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FITNESS CONSEQUENCES OF NEST DESERTION IN AN ENDANGERED HOST, THE LEAST BELL'S VIREO

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Abstract. Recent analyses of the impact of cowbird parasitism on host productivity suggest that while parasitism reduces productivity on a per-nest basis, the ability of pairs to desert parasitized nests and renest allows them to achieve productivity comparable to that of unparasitized pairs. This has implications for the management of several endangered species that are highly vulnerable to parasitism and consequently the target of cowbird control programs. I calculated seasonal nesting effort (number of nests per pair) and productivity of 568 pairs of Least Bell's Vireos (*Vireo bellii pusillus*) monitored over 11 years at the San Luis Rey River in San Diego County, California (where cowbird trapping has reduced, but not eliminated, parasitism), assigning pairs to one of three groups: (1) deserters, (2) rescued (parasitized pairs with nests ''rescued'' from probable failure by the removal of cowbird eggs), and (3) unparasitized. Parasitized pairs attempted significantly more nests per season than did unparasitized pairs, with deserters producing more nests than rescued pairs. However, productivity of deserting pairs was significantly lower than that of both rescued and unparasitized pairs, largely because subsequent nests of deserting pairs were also parasitized. Seasonal productivity of rescued and unparasitized pairs was comparable, indicating that in this species, reduction of cowbird impacts through nest manipulation to remove cowbird eggs is effective. Desertion by Least Bell's Vireos does not appear to be an adequate natural defense against parasitism, suggesting the need for continued cowbird control while vireo populations are re-established.

Key words: brood parasitism, Brown-headed Cowbird, endangered species, Least Bell's Vireo, Molothrus ater, *nest desertion,* Vireo bellii pusillus.

Consecuencias de la Deserción de Nidos sobre la Adecuación Biológica en un Hospedero Amenazado, *Vireo bellii pusillus*

Resumen. Análisis recientes del impacto del parasitismo de *Molothrus ater* sobre la productividad de los hospederos sugieren que mientras el parasitismo reduce la productividad por nido, la habilidad de las parejas parasitadas de abandonar los nidos parasitados y de reanidar les permite obtener una productividad comparable a la de parejas no parasitadas. Esto tiene consecuencias para el manejo de especies amenazadas muy vulnerables al parasitismo, que son el foco de muchos programas de control de *M. ater*. Calculé el esfuerzo de anidación por temporada (número de nidos por pareja) y productividad de 568 parejas de *Vireo bellii pusillus* monitoreadas durante 11 años en el río San Luis Rey, San Diego, California (donde la captura de *M. ater* ha reducido pero no eliminado el parasitismo). Las parejas fueron asignadas a tres grupos: (1) desertoras, (2) rescatadas (parejas parasitadas ''rescatadas'' mediante la remoción de huevos de *M. ater*) y (3) no parasitadas. Las parejas parasitadas intentaron un número significativamente mayor de nidos por temporada que las no parasitadas, y las desertoras produjeron más nidos que las rescatados. Sin embargo, la productividad de las parejas desertoras fue significativamente menor que la de las parejas rescatadas o las no parasitadas, principalmente debido a que en los siguientes intentos de las parejas desertoras los nidos también fueron parasitados. La productividad por temporada fue similar entre las parejas rescatadas y las no parasitadas, indicando que la extracción de huevos de *M. ater* es una práctica efectiva que reduce el impacto del parasitismo. La deserción por parte de *V. b. pusillus* no parece ser una defensa natural adecuada contra el parasitismo, sugeriendo que debe continuarse el control de *M. ater* mientras se reestablece la población de *V. b. pusillus*.

INTRODUCTION

Declines in many sensitive bird species are attributable, at least in part, to the detrimental impacts of Brown-headed Cowbird (*Molothrus ater*) parasitism on host reproductive success and productivity (Walkinshaw 1972, Mayfield 1977, Franzreb 1987, Marshall and Stoleson 2000). Consequently, cowbird control has been employed for over a decade to promote recovery of threatened and endangered species such as Kirtland's Warbler (*Dendroica kirtlandii*; Kelly and DeCapita 1982), Golden-cheeked Warbler

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(*D. chrysoparia*), Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Whitfield et al. 1999, Whitfield 2000), California Gnatcatcher (*Polioptila californica*; Braden et al. 1997), Black-capped Vireo (*Vireo atricapillus;* Grzybowski et al. 1986), and Least Bell's Vireo (*V. bellii pusillus*; Kus 1999, Griffith and Griffith 2000). As we evaluate the effectiveness of cowbird control and design management plans for these and other species, two questions must be addressed: (1) is the control working?, and (2) is it necessary? The answer to the first question necessarily depends on the objective of the control, which within the context of endangered species recovery ultimately is to increase population size and distribution to the point that the species is no longer threatened by extinction. The second question is less straightforward, and requires knowledge of the host's natural defenses against parasitism, if any, and the conditions under which these defenses are sufficient to maintain stable populations without human intervention. These conditions are likely defined by a complex set of interacting variables including host and parasite abundance, habitat availability and configuration, and other factors that change over time as managers endeavor to create conditions favorable to host population growth. Because of this, periodic evaluation of the need for cowbird control is a necessary and appropriate component of an adaptive management program.

The most common form of defense against parasitism among small hosts is nest desertion followed by renesting (Friedmann 1963, Graham 1988, Rothstein 1990). By this mechanism, ''deserters'' are able to fledge more young than ''acceptors,'' and in some cases can achieve seasonal productivity equivalent to that of unparasitized pairs (Goguen and Matthews 1996, Budnik et al. 2001). Although parasitized pairs experience lower success per nest, their ability to renest and ultimately fledge young constitutes a defense that would allow such a host to persist in the absence of cowbird management (Pease and Grzybowski 1995, Schmidt and Whelan 1999).

I examined the fitness consequences of desertion in the Least Bell's Vireo, an endangered subspecies of Bell's Vireo confined to riparian habitat in southern California and Baja California. Least Bell's Vireos are heavily parasitized, and have been managed for the last 15 years by trapping to remove cowbirds from breeding habitat, as well as nest manipulation to remove cowbird eggs from parasitized nests (Kus 1999, Griffith and Griffith 2000). Vireo numbers have increased sixfold since the initiation of widespread cowbird control in the mid-1980s (BEK, unpubl. data), evidence that the control benefited the species during the ''crisis'' stage of recovery when vireos numbered in the low hundreds rangewide. Here, I assess the role of nest desertion in reducing the impacts of parasitism and evaluate the potential for this species to persist in the absence of cowbird management.

METHODS

STUDY AREA AND STUDY SPECIES

Least Bell's Vireos were studied during 11 years between 1988 and 2000 (excluding 1997 and 1998) along a 16-km reach of the San Luis Rey River downstream of Interstate 15 in northern San Diego county, California (33°17′N, 117°13′W). This portion of the drainage supports a riparian corridor of mixed cottonwood-willow habitat bordered by roads, golf courses, agricultural fields, residential areas, and commercial developments. Annual cowbird trapping was conducted at the site from 1988 through 1998, but constraints on the number, placement, and dates of operation of traps, as well as high cowbird abundance in the study area, limited the extent to which trapping reduced parasitism (Kus 1999). No traps were operated in 1999 or 2000.

Breeding Least Bell's Vireos begin arriving at the study site during the latter part of March and typically begin nesting in early April. Birds remain through early October, although nesting is complete by the end of July (Kus 1999). Nest construction requires approximately four days, and egg laying commences one day later. Females typically lay one egg per day for a total clutch of 3–4 eggs, and begin incubation with the penultimate egg (Brown 1993). Vireos readily renest following nest failure, attempting as many as five nests per season (BEK, unpubl. data). Predation is the major cause of nest failure at the site, averaging 37 ± 7% of completed nests per year (SD; $n = 9$ years, Kus 1999).

Cowbirds typically arrive at the study site in early April; however, prior to mid-April, most individuals are migrants (J. Wells and J. Turnbull, unpubl. data). Cowbirds breed in the area from mid-April through August, by which time

most hosts have ceased nesting. The laying period of cowbirds thus overlaps with that of vireos during all but approximately the first two weeks of the vireo's breeding season in most years.

VIREO NEST MONITORING

Least Bell's Vireos were studied each year between 15 March and 31 August. Surveys were conducted early in the spring to locate territories and identify pairs, which were then monitored for nesting activity throughout the entire season. Nests were located and their contents checked weekly using extendable mirrors to minimize disturbance to vegetation at nest sites. The number of eggs and nestlings present in nests was recorded on each visit. Any cowbird eggs encountered in nests were removed by hand using adhesive tape to avoid damage to vireo eggs. Nests were monitored until they either fledged young, were depredated, or were abandoned. Nests were considered abandoned if their contents were cold or destroyed and no longer tended by adults. Abandonment was attributed to parasitism only when cowbird eggs were present in the nest or on the ground beneath it.

STATISTICAL ANALYSES

I compared the number of nest attempts and total number of young fledged per season by vireo pairs in three groups: deserters (pairs that deserted one or more parasitized nests), rescued (pairs with one or more parasitized nests from which cowbird eggs were removed), and unparasitized pairs (pairs without any parasitized nests). Nesting effort was calculated from a dataset combining all years, after inspection of the data revealed no inconsistencies across years with regard to variance and pattern of response among the three groups. A one-way ANOVA followed by independent-sample two-tailed *t*-tests was used to compare the average number of nesting attempts per pair across the three pair types. Seasonal productivity of pairs was compared using two analyses. First, a series of logistic regressions was performed to calculate the likelihood of fledging any young in a particular season for the three groups. In these analyses, the dependent variable ''success'' was coded as 0 for pairs failing to fledge young, and 1 for pairs fledging one or more young. Independent variables included pair type (deserter, rescued, or unparasitized), year, and year × pair type.

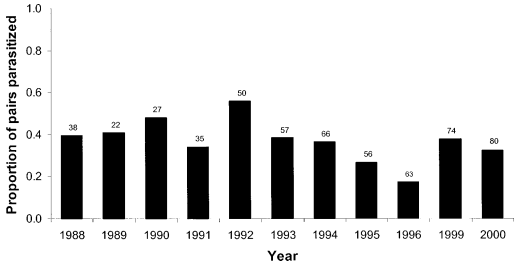

FIGURE 1. Proportion of Least Bell's Vireo pairs parasitized at the San Luis Rey River, California, 1988–2000 (excluding 1997 and 1998). Numbers above bars represent population size (number of pairs).

The categorical variable pair type was analyzed using dummy variables to allow comparisons of rescued and unparasitized pairs to deserters, the reference group (constant). Likelihood-ratio tests were used to compare models and evaluate the effects of the independent variables on pair success. Log odds of success were converted to probabilities for use in subsequent analysis using the formula $probability = odds\ (1 + odds)^{-1}$, first deriving odds by exponentiating (using natural logs) the log odds generated by the logistic regression for each pair type (Afifi and Clark 1990). I then used independent-sample two-tailed *t*-tests to compare the average number of young produced by successful pairs across pair types, excluding pairs that failed to fledge young. Finally, I multiplied the probability of success by the average number of young fledged by successful pairs to produce an estimate of pair productivity for deserters, rescued pairs, and unparasitized pairs. Significance was accepted at $P < 0.05$. Values reported are means ± SD.

RESULTS

The proportion of vireo pairs parasitized each year averaged 37 ± 10% ($n = 568$), and was generally consistent over time despite a more than doubling in size of the study population (Fig. 1). The lowest rate of parasitism observed (18% of pairs) occurred in 1996, when trapping effort was substantially improved relative to previous years (Kus 1999). The proportion of pairs parasitized in 1999 and 2000, when no traps were operated, was comparable to that observed prior to 1996, suggesting that vireos breeding at this site prior to 1996 experienced parasitism levels similar to those in unmanaged populations.

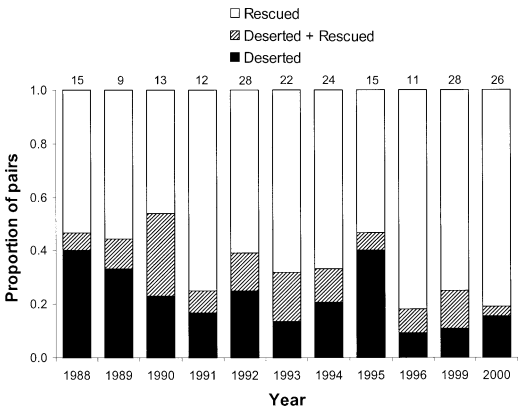

FIGURE 2. Response of Least Bell's Vireos to parasitism at the San Luis Rey River, California, 1988–2000 (excluding 1997 and 1998). Numbers above bars represent number of parasitized pairs.

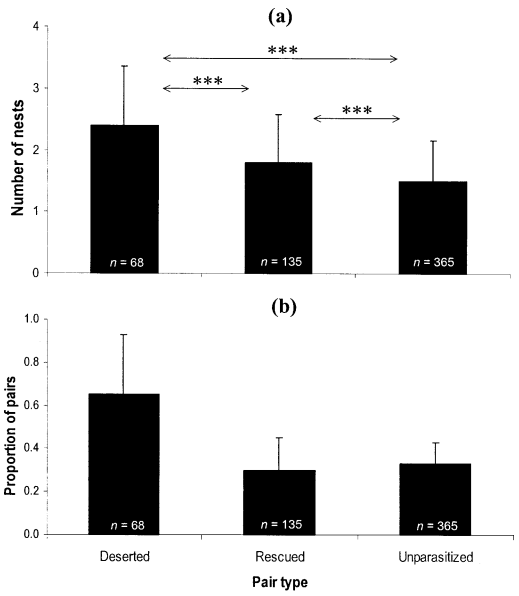

FIGURE 3. (a) Number (mean ± SD) of nesting attempts per year by deserters, rescued, and unparasitized Least Bell's Vireo pairs at the San Luis Rey River; (b) proportion (mean ± SD) of deserters, rescued, and unparasitized pairs failing to fledge young by the end of the breeding season. Sample size is the number of pairs. ***$P < 0.001$.

RESPONSE TO PARASITISM

Of the parasitized pairs each year, between 9% and 40% deserted at least one parasitized nest (Fig. 2; mean = 23 ± 11%). Most pairs did not abandon parasitized nests, and were rescued by the removal of cowbird eggs from their nests. A small number of pairs in each year both deserted nests and were rescued in later nesting attempts; in most years, this amounted to a single pair, and in no year did the number of pairs in this category exceed four. Because I considered the size of this group in each year inadequate for analysis as a separate category, I combined these pairs with deserters into a single category for further analysis.

NESTING EFFORT BY PAIRS

Pairs differed with regard to the number of nests produced per season ($F_{2,570} = 50.2$, $P < 0.001$). Deserters attempted significantly more nests than did both rescued pairs ($t_{201} = 4.9$, $P < 0.001$) and unparasitized pairs ($t_{428} = 10.1$, $P < 0.001$), averaging 2.4 ± 1.0 nests per year (Fig. 3a). Rescued pairs also renested significantly more often than unparasitized pairs ($t_{495} = -4.7$, $P < 0.001$), although the difference between these two groups was small (rescued pairs: mean = 1.8 ± 0.8; unparasitized pairs: mean = 1.5 ± 0.7).

Parasitized birds were highly likely to be parasitized repeatedly throughout the season: of pairs that renested following abandonment or failure of parasitized nests ($n = 203$), 57 ± 18% experienced one or more subsequent parasitism events.

SEASONAL PRODUCTIVITY

Between one-third and two-thirds of pairs were unsuccessful in fledging young each year, despite renesting after failed attempts. The proportion of unsuccessful pairs was consistently highest for deserting pairs, over 60% of which on average failed to fledge young (Fig. 3b), double the proportion observed among rescued and unparasitized pairs. Of the renesting attempts by deserting pairs, 31% ($n = 86$) failed from predation, comparable to the 37% of renests by rescued ($n = 90$) and unparasitized ($n = 132$) pairs that were depredated. However, an additional 34% of renests by deserters were parasitized and abandoned, and 19% of renests by deserters failed as a result of other or unknown causes such as abandonment prior to nest completion or desertion of inviable eggs, higher than the 7–9% of such failures by renesting rescued and unparasitized pairs, respectively. I therefore used logistic regression to compare the likelihood of success among the three pair types before cal-

TABLE 1. The logistic regression model that best described the likelihood of success (fledging ≥ one young per season) by Least Bell's Vireo pairs at the San Luis Rey River, California. Odds ratios reflect the likelihood of success by rescued and unparasitized pairs, respectively, relative to deserters.

Parameter	Estimate	SE	*P*	Odds ratio
Constant: deserted	−0.54	0.25	0.03	
Pair type: rescued	1.55	0.32	<0.001	4.7
Pair type: unparasitized	1.12	0.27	<0.001	3.1

TABLE 2. Seasonal productivity of Least Bell's Vireo pairs at the San Luis Rey River, California. Probability of success calculated from log $\text{odds}_{(\text{success} = 1)}$ = –0.54 + estimate (1) for each pair type (Table 1; see Methods).

Pair type	Probability of success	Mean (± SD) number young per successful pair	Productivity (young per pair per year)
Deserted	0.36	2.8 ± 1.3	1.01
Rescued	0.73	2.4 ± 1.2	1.75
Unparasitized	0.64	3.1 ± 1.4	1.98

culating the average number of young produced by pairs in each group. The model that best discriminated between successful and unsuccessful pairs was that including pair type as the sole independent variable (log likelihood of constants only model $\chi^2_2 = 25.9$, $P < 0.001$; Table 1). Inclusion of year and year × pair type did not improve the model (log likelihood $\chi^2_1 = 2.0$, $P = 0.36$; and $\chi^2_3 = 3.4$, $P = 0.34$, respectively). Unparasitized pairs were three times more likely than deserters to fledge young, and rescued pairs were nearly five times more likely to be successful than were deserting pairs.

Among successful pairs, the number of young fledged per season by deserters that renested did not differ significantly from that of rescued pairs ($t_{122} = -1.3$, $P = 0.19$) or unparasitized pairs ($t_{257} = 1.2$, $P = 0.22$; Table 2). However, production of young by rescued pairs was significantly lower than that of unparasitized pairs by approximately 0.7 young per year ($t_{331} = 4.5$, $P < 0.001$).

Seasonal productivity, calculated as the product of the probability of success and the average number of young fledged by successful pairs, differed across pair types, with deserters producing half as many young per year as rescued and unparasitized pairs (Table 2). Although rescued pairs fledged significantly fewer young per season than did unparasitized pairs, they were more likely to be successful, producing an estimate of seasonal productivity comparable to that of unparasitized pairs.

DISCUSSION

Least Bell's Vireo pairs that deserted parasitized nests and renested produced about half as many young per season as did unparasitized pairs and pairs rescued by the removal of cowbird eggs from their nests. Although successful deserters fledged as many young as successful rescued and unparasitized pairs, deserters were far less likely to be successful, and most deserting pairs failed to fledge any young.

The frequency of desertion by Least Bell's Vireo pairs studied here (mean = 23%) is lower than that reported for other subspecies of Bell's Vireo. Budnik et al. (2001), in a 3-year study of *V. b. bellii* breeding in central Missouri, found that 55% (23 of 42) of parasitized pairs deserted at least one nest, and that 51% of all parasitized nests were abandoned. Parker (1999) documented an even higher rate of nest abandonment (74% of 43 parasitized nests) among Bell's Vireos breeding in Kansas, and although he did not report the proportion of pairs that deserted parasitized nests, it was likely similarly high. Bell's Vireos (*V. b. arizonae*) nesting along the lower Colorado River deserted 43% of parasitized nests (Averill-Murray et al. 1999), suggesting that desertion among pairs in this population is more frequent than by Least Bell's Vireos in southern California, which on average abandon 29% of nests (Kus 1999). The reasons for the high variability in desertion rates across vireo populations are unknown; however, at least two lines of evidence suggest that desertion may be a conditional response to factors that vary geographically and temporally, and, perhaps, with age and experience of host pairs. First, vireo pairs in Missouri (Budnik et al. 2001) and California (this study) did not consistently desert parasitized nests. Budnik et al. (2001) observed that fewer than half of the parasitized pairs in their analysis followed a pure strategy of ''always desert'' or ''always accept,'' and that most pairs exhibited both responses in a given year. Least Bell's Vireos displayed a similar pattern through the occurrence in each year of the study

of pairs that both deserted and were rescued (termed ''acceptors'' by Budnik et al. (2001). Second, the probability of desertion in Least Bell's Vireos is a function of vireo clutch size at the time cowbird eggs are laid and the degree of clutch size reduction resulting from egg removal by cowbird females (Kus 1999). The combined effects of these factors on the likelihood of nest desertion results in a higher rate of abandonment for nests left with two or fewer vireo eggs than nests left with more than this. The observed response to reduced clutch size is probably a response to a reduction in total clutch volume (including the cowbird egg), as abandoned clutches on average have been reduced by two vireo eggs. Desertion thus appears to be mediated by several factors, the identification of which warrants further investigation.

The primary reason that deserting pairs of Least Bell's Vireos rarely succeeded in fledging young was the high probability that renests following parasitism were also parasitized, as predation of renests did not differ from that of renests by rescued and unparasitized pairs. Most deserters thus continued to renest until they either gave up or reached the end of the breeding season. This situation differs from that encountered by vireo populations in the Great Plains, where cowbirds cease breeding approximately 2–3 weeks prior to the end of the vireo nesting season (Parker 1999, Budnik et al. 2001). Under these conditions, pairs that desert and renest later in the season have a high likelihood of escaping parasitism and ultimately fledging young, making desertion a beneficial response to parasitism (Parker 1999, Budnik et al. 2001). The selective advantage of desertion in a given population is thus clearly dependent on seasonal patterns of parasitism and the corresponding probability of parasitism of renests.

Although deserting Least Bell's Vireo pairs fledge fewer young per season than do unparasitized pairs, they fledge more than they would by accepting cowbird eggs, since virtually no vireo young fledge from parasitized nests (Pitelka and Koestner 1942, Parker 1999, Budnik et al. 2001). Selection is thus predicted to favor desertion when it occurs. Why, then, are desertion rates so low in the Least Bell's Vireo? Rothstein (1975a, 1982) suggested that populations such as this with low desertion rates are actually undergoing an evolutionary transition from being largely acceptors to becoming rejectors (''evolutionary lag'' hypothesis). When the cost of accepting parasitism is high, as it is for Bell's Vireos, selection should act rapidly to bring desertion to fixation, a process that Rothstein (1975b) suggested can occur for other host defenses (e.g., cowbird egg ejection) within 100 years. Least Bell's Vireos in California have been exposed to cowbird parasitism for just under a century (Laymon 1987, Rothstein 1994), and while it is possible that vireo populations are in transition and that desertion is becoming more frequent, it does not appear from the results of this study that selection for desertion is very strong. Even though some deserting pairs are able to fledge young by renesting, most do not, and seasonal productivity of deserters is relatively low. Ironically, efforts to minimize parasitism and its effects through cowbird trapping and vireo nest manipulation are in fact hindering any evolutionary transition that might be occurring by removing the selective costs of accepting parasitism. These factors combined suggest that under current management, considerably more than 100 years will be required for desertion to achieve levels at which it could function as a natural defense against parasitism sufficient to maintain stable populations.

Recency of contact with cowbirds is often invoked to explain the lack of defenses against parasitism observed among new host populations (Mayfield 1977, Reed 1999). However, Hosoi and Rothstein (2000) in a recent analysis of nonforest species found no differences in desertion rates among old and new host populations, and concluded that new hosts retain the desertion response through shared genetic heritage with old-host relatives. Least Bell's Vireos are an exception to this pattern, suggesting that at least some new host populations may retain particular behaviors, but express them at rates different than those in populations of the old host (in this case, *V. b. bellii*, which evolved in sympatry with cowbirds in the Great Plains). Moreover, the selective environment in which desertion by Least Bell's Vireos is expressed differs from that in which the behavior evolved, yielding substantially different fitness consequences for deserters in the old and new host populations. These findings caution against generalizing from old to new hosts with regard to host-parasite relationships, and emphasize the need for population-specific assessments.

Rescued pairs exhibited seasonal productivity comparable to that of unparasitized pairs, although the two groups differed with regard to the components of productivity analyzed here. Rescued pairs were slightly more likely than unparasitized pairs to fledge young; however, this may be an artifact of the way pairs were grouped for analysis. By definition, rescued nests had to survive long enough for cowbird eggs to be laid and discovered by field investigators, a criterion that may have excluded nests failing early in the laying period to predation or other causes from this group. Although many rescued pairs produced unparasitized as well as parasitized nests, only 9% ($n = 248$) of nests in the rescued group failed early (e.g., containing fewer than two eggs on the last nest check), roughly half the 16% ($n = 543$) of early-failing nests among the unparasitized pairs. The possible over-representation of early-failing nests in the unparasitized group would result in an underestimate of this group's probability of breeding success, although the effect would be limited to pairs that either produced just one nest in a given season and experienced early nest failure, or produced multiple nests, all of which failed early. This was the case for 9% (33 of 365) of the unparasitized pairs. Rescued and unparasitized pairs did not differ with regard to other factors influencing seasonal productivity, such as predation (Kus 1999).

Rescued pairs, although at least as likely as unparasitized pairs to be successful, fledged significantly fewer young per season than did pairs escaping parasitism entirely. Responsible for this is the fact that while nest manipulation served to rescue parasitized nests from a fate of fledging only cowbirds, it could not prevent the removal of or damage to host eggs by female cowbirds (Kus 1999). As a result, clutch size was significantly smaller, and hatch rate significantly lower, in rescued as opposed to unparasitized nests (Kus 1999), reducing seasonal production of young by parasitized pairs. Nevertheless, nest manipulation as practiced at our study site has been effective in achieving a degree of productivity among parasitized pairs comparable to that of unparasitized birds, which in turn has produced a steady increase in this population over the decade and a half that it has been studied. Populations of other endangered species, such as Southwestern Willow Flycatcher, Kirtland's Warbler, and Black-capped Vireo, have shown similar increases in seasonal productivity as a result of cowbird removal and host nest manipulation, although increased productivity has not always been accompanied by increases in host population size (Rothstein and Cook 2000).

In conclusion, Least Bell's Vireos neither desert parasitized nests nor produce young from renests at rates high enough for desertion to be considered an adequate natural defense against parasitism. In the absence of other measures to reduce cowbird access to vireo breeding sites, continued cowbird control may be necessary in some areas to maintain vireo populations above the level at which they are vulnerable to local extinction. This does not imply that cowbird control need be a permanent component of vireo management, however, and identification of the conditions necessary for vireos and other riparian inhabitants to withstand parasitism with minimal management should remain a conservation priority. The challenge will be to reconcile the short-term objective of protecting existing populations with the need to facilitate the evolutionary processes that will ultimately determine the long-term prospects for this endangered species.

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