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CHAPTER 2

PARASITISM, PRODUCTIVITY, AND POPULATION GROWTH: RESPONSE OF LEAST BELL'S VIREOS (*VIREO BELLII PUSILLUS*) AND SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII EXTIMUS*) TO COWBIRD (*MOLOTHRUS* SPP.) CONTROL

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Abstract.—Cowbird (*Molothrus* spp.) control is a major focus of recovery-oriented management of two endangered riparian bird species, the Least Bell's Vireo (*Vireo bellii pusillus*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*). During the past 20 years, annual trapping of cowbirds at Least Bell's Vireo and Southwestern Willow Flycatcher breeding sites has eliminated or reduced parasitism in comparison with pretrapping rates and, thereby, significantly increased seasonal productivity of nesting pairs. Enhanced productivity, in turn, has resulted in an 8-fold increase in numbers of Least Bell's Vireos; Southwestern Willow Flycatcher abundance, however, has changed little, and at some sites has declined despite cowbird control. Although generally successful by these short-term measures of host population response, cowbird control poses potential negative consequences for long-term recovery of endangered species. As currently employed, cowbird control lacks predetermined biological criteria to trigger an end to the control, making these species' dependence on human intervention open-ended. Prolonged reliance on cowbird control to manage endangered species can shift attention from identifying and managing other factors that limit populations—in particular, habitat availability. On the basis of our analysis of these long-term programs, we suggest that cowbird control be reserved for short-term crisis management and be replaced, when appropriate, by practices emphasizing restoration and maintenance of natural processes on which species depend.

Resumen.—El manejo orientado hacia la recuperación de dos especies de aves ribereñas *Vireo belli pusillus* y *Empidonax trailli extimus* se ha focalizado principalmente en el control de los *Molothrus* spp parásitos. Durante los pasados 20 años, la captura anual de los *Molothrus* en las áreas de nidificación de *Vireo belli pusillus* y *Empidonax trailli extimus* ha eliminado o reducido el parasitismo en comparación con las tasas previas a la captura y, en consecuencia, ha incrementado significativamente la productividad estacional de las parejas reproductivas. Ese mejora en productividad, a su vez, ha resultado en que el número de *Vireo belli pusillus* se incrementara 8 veces. La abundancia de *Empidonax trailli extimus* en cambio, ha variado poco, e incluso en algunos sitios, se ha reducido a pesar del control de los *Molothrus*. Aunque aparentemente el control de *Molothrus* fue exitoso por los resultados obtenidos a corto plazo, el control de los *Molothrus* posee consecuencias potencialmente negativas para la recuperación a largo plazo de las especies en peligro. De la forma en que es actualmente aplicado, el control de los *Molothrus* carece de criterios biológicos predeterminados que permitan dejar de aplicarlo. Esto implica que las especies que se quiera proteger dependan eternamente de la intervención humana. El hecho de que que el manejo de las especies en peligro se base en la dependencia prolongada en el control de los *Molothrus* podría distraer la atención sobre la identificación y el manejo de otros factores que limitan dichas poblaciones- en particular, la disponibilidad de hábitat. Basándonos en nuestro análisis de estos programas a largo plazo, sugerimos que el

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control de *Molothrus* quede reservado para las crisis de manejo de corto plazo. Cuando fuera apropiado, es de esperar que dicho manejo sea reemplazado por prácticas enfatizadas hacia la restauración y el mantenimiento de los procesos naturales de los cuales esas especies en realidad dependen.

Least Bell's Vireo (*Vireo bellii pusillus*; hereafter "vireo") and Southwestern Willow Flycatcher (*Empidonax traillii extimus*; hereafter "flycatcher") are two federally endangered passerines that have been managed with cowbird (*Molothrus* spp.) control for the better part of the past two decades. Along with Kirtland's Warbler (*Dendroica kirtlandii*; DeCapita 2000), the vireo was one of the earliest endangered species for which cowbird control formed a prominent component of recovery-oriented management, providing a model for management of other parasitized species, such as the Black-capped Vireo (*V. atricapilla*; Hayden et al. 2000) and the flycatcher (U.S. Fish and Wildlife Service [USFWS] 2002). That, in turn, has stimulated interest in the use of cowbird control to enhance populations of riparian birds in general, many of which are major cowbird hosts (e.g. Griffith and Griffith 2000). Because managers are increasingly considering the use of cowbird control as a tool for protecting sensitive birds, it is essential that the results of established control programs and their efficacy be made available to inform their decision making. Here, we evaluate the effectiveness of cowbird control for increasing populations of vireos and flycatchers, expanding and updating earlier assessments (Whitfield et al. 1999, Griffith and Griffith 2000, Whitfield 2000), and comment on the role of cowbird management in recovery of endangered species.

Study Species

Vireos and flycatchers share many similarities in life histories and population trends over the past half-century (Brown 1993; USFWS 1998, 2002; Sedgwick 2000). Both species are riparian obligates, limited during the breeding season to dense shrubby vegetation along the margins of rivers and lakes. Predation accounts for approximately 20–50% of nest failures annually, and pairs of both species typically attempt 1–3 nests in a season (Kus 1999, Griffith and Griffith 2000, Whitfield 2000). Breeding-site fidelity is high in both species, and vireos and flycatchers have a similar life expectancy of 1–3 years.

Despite these similarities, vireos and flycatchers differ in their vulnerability to cowbird parasitism. Vireos begin nesting approximately two weeks before the arrival of locally breeding cowbirds; thus, the earliest nesting pairs can avoid parasitism (Kus 1999). In contrast, the flycatchers' breeding season in California completely overlaps the period of cowbird laying (mid-April to late July), and flycatchers are one of the few hosts still nesting by late summer. Male vireos participate in all aspects of nesting, including nest construction and incubation, and often sing from the nest; whereas male flycatchers' contribution is largely limited to feeding nestlings, and they are generally quiet around nest sites, which may reduce parasitism (Uyehara and Narins 1995). Vireos cannot fledge their own young from nests in which cowbirds hatch (Kus 1999), but flycatchers sometimes do so (Whitfield and Sogge 1999).

Vireos and flycatchers were considered common and widespread by late-19th-century and early-20th-century naturalists (Mearns 1890, Behle 1943, Grinnell and Miller 1944, Oberholser 1974, J. Hubbard unpubl. data). By the 1950s, both species were declining concurrently with widespread habitat loss and degradation, as agriculture, grazing, flood control, aggregate extraction, and urbanization reduced southwestern U.S. riparian forests to 5% of their former extent (Goldwasser et al. 1980, Unitt 1987). Cowbird parasitism probably played a secondary role in these declines, as vireo and flycatcher populations became small, fragmented, and unable to withstand heavy parasitism (Whitfield and Sogge 1999). Vireos were particularly susceptible to parasitism, with 100% of nests parasitized in some populations (Goldwasser et al. 1980). Parasitism was also high among flycatcher nests (Hanna 1928, Unitt 1987). When the vireo was listed as endangered under the Federal Endangered Species Act in 1986, its population included only 300 males and was restricted to a few southern California drainages (USFWS 1998). Flycatchers were listed in 1995, at which time they still occupied most of their historic range but in much reduced numbers (Marshall 2000), with a rangewide population of ~350 territories in seven states (USFWS 2002).

Recovery plans for the vireo and flycatcher both emphasize the need to arrest and reverse the loss of riparian habitat throughout the southwest through preservation and restoration of remaining sites. However, they differ in their treatment of the need for cowbird management and its role in eventual species de-listing. The plan for the vireo, in its second draft but still not approved by USFWS, calls for reduction or elimination of threats "so that Least Bell's Vireo populations/metapopulations...are capable of persisting without significant intervention, or perpetual endowments are secured for cowbird trapping and exotic plant control in riparian habitat occupied by Least Bell's Vireos" (USFWS 1998, p. v). The recovery plan for the flycatcher, approved in 2002, takes a more conservative approach to cowbird control, recommending it only after baseline data document a parasitism frequency of more than 20–30% of nests for two or more successive years in the population under consideration (USFWS 2002).

Methods

We evaluated vireo and flycatcher responses to cowbird control using a combination of published and new information. We supplemented data reported for vireos at Marine Corps Base Camp Pendleton, California (Camp Pendleton) in 1981–1996 (Griffith and Griffith 2000) and flycatchers at the South Fork Kern River, California (Kern) in 1989–1997 (Whitfield et al. 1999, Whitfield 2000) with data collected at these sites in recent years, and we updated analyses comparing pre- and postcontrol parasitism frequencies and host responses. We assessed the generality of results from the two sites by expanding the analyses to include additional vireo and flycatcher populations (see below), and extended earlier investigations by performing new analyses quantifying the effect of parasitism on annual productivity of both vireos and flycatchers.

Study sites.—Our assessment draws on data from long-term studies at four California sites. In addition to Camp Pendleton and the Kern River, described in detail in Griffith and Griffith (2000b) and Whitfield et al. (1999), respectively, we analyzed data from a 16-km reach of the San Luis Rey River (Kus 1999) and a 5-km reach of the San Diego River upstream of Padre Dam in San Diego County. Breeding flycatchers occur at Kern River and at Camp Pendleton, whereas vireos nest at Camp Pendleton, the San Luis Rey, and San Diego rivers.

The four sites represent the range of conditions under which breeding vireos and flycatchers occur in California. The Kern River and Camp Pendleton are relatively large and undeveloped sites, in contrast to the San Luis Rey River, which is bordered by roads, residential and commercial developments, agricultural fields, pastures, and golf courses, all of which have increased in extent over the study period. The San Diego River site is intermediate to these sites with regard to land use, with half the narrow riparian corridor bordered by native upland vegetation and the other half lying within an urban setting.

Population size and nest monitoring.—Vireo and flycatcher numbers were determined through area searches of all riparian habitat within specified study areas. When accompanied by nest monitoring, surveys were performed at least weekly to determine the status (paired, single–floater, migrant–transient) of each bird detected and to document the nesting activities of all breeding birds (Kus 1999, Whitfield et al. 1999, Griffith and Griffith 2000). Nests were located, and their contents checked periodically, more often early in the cycle, when cowbirds are likely to deposit eggs in nests. Any cowbird eggs found in vireo or flycatcher nests were removed or addled, taking care to leave a clutch of at least two eggs whenever possible to deter abandonment (Kus 1999). Pairs were monitored throughout the breeding season to allow determination of annual nesting effort and success, parasitism frequencies, and pair productivity.

Surveys of vireos and flycatchers at Camp Pendleton have been performed each year since 1981, though surveys in 1992–1994 were less intense and are not analyzed here (Table 1). Nest monitoring was conducted for vireos in 1981–1991 and 1995–2002 and for flycatchers in 1999–2003. Vireos at the San Luis Rey River were monitored in 1984, 1986 (B. Jones unpubl. data), and annually since 1988 (except for 1997, 1998, and 2002). Monitoring data for the San Diego River vireo population were collected in 1984 (B. Jones unpubl. data), 1986 (G. Collier and B. Jones unpubl. data), and 1987–1996. At the Kern River, flycatcher surveys and nest monitoring have been conducted every year since 1989.

Cowbird control.—Cowbirds were removed from vireo and flycatcher breeding sites through annual trapping, as described in Whitfield et al. (1999) and Griffith and Griffith (2000). Cowbird trapping at vireo nesting sites was conducted between mid-March and late July, whereas trapping at flycatcher sites began in May.

Cowbird trapping was initiated at Camp Pendleton in 1983 and at the San Diego River in 1987; trapping continued at both sites throughout the study period (Table 1). Trapping was conducted annually at the

TABLE 1. Annual rates of parasitism and productivity of Least Bell's Vireos and Southwestern Willow Flycatchers at four California sites, 1981–2003.

Site	Year	Cowbird control?	Number of pairs monitored	Number of nests with eggs	Percentage of nests parasitized	Number of fledglings per pair	Source
			Least Bell's Vireos				
San Diego	1984	No	18 [a]	25	80	0.2	[b]
	1986	No	21	40	33	1.6	[c]
	1987	Yes	21	29	0	2.9	[d]
	1988	Yes	28	44	2	3.6	[d]
	1989	Yes	25	38	11	3.3	[d]
	1990	Yes	24	37	22	2.7	[d]
	1991	Yes	27	42	29	1.7	[d]
	1992	Yes	24	46	26	2.2	[d]
	1993	Yes	28	61	7	4.5	[d]
	1994	Yes	32	62	8	2.7	[d]
	1995	Yes	37	56	9	2.3	[d]
	1996	Yes	30	43	0	2.9	[d]
San Luis Rey	1984	No	8 [e]	11	64	0.3	[b]
	1986	No	18	37	62	0.9	[b]
	1988	Yes	38	75	28	1.9	[d]
	1989	Yes	25	29	38	1.4	[d]
	1990	Yes	27	45	42	2.2	[d]
	1991	Yes	35	61	28	2.3	[d]
	1992	Yes	51	102	41	2.0	[d]
	1993	Yes	60	84	37	1.3	[d]
	1994	Yes	68	104	32	1.7	[d]
	1995	Yes	71	79	22	1.5	[d]
	1996	Yes	66	72	21	2.4	[d]
	1999	No	74	89	46	1.5	[d]
	2000	No	97	115	31	1.7	[d]
	2001	No	70	119	24	2.5	[d]
	2003	No	58	125	56	1.4	[d]
Pendleton	1981	No	14	15	47	0.6	[f]
	1982	No	48 [g]	93	47	2.1	[f]
	1983	Yes	54	86	10	2.9	[f]
	1984	Yes	63	78	18	1.6	[f]
	1985	Yes	66	26	4	3.2	[f]
	1986	Yes	68	32	6	2.7	[f]
	1987	Yes	97	70	17	2.6	[f]
	1988	Yes	175	244	1	2.7	[b]
	1989	Yes	129	166	1	3.5	[h]
	1990	Yes	156	151	1	3.0	[h]
	1991	Yes	133	124	0	3.0	[h]
	1995	Yes	60	89	1	2.4	[i]
	1996	Yes	60	74	0	2.1	[h]
	1997	Yes	60	81	0	2.8	[h]
	1998	Yes	59	89	0	2.2	[h]
	1999	Yes	53	82	0	2.1	[h]
	2000	Yes	58	80	0	2.9	[h]
			Southwestern Willow Flycatchers				
Kern	1989	No	30	34	50	0.8	[j]
	1990	No	30	38	61	0.7	[j]
	1991	No	31	45	78	0.8	[j]
	1992	Yes	24	36	69	1.4	[j]
	1993	Yes	26	33	38	1.4	[j]

TABLE 1. Continued.

Site	Year	Cowbird control?	Number of pairs monitored	Number of nests with eggs	Percentage of nests parasitized	Number of fledglings per pair	Source
Kern	1994	Yes	24	32	16	1.8	j
	1995	Yes	23	34	19	1.7	j
	1996	Yes	28	29	11	2.1	j
	1997	Yes	38	51	20	1.0	j
	1998	Yes	25	31	3	1.6	d
	1999	Yes	23	29	21	1.1	d
	2000	Yes	12	19	0	1.2	d
	2001	Yes	11	13	23	1.4	d
	2002	Yes	13	16	25	1.2	d
	2003	Yes	15	26	20	2.8	d
Pendleton	2000	Yes	10	8	0	2.3	d
	2001	Yes	18	29	0	1.9	d
	2002	Yes	16	29	0	1.5	d
	2003	Yes	16	25	0	2.9	d

[a] Includes data from five territories 3 km upriver of study site.
[b] B. Jones unpubl. data.
[c] G. Collier and B. Jones unpubl. data.
[d] Present study.
[e] Includes data from eight territories 2 km downriver of study site.
[f] L. Salata unpubl. data.
[g] Includes six pairs 3 km upriver of study site.
[h] Griffith and Griffith 2000, J. C. Griffith and J. T. Griffith unpubl. data.
[i] B. Kus unpubl. data.
[j] Whitfield et al. 1999, M. Whitfield and E. Cohen unpubl. data.

San Luis Rey River from 1988 to 1998, but historically it has been insufficient to eliminate parasitism at the site (Kus 1999). No trapping has been performed there since 1998. Cowbird control was initiated at the Kern River site in 1992 with shooting of cowbirds and expanded in 1994 to include seven traps.

Analyses.—We analyzed the effect of parasitism on vireo and flycatcher productivity using linear regression to evaluate the number of young fledged per pair as a function of annual parasitism frequency, combining data from all years. We calculated parasitism frequency, or the proportion of nests parasitized, using only nests observed with eggs; we excluded nests that failed before egg-laying had been confirmed and nests not located but known by detection of family groups. Although it is unlikely that nests in the latter group were parasitized, we excluded them to avoid a potential underestimate of parasitism created by the possible nondetection of unsuccessful nests, some of which could have been parasitized. Seasonal productivity was defined as total number of young produced per pair, including young fledged from nests not located. Possible nondetection of unsuccessful nests does not affect the calculation, because seasonal productivity is a function of successful nesting and is independent of the number of nest attempts. We obtained data for calculations from original sources of information reported in Griffith and Griffith (2000) for 1981–1996 to ensure consistency with our definitions. Data were analyzed separately for each site. A general linear model was used to test for homogeneity of slopes and to determine the statistical legitimacy of pooling across sites.

We assessed the effectiveness of trapping for reducing parasitism frequency by comparing pre- and post-trapping averages at each site using independent-sample one-tailed t-tests, predicting that post-trapping parasitism frequencies would be lower. In the same manner, we compared pre- and postcontrol levels of seasonal productivity, expecting to see an increase in that parameter after control was initiated. Finally, we present data from annual surveys to evaluate population growth of vireos and flycatchers in response to cowbird control.

All statistical analyses were performed with SYSTAT 10, with significance set at $P \leq 0.05$. Means are reported ± SD.

RESULTS

Effect of parasitism on productivity.—Seasonal productivity of vireos was inversely related to parasitism frequency at all three sites. At the San Diego River, where parasitism ranged from 0 to 80% between 1984 and 1996, 71% of the variability in seasonal productivity was explained by parasitism (Fig. 1A; $F = 24.8$, df = 1 and 10,

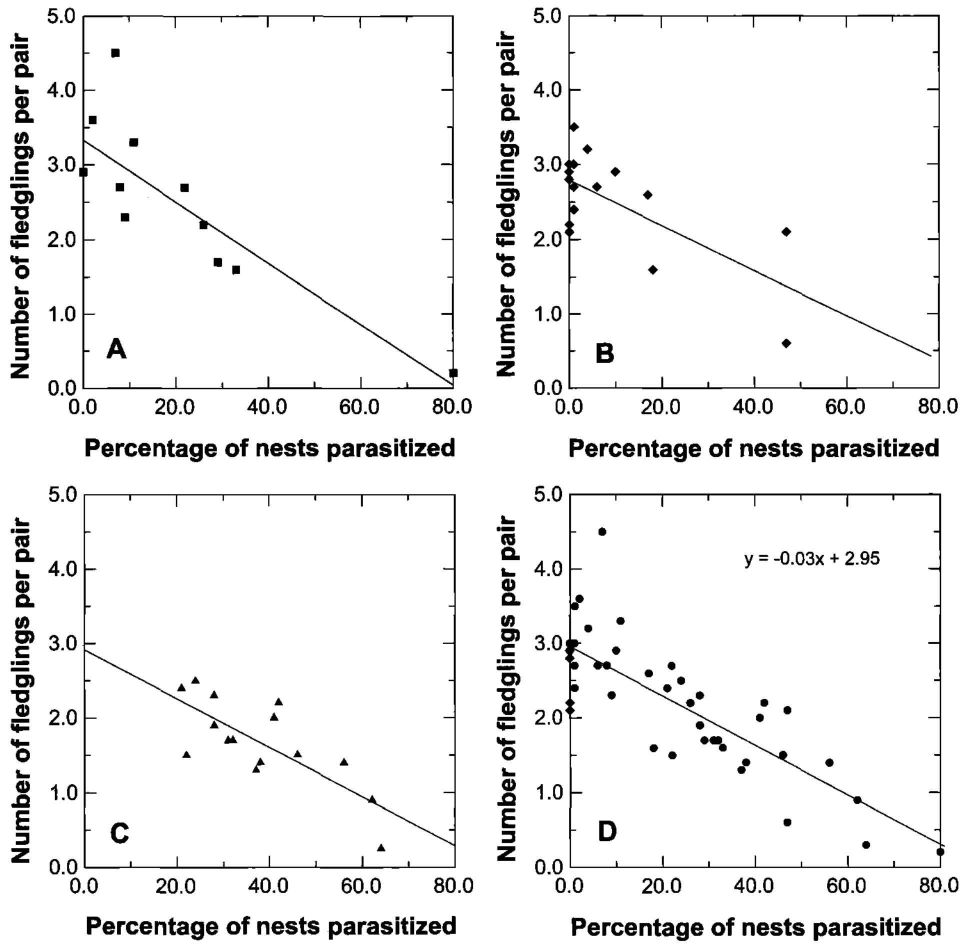

FIG. 1. Seasonal productivity of Least Bell's Vireos as a function of annual parasitism rate at (A) the San Diego River, (B) Camp Pendleton, (C) the San Luis Rey River, and (D) the three sites combined.

n = 12 years, P = 0.001). The effect of cowbirds on vireo productivity was similar at Camp Pendleton, where parasitism explained 62% of the variability in seasonal production of young between 1981 and 2000 (Fig. 1B; F = 11.8, df = 1 and 15, n = 17 years, P = 0.004). Parasitism was considerably higher at the San Luis Rey River than at the other two sites, ranging from 21% to 64% over the 20-year study period; nevertheless, vireo productivity increased with decreasing cowbird parasitism even at these high levels of parasitism (Fig. 1C; r^2 = 0.58, F = 17.9, df = 1 and 13, n = 15 years, P = 0.001). Finding no significant difference between the slopes of the three regression lines (F = 0.7, df = 2, n = 44 site-years, P = 0.53), we combined the data to determine the effect of parasitism on productivity over the full range of parasitism levels observed throughout the vireo's range, and found that parasitism explained 65% of the interannual variability in production of vireo young (Fig. 1D; F = 77.7, df = 1 and 42, n = 44 site-years, P < 0.001). Annual productivity of vireos increased by one young for each drop of 30% in parasitism frequency.

Like vireos, flycatchers at the Kern River exhibited a decline in productivity with increasing parasitism, though the relationship was not quite significant (Fig. 2; r^2 = 0.23, F = 4.0, df = 1 and 13, n = 15 years, P = 0.07). No parasitism of flycatchers occurred at Camp Pendleton during the study period, and flycatchers fledged 1.5–2.9 young per year (Fig. 2). Data from the Kern show that, over a wide range of parasitism from 0 to nearly 80% of nests, 23% of the annual variability

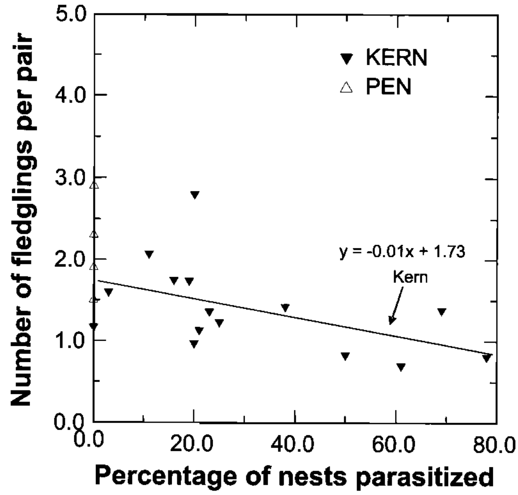

FIG. 2. Seasonal productivity of Southwestern Willow Flycatchers as a function of annual parasitism rate at Kern River (KERN) and Camp Pendleton (PEN).

in flycatcher productivity is attributable to cowbird parasitism. In flycatchers, a difference of 91% in parasitism frequency produces a change in annual productivity of one young.

Response to cowbird control.—Implementation of cowbird control at all four sites significantly reduced the incidence of parasitism of vireo and flycatcher nests (Table 1). Parasitism of vireos at Camp Pendleton dropped from an average of 47% of nests (SD = 0, n = 2 years) prior to cowbird trapping to 4% of nests (SD = 6) in the 15 years after trapping was initiated (t = 9.6, df = 15, $P < 0.001$). At the San Diego River, parasitism of vireo nests dropped from an average of 57% (SD = 33) during the two years before trapping to 11% (SD = 11) after (t = 4.0, df = 10, P = 0.001). Even at the San Luis Rey River, where parasitism has remained high in comparison with the other two vireo sites, between 1988 and 1996, parasitism declined from an average of 63% (SD = 1.4, n = 2 years) to 32% (SD = 7.9; t = 5.3, df = 9, $P < 0.001$). Since 1999 and the cessation of trapping at the San Luis Rey River, average parasitism (39%; SD = 15, n = 4 years) has not changed (t = –1.2, df = 11, P = 0.13). Parasitism of flycatcher nests at Kern River declined from 63% (SD = 14) in the 3 precontrol years to 22% (SD = 18) in the 12 postcontrol years (t = 3.66, df = 13, P = 0.001). No parasitism of flycatcher nests at Camp Pendleton has been detected during four years of monitoring since trapping began.

Associated with declines in parasitism were significant increases in seasonal productivity of both species. Vireo pairs at Camp Pendleton increased production of young from 1.4 ± 1.1 year^{-1} (mean ± SD) prior to trapping to 2.7 ± 0.5 after (t = –3.1, df = 15, P = 0.003). At the San Diego River, pretrapping productivity of 0.9 ± 1.0 young per pair increased to 2.9 ± 0.8 after trapping (t = –3.2, df = 10, P = 0.01), the highest average productivity recorded at any site with long-term monitoring. Productivity tripled at the San Luis Rey River from 0.6 ± 0.5 young per pair before trapping to 1.9 ± 0.4 in 1988–1996 (t = –4.0, df = 9, P = 0.002). The response of flycatchers to trapping, though less dramatic than that of vireos, was nevertheless significant, with pairs increasing seasonal production of young from 0.8 ± 0.1 before trapping to 1.6 ± 0.5 after (t = –2.6, df = 13, P = 0.01).

Population growth of vireos occurred at all three sites following implementation of cowbird control. At the San Luis Rey River, vireo abundance increased from 24 territories in 1984 to 132 territories in 1999; in the four subsequent years, it leveled off and declined slightly (Fig. 3A). Similarly, vireo numbers at Camp Pendleton increased from 27 territories in 1981 to >1,000 in 1998 (Fig. 3B; note different scale), then declined to an apparent equilibrium of ~800 territories. Vireos at the San Diego River exhibited a modest increase over the 13-year study period from the low 20s to the high 30s.

In contrast, flycatcher numbers at the Kern River grew for a few years post-trapping, reaching a peak of 37 territories in 1997, but then declined steeply to reach the lowest level recorded at the site in 2002 (Fig. 3C). Camp Pendleton flycatchers, in the absence of trapping, have maintained stable numbers of approximately 18–20 territories since 1995.

DISCUSSION

Least Bell's Vireo.—Cowbird control has been effective in reducing the incidence of parasitism and consequently increasing the productivity of vireos, as shown previously by Griffith and Griffith (2000). Our analysis of data collected at several sites during the past 20 years suggests that parasitism is a major determinant of seasonal production of young in vireos, illustrating another connection between cowbird control, parasitism frequencies, vireo nesting success,

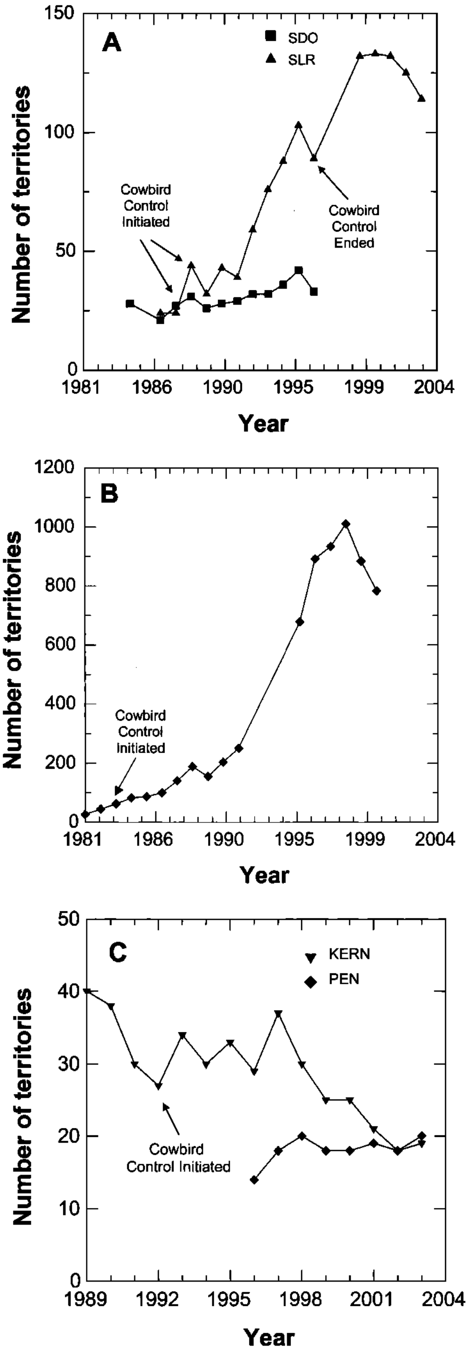

FIG. 3. Population size, between 1981 and 2003, of Least Bell's Vireos at (A) San Diego (SDO) and San Luis Rey (SLR) rivers and (B) Camp Pendleton; and of Southwestern Willow Flycatchers at (C) Kern River (KERN) and Camp Pendleton (PEN). Sources (in addition to those in Table 1): J. C. Griffith and J. T. Griffith unpubl. data.

and population size. The relationship between parasitism and productivity was consistent across several sites and maintained over a wide range of environmental conditions, including periods of drought and of high precipitation. Although other factors influenced annual productivity, parasitism accounted for ~65% of the annual variation in that measure of breeding success.

Reduction or elimination of parasitism over time and a corresponding increase in productivity have resulted in population increases in vireos at all sites where trapping has been employed. Rangewide, vireo territories now number ~2,500 (B. Kus and L. Hays unpubl. data), >8× the number that existed at the time of listing. However, allowing that trapping is clearly effective as a short-term means of increasing vireo abundance, the perspective afforded by 20 years of monitoring indicates that all of the populations described here may have reached carrying capacity, having exhibited little change during the past five years.

Despite cessation of local population growth, cowbird control is likely still contributing to vireo recovery by promoting the role of these populations as sources of dispersers that are essential for the recolonization of the vireos' historical range and maintenance of populations within an overall metapopulation. Evidence from studies of banded birds indicates that each of the populations discussed here has produced dispersers traveling as far as 250 km from their natal sites to colonize new sites, including areas along the Santa Clara and Ventura rivers in Ventura County (Greaves and Labinger 1997, Griffith and Griffith 2000, B. Kus unpubl. data) that together now support a population of >100 vireo territories (J. Greaves unpubl. data). However, saturation of habitat at vireo breeding sites that 20 years ago were among the largest remaining indicates that we have reached a pivotal point with regard to recovery, where our management priority needs to shift from enhancing numbers at historical sites to ensuring that adequate habitat exists for establishment of new populations.

Cowbird control will remain effective in increasing bird abundance only as long as suitable habitat is available to support population growth. Although no one disputes the critical need for habitat protection in recovering both vireos and flycatchers, translation of that awareness into action has been slow in coming (USFWS 1998, 2002). Practically speaking, cowbird trapping is a more straightforward and easy form of management for regulatory agencies, resource managers, and mitigants than is habitat protection, which is a complex and costly process often requiring years to accomplish. Protection of unoccupied habitat through acquisition or other agreements and creation of suitable habitat through restoration of degraded sites both present the uncertainty of whether and when sites will be colonized by the species of interest, whereas cowbird control produces immediate results. These challenges often serve as deterrents to aggressive pursuit of habitat protection, yet they underscore the need for planning and investment of resources to meet the future habitat needs of recovering species.

Southwestern Willow Flycatchers.—Unlike vireos, flycatchers have not responded to cowbird control with population increases, at least not with sustained increases. Although a significant determinant of productivity, parasitism has less of an effect on flycatchers than on vireos and minimal detectable effect on population growth, outside of a brief initial increase immediately following implementation of trapping (Whitfield et al. 1999). Today, nearly a decade after listing, flycatcher territories number only ~200 in California (Kus et al. 2003), 20% of the species' population throughout its U.S. range (Sogge et al. 2003). Clearly, factors other than parasitism are currently limiting flycatcher abundance and distribution, and exclusive emphasis on trapping will not aid in identifying or managing these factors. A similar situation was encountered in the use of cowbird trapping to increase populations of Kirtland's Warblers (DeCapita 2000). After two decades of trapping and reduction of parasitism to ~5%, Kirtland's Warbler numbers failed to increase until a wildfire created thousands of hectares of new jack pine (*Pinus banksiana*) nesting habitat, indicating that habitat availability rather than parasitism was the primary factor limiting population growth. It appears unlikely that flycatchers have saturated their existing habitat, given the decline at Kern River and the disparity in numbers of flycatchers and vireos at Camp Pendleton, where they occur sympatrically and are subject to the same management. Ongoing investigations of declining egg hatchability, possibly related to contaminants (M. Whitfield unpubl. data), and other demographic factors on both the breeding and wintering grounds, should shed light on their roles as possible limiting factors.

Cowbird control.—Cowbird control has affected the recovery of vireos and flycatchers differently. The ways that they differ are instructive when considering cowbird control in management of other species. In vireos, cowbird control has been highly effective in producing a rapid reversal of population decline, and the species is now in the process of recolonizing its historical range. Given that success, it was logical and appropriate that cowbird trapping was initiated to protect flycatchers once they were listed as endangered, and that effort, too, has advanced flycatcher recovery—not by increasing abundance, but by revealing that something other than parasitism is limiting flycatcher populations. In both cases, cowbird control has brought us to a point where a redistribution of management effort is warranted, and becoming complacent because of prior success will likely delay or prevent achievement of full recovery.

Recommendations for cowbird control.—With that in mind, we note that a critical component missing from all the cowbird control programs with which we are familiar is a plan for ending the control. Rothstein and Cook (2000) raised the same concern. Given the growth in our understanding of both the effectiveness and limitations of prolonged cowbird control and the potential for reliance on open-ended control to detract from exploring or implementing other, more appropriate forms of management, we recommend that control programs give consideration to the desired results of the control and specify criteria for ending it.

Reasons for avoiding open-ended control whenever possible include a number of economic, political, and ethical issues (Rothstein and Cook 2000, Rothstein et al. 2003). A possible biological consequence is that cowbird control interferes with the evolutionary processes necessary for establishment of genetically based natural defenses that would allow for the continued existence of host species in the absence of human intervention. We refer not to the appearance of new defenses, but to enhancement of defenses already present and expressed to some degree, a process requiring far less evolutionary time. For example, desertion of parasitized nests followed by successful renesting is a defense exhibited by many small hosts (Friedmann 1963), including other subspecies of vireos (Kus 2002). Least Bell's Vireos share an evolutionary history with these subspecies, and like them, desert parasitized nests, but at a much lower rate (29% of nests [Kus 1999] as compared with 43–74% of nests [Averill-Murray 1999, Parker 1999, Budnik et al. 2001]) and within an ecological context different from that in the Great Plains portion of the Bell's Vireo's range, where cessation of cowbird breeding 2–3 weeks before vireos stop nesting allows renesters to be successful (Parker 1999, Budnik et al. 2001). The result is that deserting Least Bell's Vireo pairs fledge only half as many young as unparasitized pairs (Kus 2002). However, they produce more young than they would if they failed to desert, creating positive selection for desertion if that behavior is heritable. Cowbird control, done effectively, removes the selective pressure necessary for promoting an increase in such a response.

Nest manipulation is another form of cowbird control that interferes with the evolution of antiparasite behaviors. Removal of cowbird eggs from vireo nests allows rescued pairs (nondeserters with at least one parasitized nest; Kus 2002) to attain seasonal productivity comparable with that of unparasitized pairs, an outcome considered a management success—which it is, in the short term. In fact, vireo young from manipulated nests are twice as likely to survive to breeding age as those from unparasitized nests (B. Kus unpubl. data), which compensates for the reduced number of young fledged from parasitized nests (Kus 1999). Again, cowbird control in the form of nest manipulation reduces the selective costs of heritable behaviors yielding vireo nests vulnerable to parasitism, which could include those involved in nest placement, timing of nest initiation, and activity at the nest. Variability exists in all of these behaviors and, if genetically based, provides the raw material on which natural selection can act given the opportunity.

We recognize that establishing goals and endpoints for cowbird control programs is a formidable challenge requiring a commitment to the practice of adaptive management as we test and evaluate various possibilities. The data summarized here offer a starting point for addressing questions of when, how, and where trapping might be reduced and eventually discontinued. For example, on the basis of a simple estimate of two young per female as the level of annual productivity needed to maintain a stable population (Franzreb 1989), our analysis indicates that Least Bell's Vireos are apparently able to maintain equilibrium numbers at parasitism frequencies of up to ~30%, supporting the frequencies proposed elsewhere (Smith 1999, USFWS 2002) as a threshold for initiating cowbird control to protect endangered species. That may be a reasonable goal for managing populations that have reached carrying capacity. The increased cost and effort of managing for 0% parasitism as opposed to 20–30% is considerable, and unjustified if unaccompanied by corresponding biological gains. Other sites might be managed as source populations with lower parasitism thresholds, again using existing data to evaluate incremental differences in the cost:benefit ratios of different options. Experimentation with some large populations on number of traps, dates of operation, and annual trapping frequency needed to achieve desired goals will be a necessary part of research on how to minimize unproductive use of cowbird control. Further studies of hosts' natural defenses are needed to establish which are genetically based and, thus, subject to natural selection, followed by analyses combining selection models and host population dynamics to identify management regimes that minimize the risk of extinction while providing conditions under which selection can operate.

Conclusion

We believe that cowbird control is an appropriate and effective short-term management tool in recovery of endangered hosts and has been instrumental in preventing extinction of vireo and flycatcher populations in California. It is not a panacea, however, and is effective only so long as parasitism is the primary limitation to population growth. The degree to which that is the case will vary from species to species, as illustrated by differences between vireos and flycatchers in their responses to control, and over time as populations encounter other obstacles to growth. We encourage managers to be mindful of that in the design of recovery-oriented management for these and other species, and to be prepared to adapt management as species' needs change. In particular, we stress the need to consider the potential negative effects of long-term cowbird control on the ability of species to persist without management intervention, and avoid creating permanent dependence on humans for survival. We encourage research exploring natural defenses in endangered hosts to guide the design of cowbird management that balances the short- and long-term needs of averting extinction and facilitating evolutionary processes necessary for host persistence.

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