CURRENT STATUS OF THE BROWN-HEADED COWBIRD IN THE SIERRA NATIONAL FOREST

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ABSTRACT.—Seasonal distribution and abundance, habitat preferences and use, and host relationships of Brown-headed Cowbirds (*Molothrus ater*) in the Sierra Nevada of California were studied in the Sierra National Forest in 1980 and 1981. From several hundred counts, including many made in 1978 and 1979, the relative numbers of cowbirds and potential hosts were estimated for a variety of habitats and for varying distances from known loci of afternoon foraging aggregations. Intensive searches were made for nests and fledged broods of potential hosts. Cowbirds strongly prefer meadow edges as breeding habitats, using clearcuts and incompletely logged forests to some extent and unlogged forests rarely or not at all. In the preferred meadow habitats, cowbird abundance declined rapidly with increasing distance from human-based sources of food, such as pack stations. The relative abundance of Warbling Vireos (*Vireo gilvus*) was negatively correlated with that of cowbirds, supporting other evidence of high rates of parasitism on this host species in the Sierra Nevada. Because cowbirds are rare in or absent from many major habitat types and areas remote from human-based sources of supplemental food, however, we doubt that any species in the Sierra Nevada is currently threatened by cowbird parasitism. The problem needs periodic monitoring, however, as human developments become more widespread in the mountains. *Received 2 August 1982, accepted 20 December 1982.*

ROTHSTEIN et al. (1980) documented the recent range expansion of Brown-headed Cowbirds into the Sierra Nevada of California, noting that cowbirds were not reported there before 1930 but appear to be generally distributed over most or all of the mountains today. This range expansion may be significant in view of the cowbird's habit of depositing eggs in the nests of other songbirds, which then rear the young cowbirds at the expense of their own reproductive effort.

Cowbird nest parasitism may be a serious threat, especially for species with limited distributions and small populations. Cowbird parasitism has been implicated in the decline of Kirtland's Warbler (*Dendroica kirtlandii*) in Michigan (Mayfield 1978) and the Golden-cheeked Warbler (*Dendroica chrysoparia*) in Texas (Oberholser 1974, Pulich 1976). Gaines (1974), in a recent report on riparian avifauna of the Sacramento Valley of California, suggested that cowbirds were a factor in the significant declines of several passerine species there over the past 40 yr. Bell's Vireo (*Vireo bellii*) has apparently been extirpated from central California, and cowbird parasitism is considered a primary cause (Gaines 1974, Goldwasser et al. 1980). High rates of nest parasitism recorded recently in the Sierra Nevada suggest that potential hosts, especially the Warbling Vireo (*Vireo gilvus*), should be monitored closely for possible adverse effects of cowbird parasitism (Gaines 1977: 105, Rothstein et al. 1980).

The field studies of Rothstein et al. (1980) were concentrated on the eastern slope of the Sierra Nevada, in areas generally lacking extensive, unbroken stands of forest. No systematic investigation was made of cowbird occurrence in areas remote from human developments. Because cowbirds, at least in the Mammoth Lakes area of the Inyo National Forest on the eastern slope, apparently depend on human-based food resources, especially horse corrals, they may not occur in areas distant from such food resources (Rothstein et al. 1980).

Using the Sierra National Forest as representative of the western slopes of the Sierra Nevada, we attempted in the present study (1) to assess the seasonal distribution and relative abundance of cowbirds by habitat; (2) to determine whether or not cowbirds are also attracted to (dependent upon?) pack stations and other human-based sources of food on the west side; (3) to determine whether or not cowbirds

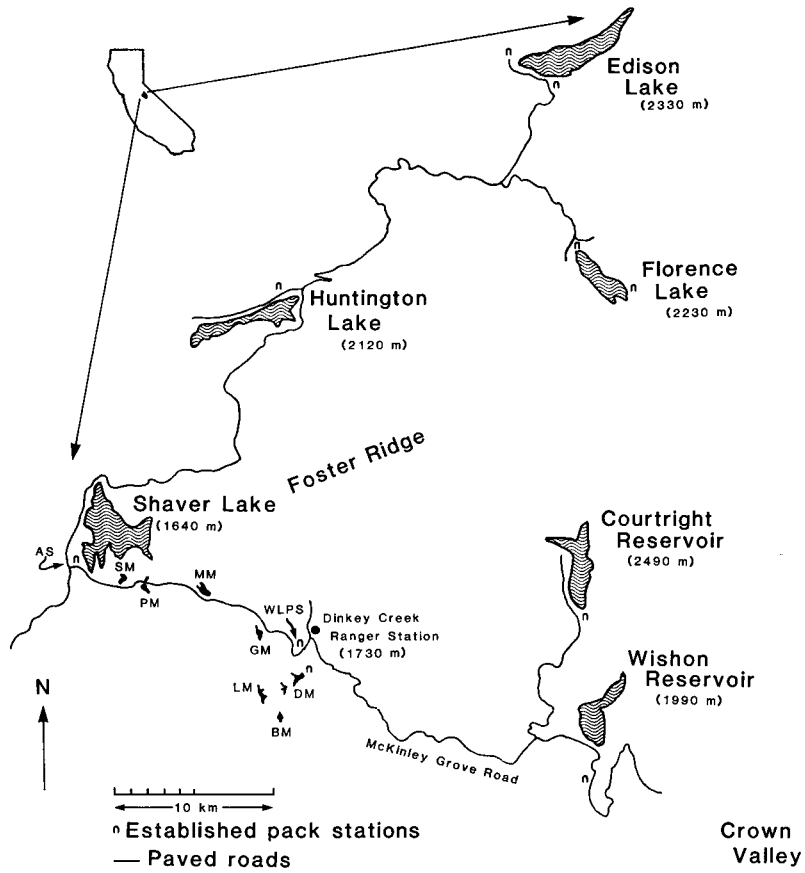

Fig. 1. Map of a portion of the Sierra National Forest showing principal study sites and selected elevations. AS = Arrow Stables, WLPS = Wishon Lakes Pack Station, SM = Swanson Meadow, PM = Poison Meadow, MM = Markwood Meadow, GM = Glen Meadow, LM = Lost Meadow, DM = Dinkey Meadow, and BM = Bear Meadow.

have penetrated deeply into extensive forest stands, remote from human developments; and (4) to determine whether or not the high rates of nest parasitism found in some hosts in other parts of the Sierra Nevada are similarly high in the Sierra National Forest.

STUDY AREAS AND METHODS

The primary study area was centered at Wishon Lakes Pack Station (WLPS), 0.8 km south-southwest of Dinkey Creek Ranger Station, Fresno County, California in a mixed-conifer forest zone at an elevation of 1,740 m (Fig. 1). This is a seasonal pack station used from late spring or early summer to late fall or early winter, depending on weather conditions. Horses were brought to WLPS for the season on 14 June 1980 and on 29 May 1981.

Cattle are also prominent in the ecology of Brown-headed Cowbirds in the Sierra National Forest. In the vicinity of WLPS, cattle were first brought to the mountains on 16 June 1980 and 6 June 1981. They were initially turned out at Dinkey Meadow and trucked from there in small numbers to most of the meadow systems we studied within 5 km of WLPS. This distribution was generally completed within a week. Cattle that grazed in and near the meadows closer to Shaver Lake (such as Poison, Swanson, and Markwood; Fig. 1) were first released near Markwood Meadow about 2 weeks later than those at Dinkey Meadow.

Most fieldwork was concentrated in a corridor along the McKinley Grove road from Shaver Lake to Wishon and Courtright reservoirs. All localities mentioned in the text are identified in Fig. 1.

Climate differed between years and may have influenced the time of arrival of migrants and the timing of breeding by birds in the mountains. The following summarizes records maintained at Wishon

Reservoir by the Pacific Gas and Electric Company. During both years, a marked and steady increase toward summer temperatures began during the week of 8–14 April. For the 9 weeks before that, the mean temperature at Wishon Reservoir was 1.2°C in 1980 and 3.1°C in 1981. Mean temperatures from 15 April to 2 June, when most species had begun nesting, were 6.6°C in 1980 and 8.6°C in 1981. More snow fell during the winter of 1979–1980 than during that of 1980–1981: a maximum snow depth of 188 cm was recorded in early March 1980, and a maximum of 107 cm was recorded in early February 1981. The combined differences of snowfall and mean temperatures between years resulted in much later meltoff of the snow pack in 1980 than in 1981. Snow on the ground was not recorded after 21 April 1981, but it lingered into the third week of May in 1980.

Cowbirds were counted at WLPS at 2-h intervals throughout the daylight period, usually twice a week from 18 June to 15 August 1980 and once a week thereafter until 2 October. A visit of about 5 min to the pack station was usually sufficient to estimate the total number of cowbirds present by sex and age classes.

Distribution and abundance of cowbirds and potential hosts were assessed by 10-min point counts, with unlimited distance, at numerous localities widely distributed throughout the Sierra National Forest in 1980 and 1981. Counts in 1981 were confined to areas within 8 km of WLPS or the Arrow Stables at Shaver Lake. No attempt is made here to translate the counts into densities.

Several habitat types were sampled, including meadows, riparian systems, clearcuts, incompletely logged forests, and unlogged forests. Sites in all habitat types were located at varying distances from pack stations, towns, and other apparent focal points of cowbird foraging activity. Included are counts at 52 locations sampled repeatedly in 1978 and 1979 by T. A. Larson (pers. comm.) and many other counts by us in 1978 and 1979 for other studies in unlogged forests and at meadow and clearcut edges. Altogether, we have data from 248 sites, counted a total of 1,057 times before 15 July of the 4 yr included. Many of the counts from 1978 and 1979 were used in the report by Rothstein et al. (1980).

Visits of several days each were made to three "remote" areas. On a National Forest map, all known mountain pack stations, communities, and campgrounds were plotted, and the sites most remote from such sources of human-based food for cowbirds were selected. Point counts were done mainly in riparian and meadow sites considered most suitable for cowbirds, and intensive searches were made at those remote areas for nests and broods of potential cowbird hosts. The three areas selected (Fig. 1) were:

Edison Lake.—Sites ranged in elevation from about 2,100 to 2,500 m and were in mixed-conifer, red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta*) forest zones. The area was visited from 23 to 27 June 1980. A small pack station was operating at Edison Lake at the time, and sampling points ranged out to about 14 km from it.

Foster Ridge.—Sites ranged in elevation from about 2,200 to 2,800 m and were in red fir and lodgepole pine forest zones. The area was visited from 30 June to 3 July 1980. WLPS was the nearest pack station, ranging from 9 to 13 km from sample sites.

Crown Valley.—Sites ranged in elevation from about 2,300 to 2,900 m and were in mixed-conifer, red fir, and lodgepole pine forest zones. The area was visited from 14 to 18 July 1980. The nearest established pack station to the Crown Valley sites was 11 km away at the Forest Service work center near Wishon Reservoir, but as many as eight horses were grazing in a meadow in Crown Valley within 1 km of some count points.

From 9 June to the end of August 1980 and from 1 June to 26 August 1981, intensive searches for nests and broods of potential hosts were concentrated in likely habitats, especially meadow edges and riparian zones. Most searches were made within 5 km of WLPS, although some sites up to 12 km away were included. Most nests were checked repeatedly for parasitism and to establish the approximate date (within a 2-week period) of first laying.

We followed the daily movements of several cowbirds fitted with radio transmitters (Verner in prep.). Certain results obtained from the radio-tagged birds are given here when they aid interpretation of other observations.

TABLE 1. Mean numbers of cowbirds per count in various habitat types in the Sierra National Forest, California, based on counts in 1978, 1979, 1980, and 1981.

Habitat	Number of cowbirds	Variance	Number of sites	Number of counts
Meadows	0.56[a]	1.02	96	168
Clearcuts	0.095	0.34	70	241
Logged forests	0.07	0.27	28	202
Unlogged forests	0		38	226

[a] Counts in meadows were significantly higher than those in clearcuts (t-test; $Z = 5.88$, $P < 0.0001$) and logged forests ($Z = 6.01$, $P < 0.0001$), but counts in clearcuts were not different from those in logged and unlogged forests ($Z = 0.33$, $P = 0.74$).

RESULTS

Habitat preference and distribution.— The relative abundances of cowbirds indicated that they are a species primarily of meadow edges (Table 1). Observations in riparian habitats were too few to analyze, but studies on the eastern slopes of the Sierra Nevada show riparian systems to be extensively used by cow-

birds (Rothstein et al. 1980). Our failure to record them in unlogged forests was unexpected, as they occur in such forests on the east side (Rothstein et al. 1980), and many of our forested sites were less than 1 km from meadow systems where we regularly observed cowbirds. Forests on the east side are seldom as dense as those on the west side, however, which may account for the difference.

We found cowbirds to be widely but not uniformly distributed throughout the Sierra National Forest. They were rare in all habitat types except meadows (and probably deciduous riparian systems), and their numbers dropped sharply with distance from pack stations, campgrounds, towns, and other such sources of human activity. At meadow sites, grouped into distance intervals of 1 km from the nearest known pack station (or horse corral), cowbird numbers were negatively correlated with distance from pack stations (Kendall's tau = -0.64, $P < 0.01$). Their numbers were also negatively correlated with elevation (Kendall's tau = -0.64, $P < 0.01$). We could not separate distance effects from elevation effects by analysis of a log-linear contingency table, because we had too few sites and because most sites at higher elevations were also far from pack stations. The Edison Lake counts, however, which were taken separately, were not significantly correlated with elevation (Kendall's tau = 0.33, $P = 0.38$), but their relation to distance from the Edison Lake Pack Station was negative and, we believe, significant (Kendall's tau = -0.52, $P = 0.07$). Interestingly, the most distant sites in the Edison Lake sample, where no cowbirds were seen, were at lower elevations than sites nearest to the pack station.

We visited numerous pack stations at elevations ranging from 2,100 to 2,600 m in the western Sierra Nevada and always found cowbirds when horses were present. Rothstein et al. (1980) reviewed records of cowbirds at high elevations in the Sierra Nevada, including four parasitized nests of Wilson's Warblers (*Wilsonia pusilla*) reported by Stewart et al. (1977) at elevations from 3,000 to 3,100 m at Tioga Lake, Tuolumne County. We believe that these records together with our results show that cowbird numbers decline with distance from pack stations and that the observed decline with elevation is spurious, resulting from the fact that most of our sites at higher elevations were also far from pack stations.

Seasonal abundance and daily movements of adults.—We do not know how early in the season cowbirds typically arrive in the Sierra National forest. Our earliest record was on 2 May 1978, when we saw 6 at Swanson Meadow and 3 at Glen Meadow. In 1981, 38 meadow sites within 8 km of an established pack station or horse corral were counted from 11 to 18 May, before any horses or cattle were present in the mountains. These counts were compared with counts of the same sites in early June 1981, when horses were present at WLPS but cattle were not yet in the meadows, and in early July 1980, when both cattle and horses were present. We found no significant difference between the May counts and either set of counts made after cattle and horses were in the mountains, suggesting that cowbirds were at normal summer abundance at least 2 weeks before any livestock were present.

Observations at WLPS and other pack stations in the western Sierra Nevada indicate that cowbirds seldom frequent pack stations before horses are brought in for the summer. We attracted several to baited traps at WLPS beginning 3 days before horses arrived in 1980. In the corresponding 3 days in 1981, no cowbirds were seen during several visits in midday hours. None came the day horses arrived (29 May, at 1615 PST), but on succeeding days the numbers gathering in the afternoon to feed in the corrals increased dramatically. Peak daily counts were as follows: 30 May, 13; 31 May, 26; 1 June, 45; and 2 June, 60 (Rothstein et al. in prep.).

Peak counts at WLPS were high in late June, lower in early July (including the count on 30 June), and higher again toward mid-July (Fig. 2). This pattern was examined more closely by comparing diurnal trends in numbers at WLPS during each of those three periods (Fig. 3). Numbers of adults, particularly males, increased early in the morning at WLPS (Fig. 3), as at pack stations near Mammoth Lakes (Rothstein et al. 1980). In late June numbers increased until just before dark, when most birds departed in small flocks during a brief period. Most of the birds regularly frequenting the pack station roosted communally in willow thickets in Dinkey Meadow or Lost Meadow, a behavior that persisted throughout their summer stay

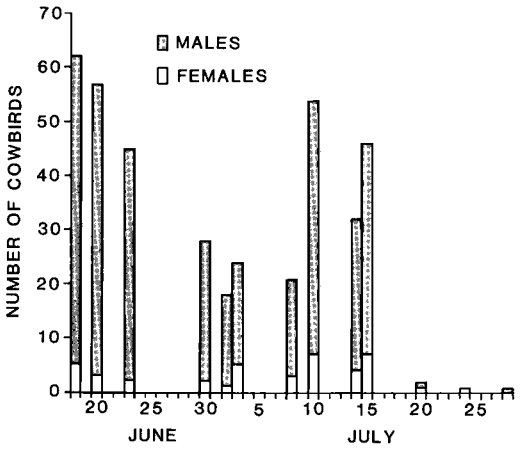

Fig. 2. Peak numbers of adult Brown-headed Cowbirds on specific count days at Wishon Lakes Pack Station in 1980.

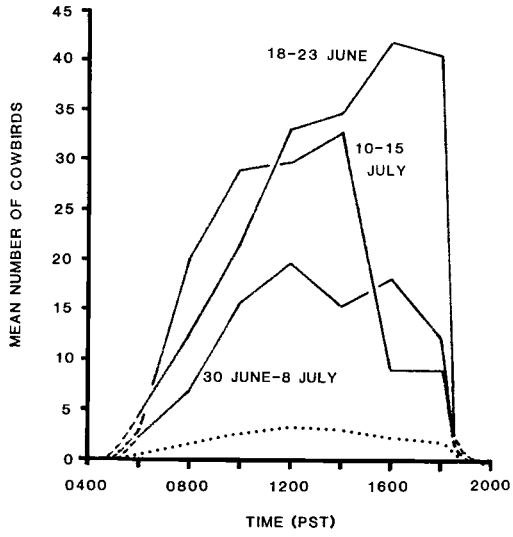

Fig. 3. Diurnal variations in numbers of Brown-headed Cowbirds at the Wishon Lakes Pack Station in 1980. Solid lines show average counts of males; dashed ends of these lines show approximate extremes of arrival and departure times. The dotted line shows average counts of females over all dates.

in the mountains (Verner in prep.). Curves for the next two periods corresponded better to those obtained by Rothstein et al. (1980) near Mammoth Lakes. The middle period (30 June to 8 July) differed in having much lower peak counts and fairly stable high counts from about 1000 to 1600 PST after which most birds went to night roosts during a short period just before dark. The final period (10 through 15 July) was similar to earlier periods during the morning, but most birds left the pack station earlier in the afternoon. Two-way analysis of variance confirmed significant differences among these curves ($F = 4.74$, $P < 0.05$) and significant interactions between period and time of day ($F = 3.34$, $P < 0.02$).

The studies of Rothstein et al. (1980 and in prep.) strongly suggest that all cowbirds in the Mammoth Lakes area regularly visit pack stations, backyard bird feeders, and other such places to obtain much of their food. This is not entirely so on the west side, as some radio-tagged birds seldom left breeding areas to visit distant feeding sites, and others never did. This was particularly true of the small sample of radio-tagged females. Instead of gathering at pack stations, many cowbirds in the Sierra National Forest gathered in mid- to late morning in the vicinity of small herds of cattle that grazed regularly in some of the meadows. The cattle typically spent long periods each day, especially when it was hot, resting in the shade of dense conifer thickets at meadow edges. There we regularly found small flocks of cowbirds, ranging from 5 or 6 birds at Lost Meadow to more than 20 at Bear Meadow and more than 25 at Markwood Meadow. Exact counts were impossible, because the cowbirds usually remained in the trees or foraged around the cattle in tall grasses and forbs in the meadow.

The sharp drop in peak numbers from 15 to 21 July (Fig. 2) marked the apparent departure of most adults from the mountains in 1980. Our latest record of an adult at WLPS was of a single male on 28 July; the latest for a female was on 24 July. Through 2 October, we visited WLPS weekly and continued regular weekly visits to likely cowbird habitats, even to locations at elevations between 2,200 and 2,600 m. The latest that adults were seen elsewhere in the mountains was on 4 August, when two males were at a horse corral near Wishon Reservoir (Fig. 1).

Evidence from five radio-tagged birds supports the observed abrupt departure of adults from the mountains. All tagged birds were present and exhibited their usual diurnal pattern of attendance at the pack station on 17 July, and the unmarked segment of the feeding

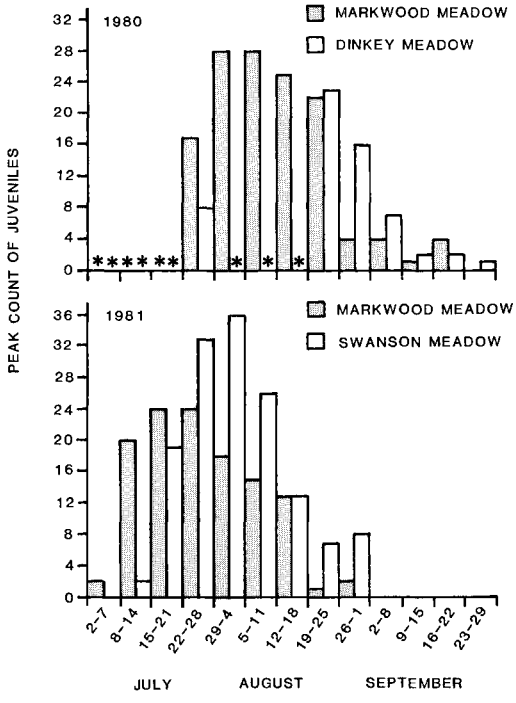

Fig. 4. Weekly peak counts of independent juvenile cowbirds at Markwood and Dinkey meadows in 1980 and at Markwood and Swanson meadows in 1981. An asterisk indicates that no count was made.

aggregation appeared to be present as usual throughout the day. The radio-tagged birds were located in their usual roosting areas after dark on the 17th. On the 21st no radio-tagged birds could be located anywhere within 15 km of WLPS. Apparently, therefore, sometime between dawn on 18 July and nightfall on the 20th, nearly all adult cowbirds left our main study area. Observations in 1981 showed a similar abrupt decline in numbers of adults in the mountains during the second week of July.

Young cowbirds.—In 1980, independent juvenile cowbirds were first seen on the afternoon of 14 July, when two were recorded at WLPS. The earliest young observed in 1981 was a fledgling, judged to be at least 2 weeks old, being fed by a pair of Yellow-rumped Warblers (*Dendroica coronata*) at Lost Meadow on 14 June (S. I. Rothstein pers. comm.).

Approximate dates of egg laying for these young can be extrapolated, given assumptions about timing of the various stages of the nesting cycle. We assume an average of 2 days elapses from laying to incubation of cowbird eggs, that incubation averages 12 days, and that young require an average of 32 days from hatching to independence [$\bar{x}$ = 31.6, range = 25–37 days, for nine young followed in Maryland and Virginia (Woodward in press)]. We further assume that juveniles begin to form flocks at independence, a view shared by P. W. Woodward (pers. comm.). Thus, eggs for the earliest juveniles seen in 1980 were probably laid no later than 29 May, or more than 2 weeks before the arrival of horses and cattle in the area. With an estimated nestling period of 12 days, the early fledgling seen in 1981 probably came from an egg laid about 7 May, or nearly 3 weeks before horses arrived at WLPS and more than a month before cattle were released in Dinkey Meadow. Such early young were apparently exceptional, however, as even small numbers of independent juveniles were not regularly observed anywhere in the Sierra National Forest until mid-July of 1980 and early July of 1981 (Fig. 4).

Including the earliest (14 July) and latest (24 September) records of juveniles at WLPS in 1980, peak daily counts at WLPS were 2 (4 days), 1 (5 days), and 0 (8 days). We believe low counts such as these are not typical of most years. On a visit to WLPS in early August 1979, we observed at least 12 juvenile cowbirds. In 1981, too, juveniles were more common at WLPS. We could usually see 5–10 there daily during the first half of July, perhaps in response to baited traps and live decoys in traps there. Seven were counted at WLPS on 27 July 1981, but none were seen there after that. This compares more favorably with the numbers of juveniles typically frequenting pack stations in late summer near Mammoth Lakes (Rothstein et al. 1980).

Although juveniles made little use of food available at the pack station in 1980, many were in the general vicinity. Late in July, after most adults had left the mountains, juveniles began to appear in the meadows that we searched regularly for nests and fledged broods of potential hosts, so additional time was given on a regular basis to estimate numbers of juveniles in some of those meadows (Fig. 4). Juveniles apparently used the meadows primarily for foraging, sometimes feeding around livestock and commonly associating with flocks of Brewer's Blackbirds (*Euphagus cyanocephalus*). Markwood Meadow and the lower end of Dinkey Meadow consistently had more juve-

niles than other meadows in 1980, but in 1981 Dinkey Meadow had few juveniles—a high count of seven on 27 July. Low counts in Dinkey Meadow may have reflected the trap and removal operation at WLPS (Rothstein et al. in prep.). Consequently, count data for Swanson Meadow are given here to provide an idea of the seasonal build-up and decline of juveniles in 1981 (Fig. 4).

The patterns in Fig. 4 suggest a rapid increase in numbers of juveniles during late July and early August, with a gradual decline to zero by the end of September in 1980 and early September in 1981. Rothstein et al. (1980) reported a similar increase at Mammoth Lakes, at about the same time of year, but they did not continue observations late enough to observe the decline in numbers as juveniles left the mountains.

Hosts.—Cowbird parasitism was confirmed for 10 of 43 species considered potential hosts (Table 2). We add the Golden-crowned Kinglet (*Regulus satrapa*) and Hermit Warbler (*Dendroica occidentalis*) to the list of known hosts in the Sierra Nevada. Clutches in most potential host nests were laid between 14 May and 8 July in 1980 and between 28 May and 8 July in 1981 (Fig. 5). The low rate of parasitism in our samples (Table 2) suggests that nest parasitism by cowbirds does not have a significant impact on potential hosts in the Sierra National Forest. If the impact of nest parasitism on a species were significant, we should expect to find the numbers of that species depressed in areas where cowbirds are more abundant. To test this, we examined correlations between relative abundances of cowbirds and several likely hosts. Only the relative abundance of Warbling Vireos was negatively correlated with that of cowbirds (Kendall's tau = -0.35, $0.05 > P > 0.025$). This relationship was independent of differences in habitat preference between the vireos and cowbirds, because it held even in meadow-edge habitats, where cowbirds were most abundant.

Chronology, comparing years.—Timing of major events thought to be important in the breeding cycle of Brown-headed Cowbirds in the Sierra Nevada was consistently later, by 1 to 2 weeks, in 1980 than in 1981 (Fig. 6). Only the latest record of an adult in the mountains was earlier in 1980. The latest bird seen in 1981 appeared to have a head injury, however, so its late stay may have been anomalous.

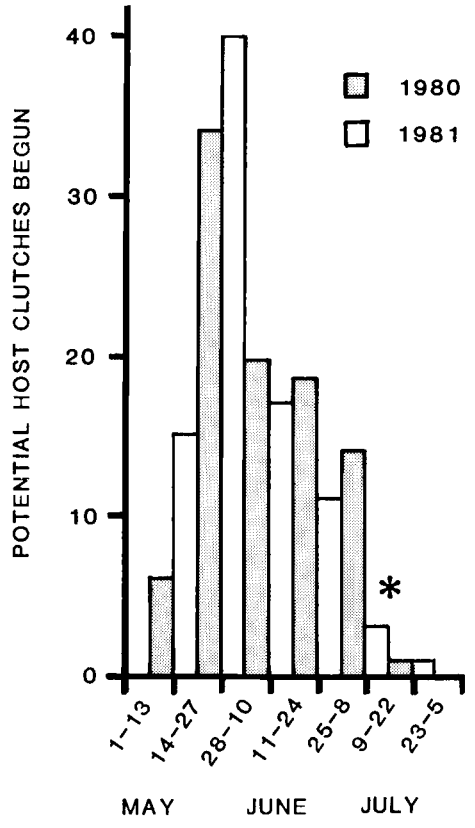

Fig. 5. Seasonal pattern of estimated dates upon which clutches were begun by potential cowbird hosts in the Sierra National Forest in 1980 and 1981. The asterisk shows the 2-week period during which most adult cowbirds left the mountains in both years.

Discussion

Seasonal chronology.—Although we cannot reach definite conclusions from such a limited sample, we suspect that differences in the timing of egg laying by potential hosts were related to differences in the rate of snowmelt between 1980 and 1981. Possibly birds were delayed in their laying by the slower advance of spring in 1980, relative to 1981, or perhaps a higher proportion of early nesters failed in 1980 and had to renest at a later time. We know these climatic differences between years influenced the dates that cattle and horses were brought into the mountains, and this probably influenced the timing of some cowbird activities.

Distribution and habitat preference.—We interpret the cowbirds' daily patterns of activities

TABLE 2. Passerine nests and family groups checked for parasitism in the Sierra National Forest in 1980 and 1981.

Species	Nests		Family groups	
	1980	1981	1980	1981
Willow Flycatcher (*Empidonax traillii*)	1			
Hammond's Flycatcher (*Empidonax hammondii*)			1	1
Dusky Flycatcher (*Empidonax oberholseri*)	4	8		2 (1)[a]
Western Wood Pewee (*Contopus sordidulus*)	2	8	6	1 (1)
Olive-sided Flycatcher (*Contopus borealis*)	1			
Northern Rough-winged Swallow[b] (*Stelgidopteryx serripennis*)			2	
Barn Swallow (*Hirundo rustica*)	3			1
Steller's Jay[b] (*Cyanocitta stelleri*)	4	3	3	2
Mountain Chickadee[b] (*Parus gambeli*)		2	2	1
Brown Creeper (*Certhia americana*)	2	2		1
Canyon Wren[b] (*Catherpes mexicanus*)	1			
Winter Wren[b] (*Troglodytes troglodytes*)			1	
American Robin (*Turdus migratorius*)	7	10	16	17
Hermit Thrush (*Catharus guttatus*)		1	1	1
Mountain Bluebird (*Sialia currucoides*)	1		1	
Western Bluebird (*Sialia mexicana*)			1	3
Townsend's Solitaire (*Myadestes townsendi*)	1			
Golden-crowned Kinglet (*Regulus satrapa*)	1		13 (1)	2
Hutton's Vireo (*Vireo huttoni*)	1			
Solitary Vireo (*Vireo solitarius*)			1 (1)	
Warbling Vireo (*Vireo gilvus*)	1		3	3 (1)
Nashville Warbler (*Vermivora ruficapilla*)			3	
Yellow Warbler (*Dendroica petechia*)	1	2	4 (1)	1
Yellow-rumped Warbler (*Dendroica coronata*)	2	1	16 (3)	15 (4)
Hermit Warbler (*Dendroica occidentalis*)	1		5	3 (1)
MacGillivray's Warbler (*Oporornis tolmiei*)	2			4 (1)

TABLE 2. Continued.

Species	Nests		Family groups	
	1980	1981	1980	1981
Wilson's Warbler (*Wilsonia pusilla*)	4		4	1
Red-winged Blackbird (*Agelaius phoeniceus*)	1	3	2	4
Brewer's Blackbird (*Euphagus cyanocephalus*)	6	15	5	2
Western Tanager (*Piranga ludoviciana*)		8		5
Black-headed Grosbeak (*Pheucticus melanocephalus*)	4		3	
Lazuli Bunting (*Passerina amoena*)			2	3
Purple Finch (*Carpodacus purpureus*)			3	3
Cassin's Finch[b] (*Carpodacus cassinii*)			1	
Lesser Goldfinch (*Carduelis psaltria*)		1	1	2
Green-tailed Towhee (*Pipilo chlorurus*)	3	1	4	8
Rufous-sided Towhee (*Pipilo erythrophthalmus*)				1
Dark-eyed Junco (*Junco hyemalis*)	29	19 (1)	39	39
Chipping Sparrow (*Spizella passerina*)	2	2	20	20
White-crowned Sparrow (*Zonotrichia leucophrys*)		1		
Fox Sparrow (*Passerella iliaca*)	1	1	10	9
Lincoln's Sparrow (*Melospiza lincolnii*)	3	3	3	1
Song Sparrow (*Melospiza melodia*)		2	2	9
Yearly totals: 1980—41 species	89 (0)		185 (6)	
1981—31 species		84 (1)		165 (9)
Grand totals: 43 species	173 (1)		350 (15)	

[a] Numbers in parentheses indicate confirmed cases of parasitism.
[b] These species were not recorded as cowbird hosts by Friedmann (1963, 1966, and 1971) or Friedmann et al. (1977), but closely related species with similar breeding ecologies have been parasitized.

in various areas as Rothstein et al. (1980) did for the Mammoth Lakes area. The birds are apparently dispersed on the breeding grounds during most or all of the morning. From about midmorning on they gather into feeding flocks, typically of about 20–30 birds (about 50 in a few places, as at WLPS), mainly at places where horses are kept or where cattle gather in small herds in and near meadows. Data show that most cowbirds in the Sierra National Forest typically roost in large flocks in willow thickets, away from both their breeding and feeding areas (Verner in prep.). In late afternoon or early evening, they leave the feeding sites and form roosting aggregations. Some of those that normally forage in and around meadows, especially the females, remain in those meadows, while others join roosting flocks elsewhere. This pattern contrasts with that at Mammoth Lakes, where most cowbirds of both sexes typically roosted alone on their breeding areas (Rothstein et al. in prep.).

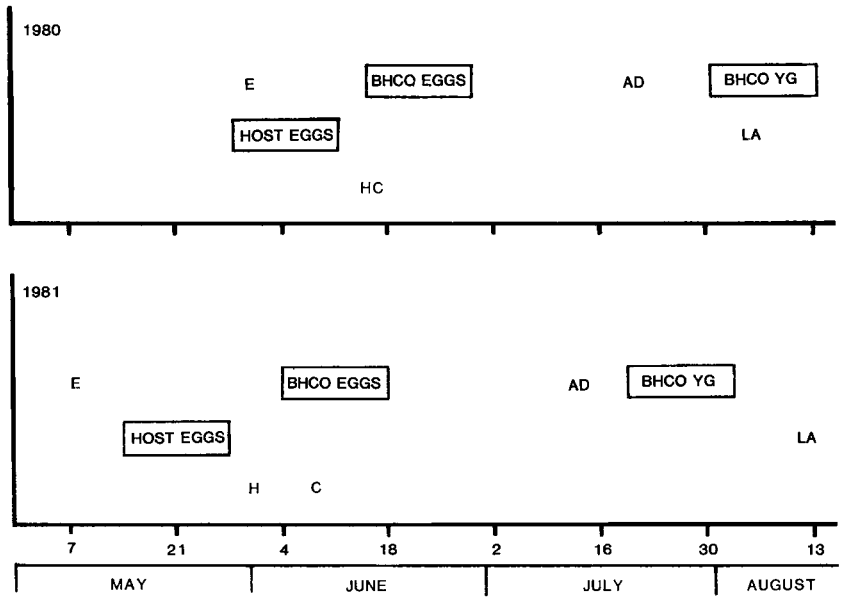

Fig. 6. Summary of principal chronological events associated with Brown-headed Cowbirds in 1980 and 1981. Bars show estimated 2-week peak periods of egg laying by cowbird hosts (HOST EGGS), egg laying by cowbirds (BHCO EGGS), and counts of independent juvenile cowbirds (BHCO YG). E = estimated date egg was laid for first young cowbird seen, H = date horses first brought to WLPS, C = date cattle first turned out in meadows near WLPS, AD = approximate date most adult cowbirds left the mountains, LA = latest date an adult was seen in the mountains.

Rothstein et al. (1980: 253) reported that cowbirds appear to be "ubiquitous over most or all of the mountains at this time. We did not investigate their presence in areas remote from human developments, however, so it is possible that the species has not invaded such areas, particularly if they support large, unbroken stretches of mature forest." Results of the present study clearly show that cowbirds are largely or totally absent from extensive stands of old-growth forest, even when such stands are close to the centers of cowbird abundance. Their strong preference for meadow and riparian habitats for breeding areas most likely is a response to more host species being there, as Rothstein (pers. comm.) found a significant correlation between cowbird abundance and species richness of potential hosts. It is possible, of course, that meadows attract cowbirds in part because they conform more to some sort of habitat gestalt retained from their ancestral evolution in shortgrass prairies.

We found cowbirds to be rare even in preferred habitats (meadows and riparian systems) that were more than about 10 km from centers of human activities that provided food sources for afternoon feeding aggregations. Because we found numerous cowbirds of both sexes apparently independent of pack stations, meeting all their needs in meadows with small herds of cattle, we believe that cowbirds in the western Sierra Nevada could extend their distribution to the more distant localities. That they have not done so is probably explained by the distribution of cattle during the period when cowbirds are in the mountains. Cattle are brought into the mountains and released beginning about mid-June. Most release points are near pack stations or other human developments. The cattle then spread out over the forest, but by mid-July, when most adult cowbirds leave the mountains, cattle still have not reached many remote areas.

The importance of supplemental food sources.—Rothstein et al. (1980) speculated that invasion of the Sierra Nevada by cowbirds was made possible by the artificially rich sources of food associated with campgrounds, towns (bird feeders), and especially pack stations and other horse corrals. In the western Sierra Nevada,

grazing and resting by small herds of cattle in and around meadows apparently provide many additional focal points for feeding aggregations of cowbirds. The Mammoth Lakes area lacks an extensive network of scattered meadows, such as that in the Sierra National Forest, and free-ranging cattle do not use forested areas near Mammoth Lakes to any great extent.

Although we agree that supplemental food sources are probably essential for successful exploitation of the Sierra Nevada by cowbirds, two observations challenge that interpretation. First, the fact that cowbirds regularly migrate into the mountains late in the spring before cattle or horses are present shows that they are not dependent on livestock, at least for short-term maintenance. Second, the earliest young seen in both years probably came from eggs laid before livestock were present (Fig. 6).

In spite of these apparent contradictions, we find the evidence compelling that supplemental food sources are critical. Given earlier assumptions about the timing of the phases of the nesting cycle (a total of 46 days from egg to independence) and the forming of flocks by juveniles as soon as they are independent, our data suggest that the peak period of egg laying by cowbirds in both years started about 17 days later than the beginning of the peak of availability of potential host nests (Fig. 6). We believe these peaks should coincide, unless something restricts the ability of the cowbirds to lay during peak availability of host nests. In both years, apparently the start of the peak period of egg laying by cowbirds followed soon after the arrival of horses at WLPS. In 1980 it also corresponded with early releases of cattle, but in 1981 it apparently preceded release of cattle by about a week (Fig. 6). Although earlier egg laying occurred during both years, it may have resulted in too great a weight loss by the females to permit laying of many eggs.

Delayed breeding among Brown-headed Cowbirds, relative to their hosts, may be a widespread phenomenon in the West (S. I. Rothstein pers. comm.), so our observations in the Sierra National Forest may simply be indicative of a more general phenomenon. Nonetheless, the data strongly suggest that maximum breeding efforts by cowbirds in the western Sierra Nevada begin only after livestock are available to provide supplemental food sources.

If cowbirds were regularly able to breed successfully in Sierran environments without access to livestock or some other supplemental food source, they should spread to all meadow systems in the Sierra National Forest, regardless of accessibility to horse corrals or grazing cattle. The fact that cowbird numbers decline with distance from human developments indicates continued dependence on supplemental food, unless we assume that a spread into the mountains is still underway and that cowbirds simply have not yet reached all potentially suitable habitats. This is possible, of course, but some of the sites free of cowbirds in the Edison Lake area were down the San Joaquin River drainage from the lake, in the path of the most logical migration route to and from the San Joaquin Valley. We suspect that adults regularly migrate through these sites on their way to and from breeding areas near Edison Lake. Moreover, it is unlikely that meadow systems not yet reached by cowbirds would coincidentally be those not reached by cattle at all or, at least, before adult cowbirds leave the mountains in mid-July.

The abrupt departure of adults from the mountains in mid-July is also consistent with the supplemental food hypothesis. The departure coincides with the near disappearance of available host nests (Fig. 5), which certainly requires a change in activities of adult cowbirds. They must complete a molt and recover any weight lost during breeding. That they then leave the mountains suggests that food supplies may be insufficient. In contradiction to this interpretation are the facts that juveniles have been observed in the mountains well into September and our observations showing that they undergo extensive molt before migrating from the mountains. Independent juveniles began to appear not long before adults left the mountains, however, reaching a peak within about a month and then declining steadily but more gradually than the decline in numbers of adults. The pattern of decline suggests a short period in the mountains for most juveniles. Because cowbirds probably lack an innate system regulating altitudinal migration (occupation of the Sierra Nevada is too recent), juveniles, too, may be driven from the mountains by a negative energy balance, especially as nighttime temperatures begin to drop noticeably in late summer and early fall.

The energy demands on females during the breeding period are undoubtedly greater than

those on males, and yet females were observed to meet all their needs without leaving a given meadow system, so long as it had cattle. We must presume that males, too, could satisfy their energetic needs in the same fashion. Because of this, we have seriously considered the alternative that adult cowbirds gather to feed in places with rich food resources primarily for social purposes rather than to supplement an otherwise inadequate food supply. Adult males, especially, could use these aggregations to establish dominance that might benefit them later in competition with some of the same males for access to females, and yearling males could benefit from learning how to function better in the hierarchical system of their species. This hypothesis is supported by the fact that radio-tagged males traveled considerable distances more commonly than females to join these groups.

Alternatively, males may move about much more than females in order to gain occasional opportunities for mating, and, because a number of females regularly visit pack stations, the stations could be ideal places for such opportunistic mating. West et al. (1981), however, showed that female Brown-headed Cowbirds in aviaries almost exclusively copulate only with males with which they have had a prolonged association. Their data suggest that a less dominant male or a nomadic male could not mate with a female, because familiarity between the male and female, established during at least a week's consortship, is essential for the female to accept copulation by any male. Accepted males also had to maintain dominance over other males during the period of consortship.

Social interaction cannot be ruled out, especially among males, as being an important benefit of the social foraging observed on both sides of the Sierra Nevada. We are compelled by the evidence, however, to conclude that cowbirds must forage in places that provide unusually rich, artificial food resources to maintain a replacement-rate reproductive output in the mountains. Social benefits, if they occur, may simply be byproducts of group foraging. Thus, we conclude that cowbird abundance and distribution in the Sierra Nevada result from a dynamic interplay between habitats with suitable hosts and accessibility to artificial concentrations of rich food sources. An important implication is that, as more pack stations, campgrounds, and communities are established in the mountains, so too will the general abundance of cowbirds increase.

Seasonal abundance.—Most or possibly all cowbirds reach their summer breeding localities well in advance of the arrival of cattle or horses, as shown by counts in May 1981. Even before horses were brought in, substantial numbers of cowbirds began to visit WLPS in 1980, probably in response to baited traps. This was not true in 1981 (Rothstein et al. in prep.). The rapid buildup to maximum, seasonal, peak numbers of adults visiting WLPS after horses arrived suggests that they regularly monitor the pack station in anticipation of the arrival of horses, probably remaining there only briefly before some source of supplemental food is available.

The marked reduction in peak numbers of male cowbirds at WLPS in late June and early July 1980 could indicate that most males remained on their breeding areas at that time. This period corresponds approximately with the peak period of egg laying by cowbirds, as determined from the timing of the buildup in numbers of independent juveniles in meadows within 8 km of WLPS (Fig. 6). In leaving females on the breeding grounds to visit WLPS, or any other separate feeding area, males would run the risk of having their female consort(s) fertilized by other males. We are unable to characterize the mating system of cowbirds in the Sierra Nevada, but prolonged association was observed between radio-tagged males and females. Nevertheless, birds of both sexes were regularly seen with birds of the opposite sex other than their usual consort, and Elliott (1980) documented promiscuous mating in a group of color-banded cowbirds in Kansas.

We agree with Rothstein et al. (1980) that the departure of adults from the mountains in mid-July is probably a response to the declining availability of host nests (Fig. 5), coupled with suboptimal food supplies (see discussion in previous section). The usual pattern of departure appears to be an initial, sharp decline, with remaining adults leaving the mountains during the next 2 weeks. This is apparently typical in the Mammoth Lakes area as well (Rothstein et al. 1980, Rothstein pers. comm.), and Gaines' (1977: 121) observations suggest a similar pattern in Yosemite National Park.

The early departure of the adults raises an interesting question about the pattern of altitudinal migration and its expected direction

from the breeding grounds. Because cowbirds only recently expanded their breeding range into the high Sierra Nevada, we should not expect their migratory behavior to exhibit well-defined directionality. Adults leave the breeding grounds well in advance of the juveniles, so they are not availble for the juveniles to follow during fall migration. It is thus reasonable to expect the juveniles to migrate in the fall in a variety of directions from the breeding grounds. This may explain recoveries of two adults banded at Mammoth Lakes. A female banded on 27 July 1978 was recovered in November 1978 near Santa Cruz (about 300 km to the west and across the Sierran crest). A male banded on 7 July 1979 was found near Bishop on 6 August 1979 (about 50 km to the southeast) (Rothstein pers. comm.).

Hosts.—The low rate of parasitism observed—1% of 173 nests and 4.3% of 350 family groups—among potential hosts in this study is puzzling when compared with results from other studies in the Sierra Nevada. For example, White (1973: 62) found no cases of cowbird nest parasitism of Dark-eyed Juncos (*Junco hyemalis*) in 1969 at Sagehen Creek Basin, Nevada County, east of the Sierran crest at an elevation of 1,950 m. She stated, however, that ". . . over the following three years the cowbirds increasingly used juncos as nest hosts, so that by 1972 36% of the observed junco nests contained cowbird eggs or young." We found only one parasitized nest among 48 junco nests and no parasitized broods among 78 family groups. In the Mammoth Lakes area in 1975, 1977, and 1978, Rothstein et al. (1980) found evidence of parasitism in 10 of 48 nests (21%) of 15 potential host species, including 3 of 6 junco nests. Gaines (MS, cited in Rothstein et al. 1980) found 2 instances of parasitism among 45 nests (4%) and 11 instances among 122 fledged broods (9%) of 8 and 22 potential host species, respectively.

Observed rates of parasitism among family groups in the Sierra National Forest in 1980 and 1981 were not much lower than those found by Gaines in Yosemite Valley in 1978, the only available comparison for family groups. If American Robins (*Turdus migratorius*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Brewer's Blackbirds are eliminated from both samples (none has been found to be parasitized in the Sierra Nevada) parasitized family groups in our sample are much less frequent (4.9%) than those in Gaines' (16.9%). Moreover, observed rates of parasitized nests during both years of our study probably represent a significant difference from results of other studies in the Sierra Nevada. Examination of the species for which parasitized family groups were found suggests that, at least in the Sierra National Forest, cowbirds have specialized in parasitizing tree-nesting hosts whose nests cannot be easily found or examined. Results from both years support this hypothesis.

Another possible explanation for the low rate of parasitism observed in this study is that cowbirds were forced to delay most egg laying until livestock were present to provide a supplemental food source. In 1980, an estimated 63% of all clutches of potential hosts were completed before the peak period of egg laying by cowbirds began. In 1981, 43% of potential host clutches were laid before the peak of egg laying by cowbirds. Consequently, the number of host nests vulnerable to parasitism was already on the decline by the time cowbirds were most actively seeking them.

Because the abundance of the Warbling Vireo, known to be a preferred host in the Sierra Nevada, was shown by counts in 1980 to be negatively correlated with the abundance of cowbirds, we suggest that cowbird parasitism has a significant impact on this species. This conclusion is supported by the high rate of nest parasitism found by Rothstein et al. (1980) near Mammoth Lakes and the high rate of family-group parasitism found by Gaines (MS, cited in Rothstein et al. 1980) in Yosemite Valley in 1978. The Warbling Vireos parasitized at Mammoth Lakes reared only cowbirds (Rothstein et al. 1980).

Management implications.—Given that cowbirds apparently began expanding their range into the Sierra Nevada sometime between 40 and 50 yr ago (Rothstein et al. 1980), their abundance and distribution probably have stabilized in relation to present conditions. We believe that no host species is seriously threatened by cowbird parasitism at the present time, because cowbirds are rare in areas remote from human developments and even in some extensive habitat types near human-based food sources, and because their laying season is delayed in relation to that of most host species. This is not necessarily a stable situation for at least four reasons: (1) Human use of the Sierra Nevada will undoubtedly increase in future

years. Unless future developments are confined to areas already developed, they will no doubt increase the abundance and distribution of cowbirds in the mountains. At their worst, future developments could result in pack stations, horse corrals, small communities, and large campgrounds scattered in a distribution that, together with grazed meadows, would provide rich food sources for cowbirds within 5 or 10 km of any point in the Sierra Nevada. (2) Fractionation into ever-smaller patches of habitats presently not used much by cowbirds could subject potential hosts to cowbird parasitism even in those habitats. (3) Increasing the numbers of cattle released for summer grazing in the mountains, releasing cattle earlier, or releasing them at higher elevations could result in cattle becoming more widespread in the mountains and, hence, available for use by cowbirds for supplemental food sources during their breeding period. (4) Earlier transportation of horses to mountain pack stations could result in an earlier breeding season for the cowbirds and a higher percentage of hosts being vulnerable to parasitism.

Because future developments in the Sierra Nevada are uncertain, we strongly recommend continued monitoring of the relationships among populations of cowbirds and their various host species at various localities in the Sierra Nevada. The evidence that cowbird parasitism in certain portions of the mountains is significantly affecting populations of the Warbling Vireo particularly warrants serious, continued attention.

Some control of cowbird numbers, especially males, in the Sierra Nevada might be possible through trapping and removal operations at pack stations. The feasibility of this procedure is currently under study.

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