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BEHAVIORAL DIFFERENCES AMONG SEX AND AGE CLASSES OF THE BROWN-HEADED COWBIRD AND THEIR RELATION TO THE EFFICACY OF A CONTROL PROGRAM

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Abstract.—The recent colonization of the Sierra Nevada by the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, may constitute a threat to some passerine populations. Because radio-telemetry studies have demonstrated that cowbirds commute up to 7 km between breeding sites in natural habitats and man-made feeding sites such as pack stations (horse corrals), it seemed possible to control cowbirds over a large area by removing them from a small number of man-made feeding sites. The feasibility of such a control program was tested by removing 125 cowbirds from a pack station in the western Sierra Nevada. Although cowbird numbers at the removal site declined markedly, there was only a moderate decline in male cowbirds, and at best only a slight decline in female cowbirds in the general area surrounding the removal site. The removal program had a limited impact because many cowbirds in the area, especially females and adult males, often fed in the vicinity of cattle grazing in meadows, unlike cowbirds in the area where the radio-telemetry study was done. Because free-ranging cattle are widespread in the Sierra, short-term removal programs at localized sites may have limited value, except in the few areas where there are no free-ranging cattle. Our results indicate that cowbirds are highly attracted to horses and make only limited use of corrals in the absence of livestock. Yearling males spent more time at a social feeding site than did adult males and females which, along with other evidence, indicates that cowbirds form afternoon social groups for purposes of feeding, rather than to partake in social behavior in a lek-like situation. *Received 23 Aug. 1986, accepted 13 Feb. 1987.*

The phenomenal increase in the distribution and abundance of the Brown-headed Cowbird (*Molothrus ater*) over the last 200 years probably exceeds that of any other native North American bird (Mayfield 1965, Rothstein et al. 1980). Because the cowbird is a brood parasite, victimizing nearly all passerines with which it is sympatric (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985), its range extension may have placed a new and potentially serious limit to the reproductive potential of some host populations. Indeed, the cowbird has been implicated in the decline of both endangered and common species (Mayfield 1977, Brittingham and Temple 1983). We report on the efficacy of a possible control program thought to be especially well suited to the Sierra Nevada

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of California and other semiwilderness areas. We also describe behavioral differences among sex and age classes of cowbirds, as indicated by the results of intensive trapping. These behavioral differences are significant to studies of the behavioral ecology of the cowbird (see review in Rothstein et al. 1986) and to understanding shortcomings in the control program we tested.

The Sierra Nevada constitutes one of the last major biotic units in the continental United States to be colonized by the cowbird (reviewed in Gaines 1977, Rothstein et al. 1980). Colonization is still apparently in progress, as cowbirds are rare or absent from some wilderness regions and heavily forested areas (Verner and Ritter 1983). The recent arrival of cowbirds may be especially threatening to Sierran passerines. These populations have had no recent contact with parasitic birds, and thus their members may have relatively few or no adaptations to reduce the impact of cowbird parasitism. Furthermore, some Sierran passerines occur in small disjunct populations limited to patches of suitable habitat. Cowbird parasitism is especially likely to extirpate birds in such situations because there is no feedback between their abundance and that of the parasite. Parasite numbers may decline little if at all as the host declines, because most of the recruitment into the cowbird's population may come from more abundant, widespread host species. Passerines that seem to be endangered by cowbird parasitism in other regions have small, patchily distributed populations (Gaines 1974; Oberholser 1974; Post and Wiley 1976, 1977; Mayfield 1977, 1978; Pulich 1976). Evidence suggests that one favored host, the Warbling Vireo (*Vireo gilvus*), has already declined in Sierran areas where cowbirds are most common (Verner and Ritter 1983; see also Airola 1986). Therefore, it is important to develop techniques that can control cowbird populations if it is confirmed that Sierran passerines are undergoing serious declines due to cowbird parasitism.

Our earlier studies (Rothstein et al. 1980, 1984; Verner and Ritter 1983) suggested a feasible control technique. Throughout North America, cowbird distribution seems to be limited primarily by the availability of suitable foraging habitat, with the birds feeding mostly on the ground in areas of short grass, preferably in the immediate vicinity of grazing mammals (Friedmann 1929, Hamilton and Orians 1965, Mayfield 1965). Human development has created new foraging habitat as forests have been cut, arid land irrigated, and livestock introduced. Because it is largely undeveloped, however, the Sierra has relatively few such patches of "artificial" feeding habitat. Radio-tracking (Rothstein et al. 1984) demonstrated that Sierran cowbirds commute daily up to 7 km between widespread morning breeding ranges, where they are largely asocial in natural habitats; and localized artificial feeding sites (horse corrals, bird feeders, etc.), where they are highly social in the afternoon. Thus, it may be possible to remove most cowbirds from an area within a radius of 7 km (154 km^2) or more by trapping birds at a single site for a short time. The effectiveness of such a removal program was tested in this study by removing cowbirds visiting a pack station over a one-month period in an area thought to contain little else in the way of artificial feeding habitat. In contrast to the trapout program currently used to remove cowbirds from the range of the Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1978, Kelly and De Capita 1982), our design relied on traps at one established feeding site, rather than on an extensive grid of traps designed specially for the trapping regime.

METHODS

The primary removal site was the Wishon Lakes Pack Station (WLPS), 1.2 km SSE of the Dinkey Creek Ranger Station, Sierra National Forest, Fresno County, California. Small numbers of cowbirds were also captured at the Camp El-O-Win horse corrals, 1.75 km southeast of WLPS. Both sites are at an elevation of 1710 m. Prior work (Verner and Ritter 1983 and Rothstein pers. obs.) showed that WLPS was the only feeding site within 15 km, an area covering 707 km^2, that attracted large numbers of cowbirds, often 40 or more at a time. To estimate the number of cowbirds visiting WLPS, we counted individuals present during 5-min periods spaced throughout the day (>0.5 h apart). Cowbirds were captured with "Potter" traps and, to a lesser extent, with a large (approx. 1.5 m^2) decoy trap baited with "wild bird seed." Yearling and adult males were differentiated by plumage (Selander and Giller 1960). Females were not aged.

To assess the area-wide effects of removing cowbirds from the 2 capture sites, birds were surveyed before and after the removal in 1981 at 38 points in all 15 meadows within 7 km of WLPS. We counted individuals of all bird species visually or aurally detected from a fixed point during a 10-min period between 05:30 and 09:30 PST. Meadows were chosen because cowbirds in this area are most common in these habitats and occur rarely in forests, the predominant local habitat (Verner and Ritter 1983). Because some survey sites within the same meadow were as little as 0.2 km apart, and hence well within the range of a single individual cowbird (Rothstein et al. 1984), each site did not constitute an independent datum. Rather, each meadow was treated as an independent datum, and analyses were done by analyzing the changes, between sampling periods, in total cowbird detections per meadow. We never detected cowbirds in 3 meadows, and these meadows are deleted from results reported here. The remaining 35 sites in 12 meadows ranged from 0.3 to 4.6 km from WLPS ($\bar{x}$ = 2.7, median = 2.6 km).

Observers surveyed each of the 35 sites during 3 periods: 7–13 July 1980, one year before the removal experiment (period A); 2–11 June 1981, immediately before cowbird removal at WLPS was initiated (period B); 29 June–8 July 1981, after the removal was nearly completed (period C). All 3 periods were within the early June to mid-July interval when Sierran cowbirds are at peak abundance (Rothstein et al. 1980). Although the peak of cowbird egg laying may vary from year to year and the use of afternoon feeding sites may vary within one season (Verner and Ritter 1980), we have found no variation in numbers of cowbirds occurring during the morning in breeding habitat from early June until mid-July when the birds leave the Sierra (Rothstein et al. 1980, Verner and Ritter 1983). To control for different observers, only bird counts made by the same individual were compared. L.V.R. did counts at each site during all 3 periods; E.S. did counts only during periods B and C, the most critical ones for assessing effects of the removal. The 2 observers visited the same meadows on different days.

RESULTS

Cowbird occurrence at Wishon Lakes Pack Station.—We did frequent 5-min counts of cowbirds at WLPS during the time of day when cowbird numbers typically peak at pack stations (12:00–18:45). Observations began at 16:46 on 29 May, shortly before the first horses of the season arrived at 17:15. No cowbirds were detected that day despite nearly continuous observations from 16:46 until sunset; but cowbird numbers increased dramatically over the next 4 days (Fig. 1). The mean numbers of birds seen per 5-min count (Fig. 1) showed a significant rise between 29 May and 2 June (Kendall rank correlation tests: males, $\tau = 1.00$, $P = 0.008$; females, $\tau = 1.00$, $P = 0.008$), as did the peak numbers (Fig. 1) observed on each day (males, $\tau = 1.00$, $P = 0.008$; females, $\tau = 0.90$, $0.008 < P < 0.04$). Although it occurred in both sexes, the increase was much greater in males. This strong differential between the sexes is typical of Sierran pack stations and is especially pronounced at WLPS (Rothstein et al. 1980, Verner and Ritter 1983).

After a rapid increase, cowbird numbers became relatively stable by 2 June. The relation between time of day and cowbird numbers on 1 June (Fig. 2), the day on which we did the most 5-min counts, was typical of the diurnal pattern in cowbird numbers at Sierran feeding sites as shown by previous analyses in which data from many days were lumped (Rothstein et al. 1980; Verner and Ritter 1983). After numbers stabilized, they remained consistently above those seen shortly after the horses arrived (compare 29–31 May with 3–11 June) (Fig. 1).

The removal phase and trapping data.—The removal at WLPS began on 12 June, although 6 birds were captured on 8 June to provide decoys for our traps and for other cowbird studies. Traps were kept open and baited for 6–7 h on 8 of the next 9 days and sporadically thereafter (Fig. 3). Nearly all birds were captured in Potter traps. To determine if trapping had a detectable effect on numbers of cowbirds visiting the site, frequent 5-min counts were begun on 22 June. By 22 June, 102 (81.6%) of the 125 cowbirds ultimately caught at WLPS had already been removed (Fig. 3). The 5-min counts demonstrated significant decreases in cowbird numbers (*P*s with Mann-Whitney *U*-tests were each <0.001 for both males and females for numbers recorded during 3–11 June vs 22 June–1 July; data in Fig. 1). For example, male and female numbers, before the removal, peaked at 51 and 9, respectively, whereas the comparable numbers were

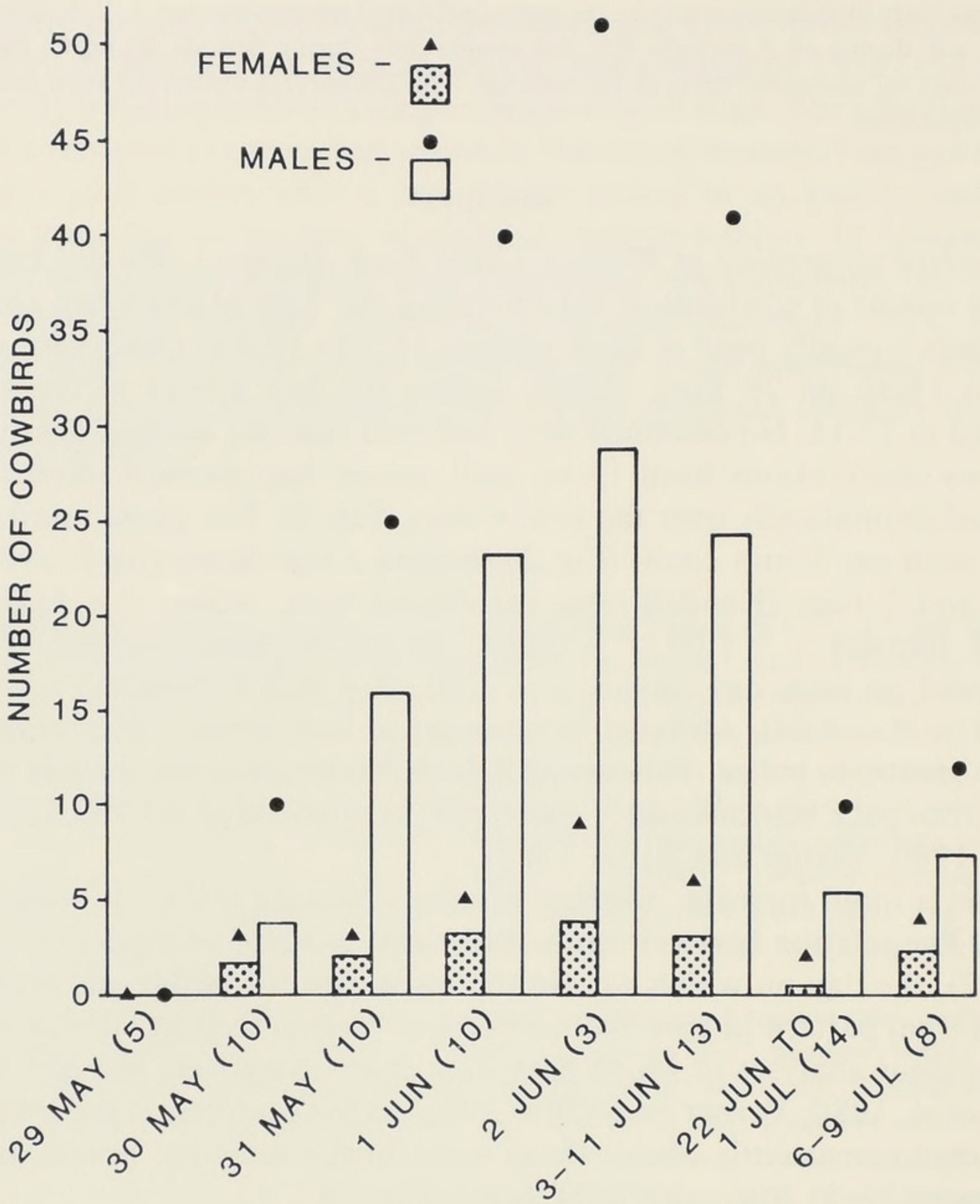

FIG. 1. Numbers of cowbirds recorded during 5-min counts at Wishon Lakes Pack Station during the daily period of peak abundance (12:00–18:45) on various dates. Bars represent mean numbers for the indicated dates; points (males) and triangles (females) indicate maximum counts. Sample sizes are given in parentheses after dates (i.e., number of 5-min counts taken ≥0.5 h apart). Horses were first brought to the pack station on 29 May. Peak counts of cowbirds stabilized by 2 June. Cowbird removal began on 12 June and was mostly completed by 22 June.

10 and 2 for the 22 June–1 July post-removal period (Fig. 1). However, cowbird numbers increased slightly by 6–9 July (Fig. 1), as the numbers of males and females seen at WLPS then were significantly higher than during 22 June–1 July ($P \leq 0.05$ and $P < 0.01$, respectively). This increase probably reflects immigrants from nearby regions, as banding studies (R. C. Fleischer and S. I. Rothstein, unpubl. data) have shown that some

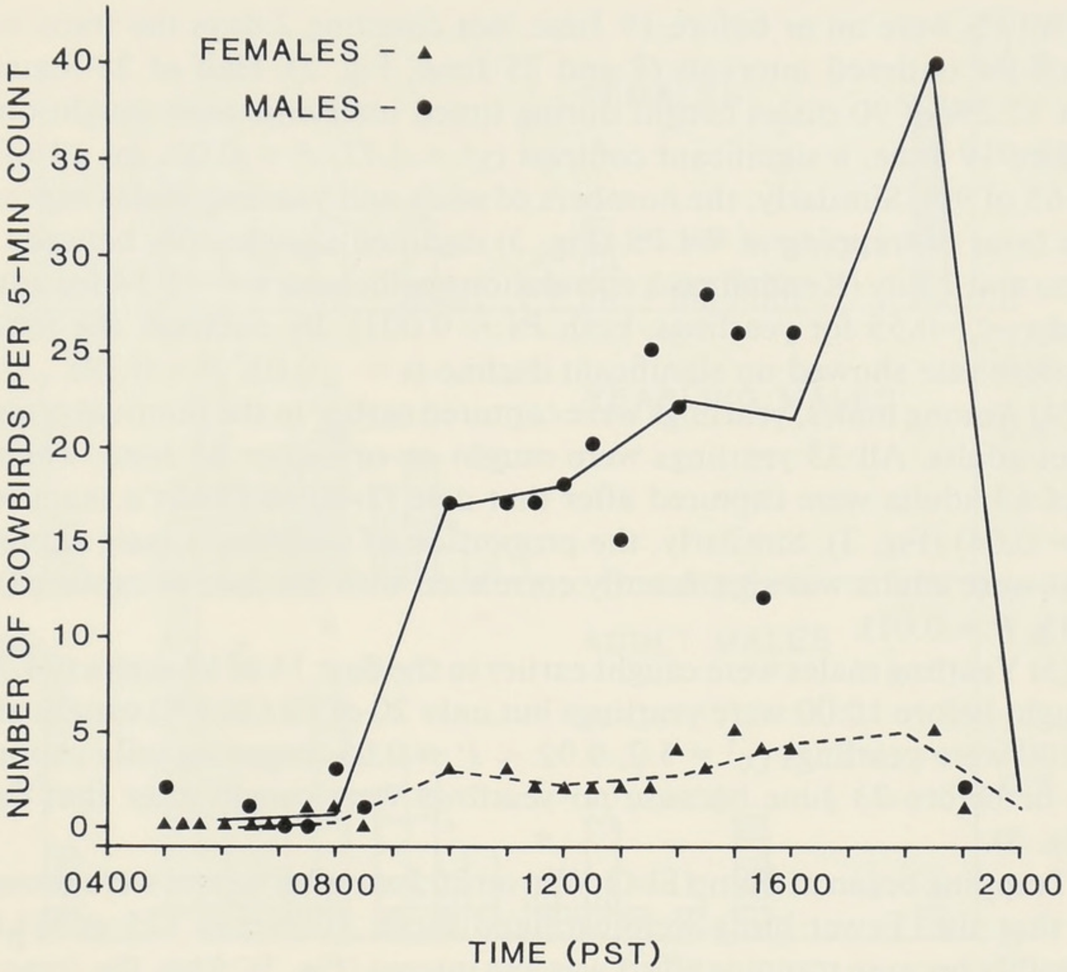

FIG. 2. Typical pattern of diurnal variation in cowbird numbers at Wishon Lakes Pack Station. The data are for 1 June when numbers began to stabilize. Solid and dashed lines represent 2-h means for males and females, respectively (05:01–07:00, 07:01–09:00, etc.).

Sierran cowbirds change their entire range during the breeding season and begin to use feeding sites 10 km or more from sites used earlier in the season.

The trapout data for WLPS showed 5 trends related to aspects of cowbird biology:

(1) The total number of birds caught, 96 males and 29 females, exceeded the largest numbers seen at one time, 51 males and 9 females.

(2) The sex ratio of captured birds differed from that of birds seen during counts. The former ratio was 3.3:1 (96M:29F); the latter was 5.7:1 (51:9) for the maximum numbers of each sex observed in one 5-min count and 7.6:1 (25.2:3.3) for the average number of each sex seen during the afternoon peak (12:00–18:45) in numbers between 2–11 June (Fig. 1).

(3) The numbers of captured adult and yearling males declined much more rapidly than did the numbers of females. Half of the trapping hours

at WLPS were on or before 19 June, not counting 2 days the traps were open for untimed intervals (8 and 25 June, Fig. 3). Half of 28 females, but 72.2% of 90 males caught during timed intervals, were caught on or before 19 June, a significant contrast ($\chi^2 = 4.77$, $P < 0.05$, for 14 of 28 vs 65 of 90). Similarly, the numbers of adult and yearling males captured per hour of trapping at WLPS (Fig. 3) declined significantly between 12 June and 7 July (Kendall rank correlation coefficients $\tau = -0.54$ for adults and $\tau = -0.55$ for yearlings, both *P*s < 0.001). By contrast, the female capture rate showed no significant decline ($\tau = -0.05$, $P = 0.39$).

(4) Among males, yearlings were captured earlier in the removal process than adults. All 33 yearlings were caught on or before 23 June, whereas 9 of 63 adults were captured after that date (2-tailed Fisher's exact test, $P = 0.04$) (Fig. 3). Similarly, the proportion of each day's male captures that were adults was significantly correlated with the date of capture ($\tau = 0.45$, $P = 0.01$).

(5) Yearling males were caught earlier in the day: 11 of 17 males (64.7%) caught before 10:00 were yearlings but only 20 of 65 (30.8%) caught after 10:00 were yearlings ($\chi^2 = 5.2$, $0.02 < P < 0.05$, counting only captures on or before 23 June because no yearlings were caught after that date) (Fig. 3).

Trapping began at Camp El-O-Win on 26 June after horses were brought to that site. Fewer birds were captured there, 10 versus 125 at WLPS, possibly because trapping effort was less intense (Fig. 3). Also, the removal at WLPS had probably already resulted in a decline in area-wide cowbird numbers, and even under normal conditions El-O-Win attracted fewer birds than WLPS (unpubl. observations in 1980). The limited trapping data from El-O-Win support trends 2 and 4 (above) in the WLPS data and conflict with none of the others. The sex ratio for birds trapped at El-O-Win was unusually even (5M:5F) (Fig. 3), relative to the ratio for birds seen at Sierran feeding sites. Trapping at El-O-Win was late in the trapping period, and all the males captured were adults, as would be expected from the data for WLPS.

Eleven 5-min counts at WLPS from 14 June to 15 July 1983, averaged 5.0 males (range = 0–12) and 1.7 females (range = 0–3), with both distributions being significantly below the data for 2–11 June 1981 (Mann-Whitney *U*-tests, $P < 0.001$ for males and $P < 0.01$ for females) (Fig. 1). Data from 1984 also showed reduced numbers (M. D. Stafford pers. comm.), as did limited observations in 1982. We were unable to determine if this apparent long-range decline in cowbird numbers at WLPS was due to the 1981 trapout or to the fact that the proprietor of WLPS switched to a new horse food in 1982. This new food was "cubed hay" (densely

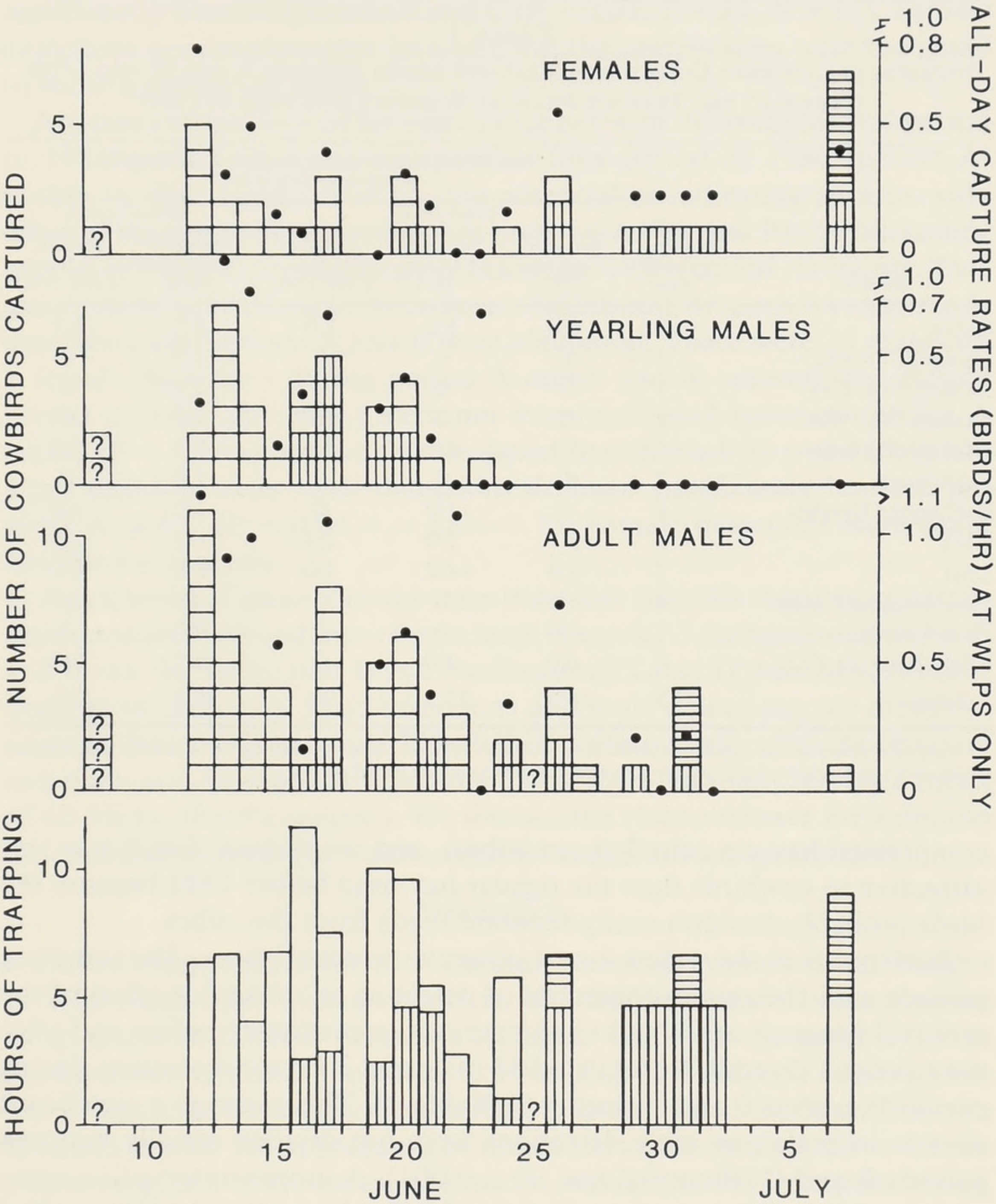

FIG. 3. Numbers of cowbirds captured and numbers of hours traps were kept open at 2 removal sites, Wishon Lakes Pack Station (vertical cross-hatching before 10:00, open blocks after 10:00) and Camp El-O-Win (horizontal cross-hatching). The hourly capture rates (solid dots) for each day of trapping at WLPS are also shown (except for 2 days, question marks, when times were not recorded).

TABLE 1

NUMBERS OF COWBIRDS DETECTED IN MEADOWS BEFORE (PERIODS A AND B) AND AFTER (PERIOD C) THE TRAPOUT PHASE AT WISHON LAKES PACK STATION

		Number of cowbirds (males : females) detected during sampling periods A to C				
		Ritter counts			Stevens counts	
Meadow	No. observation sites[a]	Period A (7–13 July 1980)	Period B (2–11 June 1981)	Period C (29 June–8 July 1981)	Period B (2–11 June 1981)	Period C (29 June–8 July 1981)
Cabin	4	6:0	5:0	2:0	5:0	8:1
Camp El-O-Win	1	0	0	0	1:0	0
Dinkey Crk. Dry	1	0	0	0	2:0	0
Dinkey Crk. Wet	1	0	0	1:0	1:0	0
Dinkey (Forbes)	5	1:1	8:1	2:0	6:3	2:0
Exchequer	2	0	0	0	2:0	0
Exchequer Heights	4	0	1:0	0	1:0	1:0
Glen	6	3:1	2:0	2:4	6:3	2:0
Lost	7	4:4	14:2	2:0	8:0	6:0
Pine Logging Camp	1	1:0	0	0	0	1:0
Pack Station	1	5:0	0	0	2:0	0
Flight Line 28 #221	2	6:0	3:0	0	4:3	2:0
Totals	35	26:6	33:3	9:4	38:9	22:1

[a] Number of points in each meadow at which 10-min counts were done. All points were surveyed once by each observer during each sampling period (except that Stevens did no counts during period A).

compressed hay cut into 3–4 cm cubes), and we suspect that it was less attractive to cowbirds than the regular hay used before 1982 because the birds probably couldn't easily separate seeds from the cubes.

Bird counts in the region surrounding the removal sites.—The sampling periods with the greatest potential of detecting an area-wide effect of the removal program are B and C, the periods immediately before and after the removal. Overall, Ritter listed 33 male and 3 female detections during period B, versus 9 and 4 during C (Table 1). This suggests a significant decline in males, as male detections were not divided equally between periods B and C (Binomial test, $P < 0.001$). A more conservative comparison using a Wilcoxon test (Siegel 1956, Rohlf and Sokal 1969) applied to the numbers of male cowbird detections per meadow showed a significant decline between periods B and C ($0.03 < P < 0.05$, $t = 1.5$, N = 6 meadows with changes in numbers of male detections). The data for females were too few for meaningful analyses.

Overall, Stevens had 38 male and 9 female detections during period B and 22 and 1 during C. Neither male nor female detections were divided equally between periods B and C (for males, $P = 0.026$; for females, $P = 0.01$). The number of male cowbird detections per meadow declined significantly between periods B and C ($P = 0.03$, $T = 11$, $N = 11$). Female detections per meadow also declined, but the sample sizes were too small to show a significant result.

Another comparison of interest is that between the postremoval period in 1981 (period C) and a comparable time period in 1980 (period A) (Table 1). This comparison has the potential of indicating an area-wide effect of the removal, assuming that preremoval (period B) cowbird numbers in 1981 were not significantly below the 1980 (period A) counts. This assumption is reasonable because no significant or even strong trends emerged when periods A and B were compared. There were 26 male and 6 female detections during period A and 9 and 4, respectively, during period C. Male detections were not evenly divided between periods A and C ($P < 0.005$) but the female detections showed no trend (6:4). On a per meadow basis, male detections declined significantly between periods A and C ($P = 0.04$, $t = 5$, $N = 8$). Female detections were again too few for analysis.

A synthesis of these various tests indicates that the removal program depressed male abundance over a large area. All 3 comparisons (A vs C and B vs C for Ritter plus B vs C for Stevens) (Table 1) showed significant declines in both total male detections and male detections per meadow. Overall, Ritter detected only 27% (9/33) as many males after the removal as before, and Stevens detected only 58% (22/38) as many, giving a mean of 42.5% for these 2 samples. We found little clear evidence for a decline in female abundance, but most analyses suggested a slight decline.

DISCUSSION

Cowbird responses to horses.—The date on which horses are first brought to WLPS and other Sierran pack stations for the summer season varies by as much as 2 weeks (Verner and Ritter 1983), so the sudden rise in cowbird numbers after the horses arrived (Fig. 1) is unlikely to have been due to cowbirds accurately timing their migration into the Sierra Nevada to coincide with the appearance of horses. Also, 10-min counts in meadows during mid-May, before the horses arrived in 1981 (unpubl. data), indicated that there were nearly as many cowbirds present then as there were later in the season (period B) (Table 1). Thus the rapid increase in cowbird numbers at WLPS indicates that cowbirds were in the general area before the horses were present and that they frequently checked WLPS to assess its suitability for foraging. Although cowbirds were present in the area before horses arrived, the onset of peak egg-laying rates coincided closely with the arrival of horses and other livestock, thereby suggesting that the birds depend on these unnatural foraging associates for sustained breeding (Verner and Ritter 1983).

By monitoring cowbird numbers immediately after horses arrived at WLPS, we found that cowbirds were attracted to horse corrals by the presence of horses per se, not by the artificial habitat of corrals, i.e., bare dirt with hay and horse manure. Horses may increase the foraging value of pack stations because they and their fresh manure attract flies and other insects, their manure may have parasites, and pack station operators put out grain and fresh hay only when horses are present (although old manure and hay are usually abundant before horses arrive). Also, we found numerous insect larvae under hard caked manure and dirt at WLPS before the horses arrived, but the birds were unable to secure these until the horses walked over the area and broke up the soil.

The differing trapping patterns of adult and yearling males and of females.—That we were able to catch so many cowbirds and reduce the population size so effectively at WLPS, suggests that birds congregated there primarily for foraging rather than to engage in social behavior. This view agrees with our finding that the birds did not congregate at WLPS until horses were present. Although courtship and agonistic behavior are common at pack stations in the Sierra, and cowbirds often seem to be participating in a lek-like situation, we suggest that this social behavior is primarily or solely an outcome of the birds congregating to feed at a prime spot, not an inducement for the gregariousness itself. Significantly, the female capture rate (Fig. 3) did not decline towards the end of the removal phase despite the fact that male numbers at WLPS were greatly reduced. Had females visited WLPS to assess males in a lek-like situation, their visitation rates should have declined as male numbers went down.

It does not seem that a critical number of birds must be present for continued use of a feeding site. Thus cowbirds will apparently continue to feed at a site and become trapped even after their numbers begin to decline. However, radio-tracking studies conducted simultaneously with the removal experiment suggested that the birds visiting WLPS at any one time were a biased subsample of the local population. Some female cowbirds in this area often spent the afternoon in meadows, foraging among cattle (Verner 1983) and usually accompanied by 1 or 2 males. Thus the sex ratio in meadows was much closer to being even than it was at WLPS, and many cowbirds, especially females, in the area around WLPS did not show a consistent commuting pattern between disjunct morning and afternoon ranges. By contrast, all birds commuted to social feeding sites nearly every day in the eastern Sierra near Mammoth Lakes, where there is no network of mesic meadows used by range cattle (Rothstein et al. 1984). Although some or perhaps all local females visited WLPS on occasional days, trapping at WLPS was not a highly efficient way to reduce the local breeding population because it is more critical to remove females than the more numerous males (sex ratios reviewed in Rothstein et al. 1986), yet the former made less use of WLPS.

The various trends in the trapout data support the view that the birds visiting WLPS at any one time were a biased subsample of the local population. A segment of the local population that did not visit WLPS every day accounts for the fact that the total numbers of both males and females caught greatly exceeded the highest numbers of each ever seen at one time. This discrepancy between numbers of birds observed and trapped at WLPS is probably also due to cowbirds sometimes perching high in trees surrounding the pack station and being less observable during our 5-min counts. The more even sex ratio among trapped birds than among birds seen at WLPS probably occurred because females, more than males, often failed to commute to WLPS every day. As the length of the trapout phase increased, more of these irregular visitors to WLPS were presumably added to the sample of trapped birds. This also explains the third trend in the trapout data, which showed that the capture rates for males declined over time whereas those for females did not. This latter result indicates that the relatively even sex ratio among trapped birds was not due solely to females being more likely to enter traps, as has been found for wintering cowbirds (Johnson et al. 1980).

The female capture rate at WLPS declined initially ($\tau = -0.47$, $P = 0.017$ for 12–24 June), although the overall rate showed no significant decline (Fig. 3). We suggest that this initial decline occurred because females with breeding ranges near WLPS visited it frequently, perhaps daily, and hence were rapidly trapped out.

Because yearling males were caught earlier in the trapout period and earlier in the day than adult males, we conclude that they spent more time at WLPS. Yearling cowbirds in California are much less successful at securing mates than are adults (Payne 1973, Rothstein et al. 1986, Yokel 1986), although the 2 age classes have similar success rates in the East (Darley 1968, Dufty 1982a). Thus among males, individuals that engaged in little or no breeding probably made greater use of WLPS than did more successful breeders. Although they do not maintain mutually exclusive territories (Dufty 1982a, b), male cowbirds interact agonistically (Rothstein et al. 1986, in press), perhaps in competition for local dominance. Yearling males are subordinate to adult males in the Sierra (D. A. Yokel pers. comm.), and some may be so effectively dominated in breeding habitat that they pursue a default strategy by investing less effort in mate procurement than do adults and by spending more time at prime feeding sites. That the ages of males at WLPS were skewed towards yearlings, which rarely mate (Rothstein et al. 1986), is further evidence that females visited WLPS to feed rather than to assess potential mates.

Efficacy of the removal experiment, and management implications.— The mean number of male cowbirds seen per 5-min count during the afternoon at WLPS after the removal was only 23.0% of the mean before the removal (5.6 for 22 June–1 July vs 24.3 for 3–11 June; data in Fig. 1). The comparable figure for females was 12.5% (0.4 vs 3.2). These changes in numbers of cowbirds were much greater than those that occurred at WLPS during the 1980 breeding season (Verner and Ritter 1983), when no removals occurred. Thus, we conclude that the removal experiment brought about large and statistically significant declines in both males and females feeding at WLPS during the afternoon. However, the removal at WLPS apparently caused only moderate declines in the numbers of cowbirds occurring in the morning in breeding habitat in the area surrounding WLPS, and this decline was demonstrable only for males (Table 1). These results are in accord with the discovery that many females and some males did not commute to WLPS on a daily basis and with the various trends in the trapout data. Thus in the WLPS region, removal at 1 or 2 heavily used feeding sites over the one-month period we employed is not an efficient means of controlling cowbird numbers over a large area because of the availability of dispersed feeding habitat in the form of meadows with grazing cattle.

Because the female capture rate did not decline over our one-month trapout period, it is probable that we caught only a small fraction of the local female population. Thus future trapout programs should be continued for a longer period, because the lack of a significant decline in capture rate indicates that more and more females could have been caught at WLPS as they made occasional visits to the site. Another improvement would be to continue the trapout program for several years, as this too would result in the capture of an increasing proportion of the local females. Lastly, removal activity in meadows might also be an effective improvement to our trapout program. Such removal could be achieved by use of traps, but we suspect that simply shooting the small numbers of cowbirds present in each meadow would be more efficient. Both male and female cowbirds are attracted to playback of the female's chatter call if they are alone or in small groups of five or fewer (Dufty 1982b; Rothstein et al., in press), thereby making it easy to shoot cowbirds.

Unless they incorporate some of the improvements mentioned above, short-term removal programs such as the one we tested are likely to have only limited success in much of the Sierra Nevada because free-ranging cattle occur throughout most of the mountain range. Known major exceptions are the national parks (Yosemite, Sequoia, and Kings Canyon), where cattle grazing is not allowed, and some east slope areas such as the Mammoth Lakes region, where most of the local meadows are apparently too dry to provide sufficient forage for cattle. Thus the removal technique tested in this study might be more effective in those parts of the Sierra, and in others where there are isolated pack stations or other forms of human development but no free-ranging cattle. However, even in the national parks and in the Mammoth area, cowbirds make use of alternative unnatural feeding sites, such as bird feeders and campgrounds (Rothstein et al. 1980), and the high availability of such sites in heavily visited national parks may offset the lack of cattle. Short-term removals are likely to be most successful in remote, high-altitude areas that are not reached by range cattle until cowbird breeding is over in mid-July (Rothstein et al. 1980, Verner and Ritter 1983) and that contain only one or several foci of human development such as pack stations or campgrounds.

Besides continuing the trapout phase for a longer period, we recommend that future programs continue to remove males, even though the number of females is obviously the most critical factor reducing host reproductive success. As indicated here, removal of males did not seem to make WLPS less attractive for females, and reduction of male numbers means that more traps are open and available for female captures.

Our most important finding relevant to cowbird control is that although Sierran cowbirds are most conspicuous while feeding during the afternoon in large groups at pack stations, they are adept at finding other sources of food due to human development. Furthermore, the birds in some large, conspicuous feeding groups may account for a disproportionately small share of the local breeding. Thus any plan to control cowbirds by trapping at a pack station must also consider all other forms of human activity in the area under consideration. Also, we repeat the suggestion made previously (Verner and Ritter 1983) that the impact of cowbirds can be managed by placing new foci of human activity (pack stations, campgrounds, etc.) in the Sierra Nevada and other semiwilderness regions near existing sites of human influence. Such a strategy will not open new areas to cowbird parasitism. The commuting distances over which cowbirds travel between breeding and feeding sites (Rothstein et al. 1984) can be used as a guide for siting new facilities.

We detected so few females in breeding habitat before the trapout procedure that there was little potential to find a significant decline in their numbers. Female detections were few, relative to male detections, because females are outnumbered by males (Rothstein et al. 1986) and are harder to detect in breeding habitat (Dufty 1981). Playing female chatter calls for a fixed time interval, instead of only counting birds under natural conditions (as in the present study), should be a more effective way to quantify cowbird numbers. However, repeated use of playbacks to detect cowbirds must incorporate suitable controls for habituation.

Dufty (1981) found that males were less likely to approach chatter playback if they had been exposed to playback on a previous day. Females showed no such change in responsiveness, and our playback experiments (Rothstein et al., in press) also indicate that female responses to chatter playback decline more slowly than male responses.

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