RANGE EXPANSION AND DIURNAL CHANGES IN DISPERSION OF THE BROWN-HEADED COWBIRD IN THE SIERRA NEVADA

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ABSTRACT.—An extensive literature search and survey of specimens in major scientific collections in California showed that the Brown-headed Cowbird (*Molothrus ater*) was absent from virtually the entire Sierra Nevada of California prior to 1930. Present distribution, diurnal patterns of dispersal, seasonal occurrence, and host species were studied directly in the field from 1975 to 1978. The evidence of a recent range expansion of cowbirds into the Sierra is clearcut, the birds appearing 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. Cowbirds apparently exploit horse corrals and other human developments for group foraging during midday, scattering by evening or early morning to dispersed breeding sites. Human influence may have been a necessary precursor to cowbird invasion of the Sierra, which is probably prime cowbird habitat in terms of host availability but marginal habitat in terms of food for adults. Twenty-two host species have thus far been discovered in the Sierra Nevada. Preliminary data suggest that among these the rate and consequences of nest parasitism may be severe enough to threaten continued survival in the Sierra of some species, especially the Warbling Vireo (*Vireo gilvus*). We believe the situation is serious enough to warrant close monitoring of these species' populations in the future. *Received 28 August 1979, accepted 3 December 1979.*

MAYFIELD (1965) documented the expanded distribution and increased abundance of Brown-headed Cowbirds (*Molothrus ater*) in eastern North America over the last three centuries. Although no similar, comprehensive analysis has been published for the western portion of the continent, data from many sources show similar trends there as well (see below). This study was initiated to determine (1) whether cowbirds have expanded their range and increased in abundance in the Sierra Nevada of California; (2) whether human activities contributed in any way to the changes; (3) whether cowbirds presently are a threat to any songbird population in the Sierra Nevada; and (4) if so, to identify possible ways to minimize the threat. The present report focuses on range expansion and increasing abundance of cowbirds in the Sierra, as we believe these phenomena are established without question. We also report data relevant to the cowbird's diurnal pattern of dispersion in the Sierra Nevada. This pattern may be unique among breeding birds in that most cowbirds appear to abandon their dispersed breeding areas after mid-morning and commute to localized feeding sites that support large numbers of individuals. We particularly hope that the present paper will stimulate other workers to report their relevant observations in the Sierra, as our work there is continuing.

The cowbird's invasion of the Sierra is especially interesting in terms of range extensions in general and of cowbird biology in particular because: (1) The invasion apparently began within the last 50 yr and probably is not yet completed. Hence, it can be documented more accurately than the major eastern invasion, much of which was completed 100–200 yr ago. (2) Unlike the invasion of the East and that of lowland California, the Sierran penetration has not been associated with wholesale habitat alteration. (3) Many potential hosts of this parasitic species are patchily

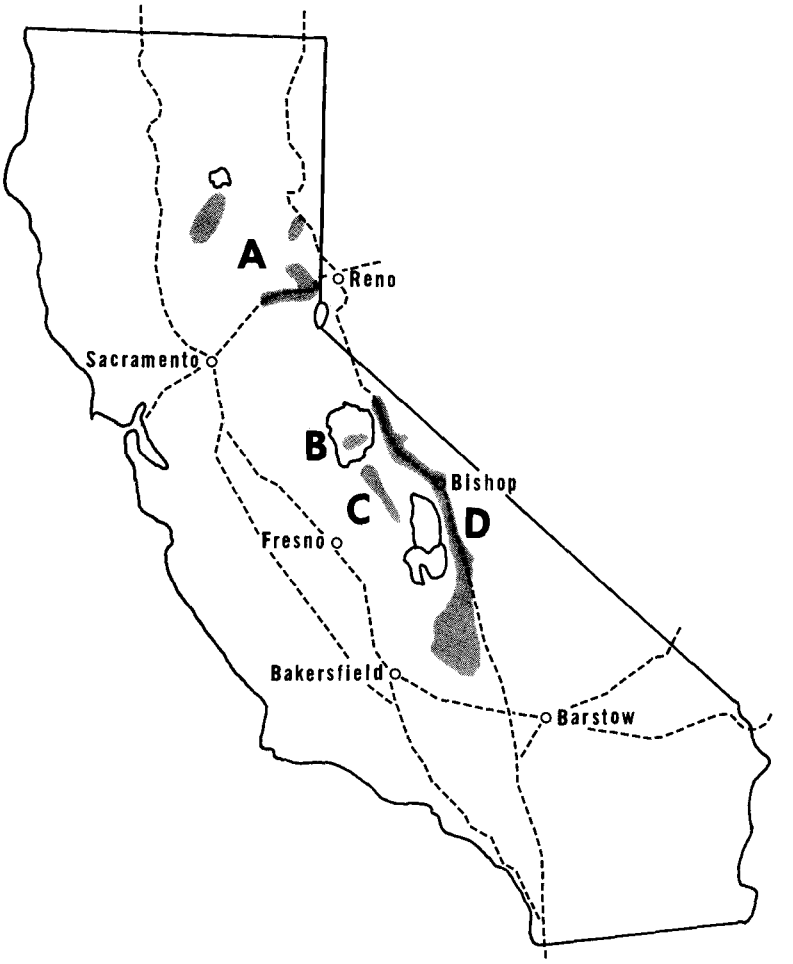

Fig. 1. Outline map of California showing approximate locations of study areas (shaded) as follows: A—Northern Sierra, B—Yosemite Valley, C—West-Central Sierra, and D—Southeastern Sierra. National Parks are shown in outline for reference. Lassen is the northernmost; Yosemite surrounds study area B; Kings Canyon and Sequoia are the two southernmost. Dashed lines represent major highways. Most of study areas A and D and all of areas B and C are beyond the cowbird's range as shown by Grinnell and Miller (1944).

distributed in the Sierra and breed in small populations that may be especially vulnerable to extirpation by the cowbird. Species with limited distributions and small populations in other areas seem to be the ones most prone to declines induced at least in part by cowbird parasitism (Gaines 1974; Oberholser 1974: 701, 752; Pulich 1976; Mayfield 1978).

METHODS AND STUDY AREAS

Documentation of the past distribution of cowbirds in the Sierra Nevada is based on extensive review of the literature and a survey of specimens in four major scientific collections in California—the Museum of Vertebrate Zoology, University of California, Berkeley; University of California, Los Angeles; the Moore Laboratory of Zoology, Occidental College, Los Angeles; and the California Academy of Sciences, San Francisco. The first three collections were also surveyed for specimens of Brewer's Blackbirds

(*Euphagus cyanocephalus*) on the assumption that blackbird specimens would establish the presence of collectors who likely would have collected cowbirds also, had they beeen available. We believe this is a reasonable assumption, because cowbirds and Brewer's Blackbirds occur in the same habitats and early collectors tried to secure series of all species. Furthermore, ornithologists collecting in earlier decades of this century showed considerable interest in the distribution and taxonomy of California cowbirds (Grinnell 1909, 1934; Dickey and Van Rossem 1922; Miller 1935), and thus would probably have made special efforts to obtain specimens.

The Sierra Nevada, for purposes of the specimen survey, was taken to include all localities above 900 m elevation between the Pit River (Modoc, Lassen, and Shasta counties) in the north and Walker Pass, Kern County, in the south. The only exception was that the Owens Valley, Inyo and Mono counties, which runs north–south along the eastern base of the Sierra at 900 to 1,300 m, was not considered part of the Sierra (although it was included in the fieldwork described below). The breeding season was assumed to range from April to August.

Documentation of the present distribution and abundance of cowbirds in the Sierra is based on field sampling in the early morning (most counts before 0830 PST) from late May to early August 1978 in four general study areas (Fig. 1). Our principal study area, the Southeastern Sierra, was located in the southern half of the eastern slope, from the Bridgeport Valley, Mono County, in the north to the Walker Pass area in the south. Adjacent nonmountain areas, such as the Owens Valley, were included also.

In the Southeastern Sierra, we sampled the avian community at least once at each of 400 sites, grouped into 29 survey routes, most of which followed improved roads.[1] Fifty-three of the 400 sites were sampled two or three times to obtain information on seasonal changes in occurrence. Although the surveys did not penetrate far into the mountains in a lateral sense, most counts were at high altitudes due to the steepness of the eastern slope and to the proximity of the Sierran crest to the eastern edge of the mountain range. Twelve of the roads surveyed ascended the mountains to above 2,400 m, and 71.0% of all counts were done above 1,700 m (Table 1). Areas within 16 km of Mammoth Lakes, Mono County, were the most intensely studied, with 116 counting stations located there.

Counts in the Southeastern Sierra Study Area were done in all types of habitats, but the majority of sites were purposely selected in habitats that appeared to be suitable for cowbird utilization, such as riparian zones, meadows, forest edges, towns, and horse corrals. Most counting sites were at least 1.6 km apart, but when two observers traveled together, they often did counts within 300 m of each other, with at least 1.6 km separating successive pairs of sites along the same survey route. Only in the Mammoth Lakes area, where coverage was especially complete, were sites ever less than 300 m apart.

The sampling procedure involved counting from a fixed point all birds detected during a 10-min period. Cowbirds detected during the 10-min counting period are identified as "Type 1 detections"; those detected at or near the site within the 5 min or so spent in the area before and after the formal counting period but not during the period are identified as "Type 2 detections."

Secondary study areas indicated in Fig. 1 are the West-Central Sierra, the Yosemite Valley, and the Northern Sierra. Ninety-six sites in the West-Central Sierra were grouped into six survey areas, all within the boundaries of the Sierra National Forest in Madera and Fresno counties. The sites were selected in mixed conifer and red fir forest zones, by a stratified random procedure, to sample avian community structure for purposes other than just sampling cowbirds. Most sites were not near improved roadways; they ranged in elevation from 1,645 to 2,316 m; most were sampled from 7 to 10 times each, and most sites were no closer together than 300 m. Counting methods were identical to those used in the Southeastern Sierra.

Yosemite Valley sites were sampled by Gaines (MS). They ranged in elevation from about 1,200 to 2,200 m. Thirty-one circular plots 25 m in diameter were sampled for 10 min one to three times each. Sites were selected in a manner assuring coverage of a broad range of habitats on the valley floor and between the floor and the rim.

Sampling in the Northern Sierra area was entirely opportunistic, depending upon personnel traveling across the mountains before 0900 PST. Twenty-five sites, ranging in elevation from 660 to 1,890 m, were sampled once each using techniques identical to those employed in the Southeastern and West-Central Sierra Study Areas.

Studies of diurnal dispersal patterns were done only in the Southeastern Sierra Study Area. Cowbird

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[1] More detailed information on specific site locations is in: Rothstein, S. I. 1979. Past and present distribution of the parasitic Brown-headed Cowbird in the Sierra Nevada Mountains: Report on research done in 1978. 37 pp. + figures and tables. Unpubl. typescript. Request copy from Librarian, Pacific Southwest Forest and Range Expt. Stn., P.O. Box 245, 1960 Addison St., Berkeley, CA 94701.

occurrence at selected horse corrals at mountain pack stations was quantified by counting the number of birds present at the site during a 5-min observation period. Counts at each site were made throughout the day but were always at least 50 min apart; generally, only 1–4 counts were made per day. The two pack stations for which we present data were 2 km south (Sierra Meadows Pack Station) and 13 km southeast (Convict Lake Pack Station) of Mammoth Lakes.

RESULTS

Past distribution.—The cowbird has increased its range throughout the far west. In British Columbia, Washington, and Oregon, it probably bred originally only east of the Cascades, but today it is widespread in some coastal areas (Brooks and Swarth 1925; Hoffman 1927: 287; Schultz 1957; Larrison and Sonnenberg 1968: 227; Gabrielson and Jewett 1970: 529). In California, the cowbird's early presence east of the Sierra in the Great Basin (Grinnell 1909, Grinnell and Storer 1924: 399) and along the Colorado River (Dawson 1924: 81) suggests that it occupied those regions in prehistoric times, but west and south of the Sierra in the remainder of California it is not clear whether the cowbird is a recent addition to the avifauna or whether its increased prevalence in this century reflects only increased abundance. Willett (1933: 156) discussed the cowbird's increased prevalence in southwestern California and called the cowbird's increase in the previous 20 yr "remarkable" and ". . . unparalleled by any other of our native birds." Cowbird eggs were not found in the San Francisco Bay region until 1922, and specimens of breeding adults were not secured until 1934 (Grinnell 1934). Even in the intensively studied area around Berkeley, the cowbird was unknown as a breeder before 1934 (Benson and Russell 1934). In the Central Valley, Tyler (1913) found no evidence of cowbird breeding in the Fresno area between 1900 and 1912, but Payne (1973) found the cowbird to be a common breeder between 1960 and 1965. In northwestern California, the first breeding records occurred in 1941 in Humboldt County (Talmadge 1948).

Prior to the present study, the only well documented presence of cowbirds in the Sierra was for Yosemite Valley and adjacent areas. Early work in the Yosemite region demonstrated the presence of cowbirds east and west of the mountains but not within the range itself (Grinnell and Storer 1924). Cowbirds apparently invaded the Yosemite Valley in 1934; their subsequent increase there is summarized by Gaines (1977). Taking the Sierra as a whole, Grinnell and Miller's (1944) discussion and range map show that the cowbird was considered to be absent from nearly the entire mountain range in the 1940's in spite of its increased abundance in the rest of California. A more recent, semipopular account states that in regions near the Sierra the cowbird is ". . . resident at lower levels west and east of the mountains" (Storer and Usinger 1963: 310).

Careful study of numerous references describing fieldwork in the Sierra prior to 1940 revealed no evidence of cowbirds, other than the previously cited records for Yosemite Valley and a few records for portions of Mono County. Cowbirds bred in the Sierra, in Mono County, in the 1920's and 1930's, as shown by scattered reports of parasitized nests (Dixon 1934; Rowley 1939: 51; Friedmann 1963: 102, 167, 1966: 2; Friedmann et al. 1977: 28), but they must have been rare and may even have been absent in some years, because Rowley (1939) failed to find adult cowbirds during 33 days of summer fieldwork in Mono County, spread over 5 yr between 1926 and 1939.

Specimens of nine cowbirds and 49 Brewer's Blackbirds collected in the Sierra Nevada before 1940 were found in the four museum collections we searched. All

TABLE 1. Percent of counting sites at which cowbirds were detected in the Southeastern Sierra Study Area between 25 May and 18 July 1978.

Portion of area sampled	Elevation				
	<1,200 m	1,200–1,700 m	1,800–2,400 m	>2,400 m	All elevations
Northern half (Big Pine to Bridgeport)					
Type 1 detections	0	48.5	32.3	34.5	35.2
Type 1 + Type 2 detections	0	51.5	38.6	48.3	43.7
Number of sites sampled	0	33	127	87	247
Southern half (Independence to Cantil)					
Type 1 detections	26.7	13.0	32.6	11.1	23.5
Type 1 + Type 2 detections	31.7	21.7	44.2	18.5	31.4
Number of sites sampled	60	23	43	27	153
Combined data					
Type 1 detections	26.7	33.9	32.4	28.9	30.8
Type 1 + Type 2 detections	31.7	39.3	40.0	41.2	39.0
Number of sites sampled	60	56	170	114	400

nine cowbirds were from Mono County; eight were taken near Mono Lake, east of the main Sierran escarpment. By contrast, the 49 Brewer's Blackbird specimens represented localities in 10 counties. Thus, the specimen survey confirms the story derived from the literature—cowbirds generally were absent from nearly all of the Sierra before 1930–40. Only meagre information is available to document changes in Sierran occurrence of cowbirds between 1940 and the present time. Because that information does little to establish general trends, we will postpone discussion of the problem for a more detailed treatment in a later publication.

Present distribution.—Table 1 summarizes the percentages of sites in the Southeastern Sierra Study Area where Type 1 and Type 2 detections were made. The cowbird was one of the most widespread species in this area, being detected at 39.0% of all counting sites. Cowbirds were detected on all 13 survey routes that went beyond the historical limits of the species' distribution in the region, as shown by Grinnell and Miller (1944). In fact, cowbirds were detected at 41.2% of 114 sites above 2,400 m. A possible trend of increasing abundance is suggested from south to north, but there is no overall trend with increasing elevation (Table 1). Interestingly, we detected no cowbirds on only 4 of the 29 survey routes in the Southeastern Sierra Study Area, and all 4 were within the historical range of cowbirds prior to 1940.

Cowbirds were detected in all six survey areas in the West-Central Sierra Study Area, being recorded at 42.7% of the 96 counting sites. All sites were in areas not frequented by cowbirds prior to 1940. Because these sites were sampled as many as 10 times in some cases, it is not reasonable to use this percentage in comparing cowbird frequency in this study area with that in the Southeastern Sierra Area (Table 1). To equalize sampling effort for the two areas, we used one count per site in the West-Central Sierra Area, using the middle count when counts for each site are ranked chronologically. For sites with an even number of counts, we used the earlier of the two counts at the midpoint. Under these criteria, only 17.7% of the 96 sites in the West-Central Sierra Area had Type 1 and/or Type 2 detections. This suggests that the West-Central Study Area has a lower cowbird abundance than our other major study area, the Southeastern Sierra, which had cowbird detections at 39.0% of all sites. Many of the Southeastern Sierra sites, however, were chosen

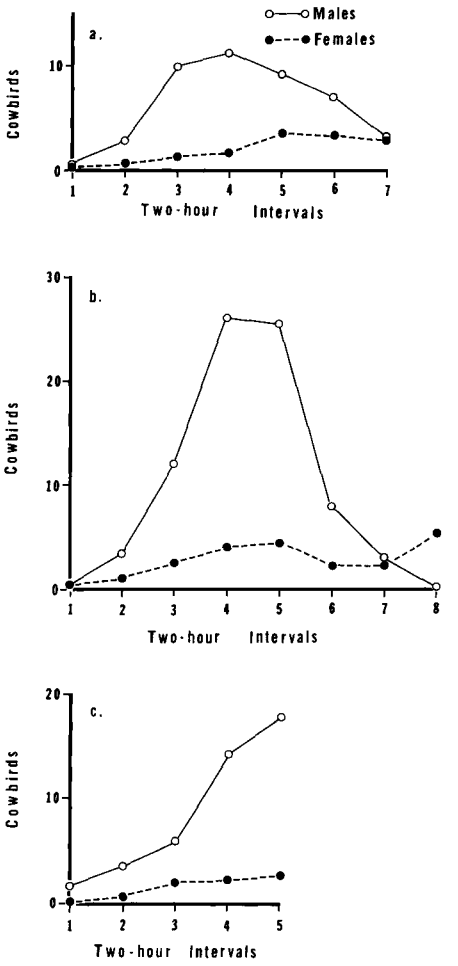

Fig. 2. Diurnal variation in numbers of adult cowbirds at pack stations in Mono County, California. Points represent mean numbers of birds present during 5-min counting periods within 2-h intervals, starting with interval 0500–0700 PST (with the mean entered at 0600). Noon is represented by interval number 4. Figure 2a presents data for the Sierra Meadows Pack Station (along Mammoth Creek, elevation = 2,390 m) from 25 June to 5 July 1978 (n = 28 5-min counts). Figure 2b presents data for the same pack station from 6 to 15 July 1978 (n = 38) when male cowbirds were more numerous. Figure 2c presents data for the Convict Lake Pack Station (along Convict Creek, elevation = 2,316 m) 22 June and 3–15 July 1978 (n = 15).

because they represented relatively good cowbird habitat, so the apparent west slope-east slope difference in cowbird abundance is not conclusive.

In the Yosemite Valley, Gaines (MS) reported Type 1 and/or Type 2 detections at 32.3% of 31 circular counting plots, taking only the first count at each plot, and, in the Northern Sierra Area, Type 1 and/or Type 2 detections were made at 40.0% of the 25 counting sites. Again, nearly all of these observations extend the pre-1940 distribution of cowbirds in the Sierra Nevada.

Specific localities visited earlier in this century and during our study further confirm the range extension of cowbirds into the Sierra. Rowley (1939) failed to detect cowbirds after much fieldwork along Mammoth and Convict creeks in Mono Coun-

ty. In 1978, we detected cowbirds at 9 of 17 counting sites along these creeks early in the morning, and later in the day we typically observed at least 15 cowbirds at a time at horse corrals within 0.6 km of each creek (Fig. 2). Tracy Storer made a special effort in 1930 to detect cowbirds in the Bridgeport Valley, Mono County, but failed to do so (Gaines 1977: 120). We detected cowbirds at four of our 14 counting sites in and near the valley in 1978. J. S. Dixon (1943) reported on birds observed in Kings Canyon National Park between 1916 and 1942 and did not list the cowbird. On 14 July 1978, M. Cannon (pers. comm.) observed three cowbirds near the center of the park in the Paradise Valley at 2,000 m elevation along the South Fork of the Kings River. Tyler (1909, 1913) reported that neither cowbirds nor Brewer's Blackbirds bred near Fresno between 1900 and 1912 but that the latter nested at Shaver Lake, Fresno County, at an elevation of about 1,700 m. Undoubtedly Tyler would have reported the cowbird as a breeder at Shaver Lake had there been any evidence of its occurrence there. In our West-Central Sierra Study Area, we detected cowbirds at 2 of 3 counting sites within 1.5 km of Shaver Lake and at 18 of 36 sites in a survey area extending southeast from Shaver Lake for 20 km.

Additional supporting observations and reports are as follows: (1) A Warbling Vireo (*Vireo gilvus*) was observed feeding a cowbird 8 km east of Sierra City, Sierra County, at 1,676 m elevation, on 13 August 1978 (A. H. James pers. comm.). (2) Cowbirds were first detected at Sage Hen Valley, Nevada County, in 1968 after about 20 yr of observations (J. M. White pers. comm.). (3) A Warbling Vireo was seen feeding a cowbird about 8 km south of Truckee along the Truckee River, Placer County, on 1 August 1978 (E. Stevens unpubl. obs.). (4) At the headwaters of the North Fork of the American River in Placer County, repeated counts in 1974 of a 1.9-ha plot in an "open canopy" mixed conifer forest, at an elevation of about 1,830 m, gave an estimated density of 2.6 cowbirds per 40 ha. Similar counts at three other plots (mixed conifer with closed canopy at 1,890 m elevation, red fir with open canopy at 2,200 m elevation, and red fir with closed canopy at about 2,270 m elevation) did not detect any cowbirds (Beedy 1976). (5) Four nests of Wilson's Warblers (*Wilsonia pusilla*) were found to be parasitized by cowbirds between 1973 and 1976 at Tioga Lake, Tuolumne County, at elevations of 3,000–3,100 m (Stewart et al. 1977). (6) Ten cowbirds were seen on 7 July 1977 at Topaz Lake on the California-Nevada boundary near northern Mono County (T. Heindel pers. comm.). (7) M. Morton (pers. comm. and Morton et al. 1972) has studied White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on the east side of Tioga Pass, Mono County, at an elevation of about 3,000 m, each year since 1968. He first observed cowbirds there in 1976 and that same year discovered his only case of cowbird parasitism of White-crowned Sparrows.

Daily dispersion patterns.—Our observations suggest that each day Sierran cowbirds used two types of habitats—breeding and feeding sites—and that these habitats were usually separate. In the morning, when our counts were done, cowbirds were dispersed over a variety of habitats but were most prevalent in those with high passerine species richness such as riparian areas and meadow-forest interfaces. These apparently were preferred breeding habitats, with cowbirds typically observed singly or in groups of 2–4. The birds were usually vocal, especially the males. They were active, and males were often detected only as they quickly flew over the area. Individuals were occasionally detected for all or most of a 10-min count, but more often they left an area after perching for only a minute or two. We virtually never detected cowbirds on the ground in these sites. Cowbirds in these habitats probably

were searching for mates and host nests and may have maintained home ranges and possibly even territories. We assume that these habitats were the primary site of breeding activities because cowbirds lay eggs in the morning, and nest building, a cue cowbirds use to find host nests, is most intense then (Friedmann 1963).

Many, perhaps most, cowbirds apparently left their breeding sites by late morning or early afternoon to form foraging aggregations sometimes numbering dozens of birds. Foraging opportunities probably were limited in habitats frequented early in the morning, as cowbirds normally feed on the ground in areas of short grass and near large grazing mammals (Mayfield 1965). We found midday feeding aggregations most often around horse corrals at mountain pack stations. Cowbirds foraged on the ground and seemed to obtain much of their food by probing through and pecking into horse manure. Counting the cowbirds at two pack stations at various times during the day indicated rapid buildup in the morning, with decline in the late afternoon (Fig. 2). To analyze statistically the numbers of cowbirds at pack stations, we divided the day into early, mid, late, and evening periods, corresponding to intervals 1–2, 3–4–5, 6–7, and 8 in Fig. 2. Mann-Whitney U tests showed that males increased significantly ($P < 0.001$) between intervals 1–2 and 3–4–5 in Fig. 2a, 2b, and 2c and decreased significantly ($P < 0.025$) between intervals 3–4–5 and 6–7 in Fig. 2a and 2b. Females showed significant ($P < 0.01$) increases between intervals 1–2 and 3–4–5 in Fig. 2a, 2b, and 2c and a significant ($P = 0.05$) decrease between intervals 3–4–5 and 6–7 in Fig. 2b. Curiously, the data for interval 8 (Fig. 2b), which consist of five counts between 1905 and 1925, show that females had a second peak just before dark ($P < 0.01$ for intervals 6–7 vs. 8), whereas males continued their late day decline ($P < 0.01$).

At least one campground in the Mammoth Lakes area also hosted midday aggregations of foraging cowbirds. The Glass Creek Campground (11 km north of Mammoth Lakes), in a mixed riparian-pine forest (*Pinus jeffreyi* and *P. murrayana*), apparently provided conditions suitable both for breeding and foraging. Two morning counts produced 3 and 4 cowbirds, all of which were flying over the area or perched off the ground, whereas three afternoon counts produced 6, 13, and 23 cowbirds, which foraged on the ground.

We did no formal 10-min counts in breeding habitats after late morning in the Sierra, but numerous casual observations indicated that cowbirds were rarely encountered in these habitats in the afternoon. Formal afternoon counts were done in the Owens Valley, however, and the results clearly suggested that most cowbirds leave the breeding sites by the afternoon. Ten-minute counts were done at 18 sites in the afternoon (from 1649 to 1750 PST) and again early the following morning. None of these sites was near an obvious source of cowbird food, such as a horse corral. Cowbirds were never noted at nine of the sites but were detected only in the morning at seven and in both the afternoon and the following morning at two sites ($P < 0.01$, sign test).

Distances traveled between breeding and feeding sites by cowbirds in the Sierra Nevada are unknown. Clearly, some birds need not travel any distance at all, because suitable breeding and feeding localities can be intermingled as in the case of the Glass Creek Campground. But because cowbirds are not restricted by parental care and can leave the area in which their young are reared for extended periods, the round trip between breeding and feeding sites need be made only once each day and hence might be long. We often saw cowbirds leaving the Sierra Meadows Pack Station (Fig. 2) and disappearing from view after flights of at least 2–3 km.

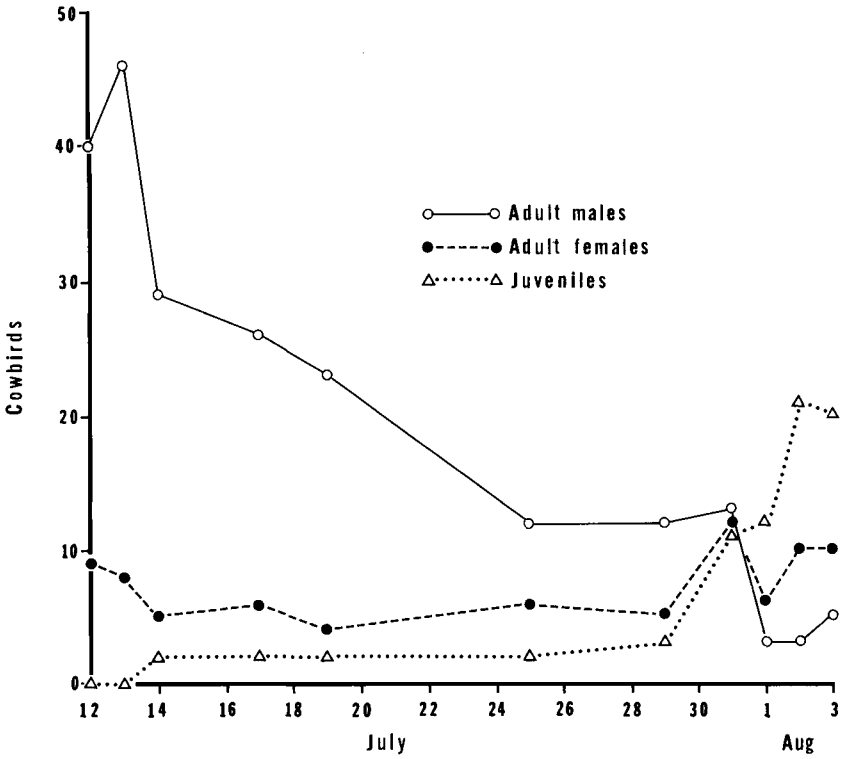

Fig. 3. Peak numbers of adult male, adult female, and juvenile cowbirds recorded daily at the Sierra Meadows Pack Station. An observer was at the pack station for nearly the entire midday peak of cowbird occurrence on each date for which an entry is made. The number shown on the graph is the largest number of cowbirds present per day.

Seasonal changes in numbers and activity.—Forty-six sites near Mammoth and June Lakes in the Southeastern Sierra Study Area were sampled between 23 June and 13 July (data included in Table 1) and again between 28 July and 3 August. These sites were in areas that seemed suitable for cowbird breeding; none was near an obvious concentration of food, such as a pack station. Cowbirds were never detected at 22 of these sites. Among the remaining 24 sites, there were Type 1 detections during only the first count at 21 sites, the second count at one site, and during both counts at two sites ($P < 0.001$, sign test). Cowbirds obviously showed a marked and rapid decline in their detectability, and probably occurrence, by late July. Similarly, Gaines (1977: 121) noted that adult cowbirds in Yosemite Valley and adjacent east slope areas "depart by the end of July." By contrast, the numbers of other passerine species declined only moderately. The 46 sites averaged 6.0 passerine species other than cowbirds on or before 13 July and 4.8 on or after 28 July. Thus the cowbird's apparent decline in numbers occurs sooner than that of most seasonally occurring passerines in these mountain habitats.

As with the east slope sites near Mammoth and June Lakes, west slope sites also showed an abrupt decline in cowbird detectability by late July to early August. Forty sites in the West-Central Sierra Study Area were counted 6 times by 1 August and 2 times between 5 and 16 August. Overall, there were Type 1 detections of cowbirds at 20 sites on or before 1 August but at none between 5 and 16 August.

TABLE 2. Passerine nests and family groups checked for parasitism in the Sierra Nevada study areas.

Species	Mammoth Lakes area, 1975, 1977, and 1978[a]	Yosemite Valley, 1978[b]	
	Nests	Nests	Family groups
Western Flycatcher (*Empidonax difficilis*)	1 (0)[c]		1 (0)[c]
Empidonax spp.	2 (1)		
Western Wood Pewee (*Contopus sordidulus*)	5 (0)	6 (0)	3 (0)
Olive-sided Flycatcher (*Nuttallornis borealis*)	1 (0)		
Steller's Jay (*Cyanocitta stelleri*)		2 (0)	3 (0)
Mountain Chickadee (*Parus gambeli*)			2 (0)
Chestnut-backed Chickadee (*Parus rufescens*)			1 (0)
Brown Creeper (*Certhia familiaris*)		1 (0)	
Dipper (*Cinclus mexicanus*)			2 (0)
House Wren (*Troglodytes aedon*)	1 (0)		
Cañon Wren (*Catherpes mexicanus*)			2 (0)
American Robin (*Turdus migratorius*)	6 (0)	9 (0)	23 (0)
Mountain Bluebird (*Sialia currucoides*)	2 (0)		
Solitary Vireo (*Vireo solitarius*)		3 (2)	3 (3)
Warbling Vireo (*Vireo gilvus*)	5 (4)		2 (2)
Nashville Warbler (*Vermivora ruficapilla*)			4 (0)
Yellow Warbler (*Dendroica petechia*)	4 (2)		3 (2)
Black-throated Gray Warbler (*Dendroica nigrescens*)			9 (1)
MacGillivray's Warbler (*Oporornis tolmiei*)			4 (1)
Red-winged Blackbird (*Agelaius phoeniceus*)	1 (0)		12 (0)
Northern Oriole (*Icterus galbula*)			2 (0)
Brewer's Blackbird (*Euphagus cyanocephalus*)	11 (0)	17 (0)	22 (0)
Western Tanager (*Piranga ludoviciana*)		1 (0)	
Black-headed Grosbeak (*Pheucticus melanocephalus*)		6 (0)	17 (0)
Evening Grosbeak (*Hesperiphona vespertina*)			1 (0)
Green-tailed Towhee (*Pipilo chlorurus*)	1 (1)		
Chipping Sparrow (*Spizella passerina*)			1 (0)
Dark-eyed Junco (*Junco hyemalis*)	6 (3)		
Fox Sparrow (*Passerella iliaca*)	1 (0)		
Lincoln's Sparrow (*Melospiza lincolnii*)			2 (0)
Song Sparrow (*Melospiza melodia*)	1 (1)		3 (2)

[a] All nests were within 16 km of the town of Mammoth Lakes.
[b] Data from Gaines (MS).
[c] Number of nests or family groups observed (number parasitized).

Considering all counts at those 40 sites, cowbirds were recorded on 42 of 240 counts before 1 August but on none of 80 after 5 August ($P < 0.001$, $\chi^2 = 14.6$, d.f. = 1). Other passerine species also declined between the first and second groups of counts, but only slightly, from a mean of 9.2 to 8.2, so again the cowbird's substantive decline was early relative to other passerines.

Data from the counting sites were partially supported by those from feeding aggregations at the pack stations. Figure 3 shows a late seasonal decline in peak numbers of male cowbirds at the Sierra Meadows Pack Station, beginning on 12 July. There were no declines in males or females before 12 July. It appears from these data that the major late July exodus of cowbirds involves adult males and that the pack stations actually attract an increasing number of juveniles at that time. Our field season in 1978 ended too early to determine how long juveniles and adult females continued to visit these feeding sites.

Early evacuation of breeding grounds may not occur at lower elevations. Seven sites at an elevation of about 1,200 m along the Owens River near Bishop, Inyo County, were sampled on 31 May, 11 July, and 26 July. Six of the sites had cowbirds on the first count, 4 on the second count, and 5 on the last count. Respective mean numbers of passerine species, other than cowbirds, were 6.1, 5.9, and 6.1. Cowbirds

on all three counts appeared to be engaged in breeding activities. They were vocal and were not seen foraging. No doubt cowbirds at these lower altitudes begin breeding relatively early, so they seem to have a substantially longer breeding season than do cowbirds in the Sierra Nevada.

Host species.—Our fieldwork and a survey of the literature (Friedmann 1963, 1966, 1971; Friedmann et al. 1977; Gaines 1977) produced records of nest parasitism of 22 species in the Sierra Nevada. Nests found in the Mammoth Lakes area by our study team and in the Yosemite Valley by Gaines (MS) provide data (Table 2) on rates of observed, although not necessarily on actual, parasitism and thus may underestimate the degree of parasitism that occurred (Rothstein 1977). By contrast, observations of family groups (Yosemite Valley only, Table 2) may overestimate rates of parasitism of some species, because cowbird fledglings probably are noisier and less wary than fledglings of other passerine species.

The data indicate that some small passerine species, especially members of the Vireonidae, Parulidae, and Fringillidae, are being heavily parasitized by cowbirds in the Sierra. Considering only those three families, 2 of 9 (22.2%) nests in the Yosemite Valley and 11 of 18 (61.1%) nests near Mammoth Lakes were parasitized. In Yosemite Valley, 11 of 49 (22.4%) family groups of vireos, parulids, and fringillids contained a cowbird. Excluding one large fringillid, the Black-headed Grosbeak (*Pheucticus melanocephalus*), changes the value to 34.4% of 32 family groups. The apparent low degree of parasitism of flycatchers is unexpected, but most flycatcher nests were of the Western Wood Pewee (*Contopus sordidulus*), a rarely observed host (Friedmann et al. 1977). Perhaps some of the *Empidonax* flycatchers will prove to be common hosts in the Sierra after the collection of more data, as some members of the genus are heavily parasitized in other regions (Friedmann 1963, Friedmann et al. 1977).

Friedmann et al. (1977: 39) discuss a case of parasitism of Brewer's Blackbird in the Sierra, but our failure to detect any parasitism (Table 2) indicates that this species is a rare host in the mountains. Near Bishop and Big Pine, 63 and 80 km southeast of Mammoth Lakes in the Owens Valley, however, we found 20 of 38 Brewer's Blackbird nests to be parasitized in 1977 and 1978. Further south in the Owens Valley, over a 101-km route from Independence to Little Lake, Inyo County, our 10-min circular counts indicate that cowbirds are less common than at Biship, and only eight of 69 Brewer's Blackbird nests found along that route were parasitized. We found no evidence in the Owens Valley that Brewer's Blackbirds reject cowbird eggs or that cowbird nestlings have difficulty surviving in their nests. Similarly, Furrer (in Friedmann et al. 1977: 37–38) found that Brewer's Blackbirds in the Potholes region of central Washington are frequent and excellent hosts, successfully producing fledglings from about one-third of all the cowbird eggs laid in their nests. The slight extent to which Sierran cowbirds parasitize Brewer's Blackbirds is thus perplexing.

Discussion

Distribution of cowbirds in the Sierra Nevada.—We believe results of the present study conclusively show that cowbirds have undergone a significant range expansion into the high Sierra Nevada from their lower elevation distribution prior to about 1940. Large areas of the Sierra still have no records of cowbirds, but this may reflect a lack of fieldwork. We detected cowbirds in every Sierran area visited, although

most data were obtained in areas close to human influences such as roads, towns, campgrounds, or pack stations. It is unknown whether cowbirds are ubiquitous in more remote areas. They were found in a diversity of habitats, but it was our impression that areas distant from human influence, or surrounded by large, unbroken stretches of forest, had relatively few cowbirds.

What factor or factors may have permitted cowbirds to invade the high Sierra Nevada cannot be determined at this time. Perhaps agricultural developments at lower elevations favored increasing cowbird numbers there to the point that some birds simply were forced to invade the Sierra, where they found ways to survive and reproduce successfully; or perhaps human developments, such as pack stations, towns, campgrounds, and grazed meadows, have resulted in food-rich areas suited to the cowbird's foraging needs, the absence of which heretofore prevented the species' successful invasion of the Sierra Nevada. Some of our data, particularly those dealing with diurnal variation in dispersal, seem to support the latter hypothesis, although the two hypotheses are not incompatible.

The concentration of cowbirds into foraging groups during midday, particularly around pack stations, suggests that such areas may supply the foraging needs of large numbers of cowbirds, which scatter by the next morning to distant breeding areas—just how distant is unknown. The cowbird appears to be ideally adapted to such an exploitation pattern, because it is not encumbered with the duties of parental care. Moreover, qualitative observations in other regions support ours (Payne 1965 in Michigan, Payne 1973 in the Central Valley of California, Kennard 1978 in New Hampshire, Rich 1978 in Idaho, Rothstein pers. obs. in New Brunswick and Prince Edward Island). Raim (1978: 330) stated that cowbirds ". . . flew about 1.5 km to afternoon flock-feeding areas," and Darley (1971) trapped breeding cowbirds at stations 1.7 km apart. In captivity, cowbirds show diurnal behavioral changes that are consistent with our interpretation of their activity pattern in nature (Rothstein 1972). Although observations in other regions also suggest major diurnal variation in cowbird dispersion, we suspect that the separation of breeding and feeding habitats, and the distances between them, may be especially extreme in the Sierra. In most lowland areas of North America, the two habitat types may often occur side by side. By contrast, the Sierra, with its diversity of communities, may offer huge expanses of breeding habitat and only small and relatively rare pockets of suitable feeding habitats, most of which may be due to human influence.

The late afternoon and early evening decline in cowbirds at the Sierra Meadows Pack Station suggests that the birds left for roosts or returned to their breeding sites by evening, but this interpretation does not account for the fact that female cowbirds peaked just before dark (Fig. 2b). Perhaps the females present in the evening were individuals that were loading up on food and that were not scheduled to lay an egg the next morning, but they may have left the pack station at first light to search for suitable host nests in which to lay eggs on subsequent mornings. In any event, there is a clear difference between female occurrence at pack stations in the early morning (0500 to 0900 PST) and in the later part of the day (Fig. 2), and this is in accord with our hypothesis that cowbirds exhibit major diurnal variation in their pattern of dispersion.

Previous studies have shown that male cowbirds outnumber females. Darley (1971), for example, estimated that the sex ratio was between 1.3:1 and 1.5:1 at London, Ontario. The extreme sex ratio of between 3:1 and 6:1 shown by midday counts at pack stations in this study (Fig. 2) thus may be unusual. Data from early

morning counts in breeding habitat support such a ratio, however. Considering all 35 sites at which Type 1 detections occurred before 14 July in the Mammoth Lakes survey area (i.e. within 16 km of the town), there were 29 sites at which only males were detected, 5 at which both sexes were detected, and only 1 at which just a female was detected. These counts in breeding habitats are probably biased in favor of males, because males are more vocal than females, but the pack station counts are free of biases, as all birds were easily visible at close range. If birds at pack stations are an unbiased subsample of all Sierran cowbirds, then it is clear that the population in our study area had a highly aberrant sex ratio. It is possible, however, that a higher proportion of males visit pack stations and/or that males stay there for longer periods.

The hypothesis that human development has been necessary for cowbirds to invade the Sierra must be considered tentative at this time. We never observed large groups of cowbirds in natural habitats, except in early August when cowbirds may have been migrating downslope. But we did not exhaustively search natural habitats, such as mountain meadows or early successional stages of recent burns, that might be suitable for cowbird foraging. So, although Sierran cowbirds obviously make considerable use of man-made habitats for feeding, the extent to which they are dependent upon such habitats is unknown.

Midsummer decline in numbers.—The precipitous decline in numbers of adult cowbirds, especially males, at feeding sites in late July coupled with our failure to detect adults in any numbers at our counting sites in suitable breeding habitat after 28 July, strongly suggest that large numbers of the birds leave the mountains at that time. During the period of adult cowbird decline at pack stations, Brewer's Blackbirds increased from an average of 1.4 birds during 66 5-min visits to the Sierra Meadows Pack Station between 25 June and 15 July to at least 40 birds on 2 and 3 August. The same trend was seen at the Convict Lake Pack Station. These increases in Brewer's Blackbird numbers suggest that a general deterioration in feeding conditions at the pack stations was not responsible for the decline in adult cowbirds. Nor was there evidence of competitive exclusion of cowbirds by Brewer's Blackbirds, because the decline in cowbird numbers began considerably in advance of any marked increase in numbers of blackbirds, and the two species rarely engaged in agonistic interactions.

The fact that cowbirds seem to decline in abundance in their breeding habitats earlier than do most passerines is to be expected of a brood parasite if those habitats offer little in the way of feeding opportunities. A parasite can do little to increase its fitness by visiting areas that provide little food and in which most potential hosts are no longer laying eggs. It is surprising, however, that adult cowbirds, at least males, appear to completely leave the mountains unusually early, as evidenced by our data. By contrast, some passerines, such as Brewer's Blackbirds and Orange-crowned Warblers (*Vermivora celata*), move up to higher altitudes in late summer (Gaines 1977). This suggests that conditions in the mountains, even at sites such as pack stations, are not especially good for cowbirds and that, when there are few opportunities left for breeding, the most adaptive option is to descend to lower altitudes for feeding and molting. If this interpretation is correct, it is consistent with the hypothesis that human developments in the Sierra were a necessary precursor to cowbird invasion.

We are unable to account for the fact that adult females do not appear to leave the mountains as early as adult males (Fig. 3). Perhaps many females continue to

lay eggs until early August [in 1975 two cowbird eggs were laid in a Dark-eyed Junco (*Junco hyemalis*) nest between 1 and 3 August (Friedmann et al. 1977)], but the only males who stay may be those who, because of pair bonds or high dominance, are the ones most likely to secure matings. It is also possible that breeding incurs greater physiological costs on females than on males (Darley 1971) and that the former load up on food at pack stations before attempting their downslope migration. The fact that juvenile cowbirds peak at pack stations after adults have declined may be due to the late date at which they become independent from their hosts. Also, juveniles may benefit by continuing their growth and development at a site rich in food (relative to other mountain areas) before attempting their downslope flight.

Host species.—The cowbird's invasion into the Sierra means that its host populations have no recent history of exposure to nest parasitism. Consequently, these populations are unlikely to have evolved defensive strategies and thus may be particularly vulnerable to reproductive failure as a result of cowbird parasitism. The data presented in Table 2 suggest that at least some species ought to receive special monitoring in the years to come. Certainly the Warbling Vireo and perhaps also the Solitary Vireo and Yellow Warbler deserve further investigation in this regard.

Data for the Warbling Vireo, especially, suggest that cowbird parasitism may be severe enough to depress numbers of this species in the Sierra Nevada. In addition to observed parasitism in the areas covered by Table 2, parasitism on this species was observed near Sierra City, Sierra County (A. H. James pers. comm.), and near Truckee, Nevada County (E. Stevens unpubl. obs.). Each of the four parasitized nests in the Mammoth Lakes area fledged only a cowbird. Thus, our sample of five nests lost 80% of its reproductive potential to parasitism. If this is an unbiased sample, it is likely that the Warbling Vireo is decreasing in abundance and/or distribution in the Sierra. Both family groups observed in Yosemite Valley contained cowbirds, and Gaines (1977: 105) noted that Warbling Vireos began to decrease in number in Yosemite in the 1930's, about the time the cowbird first appeared.

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