

A MODEL OF THE DYNAMICS OF COWBIRDS AND THEIR HOST COMMUNITIES

JOSEPH A. GRZYBOWSKI^{1,3} AND CRAIG M. PEASE^{2,4}

¹College of Mathematics and Science, University of Central Oklahoma, Edmond, Oklahoma 73034, USA; and

²Department of Zoology, University of Texas, Austin, Texas 78712, USA

ABSTRACT.—Few studies have examined the potential consequences of cowbird (*Molothrus* spp.) parasitism on entire avian communities. Because cowbirds are host generalists, an obvious opportunity exists for such community-level effects. We developed a model to predict how cowbird abundance affects and is affected by the relative abundances of different types of host species. Toward this end, we divided the passerine hosts of cowbirds into three categories, each having different population dynamic properties: (1) ejectors of cowbird eggs; (2) extinction-prone acceptors of cowbird eggs (species that decline in abundance in response to high levels of cowbird parasitism); and (3) insensitive acceptors of cowbird eggs (species that maintain their abundance even at high levels of cowbird parasitism). Ejectors are sinks for cowbird eggs and thus indirectly benefit extinction-prone hosts. Conversely, insensitive acceptors can raise cowbird young without a concomitant decrease in their own abundance; as such, they indirectly harm extinction-prone species. Although cowbird abundance is determined by the abundance of both ejectors and insensitive acceptors, the reverse is generally not true (i.e. their abundance is independent of cowbird abundance). The mathematical model of cowbird/host community dynamics we present consists of two ordinary differential equations that incorporate the above assumptions about the different classes of hosts and the manner in which they interact with cowbirds. The model predicts that extinction-prone species will have a higher potential to persist when one or more of the following exist: (1) ejectors are relatively more abundant than insensitive acceptors; (2) ejectors are abundant relative to extinction-prone carrying capacity; (3) maximum potential cowbird per-capita population growth rate is small; and (4) the potential effect of cowbirds on extinction-prone population growth rate is small. Extinction-prone species will decline or go extinct in reverse situations. Received 15 July 1996, accepted 22 June 1998.

THE BROWN-HEADED (*Molothrus ater*), Shiny (*M. bonariensis*), and Bronzed (*M. aeneus*) cowbirds are brood parasites that range broadly over the Americas (Friedmann 1929). They have been widely implicated in the decline of Neotropical migratory passerines (Brittingham and Temple 1983, Robbins et al. 1989, Terborgh 1989) and may threaten populations of some hosts at both local and regional scales (Wiley 1985, 1988; Robinson 1992; Sauer and Droege 1992).

Although cowbirds are host generalists (Friedmann and Kiff 1985; Wiley 1985, 1988; Carter 1986) and simultaneously interact with an array of host species, few studies have focused on interactions between cowbirds and their host communities. Those that have are limited to responses of cowbirds to compo-

nents of host density (Lowther and Johnston 1977, Robinson and Wilcove 1994, Barber and Martin 1997), or the correlations of host density and species type on parasitism levels for species within a host aggregation (Barber and Martin 1997). However, the population consequences of cowbird parasitism on both hosts and cowbirds are poorly understood, and cowbird/host community population dynamics are virtually unstudied (Smith and Rothstein 1999).

Cowbird parasitism reduces host reproductive performance in many species (Rothstein 1990) and thus the potential abundance of hosts in a host community. Any differences in interactions between cowbirds and components of the host community may affect both the relative and absolute densities of the different hosts as well as cowbirds. From the cowbirds' perspective, we expect that their abundance will be insensitive to the availability of any particular host species, and rather, will be determined by combined attributes of the en-

³ E-mail: grzybow@aix1.ucok.edu

⁴ Present address: Vermont Law School, South Royalton, Vermont 05068, USA.

tire host community. The abundances of individual host species may be influenced by their interactions with cowbirds but also by cowbird interactions with other host species. That is, cowbird eggs laid in nests of one host species are eggs not laid in nests of alternative host species; cowbirds fledged from the nests of one species may, as adults, parasitize nests of other host species.

Considerable heterogeneity exists among different host species in how they respond to cowbirds. Cowbird nest parasitism may severely decrease the reproduction of some hosts. Populations of Yellow-shouldered Blackbird (*Agelaius xanthomus*; Post and Wiley 1977), Least Bell's Vireo (*Vireo bellii pusillus*; Franzreb 1989), Black-capped Vireo (*Vireo atricapillus*; Grzybowski 1995), and Kirtland's Warbler (*Dendroica kirtlandii*; Mayfield 1960, Walkinshaw 1983) have suffered heavily from cowbird parasitism. Other hosts have high reproduction even while raising cowbird young. Examples include hosts with larger body size and those that reproduce early in the year before cowbirds arrive (e.g. Finch 1983, Eckerle and Breitwisch 1997). Still other hosts eject cowbird eggs from their nests (Rothstein 1975), an action that decreases cowbird reproductive success.

We postulate that the different reproductive and behavioral responses of different types of hosts to cowbird parasitism have population-dynamic consequences. Cowbirds determine the relative abundances of these types of hosts. The abundances of different types of hosts and host responses to cowbird eggs help determine the abundance of cowbirds. We model these dynamic interactions here.

THE MODEL

Three types of cowbird hosts.—To model the heterogeneity among different host species in their behavioral and population responses to brood parasitism, we partition hosts into: (1) ejectors of cowbird eggs (species that are sinks for cowbird eggs); (2) insensitive acceptors of cowbird eggs (species that raise cowbird young, but do not have their abundances determined by cowbirds); and (3) extinction-prone acceptors of cowbird eggs (species that raise cowbird young, and have their abundances determined, at least in part, by cowbirds).

Ejectors remove all or most cowbird eggs placed experimentally in their nests ("rejecters" of Rothstein 1975). Reported parasitism levels generally are low in ejectors (Friedmann and Kiff 1985); however, this may be so because ejectors remove most cowbird eggs from their nests before they are detected by observers. For example, Scott (1977) visited nests of the Gray Catbird (*Dumetella carolinensis*), an ejector, shortly after dawn (when parasitism occurs) and found that parasitism was substantially higher (44%) than reported previously (1.5%; Nickell 1958).

The remaining two categories of hosts are acceptors; i.e. they do not remove cowbird eggs from their nests (Rothstein 1975). They are distinguished by the observation that, although brood reduction occurs in virtually all parasitized nests of acceptors, populations of some species (extinction prone) are detrimentally affected by cowbird nest parasitism, whereas others (insensitive acceptors) apparently are not (Post and Wiley 1977, Friedmann et al. 1977, Franzreb 1989, Weatherhead 1989, Roskaf et al. 1990, Eckerle and Breitwisch 1997). Obviously, high levels of parasitism may cause serious declines in the abundance of extinction-prone hosts. Conversely, even at high levels of parasitism, the populations of insensitive acceptors are not regulated by cowbirds.

A mathematical model.—Our mathematical model incorporates several qualitative features of the cowbird/host interaction. The reproductive success of extinction-prone species decreases as cowbird abundance increases, and as the relative abundance of ejectors decreases (because cowbirds "waste" fewer eggs in ejector nests). Cowbird reproductive success decreases as the probability of nest abandonment after parasitism increases, and as the abundance of ejectors relative to extinction-prone and insensitive acceptors increases. Increasing cowbird abundance relative to host abundance causes the percentage of host nests that are multiply parasitized to increase, with a resulting decrease in cowbird reproductive success. Our differential equation model predicts the ultimate changes in cowbird and host abundances given these proximate effects on reproductive success.

Although our analysis recognizes four types of species (cowbirds, extinction-prone hosts, insensitive hosts, and ejectors), only the abun-

TABLE 1. Model parameters for cowbird/host community dynamics.

Fundamental parameters	
<i>C</i>	Cowbird abundance
<i>E</i>	Extinction-prone abundance
<i>I</i>	Insensitive acceptor abundance
<i>R</i>	Ejector abundance ("rejecter" of Rothstein 1975)
<i>K</i>	Extinction-prone carrying capacity
<i>d_c</i>	Cowbird per-capita death rate (per year)
<i>d_E</i>	Density-independent extinction-prone per-capita death rate (per year)
<i>r_c</i>	Density-independent cowbird per-capita birth rate (per year)
<i>r_E</i>	Density-independent extinction-prone per-capita birth rate (per year)
<i>a</i>	Nest abandonment probability (dimensionless)
<i>f</i>	Fraction of host brood fledged under parasitism (dimensionless)
<i>m</i>	Cowbird auto-interference coefficient (dimensionless)
Derived parameters	
<i>R/I</i>	Ratio of ejectors to insensitive acceptors
<i>R/(I + K)</i>	Ratio of ejectors to acceptor carrying capacity
ϵ	Extinction-prone critical ratio
χ	Cowbird critical ratio

dances of cowbirds and extinction-prone species need be modeled as dynamic variables. The abundances of insensitive acceptors and ejectors are unaffected by cowbird density (insensitive species by definition, ejectors because they immediately remove cowbird eggs from their nests and thus suffer minimal brood reduction).

Appendix 1 derives equations (1a) and (1b) below from an underlying mathematical model describing both host and cowbird reproduction. This model accounts for host abandonment of parasitized nests immediately after the nest is parasitized (probability *a*), cowbird eggs "wasted" on ejectors, and the loss of part or all of a brood when a nest is parasitized (quantified by *f*, the fraction of the potential unparasitized host brood fledged when the brood is parasitized). This underlying model produces expressions describing both cowbird and extinction-prone reproductive success (i.e. per-capita birth rates). We combine these with some simple assumptions about cowbird and extinction-prone per-capita death rates to derive a model describing the coupled population dynamics of cowbirds and extinction-prone hosts.

We denote the abundances of cowbirds, extinction-prone hosts, ejectors, and insensitive species as *C*, *E*, *R*, and *I*, respectively (Table 1). Then, as derived in Appendix 1, the following differential equations describe the extinction-prone (equation 1a) and cowbird (equation 1b) population dynamics:

$$\frac{dE}{dt} = E \left(-d_E \left[1 - \frac{E}{K} \right] + r_E \left[\frac{I + R + E + f(1-a)mC}{I + R + E + m(1-a)C} - \frac{E}{K} \right] \right) \quad (1a)$$

$$\frac{dC}{dt} = C \left(-d_c + r_c \frac{(1-a)(E + I)}{I + R + E + m(1-a)C} \right). \quad (1b)$$

These equations model the influence that cowbirds and extinction-prone species have on one another's reproductive success. Maximum cowbird success of *r_c* is obtained when both ejectors and cowbirds are rare and few nests are abandoned after parasitism (set *R* = 0 and *C* = 0 in the denominator of equation [1b], and *a* = 0 in the numerator). Maximum extinction-prone reproductive success of *r_E* is obtained when *C* = 0 (cowbirds do not reduce extinction-prone reproductive success) and *E* = 0 (extinction-prone hosts do not decrease their reproductive success via density-dependent processes). Under our assumptions, reproductive success, rather than mortality, mediates the cowbird/host community interaction. The model assumes that extinction-prone hosts have a density-independent per-capita death rate of *d_E*. The model also assumes cowbird per-capita death rate is a density-independent constant, *d_c*. The model incorporates density-dependent feedback of extinction-prone abundance on its own mortality. In the absence of cowbirds, extinction-prone abundance equilibrates at *K*. Cowbird reproductive success is also density-dependent in the model. The mod-

el assumes that cowbirds do not avoid host nests that are already parasitized, and that host nests parasitized multiple times produce no more cowbird offspring than do nests that are parasitized but once. As a consequence, per-capita reproductive success of cowbirds decreases as their abundance increases. The cowbird auto-interference parameter, m , quantifies this.

Analytical methods.—To determine the parameter values under which extinction-prone species and cowbirds persist, and, conversely, the conditions under which one or the other will go extinct, we used graphical (phase-plane) and analytic (primarily linear stability) methods (see May 1975) together with a few computer simulations. Throughout, we make the biologically reasonable assumptions that $0 \leq a \leq 1$, $r_C > d_C$, $r_E > d_E$, $m > 0$, $R \geq 0$, $I \geq 0$, and $0 \leq f \leq 1$. We also assume that $d_E \geq fr_E$.

These analyses proceeded by first finding all the equilibrium points of the extinction-prone host and cowbird differential equations and then determining the feasibility and local stability of these points. This allowed us to identify critical parameter combinations for ecologically feasible outcomes. Appendix 2 presents the details of this analysis. We also used a graphical sensitivity analysis to assess the robustness of our model to its assumptions.

Classification of hosts.—Numerous factors, including body size (Rothstein 1990), level of host brood reduction in parasitized nests, and length and timing of the host's breeding season relative to the cowbird's (Pease and Grzybowski 1995, Grzybowski and Pease 1999) determine the category of each host species. Ejectors tend to have larger body sizes. Conversely, both types of acceptors may be physically unable to remove cowbird eggs from their nests (Rohwer and Spaw 1988), although they can abandon parasitized nests soon after they are parasitized (e.g. Graber 1961, Nolan 1978, Graham 1988). Most Neotropical migrants have short breeding seasons that overlap that of cowbirds, and this may cause them to be extinction prone. By contrast, host species that are evidently insensitive to cowbird parasitism tend to be closer in size to cowbirds and/or be resident (i.e. nonmigratory) with a longer breeding season. In such species, some reproduction may occur when cowbirds are not present, and/or because the host young may be of similar or larger size than cowbird young, the

host young can compete more successfully with young cowbirds (Weatherhead 1989, Roskaff et al. 1990, Eckerle and Breitwisch 1997).

We examined the relative abundances of cowbirds and several host classes in a series of natural communities. We classified as ejectors all *Tyrannus* flycatchers, the Mimidae, the American Robin (*Turdus migratorius*), the Baltimore Oriole (*Icterus galbula*; Rothstein 1975, Finch 1982), eastern populations of the Warbling Vireo (*Vireo gilvus*; Sealy 1996), and Great Plains meadowlarks (*Sturnella* spp.; S. Brown pers. comm.). Rothstein (1975) included the Northern Mockingbird (*Mimus polyglottos*) as an acceptor from a small sample of observations (4), but Cruz et al. (1985) found that Northern Mockingbirds reject cowbird eggs and observed parasitism at the low levels expected of an ejector.

We classified blackbirds (*Xanthocephalus*, several *Agelaius* and *Euphagus* spp.), *Cardinalis* spp., the Dickcissel (*Spiza americana*), and *Pipilo* spp. (except *P. erythrophthalmus* and *P. maculatus*) as insensitive acceptors (Elliott 1978, Finch 1983, Weatherhead 1989, Freeman et al. 1990, Roskaff et al. 1990, Eckerle and Breitwisch 1997, D. Scott pers. comm.). The decision to classify Dickcissels as insensitive acceptors was somewhat arbitrary and was based on the low brood reduction caused by parasitism of their nests (Elliott 1978, Grzybowski and Pease 1999). We regarded most other regularly parasitized open-cup nesting passerines (see Friedmann 1963, Friedmann and Kiff 1985) as extinction prone. In some cases, we assigned species to one or the other of these groups based on the classification of a closely related species.

Some passerines were excluded from this summary and were thus not assigned to any host category. Most often, this occurred because they are cavity nesters, have very large body sizes, or are very aggressive near their nests. These included *Myiarchus* flycatchers, swallows, corvids, parids, nuthatches, creepers, wrens, bluebirds and solitaires, waxwings, European Starling (*Sturnus vulgaris*), grackles, fringillids, and ploceids. We also excluded shrikes and *Aimophila* sparrows, which are parasitized only occasionally (Friedmann 1963, Friedmann and Kiff 1985). Some excluded species may be parasitized at high enough rates to have been included in our analyses (e.g. some

TABLE 2. Parameter combinations implying persistence (present) or extinction (absent) of cowbirds and their extinction-prone hosts.

Long-term behavior		Mathematical condition ^a
Cowbirds	Extinction-prone hosts	
Present	Absent	$\chi > \epsilon (1 + R/I) + R/I$
Present ^b	Present ^b	$R/(I + K) < \chi < \epsilon (1 + R/I) + R/I$
Absent	Present	$\chi < R/(I + K)$

^a All inequalities assume $d_E > fr_E$. See text for further discussion.

^b For these parameter values, there is either a globally stable equilibrium point with both species present at positive abundance, or a stable limit cycle.

wrens, bluebirds, waxwings [Rothstein 1976], and fringillids [Kozlovic et al. 1996]. Conversely, some flycatchers included in our classification (*Tyrannus* spp. and *Contopus* spp.) may avoid parasitism largely by being aggressive near their nests (Sealy and Bazin 1995).

Clearly, variation exists among host species in their response to cowbird parasitism that is not accounted for by our classification scheme. For example, some species, such as Red-winged Blackbirds (*Agelaius phoeniceus*), are heavily parasitized in some regions but not in others (Freeman et al. 1990, Robinson et al. 1995); thus, in some regions they will function as insensitive species, whereas in others they will not belong to any category. Similarly, Eastern Meadowlarks (*Stunella magna*) eject cowbird eggs in some regions (S. Brown pers. comm.) but not in others (S. Robinson pers. comm.), where functionally, they may be insensitive acceptors. The House Finch (*Carpodacus mexicanus*) has a vegetarian diet. It accepts cowbird eggs and may incur significant reduction in its own reproduction; however, because its nests produce few to no cowbirds, from the viewpoint of cowbirds, it is effectively an ejector (Kozlovic et al. 1996). Additionally, variation exists within the acceptor classes in the extent of brood reduction; our model assumes a single average value.

RESULTS

Mathematical analysis of the model.—The analysis of equations (1a) and (1b) presented in Appendix 2 shows that although the equations contain 12 parameters, only four combinations of them are needed to fully determine whether cowbirds and extinction-prone species persist or go extinct (Table 1). These four parameter combinations are all non-dimensional: (1) the ratio of ejector to insensitive acceptor abun-

dances, R/I ; (2) the ratio of ejector density to the sum of insensitive acceptor density and extinction-prone carrying capacity, $R/(I + K)$ (note that extinction-prone carrying capacity is their abundance in the absence of cowbirds); (3) a ratio comparing extinction-prone population growth rate when cowbirds are absent with its value when cowbirds are very abundant, $\epsilon = (r_E - d_E)/(d_E - fr_E)$; and (4) a ratio comparing cowbird population growth rate when cowbirds and ejectors are both rare to its value when cowbirds and/or ejectors are very abundant, $\chi = [r_C (1 - a) - d_C]/d_C$. As regards the denominator of this last expression, note that cowbird reproductive success is 0 when cowbirds and/or ejectors are very abundant, making the population growth rate $0 - d_C$.

Three ecological outcomes of the interaction between cowbirds and extinction-prone species are possible. Table 2 presents parameter values corresponding to cowbirds alone persisting, to cowbirds and extinction-prone hosts coexisting, and to extinction-prone species alone persisting. Extinction-prone hosts persist most readily when cowbirds have a small effect on extinction-prone population growth (ϵ large), when maximum cowbird population growth rate is modest (χ small), when there are relatively more ejectors than insensitive acceptors (R/I large), and when ejectors are common relative to insensitive acceptors and extinction-prone abundance ($R/(I + K)$ large).

This model provides insight into the distinction between extinction-prone hosts and insensitive acceptors. When $d_E < fr_E$, extinction-prone reproductive success exceeds mortality even when all extinction-prone nests are parasitized. Thus, the "extinction-prone" hosts always persist when this inequality holds, effectively causing them to be insensitive acceptors in that they cannot be driven to extinction by

TABLE 3. Relative abundance^a of different types of passerine hosts in various habitats. The number of sample host communities is given in parentheses in the Habitat column.

Habitat	E^a	I	R	C	R/I	$R/(I + \hat{E})$	Source ^b
Forests							
E. deciduous forest (19)	79.7	9.1	11.3	2.1	1.24	0.13	1
E. deciduous forest (6)	96.7	0.3	3.0	0.0	10.30	0.03	2
E. mixed forest (5)	91.5	2.9	5.5	1.3	1.89	0.06	1
E. coniferous forests (1)	88.2	5.9	5.9	0.0	1.00	0.06	1
Cen. deciduous forest (1)	93.5	0.0	6.5	0.0	—	0.07	1
Cen. deciduous forest (3)	92.5	2.8	4.7	9.4	1.69	0.05	4
Cen. mixed forest (5)	92.3	0.0	7.7	+	—	0.08	5
W. deciduous forest (10)	88.0	4.1	7.9	3.1	1.94	0.09	1
W. mixed forest (6)	88.3	7.0	4.8	2.2	0.69	0.05	1
S. forest (5)	85.2	14.1	0.7	0.0	0.05	0.007	3
Scrublands							
E. mixed forest-scrub (9)	77.2	7.7	15.2	2.0	1.97	0.18	1
W. mixed forest-scrub (9)	87.4	3.6	8.9	2.6	2.45	0.10	1
W. desert scrub (6)	63.3	20.7	16.0	1.3	0.77	0.19	1
S. scrub (2)	86.5	11.7	1.8	0.0	0.15	0.02	3
Grasslands							
S. grassland (2)	72.7	0.0	27.3	0.0	—	0.38	3
Cen. prairie (7)	48.5	41.7	9.9	4.9	0.24	0.11	1
Cen. grassland (1)	98.1	0.0	1.9	1.9	—	0.02	5
Other							
Wetlands (8)	74.4	13.7	12.0	8.5	0.88	0.14	1
Fields/abandoned (3)	60.9	21.9	17.2	7.8	0.79	0.21	1

^a Relative densities are scaled as percent of potential host densities; cowbird densities are scaled against total host densities. E = extinction-prone acceptor; I = insensitive acceptor; R = ejector, C = cowbird.

^b 1. Van Velzen and Van Velzen (1984); 2. Kendeigh (1946); 3. Johnston and Odum (1956); 4. Bond (1957); 5. Kendeigh (1948).

cowbirds. Consequently, the analyses assume that $d_E > fr_E$.

Empirical observations and estimates of critical parameter combinations.—Table 3 shows relative abundances of ejectors, insensitive acceptors, extinction-prone species, and cowbirds for a broad range of communities of North American passerines. R/I ratios for these communities tend to be < 2 , with few outliers. The generally narrow range implies similarity of community structure across diverse habitats, although more southerly and open habitats tend to have relatively more insensitive acceptors. Table 3 also shows that extinction-prone species are generally much more abundant than ejectors or insensitive acceptors. These data actually estimate $R/(I + \hat{E})$, where \hat{E} is the empirically estimated extinction-prone abundance. By contrast, the model inequalities involve $R/(I + K)$. We expect $R/(I + K) < R/(I + \hat{E})$ because $\hat{E} < K$. We conclude that $R/(I + K)$ is usually $\ll 1.0$ (Table 3).

Cowbirds potentially have very large population growth rates (Scott and Ankney 1983, Kattan 1997), which is precisely why they pose

a potential threat to songbirds. We estimate that the parameter that quantifies this potential cowbird population growth, χ , is about 3, with a range from, perhaps, 2 to 4. The parameter r_C is approximately 3.0, computed as the product of: (1) the annual number of eggs laid per female cowbird (30 to > 40 ; Scott and Ankney 1983, Rothstein et al. 1986, Holford and Roby 1993); (2) the fraction of these eggs that are female (assumed 0.5; Darley 1971); (3) the fraction of host nests that fledge young (ca. 0.4; Martin 1992); and (4) survivorship of juveniles to their first spring (0.45; Darley 1971). Estimates of cowbird annual mortality range from 0.55 to 0.70 for females (Darley 1971). The parameter χ also depends on the probability a . Abandonment probabilities exhibit some variation but typically are between 0.3 and 0.5 for many extinction-prone species (Nolan 1978, Graham 1988, Pease and Grzybowski 1995; but see Zimmerman 1982, 1983; Sedgwick and Knopf 1988).

We have been unable to obtain a meaningful estimate of ϵ , $[(r_E - d_E)/(d_E - fr_E)]$. The problem is that the denominator of this ratio can be very

near 0, and, when it is, ϵ is very large. Thus, ϵ is extremely sensitive to the difference between d_E and fr_E . In addition to this structural sensitivity of ϵ to its component parameters, in estimating ϵ , one must also contend with sampling uncertainty and with problems that arise because, in an actual empirical situation, different extinction-prone hosts have different values of ϵ .

That said, we can provide rough estimates of the various parameters composing ϵ . Annual adult passerine mortality rates (d_E) have been estimated in the range 0.35 to 0.70 (Farner 1955, Ricklefs 1973, Payne 1989; but see Roberts 1971). One can estimate r_E using the formula:

$$r_E = S_F (0.5)d_j \quad (2)$$

where S_F is seasonal fecundity (=seasonal reproductive success), 0.5 is the fraction of a brood that is female, and d_j is survival of juveniles from fledging until the following spring. The maximum seasonal fecundity (female offspring per year in the absence of cowbirds) for passerines is roughly 2.0 to 4.2 young/female (Nolan 1978, Holmes et al. 1992, Grzybowski 1995, Woodworth 1997) and obviously is dependent on a number of factors. Estimates of juvenile survivorship are 0.5 (Greenberg 1980) to 0.7 of adult survivorship (Nolan 1978, Grzybowski unpubl. data). The fraction of the host brood fledged when a nest is parasitized, f , can be zero (Grzybowski 1995), although 0.3 to 0.6 is more typical (Nolan 1978, Smith 1981).

DISCUSSION

In this century, Brown-headed Cowbirds have expanded their range in California (Rothstein 1994) and in parts of the mountain West (Rothstein et al. 1980, Hanka 1985) and across the southeastern United States (Sauer et al. 1996). The Shiny Cowbird has extended its range and numbers through the Caribbean (Cruz et al. 1985) and is currently progressing through the Florida peninsula (Grzybowski and Fazio 1991, Post et al. 1993). The Bronzed Cowbird is expanding its range in Texas (Sauer et al. 1996). The historical growth in cowbird numbers may have come from increased winter food supply (Meanley 1975, Brittingham and Temple 1983, Robinson et al. 1993) or increases in suitable foraging habitat during the summer

resulting from the widespread clearing of forests and the introduction of domestic livestock (Mayfield 1965).

Recent analyses of Breeding Bird Survey (BBS) data indicate that Brown-headed Cowbirds may be declining in some areas, particularly in the northeastern United States where reforestation may be an important factor (Robbins et al. 1986, Robinson et al. 1993, Sauer et al. 1996). However, these analyses also suggest that cowbirds are still abundant in the Great Plains and the Midwest, and are increasing in portions of the western, midwestern, and southeastern United States (Sauer et al. 1996).

Although cowbirds are host generalists, studies on how they affect entire communities of hosts have been limited to listing the proportions of nests parasitized for a collection of species at one site or in a broader geographic area (e.g. Wiley 1985, 1988; Post et al. 1990). Our model structures the components of cowbird and host communities by explicitly recognizing three different classes of hosts differing in their behavioral (ejector vs. both types of acceptors) and population-dynamics (extinction prone vs. insensitive acceptor and ejector) responses to brood parasitism.

Cowbird/host abundance.—As shown in Table 3, the abundance of cowbirds typically is 2 to 9% of the abundance of their hosts. If a female cowbird lays 30 or more eggs in a season, and if a single host individual typically makes two to four nesting attempts per year, then one female cowbird potentially can influence 10 or more host females. As cowbird density approaches 10% of host density, few host females will go unparasitized. Although these data may contain sampling biases, they still approximate ratios that indicate a clear opportunity for cowbirds to determine aspects of host community structure.

Cowbird/host community dynamics.—Our model predicts outcomes of dynamic cowbird-host interactions. Cowbirds might cause a decline or change in relative abundance in some hosts but not in others (i.e. insensitive species); these conditions, in turn, could regulate increases or decreases in cowbird abundance. The potential for cowbird-host dynamics to be coupled in these ways is most easily seen in the context of a mathematical model like that presented here.

These potential dynamics have not been previously appreciated. For example, analyses of

BBS data at regional or local scales (Robbins et al. 1986, Sauer and Droege 1992, Brawn and Robinson 1996) have searched for patterns under simplified assumptions (i.e. if cowbirds increase then hosts should decrease). Our model presents potentially more complex and dynamic interactions that may progress differently in different continental regions. Some systems may be at early stages and come into equilibrium while being observed (Sauer et al 1996), whereas other long-standing systems may approach or already be in equilibrium (Robinson 1992).

Villard and Mauer (1996) portray a mosaic of spatial differences and temporal changes for indices derived from BBS data. This suggests, as does our analysis, a need for collection and analysis of more locally detailed data bases to assess cowbird/host community interactions.

Will extinction-prone species persist?—It appears that empirically, $\chi \gg R/(I + K)$, implying that the parameter regime where extinction-prone hosts are present and cowbirds are absent will not occur in nature. Cowbirds may, however, have habitat restrictions not encompassed by our model, and these considerations, rather than population-dynamics considerations, may exclude cowbirds from certain avian communities (e.g. large tracts of forest or grassland). Nonetheless, in more heterogeneous landscape systems, we expect that both of the other two regimes will occur in nature (extinction-prone hosts and cowbirds both present; and extinction-prone hosts absent and cowbirds present).

Sensitivity analyses.—Sensitivity analyses can be used to assess how various features of natural communities omitted from equations (1a) and (1b) might alter conclusions summarized in Table 2. Some model assumptions can be relaxed fully. For example, the model assumes that cowbird eggs are distributed among nests in proportion to their relative abundances. However, cowbirds may distribute their eggs less randomly, as with one ejector studied by Sealy and Bazin (1995). This type of circumstance can be accommodated by letting b_R and b_I quantify the extent to which cowbirds bias their egg placement and avoid (or choose) nests of ejectors and insensitive acceptors, respectively, relative to extinction-prone nests. For example, if $b_R = 0.5$, then any given ejector nest is only half as likely to be parasitized by any giv-

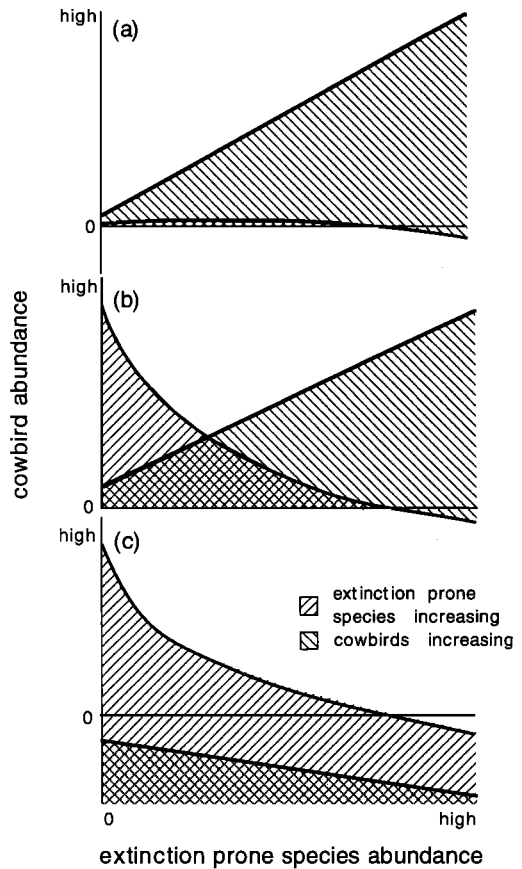


FIG. 1. Isocline analysis of the cowbird/host community differential equations under (A) parameter regime I, (B) II, and (C) III (see Table 2 and text). The cowbird isocline separates the phase plane into a region where cowbirds decrease versus a region where they increase. The extinction-prone isocline is defined similarly.

en cowbird than is an extinction-prone nest. With $R \rightarrow b_R R$ and $I \rightarrow b_I I$, the inequalities in Table 2 still hold.

Other assumptions cannot be treated so easily. However, using a graphical sensitivity analysis, the global behavior of our two-dimensional population-dynamics model can be inferred from knowledge of: (1) which isocline intersects the ordinate in Figure 1 at the largest value; (2) which isocline intercepts the abscissa in Figure 1 at the largest value (and whether the cowbird isocline intersects it at all); and (3) the assumption that the cowbird and extinction-prone isoclines intersect at most once (see May 1975). Figure 1B shows that, under parameter

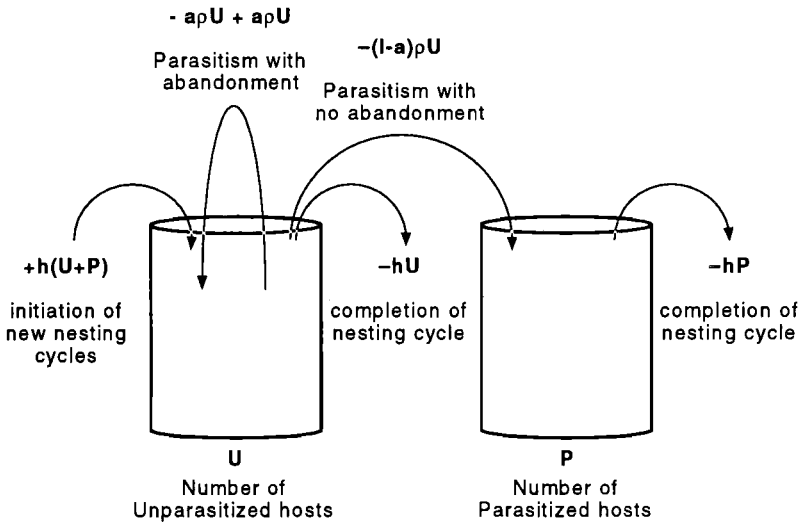


FIG. 2. Bucket diagram modeling reproduction of female passerine hosts unparasitized and parasitized by cowbirds.

regime II, there is a feasible equilibrium with both species present and abundances bounded. Under Regimes I and III, cowbirds alone or extinction-prone hosts alone will be present, respectively, in the absence of such a joint equilibrium (Figs. 1A and 1C). One can modify the isoclines shown in Figure 1 (and the underlying differential equations) in diverse ways without affecting the qualitative conclusion that there are three dynamic regimes. Although such modifications may influence the inequalities we have derived to delineate these regimes (Table 2), depending on the deviations postulated, the sensitivity analysis suggests that our conclusions are robust to any modification of the model that leaves the qualitative shape positions of the isoclines in Figure 1 unchanged.

Research needs.—Empirical assessment of the model is currently constrained by imperfect knowledge of fundamental population parameters and of how hosts should be classified. Focus on and use of imperfect indices and surrogates of host seasonal fecundity, adult and juvenile survivorship, and population size (e.g. Robbins et al. 1986, Martin 1992, Brawn and Robinson 1996) make it difficult to assess models such as ours that rely on more direct estimates of these parameters. We have incomplete knowledge of abandonment probabilities of hosts (Grzybowski and Pease 1999) and of abandonment mechanisms (Rothstein 1990).

Moreover, our knowledge of parasitism levels for ejectors is still anecdotal (Neudorf and Sealy 1992), and we know little of how cowbirds interfere with each other. Yet, our model indicates these factors are critical to understanding the community consequences of brood parasitism.

Our model suggests management options that might moderate one or more of the main parameter combinations. The ratio of ejectors to insensitive hosts (R/I) might be empirically manipulated to enhance numbers of ejectors or control insensitive acceptors, thereby bringing cowbirds and extinction-prone species closer to coexistence (i.e. no host extinctions). Habitat enhancements favoring ejector species (e.g. mimids in brushy habitats) and/or juxtaposing brushy habitats next to habitats without ejectors may provide buffers for extinction-prone species in some settings. Potentially, such manipulations, even at a small scale, could test the model while simultaneously providing effective cowbird management. Manipulations of d_c or ϵ might also be considered.

Our model focuses directly on cowbird-host interactions and omits a number of complicating factors present in actual communities. Moreover, even if these factors had not been omitted from the model, it is still difficult to obtain good, unbiased estimates of many model parameters. As such, we advocate using the model to help structure thinking on cowbird/

host community population dynamics, and for explicating qualitative features of this interaction.

ACKNOWLEDGMENTS

This research was partially supported by the National Fish and Wildlife Foundation, Texas Nature Conservancy, and a Reeder Fellowship from the University of Texas (the latter awarded to CMP). Peter Stangel, David Braun, and Jim Fries were instrumental in arranging this support. Kathy Martin, Spencer Sealy, James N. M. Smith, and an anonymous reviewer provided many useful comments for improving the manuscript. Linden Higgins assisted in figure preparation.

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Associate Editor: K. Martin

APPENDIX 1. Derivation of the cowbird/host community differential equations (1a) and (1b).

We start with an underlying mathematical model of songbird and cowbird reproduction specifying how these groups influence one another's reproductive success. We then combine fecundity expressions derived from these underlying equations with assumptions about cowbird and songbird mortality, and thereby develop the two coupled ordinary differential equations governing abundance of cowbirds and extinction-prone hosts. This derivation allows us to summarize critical assumptions implicit in our governing equations and provides a starting point from which these equations could be generalized in the future.

The model envisions placing all unparasitized host females, $U(t)$, in one "bucket," and all parasitized females, $P(t)$, in another bucket (Fig. 2). Let ρ be the per-host parasitism rate per day; i.e. the rate at which unparasitized host females first become parasitized. A fraction a of parasitized nests is abandoned immediately. We assume that breeding fe-

males (both parasitized and unparasitized) complete the nesting cycle at rate $h \cdot \text{day}^{-1}$.

Each term in equation (3a) quantifies one way in which breeding females move out of (negative terms) or into (positive terms) the bucket of unparasitized females. Specifically, various terms account for females that abandon their nests immediately after they are parasitized, $-a\rho U$; females with unparasitized nests that are parasitized and not abandoned, $-(1-a)\rho U$; unparasitized females completing their nesting cycle, $-hU$; reneesting females that abandoned their nests immediately after being parasitized, $+a\rho U$; and females that reinitiate the nesting cycle after successfully fledging young, $+h(U+P)$. Because the model assumes that females that abandon parasitized nests immediately reneest, the $-a\rho U$ and $+a\rho U$ terms cancel out. Similarly, equation (3b) accounts for females of parasitized nests previously unparasitized, $(1-a)\rho U$; and for parasitized females that complete the breeding cycle, $-hP$:

$$\frac{dU}{dt} = -a\rho U - (1-a)\rho U - hU + a\rho U + h(U+P) \tag{3a}$$

$$\frac{dP}{dt} = (1-a)\rho U - hP. \tag{3b}$$

We implicitly assume that all unparasitized females, regardless of the number of days since they initiated the nesting cycle, are parasitized at the same rate (a simplifying assumption; see Pease and Grzybowski [1995] for a more complicated example). Similarly, the model assumes that all host females complete the nesting cycle and fledge their broods at the same rate independent of the length of time since they initiated the nesting cycle. Thus, the time each female spends completing one nesting cycle (in the absence of parasitism) is distributed exponentially as $\exp(-ht)$; $1/h$ is the mean number of days it takes a female to complete a nesting cycle. In addition, brood parasitism causes host reproduction to decrease because parasitized hosts fledge reduced numbers of host young, and because of the loss of breeding-season days that parasitism causes (Grzybowski and Pease 1999). The present model accounts only for the first of these.

Equations (3a) and (3b) are linear, with eigenvalues of 0 and $-(h+\rho)$. The eigenvector associated with the first of these is $[h, (1-a)\rho]$, implying that after initial dynamics have faded, a fraction $h/[h+(1-a)\rho]$ of all the breeding females will be unparasitized, with the remainder parasitized. We let A be the mean number of cowbirds produced from each parasitized successful nest (i.e. one that fledges at least one offspring, be it host or parasite), and B and fB be the mean number of host offspring fledged from each unparasitized and para-

sitized successful nest, respectively. Then, the rate of production of host fledglings from parasitized nests equals the total number of hosts times the fraction of hosts parasitized times the per-capita rate at which parasitized hosts fledge young, times brood size, or:

$$= (U+P) \frac{(1-a)\rho}{h+(1-a)\rho} h(fB). \tag{4}$$

Analogous but slightly modified equations describe production of cowbird young and of host young by unparasitized females. Moreover, provided we set $f=1$, analogs of equation (4) are valid for insensitive hosts. Depending on the type of host, $E=U+P$, or $I=U+P$. Accounting for host offspring produced both by unparasitized and parasitized females, and recalling that the total birth rate is the per-capita rate multiplied by the population size, then:

extinction-prone total birth rate

$$= E \frac{h}{h+(1-a)\rho} hB + E \frac{(1-a)\rho}{h+(1-a)\rho} hfB \tag{5a}$$

cowbird total birth rate

$$= E \frac{(1-a)\rho}{h+(1-a)\rho} hA + I \frac{(1-a)\rho}{h+(1-a)\rho} hA. \tag{5b}$$

The population growth rate is the birth rate minus the death rate. Assuming that mortality is constant and density independent, and simplifying equations (5a) and (5b) produces:

$$\frac{dE}{dt} = hB \frac{h+f\rho(1-a)}{h+\rho(1-a)} E - d_E E \tag{6a}$$

$$\frac{dC}{dt} = hA \frac{(E+I)\rho(1-a)}{h+\rho(1-a)} - d_C C. \tag{6b}$$

To understand how abundances of the three host classes determine cowbird abundance, and how cowbirds determine extinction-prone abundance, our equations need to incorporate the idea that, with more hosts per cowbird, each host nest receives fewer cowbird eggs. We assume that cowbird eggs are divided between all classes of hosts in proportion to their relative abundance such that $\rho = \gamma C / (I+R+E)$, where γ is the rate at which a single cowbird produces eggs. We define $m = \gamma/h$, $r_C = \gamma A$, and $r_E = hB$, and substitute in equations (6a) and (6b).

To account for density-dependent processes that increase the extinction-prone per-capita death rate and decrease its per-capita birth rate, we add the term $-(r_E - d_E)E^2/K$ to the right side of equation (6a). With this modification, the extinction-prone species equilibrate at carrying capacity K when cowbirds are absent.

APPENDIX 2. Analysis of equations (1a) and (1b). See Table 1 for definitions of χ and ϵ .

Equations (1a) and (1b) have four equilibrium points: I, $\hat{E} = 0$, $\hat{C} = 0$; II, $\hat{E} = K$, $\hat{C} = 0$; III, $\hat{E} = 0$, $\hat{C} = (\chi I - R)/(m(1 - a))$; and IV, $\hat{E} > 0$, $\hat{C} > 0$. More specifically, $\hat{C} = (\chi I + \chi \hat{E} - R)/(m(1 - a))$ and \hat{E} satisfies $\epsilon(1 + \chi)\hat{E}^2 + \hat{E}(\epsilon I + \epsilon \chi I + \chi K - \epsilon K) + K(\chi I - \epsilon I - \epsilon R - R) = 0$.

Only equilibria that are feasible and locally stable will be seen in nature. Equilibrium I is always feasible but also is always locally unstable. Equilibrium II is always feasible. It is locally stable when $\chi < R/(I + K)$. Equilibrium III is feasible for $\chi I - R > 0$. It is locally stable for $\chi > \epsilon(1 + R/I) + R/I$. Equilibrium IV is feasible whenever $\chi > R/(I + K)$ and $\epsilon(I + R) > \chi I - R$. The first of these two inequalities ensures that $\hat{C} > 0$. The second ensures that $\hat{E} > 0$. When the second inequality is reversed, $\chi > \epsilon$; all terms of the quadratic equation that \hat{E} satisfies are positive. By the Routh-Hurwitz criterion, all of its roots have negative real parts (Chen 1970: 322-328), and the equilibrium is not feasible. Conversely, when the second inequality holds, the quadratic equation has exactly one sign change. By the Routh-Hurwitz criterion, there is one root with a negative real part

and one with a positive real part; the equilibrium is thus feasible.

By combining these feasibility and local stability analyses with the graphical phase-plane analysis showing global equilibrium stability, we find three qualitatively distinct parameter regimes (Table 2). Regime I occurs when $\chi > \epsilon(1 + R/I) + R/I$. Figure 1A shows that when this inequality holds, Equilibrium III is locally and also globally stable. Regime III occurs when $\chi < R/(I + K)$. In this case, Figure 1C shows that Equilibrium II is both locally and globally stable. Regime II occurs when $R/(I + K) < \chi < \epsilon(1 + R/I) + R/I$. Under this inequality, Equilibrium IV is always feasible, and Equilibria II and III are always unstable (Fig. 1B). However, Equilibrium IV is not always locally stable under Regime II. To further understand when Equilibrium IV is feasible but locally unstable, note that the equations do not permit the abundances of cowbirds and extinction-prone hosts to increase in size forever. When E and C are sufficiently large, dE/dt and dC/dt are both negative, strongly suggesting a stable limit cycle. Because the governing equations do not satisfy Kolmogorov's theorem (May 1972), we used computer simulations to verify the presence of a stable limit cycle when Equilibrium IV is feasible and locally unstable. In summary, Regime II implies simultaneous persistence of cowbirds and their extinction-prone hosts either in a stable equilibrium or a stable limit cycle.