DEMOGRAPHIC CONSEQUENCES OF BROWN-HEADED COWBIRD PARASITIZATION OF LAZULI BUNTINGS

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Abstract. Lazuli Buntings (*Passerina amoena*) have a large breeding distribution throughout western United States and southwestern Canada. They are not currently considered to be a species at risk, and have been reported to be rare hosts of Brown-headed Cowbirds (*Molothrus ater*). At some locations in west-central Montana, however, the prevalence of cowbird parasitization is high, with over 70% of bunting nests parasitized. The cost of cowbird parasitization for Lazuli Buntings is severe: about 90% of parasitized nests that fledged a cowbird chick did not fledge any bunting chicks. The demographic consequences of parasitization by cowbirds were investigated with non-spatial, age-structured population models, using a range of values for survivorship, fecundity, and cost of parasitization. These demographic analyses suggest that isolated populations of Lazuli Buntings are more at risk than currently appreciated; deterministic models suggest that the threshold parasitization levels required for bunting populations to replace themselves ($\lambda = 1.0$) are relatively low (threshold levels are 17% of nests parasitized for intermediate survivorship estimates and 44% for high survivorship estimates). When realistic environmental and demographic stochastic variation is incorporated into the demographic models, Lazuli Bunting populations appear even more at risk than suggested by deterministic models. More research is needed on documenting the spatial and temporal patterns of cowbird parasitization, refining survivorship estimates, and understanding the metapopulation structure of Lazuli Buntings.

Key Words: age-structured model, brood parasitism, Brown-headed Cowbird, cost of parasitization, Lazuli Bunting, *Molothrus ater,* neotropical migrant, *Passerina amoena,* population dynamics.

The impact of parasitization by Brown-headed Cowbirds (*Molothrus ater*) on populations of passerine hosts has been a long-standing issue in conservation biology. There are some well-publicized cases in which populations of songbirds are threatened by cowbird parasitization (usually in conjunction with other anthropogenic changes, such as loss and fragmentation of breeding habitat, and high densities of nest predators; Robinson et al. 1995b): Kirtland's Warbler (*Dendroica kirtlandii*; Mayfield 1977), Black-capped Vireo (*Vireo atricapillus*; Grzybowski et al. 1986), and Least Bell's Vireo (*Vireo bellii pusillus*; Goldwasser et al. 1980). In spite of one view that many populations of songbirds are now threatened by cowbird parasitization (Brittingham and Temple 1983, Terborgh 1989), the magnitude of this problem remains unclear. This is largely because the abundance of a species does not necessarily reflect its reproductive success at a location; because of large total populations and high juvenile and adult dispersal, birds can continue to recolonize areas in which nesting success is extremely low (Brawn and Robinson 1996). Since abundance may mask serious underlying reproductive failures at a location, there is a need for more detailed demographic analyses of the impact of cowbird parasitization on the dynamics of songbird populations (Robinson et al 1995a).

Lazuli Buntings (*Passerina amoena*) are widespread breeding songbirds throughout western United States and southwestern Canada, and

they can be very abundant in many different types of vegetation (Greene et al. 1996). Analysis of Breeding Bird Survey (BBS) data (Butcher et al. 1992) suggested that Lazuli Bunting populations were stable or perhaps increasing, and none of the monitoring criteria indicated that Lazuli Buntings were a species at risk.

However, other analyses of BBS data (Sauer and Droege 1992) suggested populations were declining in some central and western regions, although these decreasing trends were not statistically significant. More detailed analyses of BBS data that took into account magnitude of population changes (DeSante and George 1994) suggested that populations were declining in seven states, especially in Utah. These population analyses combined data from large geographic areas and many vegetation types, and therefore may mask some serious local reproductive failures and regional population declines.

If bunting populations are declining in some areas, the causes are unknown. Previous studies have suggested that Lazuli Buntings are rare hosts of Brown-headed Cowbirds (Friedmann et al. 1977, Friedmann and Kiff 1985). However, the prevalence of cowbird parasitization, the cost of parasitization on Lazuli Bunting reproductive success, and the impact of parasitization on Lazuli Bunting population dynamics are currently unknown.

The purpose of this paper is to (1) document levels of Brown-headed Cowbird parasitization

on Lazuli Buntings in western Montana, and (2) model the demographic consequences of varying levels of cowbird parasitization on Lazuli Buntings.

METHODS

DEMOGRAPHIC MODELS

The demographic consequences of cowbird brood parasitization on Lazuli Buntings were modeled using age-structured, non-spatial matrix projection models. Such models summarize the survival and reproduction of different age classes in projection matrices, and they allow a wide variety of demographic analyses (e.g., Crouse et al. 1987, Burgman and Gerard 1990, Wooton and Bell 1992; for reviews of these methods see Caswell 1989 and McDonald and Caswell 1993).

Since the survival and fecundity of buntings differ between yearling birds and older birds, but is independent of age after the first year of life (Greene et al. 1996), I constructed a female-based model with two age classes, and with a projection interval of one year. This demographic model is summarized as a life cycle diagram (Caswell 1989), which shows the transition coefficients related to survivorship and reproduction of the two age classes (Fig. 1A). Note that the age categories span a year. Thus, the yearling category integrates information about birds from just after hatching until just after their first birthday (for details see Caswell 1989, McDonald and Caswell 1993).

I investigated the consequences of cowbird parasitization on the population dynamics of Lazuli Buntings with two types of models:

1) *Deterministic population models.* These models assume time-invariant transition probabilities, density independent population growth, and do not allow for stochastic variation in vital rates (Caswell 1989). The dominant eigenvalue of a projection matrix, λ, represents the geometric rate of population growth associated with the specific transition coefficients in the matrix; a value of $\lambda = 1.0$ indicates a population is exactly replacing itself, $\lambda > 1$ indicates a population is increasing, and $\lambda < 1$ indicates a population is declining. For example, a matrix that has an associated dominant eigenvalue of $\lambda = 1.054$ indicates that a population with those vital rates would grow at 5.4% per time interval. The break-even threshold values ($\lambda = 1.0$) presented in these analyses are equivalent to May and Robinson's (1985) maximum rate of parasitization sustainable by a host population. Although long-term projections of such models are undoubtedly suspect, they are useful for investigating the short-term potential of a population
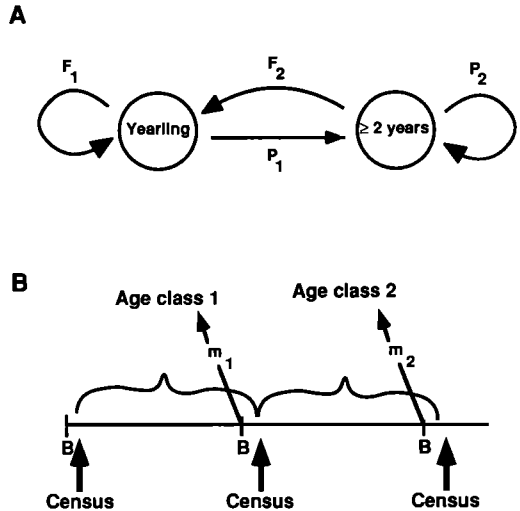

FIGURE 1. (A) Life cycle diagram of the age-structured matrix population model for Lazuli Buntings. The two nodes represent the two age classes, yearling females and females ≥2 years of age. Arrows indicate age-specific survivorship (P_i's) or age-specific fertilities (F_i's). The projection interval was one year. Specific values for the transition probabilities used in the analyses are shown in Table 2. (B) Schematic time line of a seasonally breeding bird, showing bookkeeping details used in a post-breeding census parameterization of projection matrices. B indicates the yearly pulse of breeding activity. The vertical arrows show the timing of the yearly censuses just after the breeding season. The chicks produced by females (m_i) are assigned to the age class before the birth event (Caswell 1989). See text for more details.

to grow (or decline), and to compare the effect of different vital rates on population growth rates.

The relative contribution of different transition coefficients to the overall population growth rate, λ, can be assessed through elasticity analyses. Elasticity coefficients, or proportional sensitivities, measure the relative change in λ in response to a proportional change in one transition coefficient (Caswell 1989, McDonald and Caswell 1993). Elasticity values are calculated for each matrix element independently (i.e., assuming all other transition coefficients do not change), and they represent the effect of infinitely small changes in each transition coefficient on λ (calculated as the partial derivative δ (ln λ)/δ (ln a_{ij}), where a_{ij} is the element in the ith row and j^{th} column of the transition matrix). Since elasticity values sum to 1, the relative contribution of matrix elements to overall population growth, λ, can be compared; a large elasticity coefficient associated with a particular vital rate suggests that a change in that transition will

result in a relatively large change in the population growth rate, whereas a small elasticity coefficient indicates that a change in that vital rate will have a relatively small effect on the population growth rate. See Caswell (1989) and McDonald and Caswell (1993) for more detailed discussions on the calculation and interpretation of elasticity coefficients. Wisdom and Mills (1997) commented on limitations of the elasticity approach, and offered some methods of estimating the relative contribution of transitions on population growth rates over larger ranges of variation for each transition, and when all transition coefficients are allowed to vary at the same time (see also Citta and Mills *this volume*).

2) *Stochastic population models.* All species experience variation in life history characteristics, such as survivorship and fecundity. Incorporating variation in demographic models can provide additional important insights into the population dynamics of a species, and allows probabilistic statements about the distribution of population sizes over time (Caswell 1989, Burgman et al. 1993). Thus, in addition to the deterministic demographic models with fixed vital rates described above, I also ran stochastic Monte Carlo simulations of bunting populations that incorporated both demographic and environmental stochasticity. Demographic stochasticity refers to chance variation in population size when vital rates are applied to individuals in small populations (Burgman et al. 1993). For example, it is impossible to have 9.5 individuals, and so the population would have to be either 9 or 10; the chance difference of "half" an individual represents a large proportion of such a small population. Environmental stochasticity refers to variation in survivorship and fecundity arising from variation in environmental conditions (Caswell 1989, Burgman et al. 1993).

Each of the stochastic simulations started with 100 replicate bunting populations, each with an initial size of 100 females. Vital rates were randomly drawn from normal distributions with coefficients of variation (CV) of 10% of the mean value of the vital rates. These values of yearly variation are well within the range of variation for birds, and have been used in stochastic simulations for other species (e.g., Burgman et al. 1993). For example, a 10% CV for a mean yearly survivorship of 70% implies that 95 out of 100 populations would experience survivorship values between 56–84% (i.e., $\bar{x} \pm 2$ SD).

The models used in these analyses assume closed populations, and do not allow for dispersal among sub-populations. It is clear that most populations consist of metapopulations, in which isolated sub-populations are loosely connected by immigration and emigration of individuals. The population dynamics of a metapopulation depends upon the sizes and spatial relationships of sub-populations, variation in survivorship and reproduction among patches, and dispersal among patches (Gilpin and Hanski 1991, Harrison 1991, Brawn and Robinson 1996). Hence, the results of the non-spatial models presented here are meant only to address the question of how cowbird parasitization may influence isolated bunting populations. In essence, these analyses ask the questions: at what level of cowbird parasitization is a bunting population a potential sink population (i.e., $\lambda < 1$), and at what level of cowbird parasitization is a bunting population a potential source population (i.e., $\lambda > 1$)? Analyses of potential source and sink populations of Lazuli Buntings are the subject of another paper (Greene et al. *this volume*).

PARAMETRIZATION OF DEMOGRAPHIC MODELS

As part of other behavioral studies, populations of color-marked Lazuli Buntings have been monitored in west-central Montana since 1992 (Greene et al. 1996). Data on reproductive success, survivorship, incidence of parasitization, and the cost of parasitization from three main study locations (described below) were used to parameterize these demographic models. To gather information on age-related reproductive performance and survivorship, buntings were aged using plumage characteristics; yearling birds retain brown primary coverts, whereas birds in their second year or older have primary coverts that are tinged with blue edges (Young 1991, Greene et al. 1996).

SURVIVORSHIP

Over a six year period (1992–1997), an average of 43% of banded adult males returned to the study sites the following year. This estimate of annual survivorship is undoubtedly low, since there was dispersal off of and onto the study sites between years (Greene et al. 1996). The highest estimates of yearly adult male survivorship for the congeneric Indigo Buntings (*Passerina cyanea*) are about 0.70 (Payne 1992). Yearly survivorship for adult female Indigo Buntings are generally lower than those for adult males (Payne 1992). There is little information on survivorship of buntings during their first year of life since it is extremely difficult to distinguish between mortality and dispersal. However, first year survivorship for many passerines has been suggested to be roughly half that of adult birds (Ricklefs 1973). For these analyses I have assigned juvenile survival as half of adult survival. These estimates may be too low, and thus overestimate the impact of cowbird parasitism.

TABLE 1. SUMMARY OF LIFE HISTORY PARAMETERS USED IN DEMOGRAPHIC ANALYSES

A. Yearly survivorship

	First year	Subsequent years
Low	0.20	0.40
Intermediate	0.45	0.65
High	0.50	0.70

B. Age-specific fertilities (# female offspring fledged per female per breeding season).

	Yearling female	Females two and older
No cowbird parasitization	0.61	1.13
Low effect of parasitization[a]	0.20	0.20
Severe effect of parasitization[b]	0.05	0.05

[a] Derived from congeneric Indigo Buntings (*Passerina cyanea*, Payne 1992; Payne and Payne 1998).
[b] Estimated from nest studies in western Montana.

To bracket a range of plausible survivorship values, three different estimates (low, intermediate, and high) were analyzed (Table 1A). The high survivorship schedule corresponds to the highest survivorship values estimated for *Passerina* buntings (Payne 1992).

REPRODUCTIVE SUCCESS

During six breeding seasons (1992–1997) near Missoula, Montana, the average number of young reared to fledging per breeding season per female in unparasitized nests was 1.87. However, the age of the female, but not the male, influenced fledging success; yearling females fledged an average of 1.22 chicks per breeding season, whereas older females fledged average of 2.26 chicks per breeding season (N = 60 females). The age-specific fertilities are summa-

rized in Table 1. As pointed out by Pease and Grzybowski (1995), it can be misleading to estimate how brood parasites influence the seasonal reproductive success of hosts from individual nesting attempts. For example, if a female quickly renests after nest failure or parasitization, she may produce the same number of young during the entire breeding season as unparasitized females. However, Lazuli Buntings accept cowbird eggs (Greene et al. 1996), and they rarely renest in Palouse prairie areas in western Montana. The data used to parameterize these models were from intensive nest searching and monitoring of known birds over entire breeding seasons. Thus, these estimates of reproductive success were not adjusted using the methods of Pease and Grzybowski (1995).

COST OF PARASITIZATION

The effect of cowbird parasitization on Lazuli Buntings in western Montana is severe. Most cowbird chicks hatch slightly before or at same time as bunting chicks. When this happens, the cowbird chick obtains most of the food, and the bunting chicks usually starve within 2–3 days (Greene et al. 1996, Davison 1998). In a sample of 38 nests that fledged cowbird chick(s), 73.7% fledged only 1 cowbird chick, 15.8% fledged 2 cowbird chicks, and only 10.5% fledged 1 cowbird chick and 1 bunting chick.

To bracket a range of different costs of parasitization on bunting reproductive success, two different values were used (low and severe; Table 1B). The severe effect of parasitization is from reproductive success data from study sites in western Montana; the low cost is derived from Indigo Buntings in Michigan (Payne 1992, Payne and Payne 1998).

TABLE 2. LEFKOVITCH TRANSITION MATRICES FOR LAZULI BUNTINGS USED IN DEMOGRAPHIC ANALYSES, DERIVED USING LOW, INTERMEDIATE, AND HIGH SURVIVORSHIP ESTIMATES IN TABLE 1

To	From	
	Yearling	≥ 2 years
Low survivorship, no parasitization		
Yearling	0.122 (0.060)[a]	0.425 (0.230)
≥ 2 years	0.20 (0.230)	0.40 (0.479)
	$\lambda = 0.5922$[b]	
Intermediate survivorship, no parasitization		
Yearling	0.275 (0.089)	0.73 (0.256)
≥ 2 years	0.45 (0.256)	0.65 (0.400)
	$\lambda = 1.067$	
High survivorship, no parasitization		
Yearling	0.305 (0.092)	0.791 (0.258)
≥ 2 years	0.50 (0.258)	0.70 (0.392)
	$\lambda = 1.1617$	

[a] Elasticity coefficients associated with specific transition coefficients shown in brackets.
[b] The dominant eigenvalue, λ, is shown below each transition matrix.

TRANSITION MATRICES

The demographic parameters used in matrix-based models are different from the survivorship (l_x) and maternity (m_x) functions used in life table approaches. This is worth emphasizing, since these differences continue to be a source of confusion (McDonald and Caswell 1993). In particular, as pointed out below, the fertility elements (F_i's) of matrix-based models, unlike the m_x functions of life tables, contain terms relating to survival as well as fertility rates.

To derive the coefficients for a projection matrix model, we must define the projection interval and for birth-pulse organisms, such as buntings with concentrated, seasonal reproductive periods, the time of the census of individuals relative to the breeding period. For the projection matrix for Lazuli Buntings, the projection interval and the age class is defined as one year, and I have chosen to parameterize the model with a post-breeding census. The bookkeeping aspects of the model parameterization are shown schematically in Fig. 1B.

The survival and fertility coefficients are defined as follows (Caswell 1989, McDonald and Caswell 1993):

P_i = the probability that members of age class i survive to enter the next age class i + 1.

F_i = the number of individual females in age class 1 at time t + 1 per individual in age class i at time t.

As an example, the coefficients for the projection matrix using the low survivorship and no parasitism values from Table 1 are derived as follows. With a post-breeding census, we assign the offspring that are produced by females just before their first birthday to age class 1 (Caswell 1989). Thus, for F_1, we are concerned with how the newborn individuals in age class 1 survive to the next census period and then reproduce. By definition,

F_1 = (the probability that newly hatched individuals survive to the next census period) × (the number of female offspring produced by the surviving individuals on their first birthday).

For no parasitism and low survivorship values (from Table 1), F_1 = 0.2 × 0.61 = 1.22, which is the value in the upper left of the top transition matrix in Table 2.

Similarly,

F_2 = (the probability that 1 year olds survive to the next census period) × (the number of female offspring produced by those surviving females on their second birthday).

For no parasitism and low survivorship values (from Table 1), F_2 = 0.4 × 1.13 = 0.452, which is the value in the upper right of the top transition matrix in Table 2. The age specific survivorship values are P_1 = 0.2 and P_2 = 0.4 (Caswell 1989). These are the values in the lower left and lower right, respectively, of the top matrix in Table 2.

Although I arbitrarily chose a post-breeding bookkeeping census, the model could be parameterized with any other arbitrarily chosen census time, such as a pre-breeding census. The transition coefficients in the resulting matrix would be different, but the resulting demographic analyses and conclusions would be identical. For more details on the construction and parameterization of matrix-based projection models, the interested reader is referred to the excellent treatments of Caswell (1989) and McDonald and Caswell (1993).

All demographic simulations were performed with Ramas/Age (Ferson and Akçakaya 1991) and Ramas/Stage software (Ferson 1994).

INCIDENCE OF PARASITIZATION

The prevalence of cowbird parasitization in Lazuli Bunting nests was determined at three main study sites in western Montana.

1) *Mount Sentinel and Mount Jumbo* are west-facing hillsides overlooking the city of Missoula, Montana (46° 50′ N, 114° 10′ W). This Palouse prairie grassland is dominated by several species of native bunch grasses, several invading weeds, with patches of bushes of ninebark (*Physocarpus malvaceus*), honeysuckle (*Lonicera utahenesis*), snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa woodsii*), and serviceberry (*Amelanchier alnifolia*) and chokecherry (*Prunus virginiana*) trees. During the 1995 breeding season, a communal cowbird roost was located in bushes at the base of Mount Jumbo and the north end of Mount Sentinel. This roost contained at least several hundred cowbirds. Spring floods during the 1996 and 1997 breeding seasons covered the cowbird roost sites, and they moved somewhere else.

2) *Bison Range National Wildlife Refuge* (47° 08′ N, 114° 20′ W) consists of Palouse Prairie vegetation, with steep gullies with dense patches of wild rose, ninebark, alder (*Alnus* spp.), hawthorn (*Crataegus* sp.), serviceberry, and chokecherry. Approximately 370 adult American bison (*Bison bison*) with 80–100 calves are kept on 7,492 ha, but are rotated through eight large grazing units. Ranches with large herds of cattle occur outside of the wildlife refuge. Flocks of
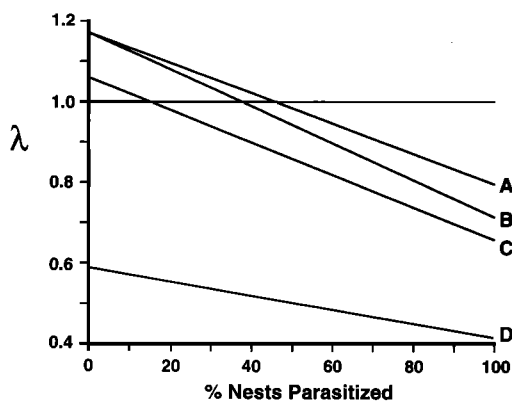
FIGURE 2. Effect of different parasitism rates and demographic characteristics on population growth rates of Lazuli Buntings in the deterministic model. The line $\lambda = 1$ indicates the break-even point at which a population exactly replaces itself; $\lambda < 1$ indicates a declining population, $\lambda > 1$ indicates a population with the potential to increase. The four different lines were calculated with the following combinations of survivorship and fertility shown in Table 3: (A) high survivorship, low effect of parasitism; (B) high survivorship, strong effect of parasitism; (C) intermediate survivorship, strong effect of parasitism; and (D) low survivorship, strong effect of parasitism.

cowbirds associate with the bison in the afternoon. I located and monitored Lazuli Bunting nests in Triskey Creek when bison were absent (the closest bison or cattle were about 4 km away), and near Indian Springs, where bison were present in large numbers throughout the breeding season.

3) *Along the Bitterroot River,* from Lee Metcalf National Wildlife Refuge (46° 40′ N, 114° 20′ W) and north to the town of Lolo, Montana. Riparian vegetation occurs in thin strips of black cottonwood (*Populus trichocarpa*) and Ponderosa pine (*Pinus ponderosa*) gallery forests and dense shrubby areas. These forests are generally less that 250 m wide. Cattle and horses are nu-

merous in the surrounding valley on farms and small "ranchettes."

RESULTS

DEMOGRAPHIC MODELS

The deterministic demographic models suggest that Lazuli Bunting populations are not self-sustaining in the face of low to modest levels of cowbird parasitization (Fig. 2). Even in the complete absence of cowbird parasitization, a bunting population experiencing the low survivorship values would decline by about 60% per year ($\lambda = 0.59$; Fig. 2, line D). For bunting populations experiencing intermediate survivorship values and severe parasitization, population growth is slightly above the break even point even in the absence of parasitization ($\lambda = 1.066$; Fig. 2, line C); the break-even point of $\lambda = 1.0$ would occur when 17% of the bunting nests were parasitized (Fig. 2, line C). Even with the highest estimates of survivorship and low effect of parasitization on bunting reproductive success, parasitism levels of higher than 44% would lead to growth rates that could not sustain the local population ($\lambda < 1.0$; Fig. 2, line A).

The elasticity coefficients associated with different transition coefficients (shown in brackets in Table 3) suggest that population growth rate is most sensitive to changes in adult survivorship, less sensitive to changes in yearling survivorship, and least sensitive to changes in fertility. These general results are illustrated graphically when adult survivorship and the effect of cowbird parasitization were independently varied (Fig. 3). For example, a 10% increase in the effect of cowbird parasitization had almost negligible demographic consequences; this change resulted in only a 0.10% change in the percentage of nests parasitized required for exact population replacement (Fig. 3, lines C to D). Furthermore, a 400% increase in the effect of parasitization resulted in only 3.5% increase in the percentage of nests parasitized required for exact population replacement (Fig. 3, lines D to B). In

TABLE 3. PERCENT OF LAZULI BUNTING NESTS PARASITIZED IN WESTERN MONTANA

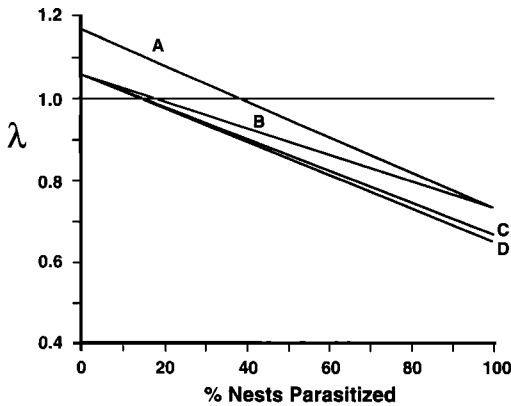| Location	Percent parasitized		
	1995	1996	1997
Bison Range NWR			
Indian Springs (bison present)	100.0 (3)[a]	87.5 (8)	100.0 (5)
Triskey Creek (bison absent)	5.9 (17)	16.6 (12)	12.5 (8)
Missoula			
Mt Jumbo and Mt Sentinel (north)	95.8 (24)	25.0 (12)	44.4 (9)
Mt Sentinel (south)	6.2 (48)	13.3 (15)	20.0 (5)
Bitterroot River			
Cottonwood forests	100.0 (4)	83.3 (12)	72.2 (18)

[a] Sample size in parentheses.

FIGURE 3. Sensitivity of population growth rate to changes in survivorship and effect of parasitism for Lazuli Buntings in western Montana. The four lines were calculated with the intermediate survivorship transition matrix (Table 3), with the following changes: (A) Intermediate adult survivorship + 10% (i.e., $P_{2,2}$ = 0.715), strong effect of parasitism; (B) Low effect of parasitism; (C) Strong effect of parasitism + 10%; and (D) Strong effect of parasitism.

FIGURE 4. Example of a stochastic simulation of Lazuli Bunting population growth, using λ = 1.0186 (high survivorship and strong effect of parasitism, with 36% of population parasitized). Simulations run with 100 populations for 25 years, with 10% coefficient of variation on vital rates. Horizontal bars indicate mean population size; vertical bars indicate range; thick bars bracket 75% of all population values for each time step.

contrast, a 10% increase in adult survivorship resulted in a 23% increase in the percentage of nests parasitized required for exact population replacement (Fig. 3, lines D to A).

The stochastic simulations show that replicate populations exposed to variation in vital rates become increasingly skewed around the average population size, with many populations smaller than the mean, and only a few populations much larger than the mean population size. This point is illustrated with the simulations for populations with a deterministic λ = 1.019; although the mean population size increased about 2% per year, the distribution of population sizes around the mean became quickly skewed over time (Fig. 4). Indeed, 82 of the original 100 populations in the stochastic simulation had decreased in size, even though the overall mean of all 100 populations increased (Fig. 4).

This result is a general one, in which the distribution of population sizes in stochastic environments became grossly skewed around the mean, with most populations much smaller than the overall mean.

INCIDENCE OF PARASITISM

There was considerable variation between sites and across years in the incidence of parasitization (range 5.9–100% of nests parasitized; Table 3). However, bunting breeding habitats that were close to agricultural land with livestock (Bitterroot River sites) or bison (Bison Range NWR, Indian Spring site), or close to
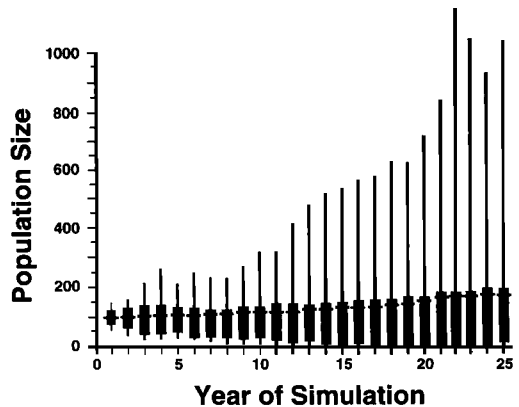
cowbird roosts (Mount Jumbo and Mount Sentinel north in 1995) had high levels of parasitization (72–100% of nests parasitized; Table 3).

DISCUSSION

These analyses suggest that Lazuli Bunting populations may be adversely effected by relatively low levels of cowbird parasitization. Even with high estimates of survivorship and reproductive success, the deterministic demographic analyses suggest that parasitization levels above about 40% of nests would cause populations to decline. Analyses for White-crowned Sparrows in the San Francisco Bay area suggested that populations can not be maintained when parasitization rates exceed about 20% (Trail and Baptista 1993).

The stochastic population models suggest that there may be even more cause for concern than suggested by the deterministic analyses; even though a λ value may be well above the break-even point of 1.0, replicate populations experiencing realistic levels of stochastic variation in vital rates become skewed around the mean population size. These results are in concordance with theoretical models of stochastic population growth, which indicate that the probability distribution of population sizes are asymptotically lognormal (stochastic ergodic theorems; Tuljapurkar and Orzach 1980, Caswell 1989). The most important implication of this result is that the lognormal distribution is skewed around its mean, with most populations below the mean,

and few populations above the mean; the mean population size, and the geometric growth rate λ, become poor measures of population dynamics in stochastic environments (Caswell 1989). Indeed, λ or the mean population size can be dangerously misleading in stochastic environments; even though the average population size can increase over time for replicate populations exposed to stochastic variation in vital rates (i.e., $\lambda > 1$), most of the original populations may have gone extinct (Caswell 1989).

Intensive monitoring of Lazuli Bunting nests at several locations revealed previously unsuspected high levels of cowbird parasitization in western Montana. Although there was substantial spatial and yearly variation in parasitism levels, generally more than 70% of buntings breeding close to livestock or cowbird roosts were parasitized. These high parasitism levels are comparable to those reported for Lazuli Buntings breeding in riparian vegetation along the Sacramento River in California (87% of 45 nests parasitized over four years, annual variation ranged from 71–100%; Gardali et al. 1998). Lazuli Bunting populations experiencing such high levels of parasitism are unlikely to be self-sustaining, and are most likely sink populations that are continually recolonized by individuals from other source populations (Robinson 1992, Brawn and Robinson 1996).

The cost of parasitization was high for Lazuli Buntings in west-central Montana. Congeneric Indigo Buntings are common cowbird hosts, but they appear to be able to commonly fledge some of their own chicks as well as a cowbird chick (Payne 1992, Payne and Payne 1998). For example, Payne (1992) found that 67% of 76 parasitized nests that fledged a cowbird also fledged an Indigo Bunting chick; the immediate cost of parasitization was about 1.2 fewer bunting chicks fledged per parasitized nest than unparasitized nests (Payne and Payne 1998). It is not clear how these differences arise; food may be less abundant in the more xeric Lazuli Bunting breeding habitat in western Montana than the more mesic areas used by Indigo Buntings. Observations at Lazuli Bunting nests indicate that cowbird chicks receive most of the food brought in by the Lazuli Bunting adults, and that bunting chicks in parasitized nests typically starve to death in a few days (Greene et al. 1996, Davison 1998). Nestling provisioning rates may be higher in more mesic areas if food is more plentiful. If this is the case, cowbird chicks may become satiated, allowing bunting chicks to obtain food after that.

It is best to view the results of these demographic analyses as cautionary. I have made a number of demographic assumptions that are undoubtedly biased on the pessimistic side.

1) *Survivorship estimates.* Juvenile survivorship was estimated as half the adult survivorship (Table 1). Survivorship is extremely difficult to estimate, especially for species, such as Lazuli Buntings, that breed in early successional vegetation and appear to have good dispersal abilities (Greene et al. 1996). Thus, both adult and juvenile survivorship may be higher than the values used in these analyses.

2) *Fecundity estimates.* Although the fecundity values used in these analyses were estimated from field data, the estimates for yearlings may be too low. Most passerines show weak age effect on reproductive success (Saether 1990). In addition, estimates of reproductive success from unparasitized nests may underestimate the true reproductive success in areas where cowbirds are common, since undetected egg destruction and egg removal by cowbirds at unparasitized nests also reduces host fecundity (Arcese and Smith in press, Pease and Grzybowski 1995).

3) *Parasitization frequency.* The estimates of parasitization frequency were from a small geographic area (all were within 50 km of Missoula, Montana). It may be that these locations happen to be cowbird "hotspots" that are unrepresentative of parasitization pressures in other places. In addition, there was considerable fluctuations in parasitization frequencies between years.

IDENTIFICATION OF RESEARCH PRIORITIES

These demographic analyses, and the uncertainties in these analyses outlined above, help focus attention on some research and management priorities. The issues outlined below are poorly understood, not only for Lazuli Buntings, but for many other species of birds as well.

Incidence of parasitization

This study has documented previously unsuspected high levels of cowbird parasitization in populations of Lazuli Buntings in west-central Montana. With the exception of similarly high parasitism levels reported in the Sacramento Valley of California (Gardali et al. 1998), there are few other estimates of the incidence of parasitization in other areas of the breeding range of Lazuli Buntings. Thus it is unclear if these results are representative of other areas. We need more information on the geographic structure of reproductive success and parasitization for Lazuli Buntings (as well as other species of birds).

Dispersal and survivorship

These life history parameters are difficult to estimate, since mortality is difficult to distinguish from dispersal. The demographic analysis

indicate that population growth rate λ is most sensitive to changes in survival estimates. How good were the ranges of survivorship values used in these analyses? Although I used a wide a range of survivorship values (0.2–0.5 for birds in their first year of life; 0.4–0.7 for older birds), Lazuli Bunting populations may be more resilient to cowbird parasitization than suggested by these demographic analyses if they tend to live longer than suggested by our current estimates. These problems are especially problematic for species, such as Lazuli Buntings, that breed in early successional vegetation types, and thus may have good dispersal abilities.

Metapopulation structure

These analyses investigated the demographic consequences of parasitization of isolated populations. However, bunting populations are connected by dispersal, and the dynamics of these interconnected populations depend on the details of the sizes and distances between populations, the geographic structure of survivorship, repro-
ductive success, parasitization, and patterns of dispersal of buntings among patches. Better data on these life history characteristics will be important to construct biologically realistic metapopulation models.