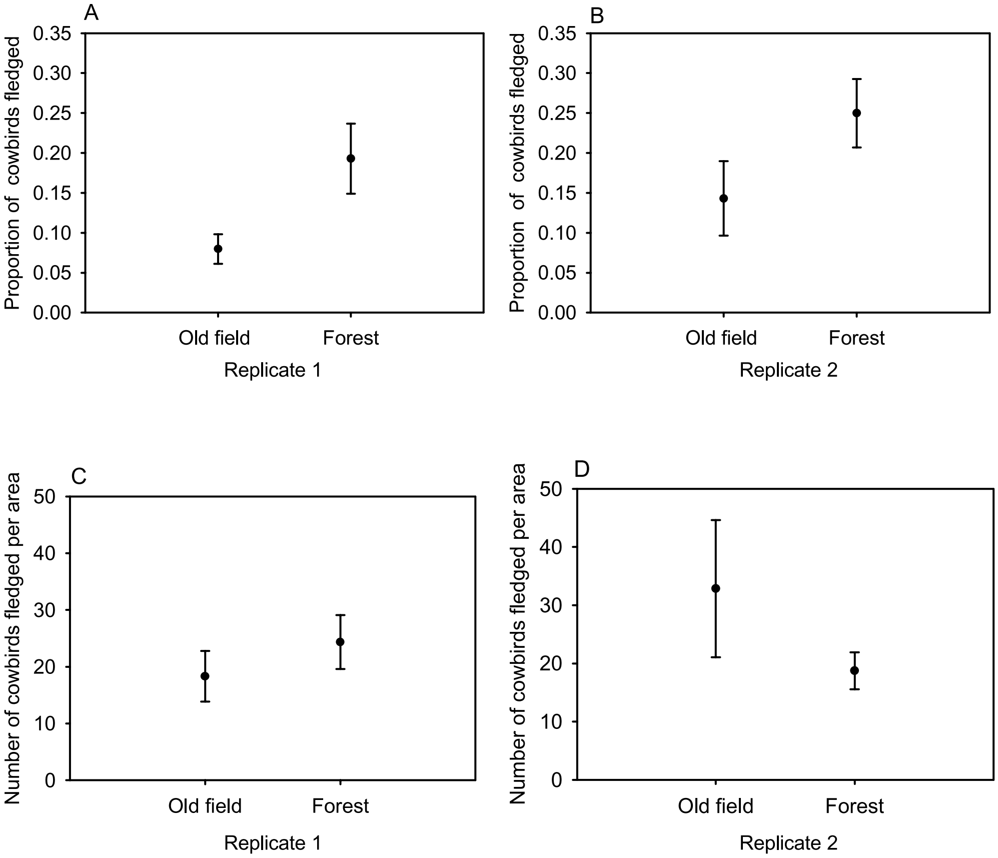

Fig. 2. Annual cowbird productivity in the presence of density dependence. The proportion of cowbirds raised to fledging in (a) replicate 1 and (b) replicate 2. The number of cowbird fledglings produced per plot (19 ha), summed across all host species and including host density, in (c) replicate 1 and (d) replicate 2. Results are simulation means ± standard errors, using input parameters that include the effects of density-dependent reduction in cowbird offspring survival.

not differ significantly between habitats in either replicate (Fig. 2c,d). The inconsistency between these two measures can be explained by the fact that significantly more cowbird eggs were laid in the old field ($t > 2.38$, $P < 0.009$ in both replicates), but most of these eggs did not survive to fledging. In other words, significantly more cowbird offspring died in the old field than in the forest ($t > 2.85$, $P < 0.003$ in both replicates).

The main cause of the difference in cowbird productivity between habitats was nest failure (likely due to predation), which was higher in the old field. Most cowbird eggs died in nest failure events in both habitats (Fig. 3a,d). However, significantly more cowbird eggs and young were lost in nest failure events in the old field ($t = 2.56$, $P = 0.005$ in replicate 1; $t = 3.07$, $P < 0.002$ in replicate 2). In the old field, high host density and high nest predation rates combined to cause rapid turnover of host nests. In other words, more nests were

Fig. 3. Fates of cowbird eggs in old field and forest host communities, in (a, b) replicate 1 and (c, d) replicate 2. Results are simulation means over 500 repetitions of the simulation, summed across all host species and including host density.

available to laying cowbirds in the field habitat, but most of these nests were subsequently depredated, thereby destroying many young cowbirds. In contrast, other forms of cowbird offspring mortality showed non-significant or inconsistent trends between habitats. The number of cowbirds that died due to abandonment by the host was not significantly different in the old field and forest in replicate 1, but in replicate 2, where the single forest species with defences against parasitism (the red-eyed vireo) was not studied, mortality due to abandonment was higher in the old field ($t = 1.65$, $P < 0.05$). Cowbird offspring mortality within active host nests was not significantly different between host communities in replicate 1, but was significantly higher in the forest in replicate 2 ($t = 2.11$, $P < 0.02$), mainly because many nests contained multiple cowbirds, and they increased each other's mortality.

When we simulated cowbird productivity in the absence of density-dependent mortality within host nests, the superiority of the forest habitat became even more pronounced. The proportion of cowbird eggs that resulted in fledglings was higher in the forest, with the difference being highly significant in both replicates ($t = 2.82$, $P < 0.003$ in replicate 1; $t = 2.56$, $P < 0.006$ in replicate 2; Fig. 4a,b). However, despite the increased productivity in the forest, the number of cowbird fledglings produced per unit area was still not significantly different between habitats (Fig. 4c,d).

When we considered host species identity and made comparisons between the two groups of host species, we found that forest-breeding hosts fledged a significantly higher proportion of the cowbird eggs they received than did old field host species in replicate 1 (Fig. 5a; Wilcoxon test, $\chi^2 = 4.46$, $P = 0.04$). In replicate 2, the difference was not significant (Fig. 5b; $\chi^2 = 1.33$, $P = 0.25$), although it becomes significant ($\chi^2 = 4.50$, $P = 0.03$) when an outlier, the common yellowthroat (*Geothlypis trichas*), is excluded. (We consider the yellowthroat in replicate 2 to be an outlier because it is predicted to be a markedly better cowbird host than any other old field species in either replicate. This is probably due to an inaccurate estimate of nest failure rate. Based on a sample size of only seven nests, yellowthroat nest failure rate in replicate 2 was 2.24 standard deviations below the mean for all other old field species.) Our second measure of cowbird productivity, the annual number of cowbirds fledged per host pair, was not significantly different between the two groups of host species, although there was a trend towards higher cowbird production in the forest in both replicates (Fig. 5c,d; Wilcoxon test, $\chi^2 = 2.80$, $P = 0.10$ in replicate 1; $\chi^2 = 1.33$, $P = 0.25$; $\chi^2 = 3.10$, $P = 0.08$ with the outlier excluded). Cowbird productivity with particular host species was positively associated between replicates only when the outlier was excluded (Fig. 6a,b; proportion of cowbirds raised to fledging by each host: $\rho = 0.31$, $P = 0.46$, and with outlier excluded, $\rho = 0.71$, $P = 0.07$; number of cowbirds fledged by each host: $\rho = 0.49$, $P = 0.22$, and with outlier excluded, $\rho = 0.78$, $P = 0.04$).

Empirical data

The empirical data used to parameterize the simulation cannot by themselves be used to draw inferences about cowbird productivity because they do not capture the season-long dynamics of the nesting and re-nesting process, and because there is no way to combine the multiple factors influencing the number of cowbirds fledged. However, the empirical data can be used to compare the relative importance of the various factors (host nest failure rates, host density, cowbird offspring mortality rates within nests, and cowbird eggs/nest) in determining community-scale outcomes. The empirical data supported the overriding

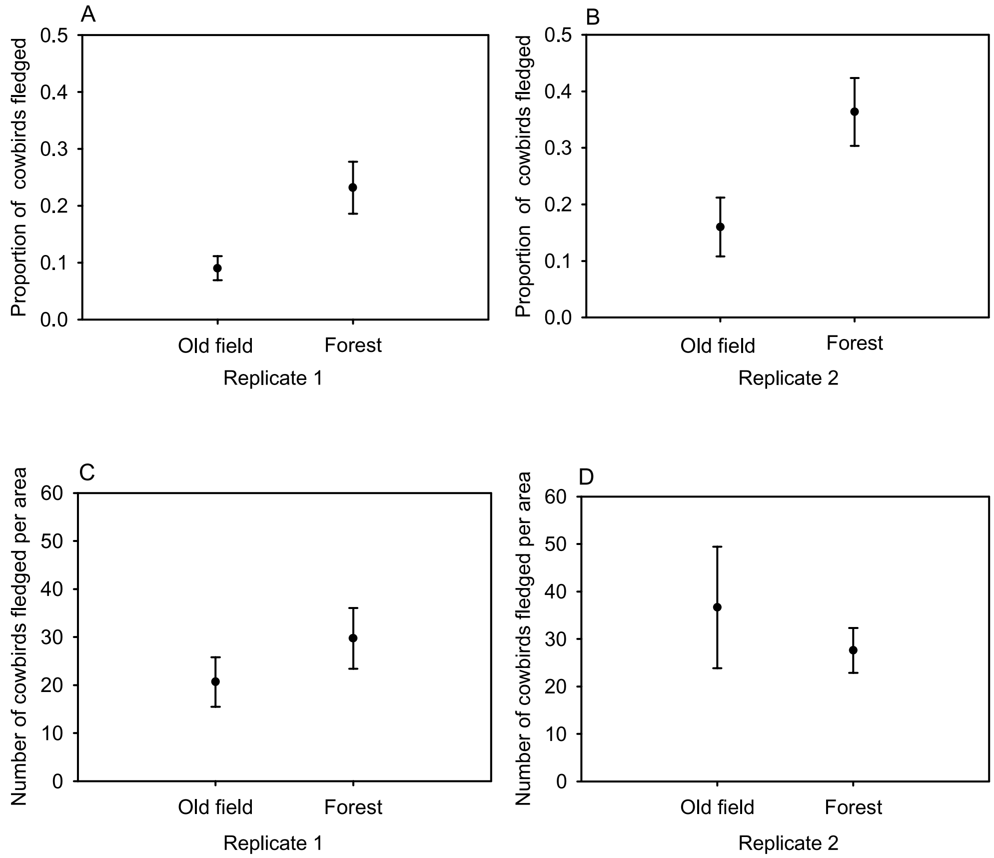

Fig. 4. Annual cowbird productivity in the absence of density dependence. The proportion of cowbirds raised to fledging in (a) replicate 1 and (b) replicate 2. The number of cowbird fledglings produced per plot (19 ha), summed across all host species and including host density, in (c) replicate 1 and (d) replicate 2. Results are simulation means ± standard errors, using input parameters that exclude the effects of density-dependent reduction in cowbird offspring survival.

importance of nest failure in determining differences between habitats. Nest failure rates were significantly higher for host species breeding in the old field in replicate 1 (Wilcoxon test, $\chi^2 = 5.01$, $P < 0.03$) and the same trend was found in replicate 2, but was not significant due to the outlier species, the common yellowthroat ($\chi^2 = 2.08$, $P = 0.15$; with outlier excluded, $\chi^2 = 4.50$, $P = 0.03$). The density of cowbird hosts was significantly higher in the old field than in the forest ($G \geq 23$, $P < 0.001$ in both years), which is a trend opposite to that found for cowbird productivity. The number of cowbird eggs per nest did not differ significantly between habitats in replicate 1 (Fig. 7a), but in replicate 2 the forest-breeding hosts were more heavily parasitized (Wilcoxon test, $U = 16$, $P = 0.05$; Fig. 7b). However, higher parasitism in the replicate 2 forest cannot be responsible for the greater proportion of cowbird eggs that survive to fledging in that habitat. The final factor, cowbird offspring mortality within host nests, did not differ significantly between habitat types in either replicate.

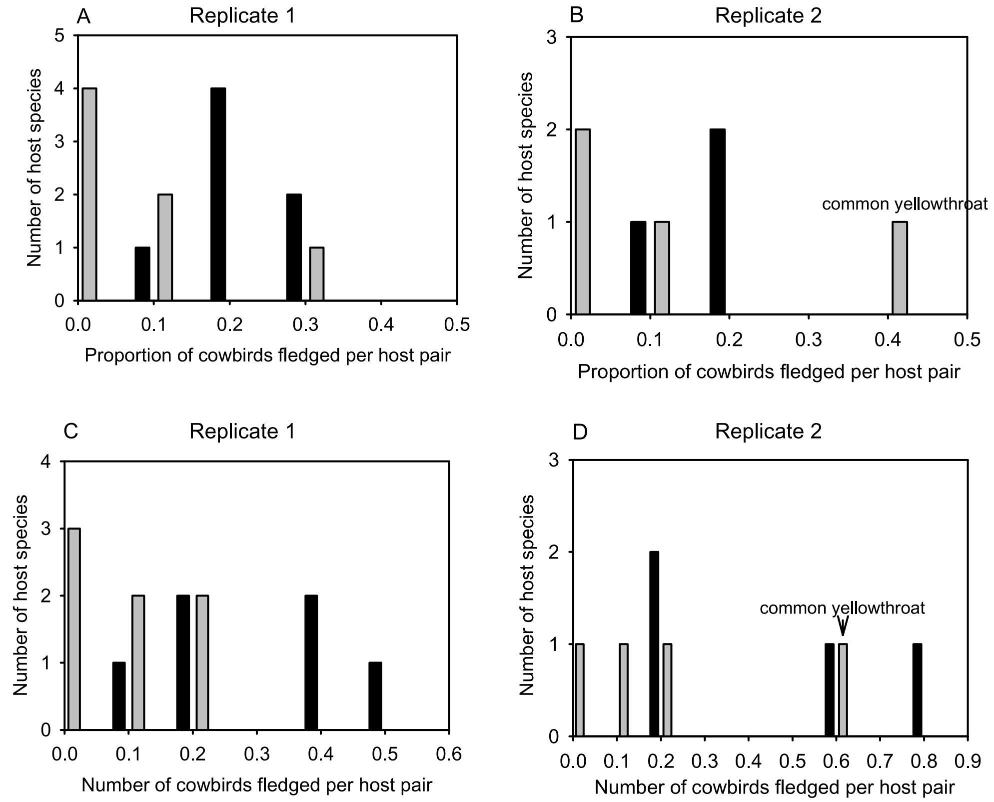

Fig. 5. Frequency distributions for annual cowbird productivity per pair of host birds, for the host species studied in each replicate. The proportion of cowbirds raised to fledging in (a) replicate 1 and (b) replicate 2. The number of cowbird fledglings produced per host pair in (c) replicate 1 and (d) replicate 2. Results are simulation means over 500 repetitions of the simulation. The outlier, common yellowthroat, is indicated.

DISCUSSION

We developed a new framework to estimate the productivity (fledglings/egg and fledglings/area) of a brood parasite across entire host communities. As far as we are aware, a solution to this estimation problem has not been attempted previously. We used Bayesian methods to generate distributions for each parameter based on observations, and Monte Carlo methods to convert these into distributions of our outcome variables. These methods offered several advantages. First, by using a simulation and sampling distributions (as opposed to single values, such as means) for all of our data, we were able to propagate error from ~50 parameters related to cowbird productivity with each host species. We were therefore able to report community-scale results with an associated aggregate error. Second, the simulation framework allowed us to accurately model the phenological components of the system, which include the season-long nesting and re-nesting process, and the degree of overlap between the breeding season of the parasite and that of each host species. Third, the simulation entails minimal assumptions. We used data for all of the parameters, and

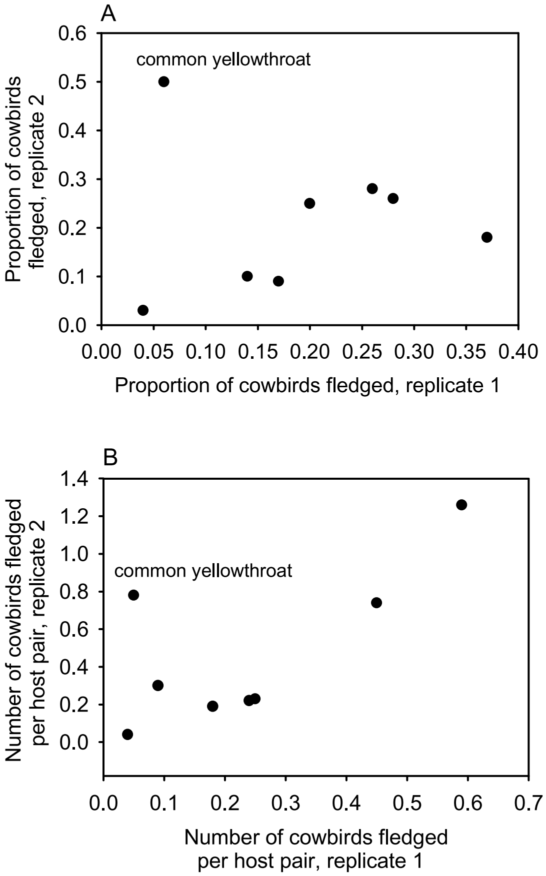

Fig. 6. Correlations between replicates in terms of cowbird productivity per pair of host birds for eight host species. (a) The proportion of cowbirds raised to fledging. (b) The annual number of cowbird fledglings produced. Two overlapping points were shifted slightly to improve visibility in (b). The outlier, common yellowthroat, is indicated.

assumed only the basic form of the sampling distributions. Using alternative, reasonable distributions had very little effect on the simulation results (R. Winfree, unpublished data). A similar approach could be used for any situation in which the productivity of a parasite needs to be integrated over multiple host species, and error propagated.

We found that cowbirds have higher productivity when they lay their eggs in deciduous forest, a habitat that they have only invaded on a large scale during the last 200–300 years, than in old fields, which are more similar to the grasslands inhabited by cowbirds for at least half a million years (Lowther, 1993). The simulation results show that a significantly greater proportion of cowbird eggs survive to fledging in the forest than in the old field in both replicate landscapes (Fig. 2a,b). We believe that the proportion of offspring that survive is the best measure of reproductive success, as it relates to per capita productivity and therefore to the cowbird population growth rate in each habitat (Winfree, 2004). However, we also used the simulation to estimate the number of cowbird fledglings produced per unit area in forest and old field habitat. The number of cowbird fledglings produced was not

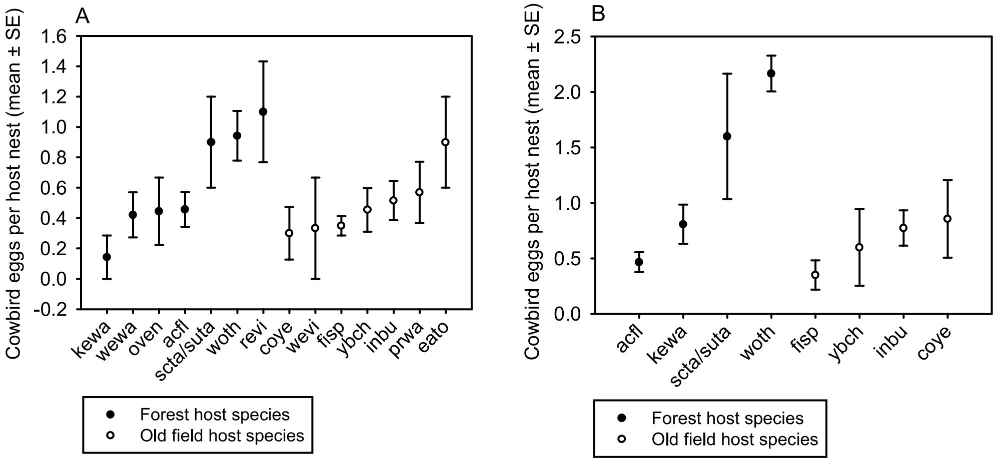

Fig. 7. Cowbird eggs laid per host nest for (a) replicate 1 and (b) replicate 2. Host species names are abbreviated using the first letters of the species' common names (see Table 2). Means ± standard errors.

significantly different between habitats in either replicate. This is a misleading finding, because it disguises the fact that many more cowbird eggs were laid in the old field, but most of them were lost to nest predation. The disjunction between the per capita and per area results highlights the importance of using a model that can estimate the annual input of parasite eggs into a community, and therefore the proportion that survive, and/or measure female parasite density so that per capita productivity can be estimated. Density is difficult to measure for brood parasites such as cowbirds, which can have large ranges [e.g. for cowbirds, up to hundreds of hectares (Thompson and Dijak, 2000)] and tend to be cryptic while they are searching for host nests. Although we tried several methods for measuring female cowbird density in our study, none generated reliable data; however, most methods indicated that density was higher in the old field (R. Winfree, unpublished data), which is consistent with our simulation results.

We also used the simulation to estimate cowbird productivity in the absence of density dependence (which in our system is manifested through reduced survival of cowbirds that share the host nest with other cowbirds) to investigate the case in which the cowbird is invading a new host community. In this 'invasion scenario', the difference in cowbird productivity between habitats increased, with the proportion of cowbirds fledged being between two and three times higher in the forest host community (Fig. 4a,b). These results support the suggestion, first made by Friedmann (1929), that the cowbird population exploded when the species gained access to hosts breeding in eastern deciduous forests, as a result of forest fragmentation in the eighteenth and nineteenth centuries.

Our results are consistent with empirical studies showing that in the eastern and midwestern Unites States, female cowbirds prefer to lay their eggs in forest habitat (Hahn and Hatfield, 1995; Thompson and Dijak, 2000), and that at a larger scale, cowbirds may seek out more forested landscapes (Gustafson *et al.*, 2002). Cowbirds in the xeric western Unites States also seek out forested, riparian habitats (Farmer, 1999), suggesting that this behaviour may have developed in the cowbirds' original grassland range. The community-scale results of the present study are also consistent with an analysis of the same data set that focused on individual host species, and did not use a simulation of the season-long breeding season, which found that on a per-nest basis most forest species are better cowbird hosts than most old field species (Winfree, 2004).

In both habitats, the majority of cowbird eggs were lost to nest failure (Fig. 3a–d), which is largely attributable to nest predation. Nest failure was also the key factor determining the difference in cowbird production between habitats. At nest failure rates typical for forest species in our study, 30–50% of nests survive long enough to fledge a cowbird. In contrast, in the old field, only 5–20% of nests survive that long. Forests in our study areas are quite fragmented, which makes them a conservative test case with regard to nest predation and cowbird productivity. Per capita cowbird productivity may be even higher in more extensive forests, where nests survive better (Robinson *et al.*, 1995; Donovan *et al.*, 1997, 2000; Chalfoun *et al.*, 2002). However, because fewer cowbirds access extensive forests, the number of fledgling cowbirds produced per area may not increase with forest size (Donovan *et al.*, 2000). It is more difficult to draw general conclusions about cowbird productivity in old fields, because the literature on old field nest predation rates is limited and reaches little consensus.

In contrast to our initial expectations, we found only a weak effect of host defences against parasitism on cowbird productivity. We had expected higher cowbird mortality due to host defences in the old field, because grassland-breeding species have a long co-evolutionary history with the cowbird and are known to have defences against parasitism (Peer *et al.*, 2000). In contrast, few forest-breeding species are known to have such defences (Hosoi and Rothstein, 2000). However, the red-eyed vireo, a forest species that preferentially abandons parasitized nests, was abundant and highly parasitized in our study, and therefore accounted for considerable cowbird mortality. Our results suggest that an ecological factor – nest predation rates, which vary with landscape context and human disturbance – may exert a stronger influence on cowbird productivity than does its evolutionary interactions with its hosts.

Cowbird offspring mortality within active host nests was low in both host communities, suggesting that the cowbird is an effective generalist parasite with both historical and more recent hosts. The main effect increasing cowbird mortality within the nest was the presence of other cowbirds, rather than any factor related to the host species.

Several limitations to our data set contributed to the uncertainty in our results and may have contributed bias; however, the known biases are contrary to the main finding of the study. First, for canopy-nesting hosts we had to include data on fledged families in our measures of cowbird eggs per nest, which means we may have underestimated the true number of cowbird eggs per nest and therefore the number of cowbirds produced in the forest. Second, we lacked data on two forest species, which again contributes to an underestimate of the cowbirds fledged in forest habitat. Third, sample sizes were small for some host species. However, all of this uncertainty was propagated through the simulation and is therefore reflected in the results.

Our results suggest that variation in the geographic spread of the cowbird might be explained by differences in the composition of the host community and cowbird reproductive potential in different regions. For example, the cowbird spread rapidly into the central and northeastern Unites States once the continuous forest was fragmented, and human activities provided feeding sites, in the 1700s (Mayfield, 1965; Rothstein, 1994). Cowbirds also rapidly colonized California alongside European settlers in the 1800s (Rothstein, 1994), possibly due to human activities which gave cowbirds access to forest-breeding hosts (Rothstein *et al.*, 1980, 1984). The reasons for the cowbird's expansion in the west remain more speculative, however, since cowbird reproduction has not yet been estimated with a western host community. The cowbird's spread into the southeastern Unites States continues to be relatively slow; for example, cowbirds are only now invading Florida (Cruz *et al.*, 1998), despite the widespread availability of feeding habitat. Possibly the inability of the host communities in this region to produce many juvenile cowbirds has limited the cowbird's invasion success. In most habitat types in Florida, nest failure rates for host species nesting in the understory are very high, and canopy-nesting species that may be better cowbird hosts exist only at low densities (S.K. Robinson, unpublished data).

Lastly, our study has management applications. Our results suggest that reducing forest fragmentation could limit the cowbird's access to this superior breeding habitat, and thereby reduce cowbird population growth. It is well known that cowbird abundance is lower in larger (ca. 3000–10,000 ha) forests (Robinson *et al.*, 1995; Donovan *et al.*, 1997; Robinson and Smith, 2000), and that they only access large forest patches that are near openings such as livestock pastures, mowed lawns and row crops, which provide feeding sites (Rothstein *et al.*, 1984; Morse and Robinson, 1999; Goguen and Mathews, 2000). Allowing the re-growth of larger forest tracts should reduce cowbird population growth, and parasitism of all cowbird host species, not only those breeding in forests. This method of managing the cowbird population is also consistent with existing recommendations aimed at increasing the productivity of forest-breeding cowbird host species, which are negatively affected by forest fragmentation (e.g. Robinson *et al.*, 1995). Furthermore, landscape management should be an efficient strategy for cowbird control because it targets the life-history stage (egg and nestling survival) to which cowbird population growth is most sensitive (Citta and Mills, 1999). In contrast, existing methods (Ortego, 2000; Rothstein and Cook, 2000) target the adult stage, to which population growth responds only weakly. Finally, landscape-scale management is more ethically defensible than large-scale killing of adult cowbirds, given that the cowbird is a native species whose population has increased in response to habitat alteration by humans, alterations which could in principle be reversed to the benefit of many species including cowbird hosts.

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APPENDIX 1

Parameter values obtained from the published literature

Several parameters necessary for our simulations were obtained from the published literature. These parameters are characteristics of the species, not the population, so using values from other studies is appropriate. First, some bird species are known to have defences against parasitism. In our study, no species rejected cowbird eggs from their nests, but three species did preferentially abandon parasitized nests (field sparrow, *Spizella pusilla*; prairie warbler, *Dendroica discolor*; and red-eyed vireo, *Vireo olivaceus*). To measure nest abandonment, nests need to be found at the beginning of the nest cycle, because abandonment usually occurs at the end of the egg-laying period. However, most of the nests in our study were found when they were further along in the nest cycle. Therefore, we based our parameter values for the probability of nest abandonment given parasitism on larger, published data sets for each of the above species. Most studies of bird nesting report a small 'background' rate of nest abandonment for unknown reasons. We expect that this is attributable to the disturbance of the nest having been found by the researcher. To avoid attributing this abandonment to parasitism, we subtracted the abandonment rate for unparasitized nests from the rate for parasitized nests in using these published studies. The data sets consisted of 147 nests for the field sparrow (Best, 1978), 138 nests for the prairie warbler (V. Nolan, unpublished data; Nolan, 1978) and 85 nests for the red-eyed vireo (Graham, 1988). A related issue is that for these three species, our empirical measures of cowbird eggs per nest will be underestimates, since some parasitized nests would be abandoned before being found. Therefore, we adjusted the parasitism parameter to assume that each species had already abandoned its characteristic fraction of parasitized nests before nests were found.

When the empirical parasitism parameter is used instead, results are qualitatively similar (R. Winfree, unpublished data).

Second, we used published values for the various species-specific phenologies associated with the nest cycle (Baicich and Harrison, 1997). These phenologies include the duration of the nest-building, egg-laying, incubation and nestling periods, as well as the number of broods a species will raise each season. For two parameter values there is very little empirical information: the number of days between the destruction of one nest and beginning a new nest; and the number of days between fledging offspring and beginning a new nest (for multiply-brooded species). We assumed that the first interval is 2 days and the second interval 7–14 days, depending on the biology of the species; this is based on two extensive published studies (Nice, 1937; Nolan, 1978) as well as personal observations. Phenological parameters used for all host species are listed in Table 2. For the cowbird, we used 12 days for the incubation period and 10 days for the nestling period (Baicich and Harrison, 1997).