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IMPACTS OF BROWN-HEADED COWBIRD PARASITISM ON PRODUCTIVITY OF THE ENDANGERED LEAST BELL'S VIREO

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Abstract. The Least Bell's Vireo (*Vireo bellii pusillus*) is an obligate riparian breeder brought to the brink of extinction in the last 50 years by habitat loss and Brown-headed Cowbird (*Molothrus ater*) parasitism. Although cowbird removal programs have effectively reversed the species' decline and promoted a rangewide population rebound, limitations on the timing, duration, location, and scope of trapping efforts permit parasitism to continue in some vireo populations. We quantified the impact of cowbirds on vireo productivity during a 9-yr study of one such population at the San Luis Rey River, California, where trapping of adults and removal of cowbird eggs from vireo nests were conducted annually to control parasitism. Cowbird parasitism occurred in every year of the study, and extended throughout the entire breeding season (April–August). Nineteen to 43% of nests (N = 667), and 19–56% of pairs (25–66), were parasitized at least once during a given year. On average, 29% of parasitized nests (N = 207) were abandoned before cowbird eggs could be removed, and parasitism was responsible for up to 29% of all nest failures. Of 139 nests from which cowbird eggs were removed, 99% remained active, and half eventually fledged vireo young. However, reduced clutch size and hatch rate in these "rescued" nests resulted in the production of up to four times fewer young per nest, and half as many young per egg, than non-parasitized nests. Nevertheless, nest monitoring and cowbird egg removal enhanced annual productivity by 11–44% over that expected in the absence of monitoring and removal. While monitoring and egg removal are effective tools in reducing impacts of parasitized nests, it is essential that appropriate trapping protocol be implemented to prevent access of cowbirds to nests and thus eliminate the impacts that monitoring cannot control. Long-term plans for management of cowbirds and their hosts should emphasize controlling landscape level factors influencing cowbird abundance as opposed to reliance solely on localized trapping programs.

Key Words: brood parasitism, Brown-headed Cowbird, endangered species, Least Bell's Vireo, *Molothrus ater,* reproductive success, species management, *Vireo bellii pusillus.*

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) has been implicated in the declines of many sensitive species of the western United States (Hanna 1928, Gaines 1974, Goldwasser et al. 1980, Laymon 1987, Unitt 1987, Harris 1991; U.S. Fish and Wildlife Service 1991, 1992; Brown 1994) . Among these is the Least Bell's Vireo (*Vireo bellii pusillus*), an obligate riparian breeder once abundant throughout the coastal and interior lowlands of California and Baja California, but currently restricted in the U.S. to a few drainages in southern California (Cooper 1861; Anthony 1893, 1895; Fisher 1893a, Grinnell and Swarth 1913, Grinnell and Storer 1924, Grinnell and Miller 1944) . The vireo, a state and federally listed endangered species, was extirpated from most of its historic range by widespread habitat loss and, secondarily, cowbird parasitism, the impact of which was evidently greater than the resultant small, fragmented populations could withstand (Franzreb 1989a). Like other vireos (Graber 1961, Friedmann 1963), the Least Bell's Vireo is particularly susceptible to parasitism, which is currently the most immediate threat to the vireo's persistence. In light of this, recovery efforts have focused on implementing cowbird removal programs in vireo breeding areas to control parasitism. Cowbird trapping, coupled with nest monitoring to detect and remove cowbird eggs from vireo nests, has virtually eliminated parasitism from many populations (Griffith and Griffith in press; B. Kus unpubl. data), and in the dozen years since listing has reversed the vireo's decline and brought about a 6-fold increase in population size (L. Hays, pers. comm.).

Although cowbird trapping has been successful in promoting a rangewide population increase, programs in some areas have been unsuccessful, allowing parasitism of vireos to continue. While undesirable within the context of short-term management goals, such circumstances afford a rare and important opportunity to quantify the impacts of cowbirds on vireos with the aim of evaluating long-term management options through an understanding of cowbird-host dynamics. One site where such an investigation has been feasible is the San Luis Rey River in northern San Diego County, California. This 80-km drainage, bordered by agricultural, residential, commercial, recreational (golf course, equestrian centers), and other types of lands attractive to cowbirds, has traditionally been difficult to manage with regard to cowbird control. Limited access to properties, vandalism of traps, and other obstacles have prevented deployment of an adequate number of cowbird traps in suitable locations within the appropriate

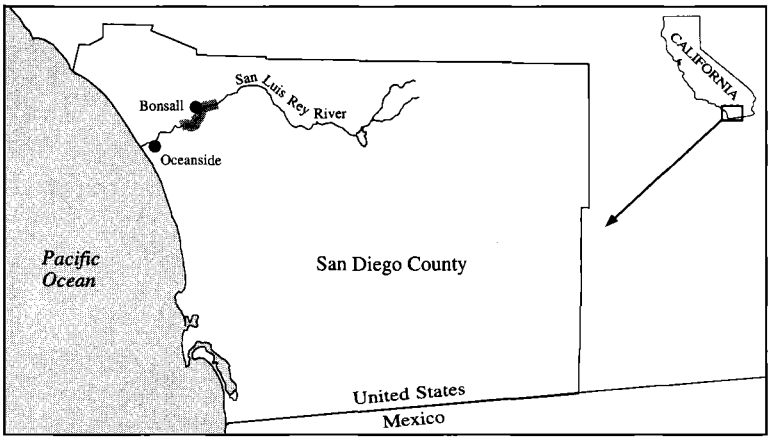

FIGURE 1. Location of study area (shaded region) along the San Luis Rey River in San Diego County, California.

time frame (1 April–15 July) to effectively remove cowbirds from vireo breeding habitat and thereby eliminate parasitism (G. Collier, pers. comm.). Consequently, the San Luis Rey River supports one of the most heavily parasitized populations of Least Bell's Vireos in the state (B. Kus, unpubl. data).

In this paper, I document the effect of cowbird parasitism on Least Bell's Vireos by drawing from the results of a 9-yr nest monitoring study of vireos at the San Luis Rey River, which at the outset of the project supported the third largest vireo population in California. I quantify the impact of parasitism on vireo productivity by comparing several reproductive parameters of parasitized and non-parasitized pairs, and conclude with an assessment of management alternatives for controlling parasitism in vireos and other species.

STUDY SITE AND METHODS

We studied vireos from 1988–1996 along a 16-km reach of the San Luis Rey River between College Avenue in Oceanside and Gird Road in Bonsall, California (Fig. 1). Cowbird trapping and vireo nest monitoring have been conducted within this portion of the drainage since 1988 as mitigation for the impacts of highway construction on vireo habitat along the river, and have been summarized in annual technical reports prepared for the California Department of Transportation, District 11, by B. Kus, G. Collier, and J. T. and J. C. Griffith. Cowbirds were captured using modified Australian crow traps baited with seed and live decoys and positioned near riparian habitat and cowbird feeding areas. Traps were serviced daily to remove cowbirds, release non-target birds, and replenish food and water. On average, 12 traps were deployed each year (range 8–15) for various lengths of time between 23 March and 1 August, with an average of 1,230 ± 444 trap-days of coverage per yr.

We studied the vireos at our site between March 15 and August 31 each year. Surveys were conducted to locate vireo territories and determine the breeding status (paired or unpaired) of all males in the study area. Pairs were visited weekly to monitor nesting activity and locate nests, which typically are placed <1m high in dense shrubby vegetation. Nests were visited according to a schedule designed to facilitate detection and removal of cowbird eggs from nests, as well as allow determination of clutch size, date of initiation, hatch rate, and fledge rate. Investigators used small automotive mirrors extendable to 1 m to examine nest contents from a distance and thereby avoid creating trails to nests. Nests were not approached if cowbirds or potential predators (e.g., Western Scrub-Jays [*Aphelocoma californica*], American Crows [*Corvus brachyrhynchos*], or Common Ravens [*C. corax*]) were in the vicinity. All cowbird eggs found in vireo nests were removed with adhesive tape to minimize disturbance to the rest of the clutch. Vireo eggs that did not hatch were examined for damage and deposited with the U.S. Fish and Wildlife Service. An attempt was made to document the fate of all nests produced by pairs in the study area.

One-tailed t-tests assuming equal variances were used to test the prediction that parasitized nests were less productive than non-parasitized nests. Correlations involving proportions were calculated using arcsine-transformed values. Variance associated with means is reported as standard deviations.

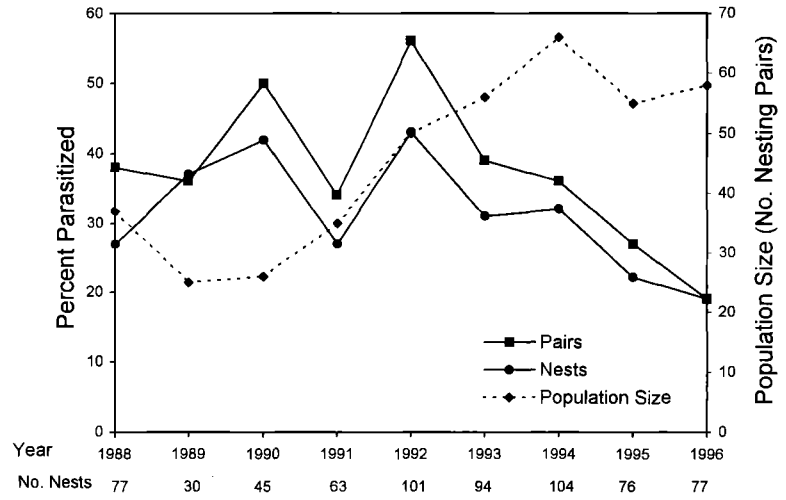

FIGURE 2. Least Bell's Vireo population size, and % of nests and pairs parasitized at the San Luis Rey River, 1988–1996. Number of trap-days = 763, 1,973, 1,784, 1,129, 1,018, 863, 820, 1,125, and 1,596 for 1988–1996, respectively.

RESULTS

Levels and Timing of Parasitism

Despite removal of several hundred cowbirds annually ($\bar{x}$ = 623 ± 258 [SD]), parasitism of Least Bell's Vireos occurred during every year of the study. The incidence of parasitism was highly variable across years, ranging from a high of 56% of pairs and 43% of nests in 1992, to a low of 19% of pairs and nests in 1996 (Fig. 2). Neither the proportion of pairs ($r = -0.35$, 7 df, $P > 0.20$) nor nests ($r = -0.43$, 7 df, $P > 0.20$) parasitized was related to vireo population size in a density-dependent manner.

Parasitism occurred throughout the entire vireo nesting season, as shown by two representative years (Fig. 3). Vireos begin arriving at their southern California breeding grounds by as early as mid-March, and typically 80% of pairs have initiated nests by the end of April, although some pairs initiate first nests as late as June (B. Kus, unpubl. data). Most nests initiated after April are re-nesting attempts following unsuccessful previous attempts. Proportionately fewer vireo nests were parasitized in early April, when most cowbirds in San Diego County are migrants en route to breeding areas elsewhere (J. Wells and J. Turnbull, unpubl. data), than during the rest of the season. Parasitism subsequently increased with the arrival of locally breeding cowbirds, occurring in 25–50% of nests initiated during 2-wk periods prior to mid-June, and 75–100% of nests initiated after that date.

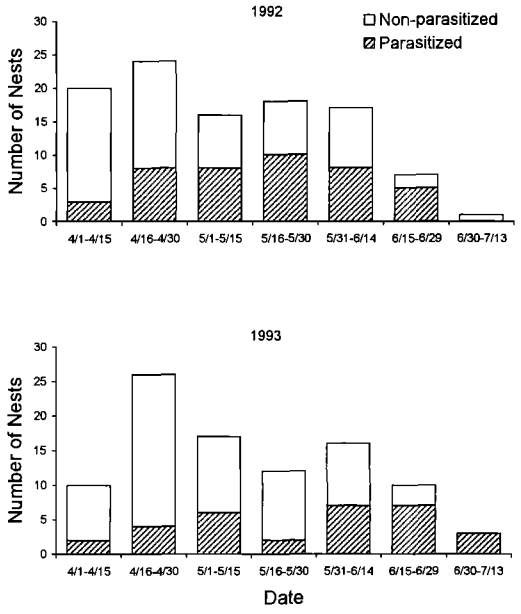

FIGURE 3. Seasonal pattern of Least Bell's Vireo nest initiations and Brown-headed Cowbird parasitism at the San Luis Rey River, 1992–1993.

Vireo Response to Parasitism

Of the 207 parasitized nests located during the study, an average of 29% (range = 12–52%, N = 9 years) were abandoned per year (Fig. 4). Of these, 97% (60/62) were abandoned by the time nest monitors detected cowbird eggs in nests, and 3% (2/62) were abandoned following removal of cowbird eggs from nests. In the latter two instances, cowbird egg removal left clutches

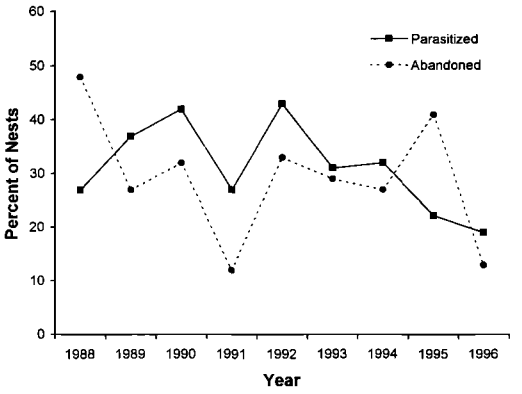

FIGURE 4. Percent of Least Bell's Vireo nests parasitized and abandoned at the San Luis Rey River, 1988–1986.

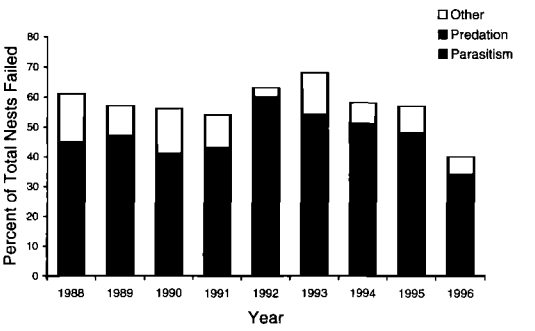

FIGURE 5. Sources of failure of Least Bell's Vireo nests at the San Luis Rey River, 1988–1996.

of two or fewer vireo eggs. The probability of abandonment (prior to egg removal) was unrelated to the rate of parasitism ($r = 0.14$, 7 df, $P > 0.50$), with pairs differing by as much as 4-fold in the likelihood of abandonment between years with similar parasitism frequencies (e.g., 1995 and 1996, 1988 and 1991; Fig. 4). Rather, abandonment appeared to be determined by clutch size (number of vireo eggs) and degree of clutch reduction by cowbirds. Clutch size reduction, presumably the result of cowbirds ejecting vireo eggs from nests at the time of laying, was particularly severe in abandoned nests. Of 31 nests for which clutch size was known prior to parasitism, clutch size reduction was documented in 90%, reducing the number of vireo eggs per nest from an average of 2.5 ± 1.1 in initial clutches to 0.5 ± 0.9 in reduced clutches ($t = 7.6$, 54 df, $P < 0.001$). Consequently, clutch size at the time of discovery of cowbird eggs was significantly smaller in abandoned nests ($\bar{x} = 0.8 \pm 1.0$, $N = 60$) than in non-abandoned nests ($\bar{x} = 2.8 \pm 0.9$, $N = 137$; $t = -14.6$, 195 df, $P < 0.001$; see below).

Eight parasitized nests still active by the time nest monitors discovered the parasitism contained only broken, dead, or no vireo eggs where eggs had been previously documented. These nests, while not abandoned, were consequently considered failures in that they had no potential to fledge vireo young. Adding these to failures resulting from abandonment, parasitism accounted for 2–17% of all nest failures in a given year (Fig. 5), adding to nest losses attributable to predation and other sources such as human disturbance and infertile clutches. The contribution of parasitism to overall nest failure was highest in years when the frequency of parasitism and the probability of abandonment of parasitized nests were simultaneously high.

Rescued Nests

Although up to half of the parasitized nests in a given year were abandoned and failed outright, the majority (137/207) of parasitized nests were "rescued" through the removal of cowbird eggs by nest monitors (Table 1). A fraction of these rescued nests subsequently failed as a result of predation, but with the exception of one year (1996), there was no evidence that predation rates of rescued nests were any higher than those of non-parasitized nests (Table 2). Between 36–70% ($\bar{x} = 48\%$, $N = 9$) of rescued nests successfully fledged vireo young, increasing annual population productivity by as much as 44% over that predicted in the absence of cowbird egg removal, where parasitized nests would either be abandoned or yield only cowbird fledglings.

Although cowbird egg removal was effective in rescuing parasitized nests, the productivity of rescued nests was significantly lower than that of non-parasitized nests as a result of the behavior of female cowbirds when depositing eggs. Vireo clutch size, calculated for nests observed

TABLE 1. Least Bell's Vireo nests remaining active following cowbird egg removal

Year	% rescued[a]	% successful	# fledglings	Increase in productivity
1988	48 (21)	70	13	24%
1989	55 (11)	50	5	18%
1990	63 (19)	50	15	37%
1991	82 (17)	36	8	11%
1992	63 (43)	55	31	44%
1993	71 (31)	41	21	38%
1994	76 (33)	44	25	27%
1995	53 (17)	44	11	12%
1996	87 (15)	39	14	10%

[a] Parasitized nests remaining active; N (total number of parasitized nests) in parentheses.

TABLE 2. PREDATION RATES OF RESCUED PARASITIZED NESTS AND NON-PARASITIZED NESTS

	Parasitized nests		Non-parasitized nests		
Year	N	% depredated	N	% depredated	P[a]
1988	10	30	43	51	0.23
1989	6	50	16	44	0.84
1990	11	45	20	35	0.34
1991	13	62	40	40	0.20
1992	27	41	56	61	0.09
1993	21	57	48	60	0.88
1994	24	54	65	49	0.70
1995	9	56	56	48	0.70
1996	13	62	57	33	0.06

[a] Chi-squared tests, 1 df.

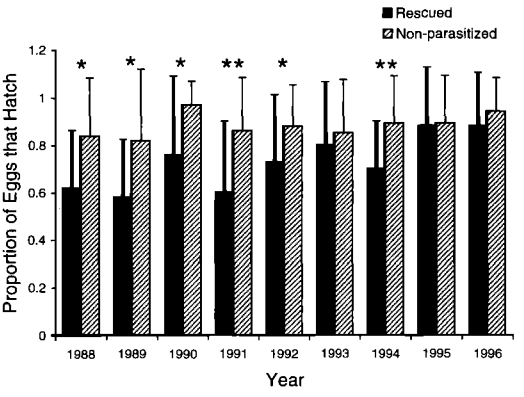

FIGURE 7. Proportion of eggs ($\bar{x}$, SD) in parasitized and non-parasitized nests that hatched at the San Luis Rey River, 1988–1996. * $P < 0.06$; ** $P < 0.01$.

with complete clutches, was significantly lower in rescued parasitized nests than in non-parasitized nests in six of the study years (Fig. 6). This was presumed to be the result of clutch size reduction by cowbirds, which was documented in 80% (8/10) of instances where it would have been possible to detect (initial clutch size: $\bar{x} = 3.6 \pm 0.52$, reduced clutch size: $\bar{x} = 2.3 \pm 0.52$; $t = 4.83$, 14 df, $P < 0.001$). In addition to, or possibly instead of, removing host eggs from nests, cowbirds frequently punctured or otherwise damaged vireo eggs, destroying egg viability and reducing hatch rates within parasitized as compared to non-parasitized clutches (Fig. 7). The difference in hatch rate between parasitized and non-parasitized nests was greatest in years when clutch size did not differ significantly between the two nest types (1988, 1989, 1991; Figs. 6 and 7).

IMPACT OF PARASITISM ON VIREO PRODUCTIVITY

The cumulative impact of cowbird parasitism on vireo productivity, produced by nest abandonment, and reduced clutch size and egg viability in non-abandoned nests, was that parasitized pairs fledged on average a half to a third as many young per nesting attempt as did non-parasitized birds (Fig. 8). Moreover, parasitized birds fledged only half as many young per egg (Fig. 9), an index of productivity reflecting reproductive effort and thus a more appropriate measure of relative fitness. This latter impact is likely underestimated in that it does not take into account undetected eggs ejected from vireo nests by cowbirds.

The predicted differences in productivity between parasitized and non-parasitized nests were observed in all years of the study, although not all differences were statistically significant (Figs. 6–9). It is likely that failure to identify significant differences in some years is due to small sample sizes, high variability, and, in

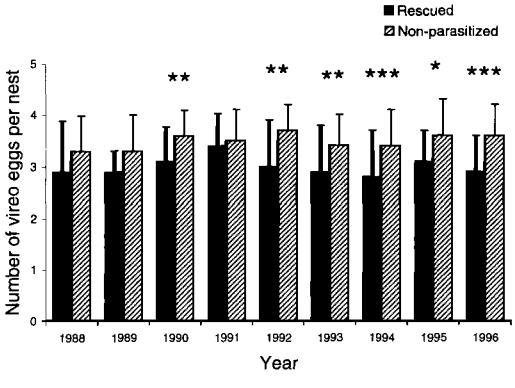

FIGURE 6. Clutch size ($\bar{x}$, SD; based on completed clutches) of parasitized and non-parasitized Least Bell's Vireo nests at the San Luis Rey River, 1988–1996. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

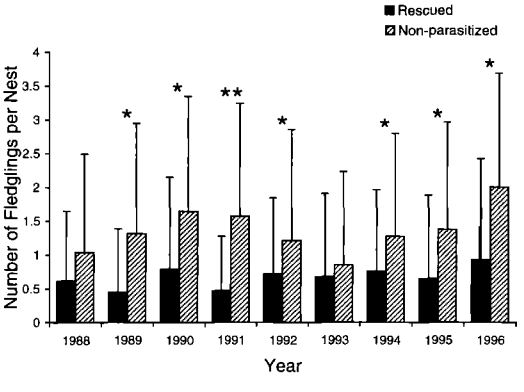

FIGURE 8. Number of fledglings per nest ($\bar{x}$, SD) in parasitized and non-parasitized Least Bell's Vireo nests at the San Luis Rey River, 1988–1996. * $P < 0.06$; ** $P < 0.01$.

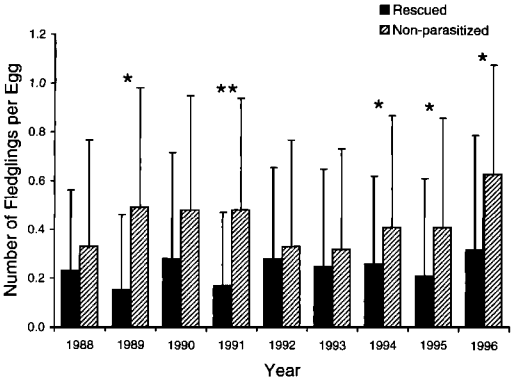

FIGURE 9. Number of fledglings per egg ($\bar{x}$, SD) in parasitized and non-parasitized Least Bell's Vireo nests at the San Luis Rey River, 1988–1996. * $P < 0.05$; ** $P < 0.01$.

some cases (e.g., clutch size in 1991, hatch rate in 1995), the lack of a true difference.

DISCUSSION

The rate of parasitism of Least Bell's Vireos in this managed population was only marginally lower than that of vireos in areas without cowbird removal programs (Gray and Greaves 1984; S. Goldwasser, unpubl. data; L. Salata unpubl. data), and varied considerably from year to year. It is likely that part of this variability stemmed from differences between years in the scope and duration of the trapping effort, with declines in recent years the result of broadening the trapping area and increasing the number of traps operated. However, environmental variables probably also contributed to annual fluctuations in parasitism, and identification of those variables is important to our understanding of cowbird-host dynamics. Clearly, a site-specific approach is necessary for properly evaluating and managing cowbird impacts on hosts, particularly in regions such as southern California that are characterized by high spatial and temporal variability.

Least Bell's Vireos in this study exhibited a strong propensity for deserting parasitized nests, at least in part a response to clutch size reduction by cowbirds. Although clutch reduction occurred in both abandoned and non-abandoned nests, the degree of reduction was significantly greater in the former, leaving vireos with clutches of fewer than one vireo egg on average as opposed to over two in non-abandoned nests. These data suggest that vireos are more likely to persist in nesting attempts where the "perceived" clutch size (vireo and cowbird eggs combined) at the time of parasitism is three or greater. Factors associated with clutch size reduction below this threshold, such as timing of parasitism and competition leading to multiple parasitism of nests, warrant further investigation to minimize abandonment of parasitized nests. Although vireos readily re-nest following nest failures, the effect of abandonment is to delay the fledging of young to the latter part of the season when post-fledging survival may be reduced by inadequate time to prepare physiologically for migration or by other factors. Parasitism during May and June, although generally less common than in April, may in fact exert a greater impact on the population in that it further delays the potential for as-yet unsuccessful pairs to fledge young within the narrowing window of time available to them. Late season parasitism may be particularly harmful; although proportionately few vireo nests are initiated after mid-June, nearly all are parasitized, preventing renesting pairs and late first-time breeders from producing any young at all and thus reducing effective population size, an important determinant of the survival of rare species.

Even if nest abandonment is averted by cowbird egg removal, parasitism reduces the potential for population growth through its effects on clutch size and hatch rate, which, combined, result in lower productivity of parasitized nests. Although pairs may ultimately succeed in fledging young, the reproductive effort required to do so exceeds that of pairs rearing young in non-parasitized nests. This is particularly so for females, which bear the cost of egg production, but also applies to males which assist with every aspect of nest-building, incubation, and rearing of young. Although spared the consequences of desertion, pairs fledging young from rescued parasitized nests realize a lower fitness return relative to investment than do non-parasitized pairs, both during the immediate season, and perhaps over their lifetimes.

An unanswered question bearing on whether rescued pairs actually experience reduced fitness is whether young fledged from rescued nests survive less well than those from non-parasitized nests. If clutch size reduction leads to reduced competition among nestlings, post-fledging survival may actually be higher in parasitized nests, offsetting part or all of the energetic costs associated with production of young. Research addressing this question will further our understanding of the costs of parasitism and the efficacy of current management techniques.

One can extrapolate from the results of this investigation and speculate on the impacts that cowbird parasitism has had on unmanaged vireo populations during the last two decades. Reports prior to the implementation of cowbird management programs indicate that cowbirds parasit-

ized 33–100% of vireo nests (Goldwasser et al. 1980, Gray and Greaves 1984; L. Salata, unpubl. data; B. Jones, unpubl. data; L. Hays, unpubl. data), and regardless of the role that cowbirds played in the initial decline of the vireo, we know from history that parasitism interacted with habitat loss to produce a precipitous and rapid decline in what was once one of California's most abundant species (Franzreb 1989a and references therein). Now well into the species' recovery, we also know that eliminating parasitism has produced an impressive population rebound. Cowbird trapping is likely to continue in the foreseeable future as a tool for promoting vireo range expansion and establishment of viable populations throughout California, and it is appropriate as we move beyond crisis management of the vireo that we consider the most biologically and economically effective options available. One option is to divorce cowbird trapping from vireo nest monitoring and apply the monetary savings to increasing the scope of the cowbird removal effort. This proposal has advantages and disadvantages; done properly, trapping is less expensive than nest monitoring, does not require specialized personnel and the same degree of state and federal permitting, and benefits all potential hosts in the area rather than just a single species. However, it results in the capture and holding of many non-target species (on average 1,285 ± 1,238 capture-events per year in this study), contributing to non-target mortality and potentially reducing reproductive success by keeping breeding birds from their nests. If not done adequately with regard to dates of operation and number and placement of traps, trapping permits parasitism to occur, which, if the trapping is performed as mitigation, is unsatisfactory, and which under any circumstances is not fully accomplishing its objective. Although trapping alone can reduce the incidence of parasitism, it cannot prevent any of the subsequent impacts on nests that are parasitized. In contrast, nest monitoring and cowbird egg removal can rescue parasitized nests by preventing total loss of vireo productivity, and do not affect non-target species. But, although it can enhance population productivity, nest monitoring cannot prevent the impacts created by egg ejection and damage done by cowbird females. Monitoring is probably the most efficient means for controlling parasitism in very small (<10 pairs) or remote populations where daily visits to check traps are prohibitively costly and time-consuming.

Presently, the most valuable use of nest monitoring within the context of cowbird control is to gauge the effectiveness of trapping programs, particularly large scale ones, and guide improvement as necessary. Once successful trapping protocols have been established, follow-up monitoring can be effectively accomplished on a 2–3 yr cycle as opposed to the annual schedule followed up to this point. Trapping by itself should suffice to eliminate parasitism in the intervening years.

Ultimately we need to develop ways to protect native birds from parasitism that do not rely on continued and invasive "topical" (localized) treatments. From a biological perspective, species like the Least Bell's Vireo will never be recovered as long as they are reliant on human intervention for their survival. Long-term funding for wildlife management is unpredictable, and it is imperative that we make progress in identifying more permanent means for controlling cowbirds and their impacts. Considerable progress has been made recently in identifying habitat and landscape features influencing cowbird densities and parasitism rates (e.g., Howe and Knopf in press, Uyehara and Whitfield in press, Petit and Petit in press, Thompson et al. in press, Robinson et al. in press, Yamasaki et al. in press, several papers in this volume). Habitat restoration to achieve conditions less conducive to cowbirds, such as enlarging or reconnecting remnants of habitat, should be pursued. Biologists should also promote changes in land use policy that discourage or restrict siting feedlots, dairies, and other operations attractive to cowbirds adjacent to host breeding habitats. Research on cowbird-host dynamics and determination of species-specific tolerable levels of parasitism should be initiated with an eye towards "weaning" sensitive species from intensive cowbird management. Only through such a long-term view can we hope to restore the native avifauna in regions where the future survival of many species is uncertain.

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