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WHAT DO DEMOGRAPHIC SENSITIVITY ANALYSES TELL US ABOUT CONTROLLING BROWN-HEADED COWBIRDS?

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Abstract. While Brown-headed Cowbird (*Molothrus ater*) control efforts are fairly common, the effects of control programs on cowbird populations are unknown. We apply analytical-based and simulation-based demographic sensitivity analysis to the problem of cowbird management. Collectively, the analyses indicate that natural variation of egg survival likely determines population growth when mean values of egg survival are low (yet plausible) or when high variation exists around mean rates. When the natural range of egg survival does not encompass low rates, yearling survival increases in importance. Due to uncertainty in vital rates, it is currently impossible to ascertain the true sensitivity of these two vital rates. Management actions that decrease only adult survival on breeding ranges are not expected to regulate population growth. In contrast, trapping on wintering ranges is expected to be more effective as this technique reduces both adult and yearling survival. However, the impacts of winter trapping may be swamped by high egg survival. When this analysis is combined with life history and logistical realities, we believe that widespread trapping efforts will be largely ineffectual for controlling cowbird populations on either breeding or wintering ranges. We suggest that cowbird vital rates be specifically examined with respect to host communities, vegetation type, and land use in order to rank management priorities.

Key Words: Brown-headed Cowbird, cowbird management, demographic analysis, *Molothrus ater*, population control, sensitivity analysis.

Land managers have long realized that Brown-headed Cowbirds (*Molothrus ater*) may decrease nesting success of passerine hosts (e.g., Hofslund 1957, McGeen 1972, Mayfield 1977, Elliott 1978, Brittingham and Temple 1983, Weatherhead 1989). Due to the negative effect cowbirds have on some host species, land managers have attempted to control cowbird populations since the early 1970s. For example, control programs in Michigan typically remove 3,000 or more female cowbirds and cowbird eggs yearly (Kelly and DeCapita 1982; M. DeCapita, pers. comm.) and trapping efforts on the Ft. Hood military reservation in Texas remove upwards of 3,000 to 5,000 female cowbirds per year (J. D. Cornelius, pers. comm.). These control programs usually target cowbirds to protect federally listed endangered species and commonly involve the removal of adults from feeding areas (Rothstein et al. 1987), the removal of adults and yearlings from communal wintering areas (J. D. Cornelius, pers. comm.), and to a much lesser extent, the removal of eggs from host nests. While cowbird control efforts are fairly common and such efforts are capable of decreasing parasitism rates, the effect of such efforts on cowbird population growth remains unknown.

Better knowledge of cowbird population dynamics is necessary to assess the efficacy of current management strategies and to aid the design of more efficient management strategies. Here we apply traditional techniques and new matrix-based techniques of sensitivity analysis to investigate how different management options may influence cowbird population dynamics. Specifically, we use sensitivity analysis to determine how we can most effectively decrease the growth rate of cowbird populations. Our objectives are three-fold: (1) to determine the relative importance of various demographic components to Brown-headed Cowbird annual population growth rates (λ); (2) to determine the robustness of model predictions when vital rate estimates vary due to measurement error and/or environmental variation; and (3) to discuss the implications of this analysis for management and research.

METHODS

We examine the sensitivity of annual population growth rate (λ) to perturbations in specific Brown-headed Cowbird vital rates with traditional analytical-based and new simulation-based techniques.

ANALYTICAL-BASED TECHNIQUES

Traditional sensitivity analysis (Caswell 1989) is an analytical technique used to evaluate expected response of population growth rates to perturbations in single vital rates (i.e., birth or death rates) one-at-a-time and by equal amounts. Sensitivity, as defined by Caswell (1989), is the absolute infinitesimal change in population growth rate given an absolute infinitesimal change in a vital rate, while all other vital rates are held constant. If *a* is a matrix of transition probabilities, v and w are the vectors of reproductive values and stable age distributions (SAD) associated with matrix *a*, respectively, and ⟨vw⟩ is the scalar product of the two vectors, the sensitivity of matrix element a_{ij} (row i, column *j*) is equal to:

$$\text{Sensitivity } (s_{ij}) \text{ of } a_{ij} = \left(\frac{v_i w_j}{\langle vw \rangle}\right). \quad (1)$$

Elasticities are similar, but are calculated on a proportional scale, where λ is the geometric population growth rate at SAD:

$$\text{Elasticity } (e_{ij}) \text{ of } a_{ij} = \left(\frac{v_i w_j}{\langle vw \rangle}\right)\left(\frac{a_{ij}}{\lambda}\right). \quad (2)$$

Intuitively, elasticity is the sensitivity of a_{ij} weighted by its proportional change with λ. The change in vital rates and λ is assumed to be infinitesimal and linear.

When matrix elements are composed of more than one vital rate, component sensitivities and elasticities can be calculated for each vital rate that appears in one or more matrix elements. Chain rule differentiation is required for each a_{ij} that contains a particular vital rate *x*. For *n* elements that contain vital rate *x*, the sensitivity and elasticity of *x* are:

Component sensitivity of vital rate *x*

$$= \sum^{n} [(s_{ij})(\text{product of non-}x\text{ components})] \quad (3)$$

Component elasticity of vital rate *x*

$$= (\text{Component sensitivity of vital rate } x)\left(\frac{x}{\lambda}\right). \quad (4)$$

What do analytical techniques of sensitivity analysis imply biologically? Because sensitivity and elasticity are partial derivatives, they represent the slope of the relationship between a small change in a vital rate to the corresponding change in λ. Traditionally, researchers and managers have assumed that vital rates with high sensitivities or elasticities should be the focus of management actions, as perturbation of these vital rates produce the greatest change in λ. This assumption is not always correct (Mills et al., in press).

SIMULATION-BASED TECHNIQUES

Traditional sensitivities and elasticities may mislead managers because inevitable variation imposed by nature, by management action, or by measurement error will not be infinitesimal or equal across all vital rates (Gaillard et al. 1998; Mills et al., in press). To account for vital rate variation on scales that are neither absolutely or proportionally equal across vital rates, we also use the sensitivity technique used by Wisdom and Mills (1997). Upper and lower limits of vital rates, determined from literature review, are incorporated into high and low matrices and a computer program constructs 1,000 matrices with each vital rate of each matrix randomly chosen from a distribution bounded by the high and low values. A population growth rate (λ) is then calculated for each matrix. The relative importance of a stage specific vital rate is assessed by regressing λ for each replicate against the value of that rate for all replicates to derive coefficients of determination (R^2). In terms of traditional definitions of sensitivity, R^2 for any component vital rate is analogous to the squared sensitivity weighted by the relative variance of a vital rate (H. Caswell, pers. comm.).

The regression method is appealing, because it allows variation in particular vital rates to alter according to the scale perceived to occur in the field. With the regression technique, variation in vital rates can be incorporated to represent natural amounts of variation, levels of variation imposed by management, or measurement error. Furthermore, vital rates can be selected from distributions that mimic natural distributions. For the selection of vital rates, we favored a uniform distribution over other distributions. Without knowing how likely different vital rates are, all vital rates should have equal likelihood of selection and this distribution evaluates the scenario where extreme changes in rates under management have the same likelihood as small changes from the current mean.

Because all possible λs are plotted, the regression technique also has the advantage of being able to detect non-linearities that traditional methods may not. This is similar to the covariance technique used by Brault and Caswell (1993), but is computationally and intuitively easier to manage. If non-linearities do not exist in the data, then varying vital rates on absolute and proportional scales should produce similar results as traditional sensitivities and elasticities (Mills et al., in press).

MODEL STRUCTURE AND INPUT FOR COWBIRD ANALYSIS

We use two-stage Leftkovitch matrices (see Appendix 1) to model cowbird populations. Stage specific demographic data form the matrix and the model projection interval is 1 year. Eigenanalysis of the matrix, or projection of the matrix over time, provides annual population growth rates (λ). Consequently, all techniques of sensitivity analysis assume populations are at stable age distribution (SAD). It is an all female model, a reasonable approach given the excess of adult males in natural populations (Darley

1971, Arnold 1983). Fecundities are divided in half to account for female eggs only and are multiplied by annual cohort survival to account for a post-breeding census.

We derive inputs to the matrix model, in terms of estimated stage-specific ranges of vital rates, from the literature (Table 1). The top row of the matrix (F_{11} and F_{12} ; see Appendix 1) contains reproductive information based on both survival of females to breed and number of eggs laid (fecundity). Historically, cowbird fecundity has been difficult to determine and estimates of the number of eggs laid per female varied widely. Much of this variation is removed when daily laying rates are considered. When multiplied by the length of the breeding season, daily laying rates are likely to be the most accurate estimator of annual female fecundity (Rothstein et al. 1986b). Consequently, we only consider daily laying rates and, to avoid non-constant laying rates over the breeding season, assume a 40-d breeding period within which laying rates are constant (Table 1). To determine the possible importance of low fecundity, we include Holford and Roby's (1993) fecundity estimates for calcium deprived individuals in captivity. From these data we estimate the suppressed daily egg laying rate to be approximately 0.37. While this figure is significantly lower than the lowest estimate of daily egg laying rate measured under natural conditions (0.51 eggs per day), inclusion in the model illustrates the consequences of extremely low fecundity on λ. Finally, we assume adults and yearlings have the same maximum and minimum daily laying rates. Although Jackson and Roby (1992) indicate that yearlings have lower fecundity than adults, the lowest measured daily laying rate for yearlings is greater than the rate for calcium deprived individuals. This implies that the lower daily laying rate used in the model (that for calcium deprived individuals) represents a worst case scenario for both adults and yearlings.

Matrix element G_{21} (Appendix 1) is the mean survival from stage 1 to stage 2, and represents a composite of egg, nestling, and yearling survival. Egg survival is defined as the probability that an egg survives to hatch. This life stage is assumed to be 15 d. While the average incubation period is approximately 10–13 d (Briskie and Sealy 1990), these estimates do not include time before incubation is initiated. In other words, because eggs are likely to remain within the nest some number of days before incubation is initiated (see Nice 1954), a 15 d pre-hatching period is realistic. Nestling survival is defined as the probability that a nestling survives to fledge, given that it hatched. This period is assumed to be 10 d (Norris 1947, Hann 1937). Yearling sur-

TABLE 1. VITAL RATES FOR THE COWBIRD TRANSITION MATRIX (SEE APPENDIX 1)

Vital rate	Average (N)	High	Low	Citations
Adult Fecundity[a]	0.69 (4)	0.8	0.51 (lab) 0.37 (calcium limited)	Scott and Ankney 1979 (California), 1980 (Ontario); Rothstein et al. 1986 (California); Holford and Roby 1993 (captive population)
Yearling Fecundity[a]	0.56 (1)	N/A	N/A	Jackson and Roby 1992
Egg survival	0.38 (pooled across 9 studies; N = 1346 eggs)	0.68 (single species study)	0.08 (host community study)	Hann 1937, Norris 1947, Berger 1951, Hofslund 1957, McGeen 1972, Elliot 1978, Weatherhead 1989, Marvil and Cruz 1989, Smith and Arcese 1994
Nestling survival	0.64 (pooled across 6 studies; N = 224 nestlings)	0.76	0.46	Hann 1937, Norris 1947, Berger 1951, Hofslund 1957, Marvel and Cruz 1989, Weatherhead 1989
Yearling survival	0.24	0.32	0.15	Dhondt 1979 for Great Tits, Woodward and Woodward 1979
Adult survival[b]	0.47 (4)	0.63	0.31	Darley 1971, Fankhauser 1971, Arnold 1983 (provides 2 estimates)

[a] Daily laying rate; we assume this constant over a 40 day laying interval (see Appendix 1).
[b] Female only rate.

vival is defined as the probability that a juvenile survives to breed, given that it fledges. This period is assumed to be the remaining 340 d of a cowbird's first year. Estimating yearling survival rates are problematic, because only one study (Woodward and Woodward 1979) quantified cowbird fledgling survival rates (only until independence at approximately 30 d). For an upper bound, we assume yearlings attain adult survival rates immediately after independence and we combine the Woodward and Woodward (1979) yearling rate for the first month after fledging (0.48) with the highest estimate of adult survival for the remaining 310 d before breeding. This yields an upper bound for yearling survival of 0.32. The lower bound for yearling survival (0.15) is assumed equal to known lower bounds for Great Tits (*Parus major*) (Dhondt 1979). While using data from other species is not ideal, Great Tits are one of the only passerine species with known yearling survival rates, thereby providing insight into a lower bound of cowbird survival.

Matrix element P_{22} is the mean survival to remain within stage 2. This is simply an adult female survival rate between annual birth events, and is estimated via return rates or recoveries (Table 1).

RESULTS

If variation is artificially constrained to be small and equal around all vital rates, we would expect the simulation-based technique to rank the importance of all vital rates similarly to the traditional analytical-based sensitivity analysis (L. S. Mills et al., unpubl. data). Although traditional sensitivities and R^2 sensitivities are not directly comparable, because they are different statistics, we do in fact find that with small and equal absolute change of ±0.10 for each rate, the rankings of vital rate effects on λ are identical for both approaches (Fig. 1a). Likewise, incorporating proportional changes in the regression technique (±10 %) produces similar rankings as traditional elasticities (Fig. 1b). The small deviations between the sensitivities or elasticities and the simulation-based measure are likely due to the effect of non-linearities on sensitivities or elasticities (Mills et al., in press). The vital rates with the highest sensitivities on an absolute scale of variation are yearling survival and nestling survival. The vital rates with the highest sensitivities on a proportional scale are egg, nestling, and yearling survival.

Of course, neither of these vital rate ranges, determined by fixed and equal absolute or proportional change, are likely biologically realistic. Therefore, we used the regression technique to determine R^2 sensitivities for the entire range of cowbird variation, letting different rates vary by different amounts according to the upper and lower bounds presented in Table 1; we refer to this as the empirical range of variation (Figs. 2 and 3). Egg survival alone appears to account for over 60% of the variation in population growth rates. The vital rate accounting for the next largest amount of variation in λ is yearling survival ($R^2 = 0.14$).

While the regression technique is likely to be more realistic than traditional methods because it selects vital rates from biologically realistic upper and lower bounds, it is possible that vital rate ranges that are too large or too small may artificially increase or decrease the R^2 value of a vital rate (Wisdom and Mills 1997). Unfortunately, the sparse data available for most species makes determination of vital rate ranges difficult. This is especially true for threatened or endangered species that we model the most, but is also true for common species such as cowbirds. A critical question is thus: what are the consequences of under- or over-estimating our range of variation in demographic parameters? If altering the range of an uncertain vital rate has little effect upon R^2, then accurate range estimation is unimportant. However, if R^2 is sensitive to small changes in the range of vital rates, then correct range estimation is critical. To assess this with our data, we altered the range of each vital rate one-at-a-time while holding the other vital rates at the empirical range width (Table 1). Vital rate ranges were decreased by 25 and 50% and increased by 25% (50% increases were not possible because some survival rates would exceed 1).

Generally, we find that increasing or decreasing range widths results in a monotonic increase or decrease in R^2 values (Fig. 4), as expected from the fact that R^2 for any component vital rate is weighted by the variance in that rate. Although in this case we do find the statistically expected change in absolute R^2 values with changes in vital rate ranges, the biologically important result is that the relative rankings do not change for the vital rates that account for most of the variation in λ.

Because egg survival was identified as the vital rate most affecting population growth when vital rates vary between empirically determined bounds, and because decreasing the range of egg survival can decrease the R^2 value of egg survival, it is relevant to ask how much of a decrease in the range of egg survival is necessary before another rate replaces egg survival as the rate most affecting λ. In the most extreme case of a 50% decline in range width, we find that most of the change in R^2 (40%) was partitioned as increased R^2 for yearling survival and that the

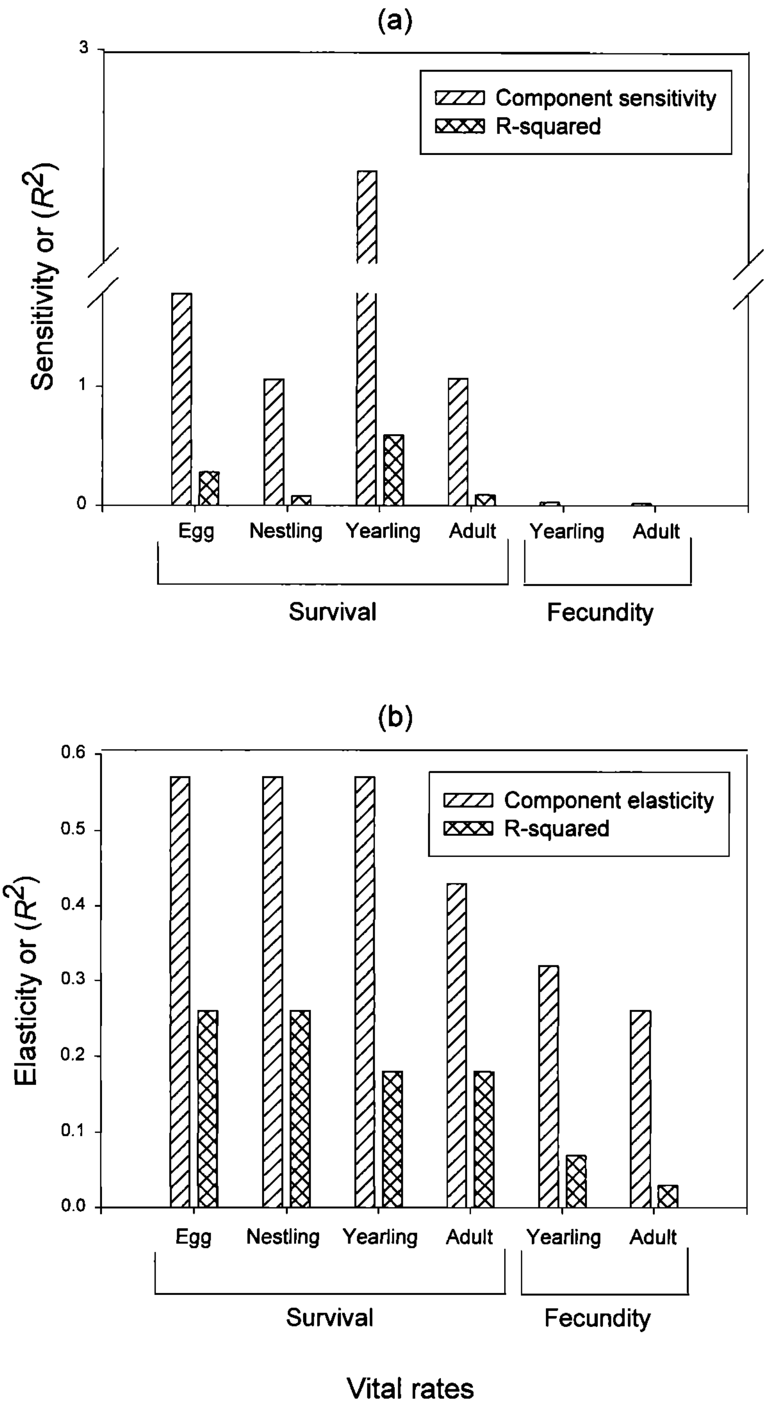

FIGURE 1. Comparison of component sensitivities and R^2 values for Brown-headed Cowbird vital rates with (a) range standardized on an absolute scale (plus or minus 0.10) and (b) range standardized on a proportional scale (plus or minus 10%). Only rankings are directly comparable between component sensitivities and R^2 values.

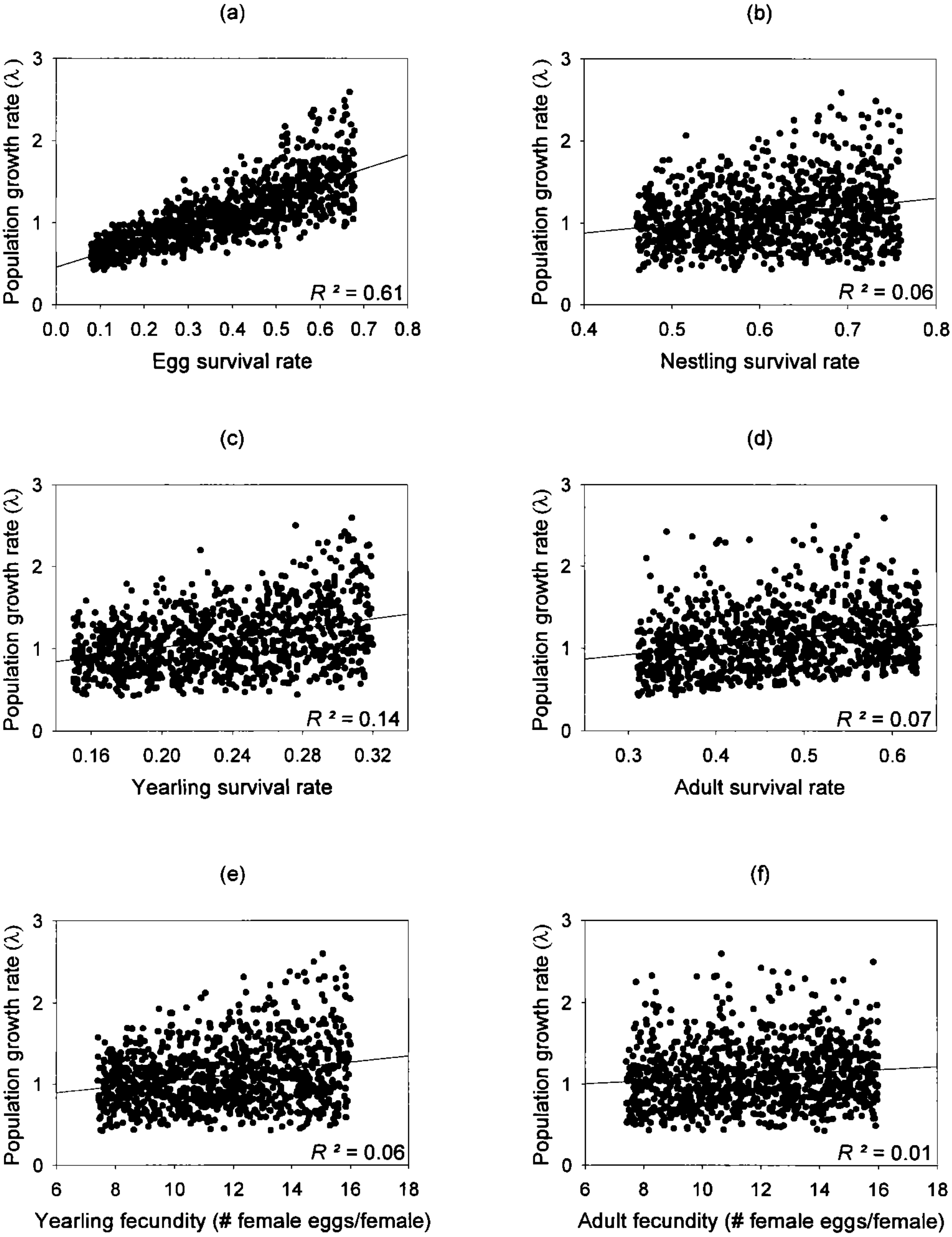

FIGURE 2. Amount of variation in Brown-headed Cowbird population growth rate (R^2) as accounted for by (a) egg survival rate, (b) nestling survival rate, (c) yearling survival rate, (d) adult survival rate, (e) yearling fecundity rate, and (f) adult fecundity rate in 1000 matrices with randomly selected vital rates. Coefficient of determination (R^2) and linear regression line presented.

total R^2 for yearling survival approached that of egg survival (compare Fig. 5 to Fig. 3).

In addition to range width, mean vital rates must also play a role in determining the effect of a change in any rate on λ. The variance around the regression line for egg survival is non-constant (Fig. 2a), indicating that R^2 values will change as the mean values of vital rates change. To investigate this further, we determined how sensitivities were affected by alter-

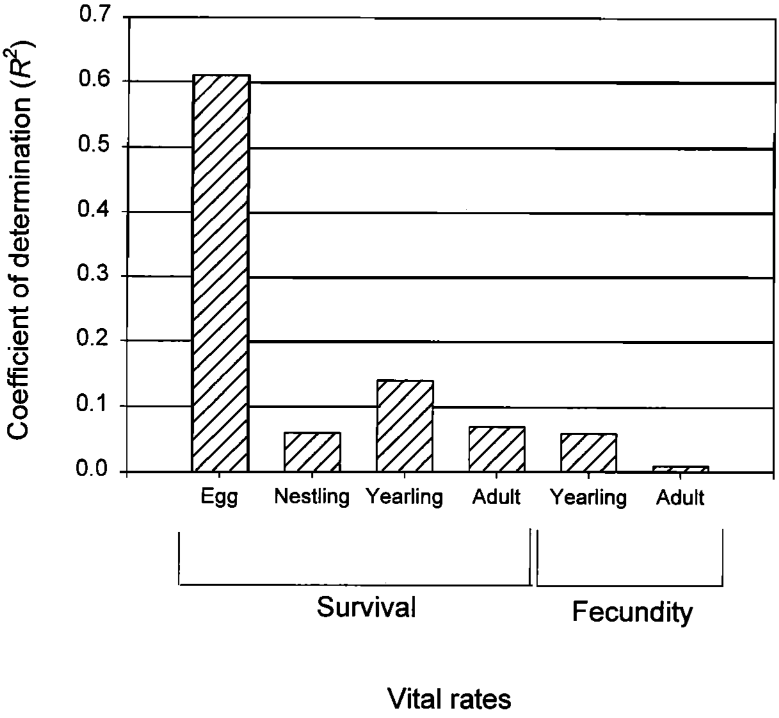

FIGURE 3. Sensitivities of Brown-headed Cowbird vital rates as indexed by the coefficient of determination (R^2) in 1000 matrices with randomly selected vital rates regressed against corresponding population growth rates.

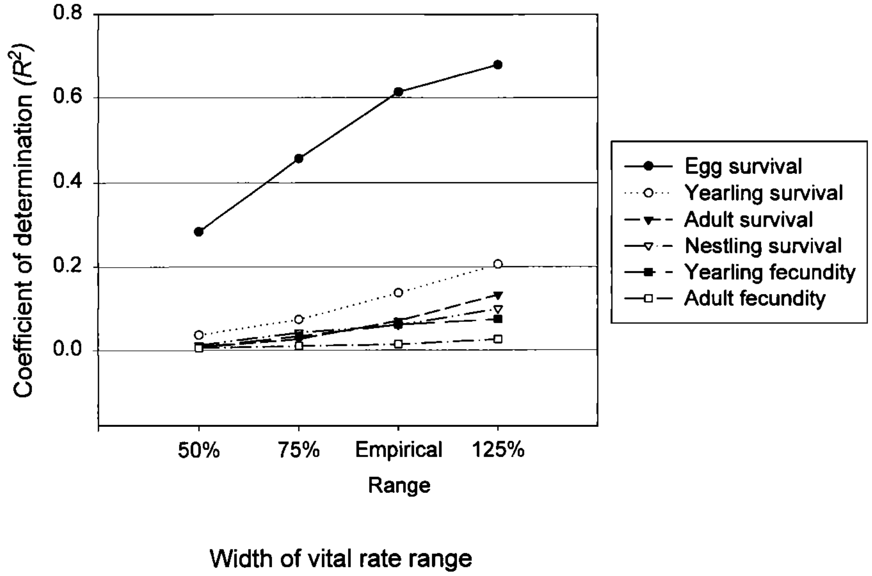

FIGURE 4. Changes in R^2 for Brown-headed Cowbird life stages when vital rate ranges are altered. Each point equals R^2 for a vital rate range which is 50%, 75%, 100%, or 125% of the original empirical range, while all other vital rate ranges are held at the empirical range.

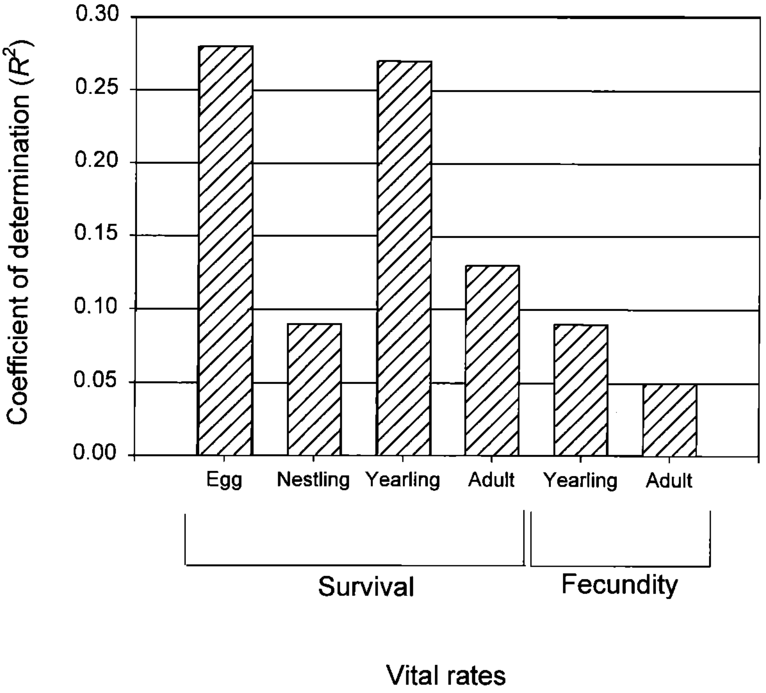

FIGURE 5. Sensitivities of Brown-headed Cowbird vital rates as indexed by the coefficient of determination (R^2) in 1000 matrices with randomly selected vital rates regressed against corresponding population growth rates when the range of egg survival is 50% of the empirical range. Compare to Fig. 3.

ing the mean egg survival rate, while holding the range of variation constant. To keep the total range of variation within the biologically plausible range of variation, we again restricted the range of egg survival (50% of the empirical range), and then increased and decreased the mean vital rate by 25%. We find that even with a small range of egg survival, if the mean egg survival rate is low, then the egg stage has the highest R^2 (Fig. 6a). Alternatively, if the mean egg survival rate is high, yearling survival has the highest R^2 (Fig. 6b).

DISCUSSION

HOW VITAL RATES AFFECT POPULATION GROWTH

The egg survival stage is likely to be the vital rate that most affects population growth rate whenever the range of variation in egg survival is high or in situations where the mean egg survival rate is low. The only studies that examine cowbird egg survival across the entire community of hosts within an area yield mean rates of 0.08 (Elliot 1978) and 0.43 (Norris 1947), indicating that the sensitivities in any of our simulations are plausible. Unfortunately, we do not know how often low rates of egg survival occur and, more importantly, how much egg survival varies within and between sites over time. In situations with high mean egg survival rates and low levels of variation around those mean rates, the yearling stage may play the biggest role in impacting λ.

An obvious question is: with what degree of certainty have we estimated our vital rate ranges? This question is most critical with regard to egg survival. Range estimation for egg survival is problematic, because most studies observe only one host. Furthermore, cowbird researchers tend to study highly parasitized hosts, hosts that accept cowbird eggs and are parasitized enough to be analyzed statistically. Unfortunately, cowbirds do not exclusively parasitize one species, but typically parasitize a number of hosts within the breeding area. Host communities likely yield rates of egg survival that differ from the rates observed in any single species. Furthermore, egg survival rates are sure to be systematically overestimated, because egg ejections or eggs laid in inactive nests are unlikely to be detected. The extent of this bias is unknown and likely dependent upon the host community and vegetation type. While many host species are known ejec-

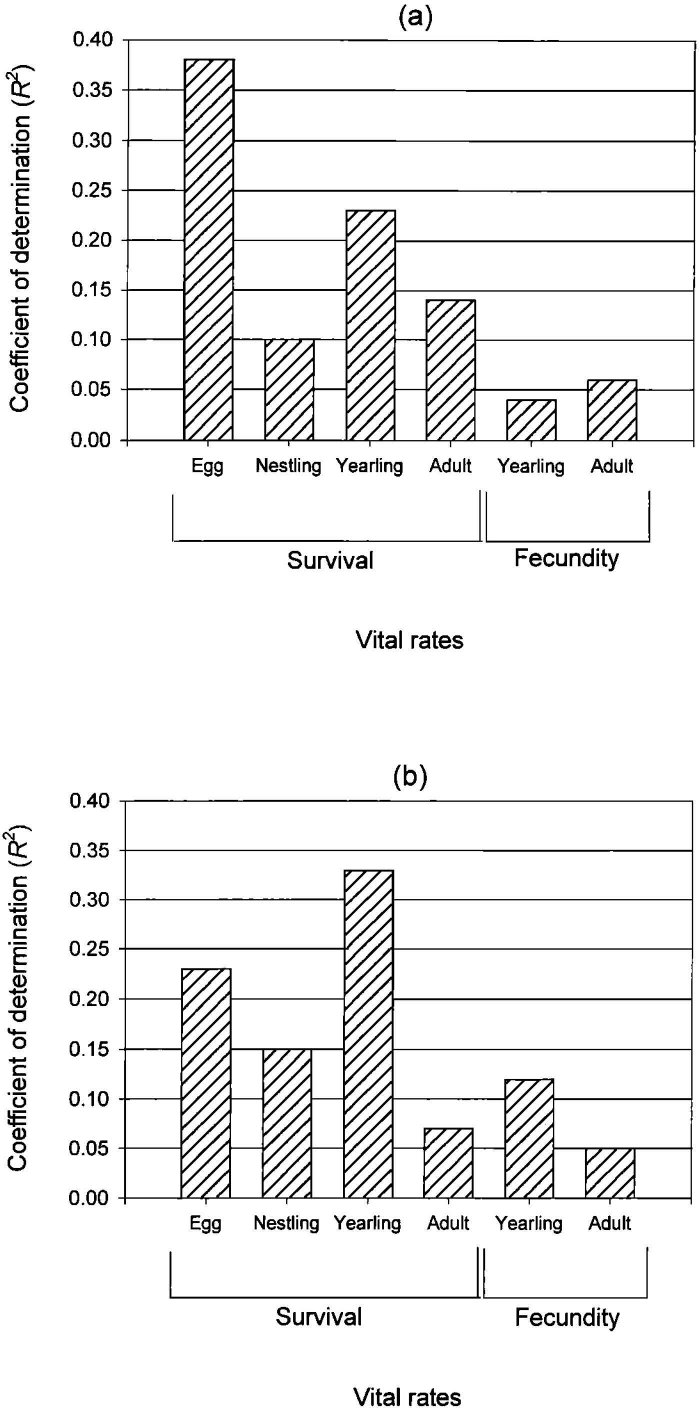

FIGURE 6. R^2 for Brown-headed Cowbird vital rates when the range of egg survival is 50% of the empirical range and the mean rate is (a) decreased 25% from the empirical mean (new mean = 0.29) and (b) increased 25% from the empirical mean (new mean = 0.48). All other vital rates have the empirical means and ranges.

tors, very little is know about how often these species are parasitized as eggs may be almost immediately ejected (Rothstein 1975b, Friedman et al. 1977). Although not well quantified, the rate at which cowbirds lay eggs in abandoned nests appears to highly variable. Berger (1951) reported a rate of 1.35% for Song Sparrows (*Melospiza melodia*) and Freeman et al. (1990) reported a rate of 21.5% for Red-winged Blackbirds (*Agelaius phoeniceus*). The high rates of inappropriate egg laying noted by Freeman et al. (1990) appear to be a function of not having perch sites; they hypothesized that without perches, the cowbirds were not able to assess correctly whether a nest was abandoned.

In summary, traditional analytical techniques indicate that egg, yearling, and nestling survival are the most sensitive vital rates. Regression-based techniques indicate that egg and yearling stages are the most sensitive. Regression-based techniques also indicate that the relative importance of egg versus yearling stages depends upon the range of variation and the mean rate of egg survival. Whenever egg survival rates are low or if the range of egg survival encompasses low rates then egg survival will most affect population growth. Adult survival, adult fecundity, and yearling fecundity were not important factors in any of the modeled scenarios.

LIMITATIONS OF MODELING TECHNIQUES

Although sensitivity analysis is capable of revealing non-intuitive relationships, several limitations must be kept in mind. First, neither the analytical- nor simulation-based technique accounts for density dependent relationships. While positive or negative correlations between vital rates could be included within either the analytical-based technique (van Tienderen 1995) or within the simulation-based technique (M. J. Wisdom et al., unpubl. data), these data are not available. Furthermore, density dependent correlations between vital rates may change as management perturbations are intensified and these changes may not be predictable under current conditions.

Second, and related to density dependence, the techniques do not account for compensatory effects. One possible compensatory effect is the replacement of breeding females and may occur as present non-breeding "floaters" occupy empty egg laying areas. If removed females are replaced, then adult survival is not functionally decreased as modeled and the predicted sensitivity is biased high. We predict that the sensitivity (traditional and regression-based) of adult survival is maximized when non-breeding floaters are not present. Conversely, if many floaters are present, adult removals will not be effective until the number of adult females drops below the amount necessary to parasitize all available nests. In short, if cowbirds exhibited extremely high replacement rates, then it is unlikely that trapping of adults near sensitive host species would be effective. Trapping records from the effort to protect the Kirtland's Warbler show that most female cowbirds are captured within the first few weeks of the breeding season (Kelly and DeCapita 1982), indicating that trapping efforts are capable of removing all females within a short time period and that floaters are not a concern to this analysis.

Third, neither technique accounts for spatial considerations. As modeled, Brown-headed Cowbirds are treated as one large population and we assume perturbations are population-wide. Management actions must consider the ratio of the size of the target population to the size of the total population, because managing only a subset of individuals dilutes population-wide effects. In other words, if we manage only a part of a cowbird population, we may have little effect on the population as a whole. Identifying exactly what effect any given management action will have on cowbird populations will require delineation of population boundaries and knowledge of movement rates between populations within and between breeding seasons. Trapping records from the effort to protect the Kirtland's Warbler (Kelly and DeCapita 1982) and the Black-capped Vireo (Barber and Martin 1997) show that trapping does not reduce the number of cowbirds in subsequent years; this indicates that there is either a large level of movement between populations or that the target population is much smaller than the total population. Unfortunately, there are little or no data identifying the spatial structure and dynamics of cowbird populations.

Finally, matrix-based calculations of λ also assume populations are at Stable Age Distribution (SAD). SAD is the proportion of individuals in any age or stage class over time, given a constant matrix. It is unlikely that populations in fluctuating environments exist at SAD for long periods of time. Currently, it is unknown how deviations from SAD in a fluctuating environment affect either traditional or the regression-based techniques.

IMPLICATIONS FOR COWBIRD MANAGEMENT

Although egg survival is likely the vital rate which most affects population growth rate in many situations, it is nearly impossible to manage with current techniques and logistical constraints. We identify four problems with egg removal programs. First, host nests are difficult and expensive to find (Martin and Geupel 1993).

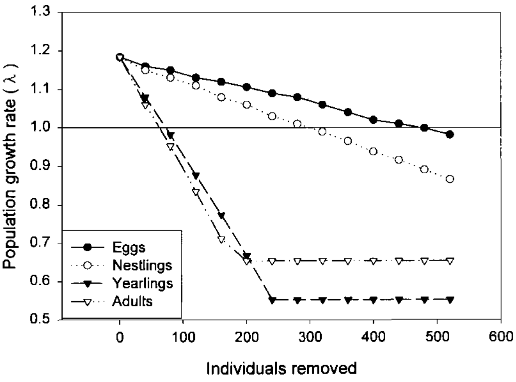

FIGURE 7. Number of individual eggs, nestlings, yearlings, and adults removed and the resulting population growth rates for a hypothetical population of 5,000 cowbirds. Removals are assumed to impose additive mortality. See Appendix 2 for details.

Second, removing cowbird eggs may increase nest predation rates or result in nest abandonment (Major 1990, Gotmark 1992), although correct protocols can reduce disturbance (Martin and Geupel 1993). Third, to be effective, egg removals must target a large proportion of the total cowbird population. Egg removals will likely have to exist at scales much larger than study sites, management areas, and wildlife refuges. The exact scale of management will depend upon the size of the cowbird population and movement rates between populations, which remain unknown. Fourth, eggs are expected to be numerous. At the time of breeding, over 90% of the population is in the egg stage at stable age distribution; consequently, management actions may remove many eggs, yet have little impact upon total egg survival rates.

To illustrate how a management imposed change in a vital rate is affected by the number in that age class, we provide an example. Using the mean matrix (Appendix 1) and assuming a population size of 5,000 cowbirds, there are over 4,600 eggs resulting from approximately 400 adults at the time of breeding (Appendix 2). Suppose that from this population we remove equal numbers of eggs, nestlings, fledglings, and adults, assuming that this mortality was additive. We find that by removing large numbers of eggs, we impact total population growth very little compared to other stages (Fig. 7). For example, on an individual basis, removing approximately 100 adults or fledglings will have the same impact as removing over 475 eggs, because there are fewer adults or fledglings in the population. In short, there are so many cowbird eggs that even large egg removals may have little impact upon total egg survival rates. While environmental variation and the consequences of having different host communities determine the population-wide survival rate of eggs, and therefore affect population growth, the effects of management on egg survival and the resulting changes in population growth are likely minuscule. When the problems of finding nests, human induced impacts upon hosts, large management scales, and the preponderance of eggs are considered jointly, we conclude that egg removal is not a viable management option.

Because reducing egg survival is not a widescale management option, we must consider what vital rates can be managed. Currently, the most common management options are trapping on the breeding grounds and trapping on the wintering grounds. Trapping on the breeding grounds typically involves the trapping of adults, while trapping on the wintering grounds involves the removal of adults and yearlings. We shall consider each of these options in turn.

Cowbird population growth rates are generally less affected by fluctuations in adult survival than other vital rates and the effects of adult removals may be masked by variation in egg and/or yearling survival. During the breeding season, the replacement of breeding females (via floaters and immigrants) exacerbates this problem and makes population growth rates even less sensitive to adult removals. To illustrate the significance of this problem, consider that cowbird trapping programs in Michigan typically remove 3,000 cowbirds per year with no noticeable decline in cowbird populations between years, despite the fact that virtually all individuals are removed during the breeding season (Kelly and DeCapita 1982; M. DeCapita, pers. comm.). The lack of any effect of trapping on cowbird populations may be due to either targeting only a small proportion of the total cowbird population or high rates of immigration. Either alternative leads to the same conclusion: adult removal programs on breeding grounds are not likely to regulate populations unless they are conducted on a much larger scale. However, this does not invalidate trapping programs during the breeding season, as such programs are usually intended to protect sensitive host species at a local scale and can successfully do so (Kelly and DeCapita 1982, Barber and Martin 1997; M. DeCapita, pers. comm.; J. Cornelius, pers. comm.).

Trapping adult and yearling cowbirds on the wintering ranges is expected to be much more effective in controlling cowbird population growth. While population growth is not sensitive to perturbations in adult survival, adults are only a small proportion of the total population.

Hence, adult survival may be greatly altered by removing only a small absolute number of adults (Appendix 2). In contrast to adult survival, population growth is likely sensitive to perturbations in yearling survival; there are also relatively few yearlings in any given population. Therefore, our sensitivity analysis and our age distributions suggest that winter trapping programs are more likely to decrease cowbird population growth rates than by removing eggs or trapping on breeding grounds. In addition to these life history considerations, winter trapping has many logistical advantages because cowbirds concentrate on large communal wintering grounds.

Unfortunately, there are also serious limitations with using winter trapping to control cowbird populations. Removing cowbirds from all wintering areas may be logistically impossible, because wintering ranges extend from Texas into Mexico (Bray et al. 1974, Arnold 1983). Also, even massive control in a limited number of wintering areas may produce extremely diffuse effects on the breeding ranges (Rothstein and Robinson 1994), because individuals in one wintering range may breed throughout North America (Bray et al. 1974, Dolbeer 1982). Finally, the large effect of egg survival on population growth rate may make trap efforts on other age classes ineffectual. For example, note that for the lowest rates of yearling and adult survival, many of the matrices have positive growth rates (Fig. 2c). So, while winter removals of adults and yearlings are expected to be more effective than removing eggs or adults on the breeding ranges, they do not have a high likelihood of regulating population growth rates unless most or all wintering areas are targeted for management. Furthermore, the effects of winter removals may be swamped by natural variation in egg survival rates.

Given the formidable logistical difficulties in lowering the vital rates that most affect cowbird population growth, we believe that the most effective method of cowbird control is likely to be the management of land uses to disfavor cowbirds. Cowbird presence is often significantly correlated with the presence of livestock (Schulz and Leininger 1991, Knopf et. al. 1988, Mosconi and Hutto 1982; but also see Kantrud 1981), agriculture (Rothstein et al. 1984, Rothstein et al. 1987, Tewksbury et. al. 1998), and forest fragmentation (Chasko and Gates 1982, Coker and Capen 1995, Tewksbury et al. 1998). By managing grazing patterns, availability of agricultural waste grain (often an important food source), and forest fragmentation, we may be able to indirectly eliminate or at least control the presence of cowbirds before they parasitize host species.

IMPLICATIONS FOR COWBIRD RESEARCH

Much research has focused upon the effects of limiting cowbird fecundity or determining what limits cowbird fecundity. We feel that this is a valid research topic for life history information, but is of little management interest unless fecundity can be decreased to rates near zero. We varied fecundity to rates lower than anything ever measured in nature (the calcium deprived rates) and then decreased that rate to assess the effect of larger variation in vital rate ranges. In all simulations but one (Fig. 6b) fecundity had the least effect on λ of any vital rate.

To date, most cowbird research has focused upon parasitism of specific host species, not upon parasitism of host communities within habitats or by land use practice. Because parasitism rates, predation rates, host communities, and the ability of hosts to fledge cowbirds vary across the landscape, it is unlikely that all vegetation types and host communities are equally productive for cowbirds. Furthermore, the presence of cowbirds may not reflect cowbird habitat quality. As long as adequate foraging habitat (feeding grounds) exist within flight range, cowbirds may parasitize host nests in habitats which barely provide positive growth rates or provide negative growth rates. By focusing research efforts upon cowbird vital rates in different vegetation types and host communities, researchers may be able to identify habitats and land use practices which are most important for (or possibly are responsible for) cowbird population growth. If the goal of management is to regulate populations of cowbirds, we suggest focusing management plans on regulating land uses which favor cowbirds in areas with positive cowbird growth rates. For example, livestock grazing in areas that have vegetation types and host communities that lead to negative cowbird population growth rates should be a lower management priority (assuming no endangered species are present) than livestock grazing in areas which lead to positive cowbird population growth rates. Currently there is no knowledge of how cowbird population growth rates may vary across combinations of vegetation types and host communities.

Last, we stress that more data are needed to understand cowbird population structure. Our model assumes that cowbirds exist in one large population, because there are no data for constructing spatially-explicit models. Without more knowledge of population boundaries and how adult and juvenile cowbirds move between populations over time, managers will not be able to predict the true efficacy of management alternatives and may choose inappropriate scales for management.

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APPENDIX 1. BROWN-HEADED COWBIRD STAGE-BASED MODEL

COWBIRD LIFE CYCLE DIAGRAM AND MATRIX

The biologically relevant projection interval for cowbirds is 1 year, so elements within the matrix represent annual rates (Fig. A1). However, in the first year of life, there are three relevant stages: egg, nestling, and yearling; thus we let the first year of life have egg, nestling, and yearling components. We only include one adult stage (as opposed to annual age classes) because age specific adult survival rates are not available and management techniques target all adults concurrently.

Transition matrix:

$$\begin{bmatrix} F_{11} & F_{12} \\ G_{21} & P_{22} \end{bmatrix}$$

DEFINITIONS OF MATRIX ELEMENTS AND VALUES FOR THE MEAN MATRIX:

Mean survival from stage 1 to stage 2 [G(2,1)] = mean egg survival (0.38) × mean nestling survival (0.64) × mean yearling survival (0.24) = 0.06

Mean survival from stage 2 to stage 2 [P(2,2)] = mean annual adult survival = 0.47

Mean yearling fertility [F(1,1)] = mean daily laying rate (0.56) × laying period (40 d) × proportion of female eggs (0.5) × mean first year survival (0.06) = 0.65

Mean adult fertility [F(1,2)] = mean daily laying rate (0.69) × laying period (40 d) × proportion of female eggs (0.5) × mean adult survival (0.47) = 6.49

These transition probabilities are incorporated into a mean matrix and have the resulting stable stage distribution and deterministic population growth rate (λ):

$$\begin{bmatrix} 0.65 & 6.49 \\ 0.06 & 0.47 \end{bmatrix}\begin{bmatrix} 0.9244 \\ 0.0756 \end{bmatrix} \qquad \lambda = 1.184$$

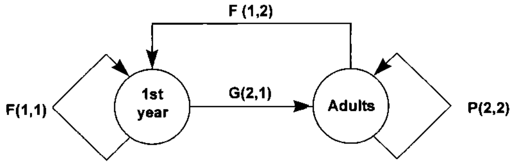

FIGURE A1. Life cycle diagram used for the Brown-headed Cowbird analysis.

STAGE SPECIFIC TIME INTERVALS

The projection interval is one year (365 d):

1st year:	
egg survival stage:	15 d
nestling survival stage:	10 d
yearling survival stage:	340 d
2nd year + (Adults):	1 yr

APPENDIX 2. ANALYSIS OF A HOW A GIVEN REMOVAL MAY AFFECT BROWN-HEADED COWBIRD SURVIVAL AND POPULATION GROWTH RATE

This analysis is included to clarify how the sensitivity analysis must be interpreted. Specifically, we were concerned that our analysis would lead to time, effort, and money being prematurely applied towards egg removal programs. When we include environmental variance in the analysis, egg survival has the largest impact upon population growth rate. However, it is not clear how removing cowbird eggs actually alters egg survival rates. We investigate this link with the following crude analysis, where we decrement cowbird vital rates one-at-a-time by removing a specified number of individual eggs, nestlings, yearlings, or adults.

We start with the following assumptions:

1. There is a population of 5,000 cowbirds at the beginning of a breeding season.
2. This population has the vital rates of the mean matrix in Appendix 1.
3. All mortality is additive (no compensatory effects) and immigration is nonexistent.
4. Populations are at stable age (stage) distribution.

To calculate the number of individuals in particular life stages within a population of 5,000, at time t, we must first determine the number of individuals at time $t-1$:

$$N_{t-1} \times \lambda = 5{,}000$$

$$N_{t-1} = 4222.97.$$

By multiplying N_{t-1} by the stage distribution vector (Appendix 1), we determine the total number of eggs and adults at time $t-1$:

$$4222.97 \times \begin{bmatrix} 0.9244 \\ 0.0756 \end{bmatrix} = \begin{bmatrix} 3903.72 \text{ eggs} \\ 319.26 \text{ adults} \end{bmatrix}$$

We then multiply the matrix by the stage distribution vector at time $t-1$ to determine the initial number of individuals in each stage at time t:

Initial number of eggs:

$$(F_{11} \times V_1) + (F_{12} \times V_2) = 4621.81$$

Initial number of adults:

$$(G_{21} \times V_1) + (P_{22} \times V_2) = 377.90.$$

Immediately after breeding, we have a population size of 377.90 adults and 4621.81 eggs. This is our total population of 5,000. To calculate the number of individuals in intermediate stages, the total number of eggs is decrement by egg, nestling, and yearling survival rates successively:

Initial number of nestlings:

Initial number of eggs × egg survival rate

= 1756.29

Initial number of yearlings:

Initial number of nestlings × yearling survival rate

= 1124.03.

We simulate individual removals by decreasing the number of individuals in a life stage by increments of 40. This mortality is assumed to occur after the initial probabilistic mortality of that stage class (i.e., it is assumed to be additive). For example, if management removes 200 eggs, then the adjusted egg survival rate is calculated as follows:

[(Initial number of eggs × original egg survival rate)

− 200 eggs]/Initial number of eggs

= New egg survival rate

$$\frac{(4621.81 \times 0.38) - 200 \text{ eggs}}{4621.81} = 0.34$$

In this example, removing 200 eggs reduced egg survival rates by only 11%. The altered survival rates are then incorporated into the mean matrix to calculate the resulting population growth rate (Fig. 7).