Studies in Avian Biology No. 15:301–315, 1994.

THE COWBIRD'S INVASION OF THE FAR WEST: HISTORY, CAUSES AND CONSEQUENCES EXPERIENCED BY HOST SPECIES

STEPHEN I. ROTHSTEIN

Abstract. No other native bird species has increased in distribution and abundance in the Far West over the last century as much as the Brown-headed Cowbird (*Molothrus ater*). Its remarkable colonizing ability is associated with its brood parasitism, which allows it to commute daily between widely disjunct feeding and breeding sites. Consequently, cowbirds use a wider range of habitats than other birds. When the western invasion began around 1900, the Dwarf Cowbird (*M. a. obscurus*) occurred along the Colorado River and farther east in the Southwest, while the much larger Nevada Cowbird (*M. a. artemisiae*) occurred east of the Sierran-Cascade axis. The former rapidly colonized southern California, the Central Valley and the Bay Region by 1922, eventually reaching western Washington and British Columbia in 1955. The advance northward, at a rate of 20–35 km/yr in California and 70–78 km/yr in Oregon and Washington, was facilitated by anthropogenic habitat changes. As they spread, cowbirds parasitized new host populations some of which declined. Cowbird removal is probably necessary to save the remnants of two taxa, Least Bell's Vireo (*Vireo bellii pusilus*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*), which would probably have survived coexistence with cowbirds had not most of their riparian habitat also been destroyed. Habitat restoration, not cowbird control, holds the most promise for the long term management of these hosts.

Key Words: Brood parasitism; colonization; cowbird; endangered species; *Molothrus*; range expansion.

Parasitic birds are significant for the basic evolutionary and ecological questions they provoke (Rothstein 1990) and for their potential effect on host species (Mayfield 1977). Among the most well-studied parasitic birds is the Brown-headed Cowbird whose parasitism makes it perhaps the most unpopular native bird in North America. It has often been condemned, e.g., Dawson (1923: 77) referred to the female cowbird as ". . . the unchaste mother of a race gone wrong . . . a blight upon the flower of Progress." whose existence means that "Evolution is at a standstill." No wonder Wheelock (1904: 412) wrote that ". . . Californians are to be congratulated that as yet the Cowbird is only an irregular winter visitant to the southeastern corner of their state." But only 29 years later, cowbirds had become so common that Willett (1933:156) called their increase ". . . remarkable; in fact unparalleled by any other of our native birds." Here I present an overview of the history and causes of the cowbird's colonization of the Far West. I also discuss the consequences experienced by some host taxa that were once abundant but are now imperiled.

GENERAL COWBIRD CHARACTERISTICS THAT ENHANCE COLONIZING ABILITY

Because cowbirds are free of parental duties they do not need to base their daily activities around a particular location, namely a single nest. Thus they can uncouple vital activities such as maintenance and reproduction by carrying them out in disjunct areas. Cowbirds in the Sierra Nevada of California, for example, "commute" up to 6.7 km between large home ranges, where they carry out breeding activities such as courtship and egg laying in the morning while alone or in small groups, and localized sites where large flocks forage in the afternoon (Rothstein et al. 1980, 1984, 1987). Cowbirds prefer and may require areas of short grass or bare ground for foraging (Friedmann 1929) and prefer to forage among large grazing mammals. Sierran feeding sites are anthropogenic, e.g., horse corrals, pastures with livestock, bird feeders, or campgrounds. The commuting behavior seems to be unique: many nonparasitic birds nest and feed in widely separated

TABLE 1. INCIDENCE OF COWBIRDS (BHCO) AND THE NEXT FIVE MOST COMMONLY LISTED SPECIES ON BREEDING BIRD CENSUSES IN VOLUMES 60–64 OF *The Journal of Field Ornithology*. FOREST CENSUSES ARE DONE COMPLETELY WITHIN FORESTS, WITH CENSUSES IN MIXED HABITATS EXCLUDED. FULL NAMES OF BIRD SPECIES, REPRESENTED BY STANDARD FOUR LETTER CODES, ARE GIVEN BELOW[1]

	Year									
	1988		1989		1990		1991		1992	
Total censuses:	87		96		98		126		132	
Forest censuses:	54.0%		54.2%		58.2%		67.5%		59.1%	
BHCO	60.9%	BHCO	62.5%	BHCO	61.2%	BHCO	61.9%	BHCO	56.1%	
AMRO	48.3	AMRO	55.2	AMRO	48.0	REVI	56.3	YETH	48.5	
NOFL	43.7	REVI	47.9	REVI	48.0	EWPE	50.8	REVI	47.7	
YETH	43.7	EWPE	45.8	YETH	48.0	AMRO	50.8	AMRO	47.0	
EWPE	40.2	NOFL	44.8	DOWO	46.9	BCCH	46.8	DOWO	41.7	
BLJA	39.1	WOTH	44.8	EWPE	46.9	BLJA	46.8	EWPE	40.2	
BCCH	39.1			BLJA	46.9	YETH	46.8			
REVI	39.1									
RSTO	39.1									

[1] AMRO: American Robin (*Turdus migratorius*), BCCH: Black-capped Chickadee (*Parus atricapillus*), BHCO: Brown-headed Cowbird (*Molothrus ater*), BLJA: Blue Jay (*Cyanocitta cristata*), DOWO: Downy Woodpecker (*Picoides pubescens*), EWPE: Eastern Wood-pewee (*Contopus virens*), NOFL: Northern Flicker (*Colaptes auratus*), REVI: Red-eyed Vireo (*Vireo olivaceus*), RSTO: Rufous-sided Towhee (*Pipilo erythrophthalmus*), WOTH: Wood Thrush (*Hylocichla mustelina*), YETH: Yellowthroat (*Geothlypis trichas*).

places but they disperse from communal breeding sites to feed at scattered sites; cowbirds by contrast disperse from communal feeding sites to scattered breeding sites (Rothstein et al. 1984).

Most or all cowbird populations show at least some degree of commuting behavior. This uncoupling of breeding and feeding activities enhances colonization in two ways. First, the tendency to fly relatively large distances on a daily basis predisposes cowbirds to disperse large distances. Even without commuting, cowbirds move large distances as their morning breeding ranges (Dufty 1982, Rothstein et al. 1984) alone are 7–68 times larger than the 1–3 ha ranges of passerines of similar body sizes (Schoener 1968).

Second, the uncoupling allows cowbirds to occur in regions with habitats that meet breeding and feeding needs in separate places. Most passerines must meet both of these needs in a single place. Indeed, my tabulations of the 1988–1992 breeding bird surveys (*The Journal of Field Ornithology*, vols. 60–64) done throughout North America show that the percentage of censuses that included cowbirds as breeders was consistently much higher than for any other species (Table 1). This result is especially impressive because most censuses were in forests, where cowbirds are not abundant. The "forest effect" can be seen in the high prevalence in Table 1 of such woodland species as the Eastern Wood-pewee (*Contopus virens*), Red-eyed Vireo (*Vireo olivaceus*), and Wood Thrush (*Hylocichla mustelina*).

Other factors that facilitate colonization are: 1) a propensity to parasitize almost every passerine with which cowbirds are sympatric (Friedmann 1963); 2) high fecundity (females lay 30–40 or more eggs per season; Rothstein et al. 1986) which gives cowbird populations an enormous growth potential; 3) a possible relative lack of defenses in host populations not previously sympatric with a brood parasite (e.g., Briskie et al. 1992).

A HISTORY OF THE COWBIRD'S INCREASE IN WESTERN NORTH AMERICA

Willett's suggestion that the cowbird has increased to a greater extent than any other native bird applies also to all of North America. Before the widespread forest clearing and agriculture brought about by the European colonization, the cowbird's favored foraging conditions of short grassy areas with grazing mammals were widespread only in the Great Plains and the Great

Basin. Cowbirds began a dramatic increase in the heavily forested East in the mid- to late 1700s (Mayfield 1965). That increase has continued into recent years as cowbirds first colonized Newfoundland in 1957 (Baird et al. 1957) and began to breed in Florida in the 1950s (Weston 1965). What is not clear, however, is whether the cowbird is completely new to all of eastern North America as Mayfield (1965) suggested. Even upon their arrival in North America, the first European colonists found some obligate grassland birds such as the Heath Hen (*Tympanuchus cupido cupido*) nesting along the East Coast. Given their daily mobility patterns (above) and tendency to disperse from one population to another (Fleischer and Rothstein 1988), it seems likely that cowbirds were originally found in small numbers in the east.

Because it occurred more recently, the cowbird's increase in the west is better documented. Around 1900, cowbirds were widespread throughout the Great Basin and adjoining parts of Oregon and Washington east of the Cascades. These birds are referable to the "Nevada Cowbird" (*M. a. artemisiae*). In addition, the "Dwarf Cowbird" (*M. a. obscurus*) was common along the Colorado River (Brown 1903, Grinnell 1914) and in the Tucson area (Bendire 1895) and presumably occurred farther east to Texas (Friedmann 1929). Cowbirds bred along the Colorado River as early as the 1860s (Cooper 1974), but even then the lower Colorado River valley was not pristine, as Spaniards brought in livestock in the late 1600s (Rosenberg et al. 1991). This could have enabled the Dwarf Cowbird to colonize the area. The Nevada Cowbird's ancient status in the west is similarly uncertain. Grinnell (1909) argued that it must have been present in the Great Basin for a long period to have evolved its large size and other distinctive features. However, Bishop (1910) described a new subspecies (*M. a. dwighti*), which later proved to be identical to *M. a. artemisiae,* from the northern Great Plains. Thus, the Nevada Cowbird could have been a recent arrival in the west as Coues (1874) reported that every wagon train passing over the prairies in summer was accompanied by cowbird flocks.

In any case, cowbird abundance in the Great Basin and adjoining areas east of the Cascades has increased greatly since the late 1800s. During extensive travels through the intermountain states in the late 1800s, Bendire (1895) noted cowbirds on "but very few occasions," and Ridgway (Baird et al. 1874) only saw cowbirds twice. Especially instructive are records from eastern Oregon. Bendire (1877) found no cowbirds in Harney County in 1875 and 1876, although he visited localities such as Malheur Lake where they are now abundant (Littlefield 1990). The first Oregon records (Woodcock 1902) were from central and northern Baker County, roughly 160 km northwest of Bendire's area. Other early Oregon records are summarized by Gabrielson and Jewett (1940). Cowbirds became common around Malheur Lake by 1918 (Willett 1919), perhaps aided by an increase in agriculture since the 1870s. A contemporaneous increase appears to have occurred in eastern Washington as Dawson (1909:44) wrote that ". . . the Cowbird is no longer rare east of the Cascades . . . ," and that "the earlier writers make no mention of it . . ." in Washington.

Cowbirds probably did not breed west of the Cascade-Sierra axis or the Colorado River prior to about 1890, except in coastal southwestern British Columbia, where small numbers may have bred sporadically (Kermode 1904, Brooks and Swarth 1925). An 1862 record from San Diego County (Cooper 1874) was early enough in spring to have been a wintering flock. Rothstein et al. (1980) and Laymon (1987a) briefly summarized the cowbird's colonization of California and here I present a more detailed account (summarized in Fig. 1 and Table 2) for the region from California to British Columbia based on all of the original literature, numerous museum specimens, *Audubon Field Notes* (1947–1965) and compilations of host use

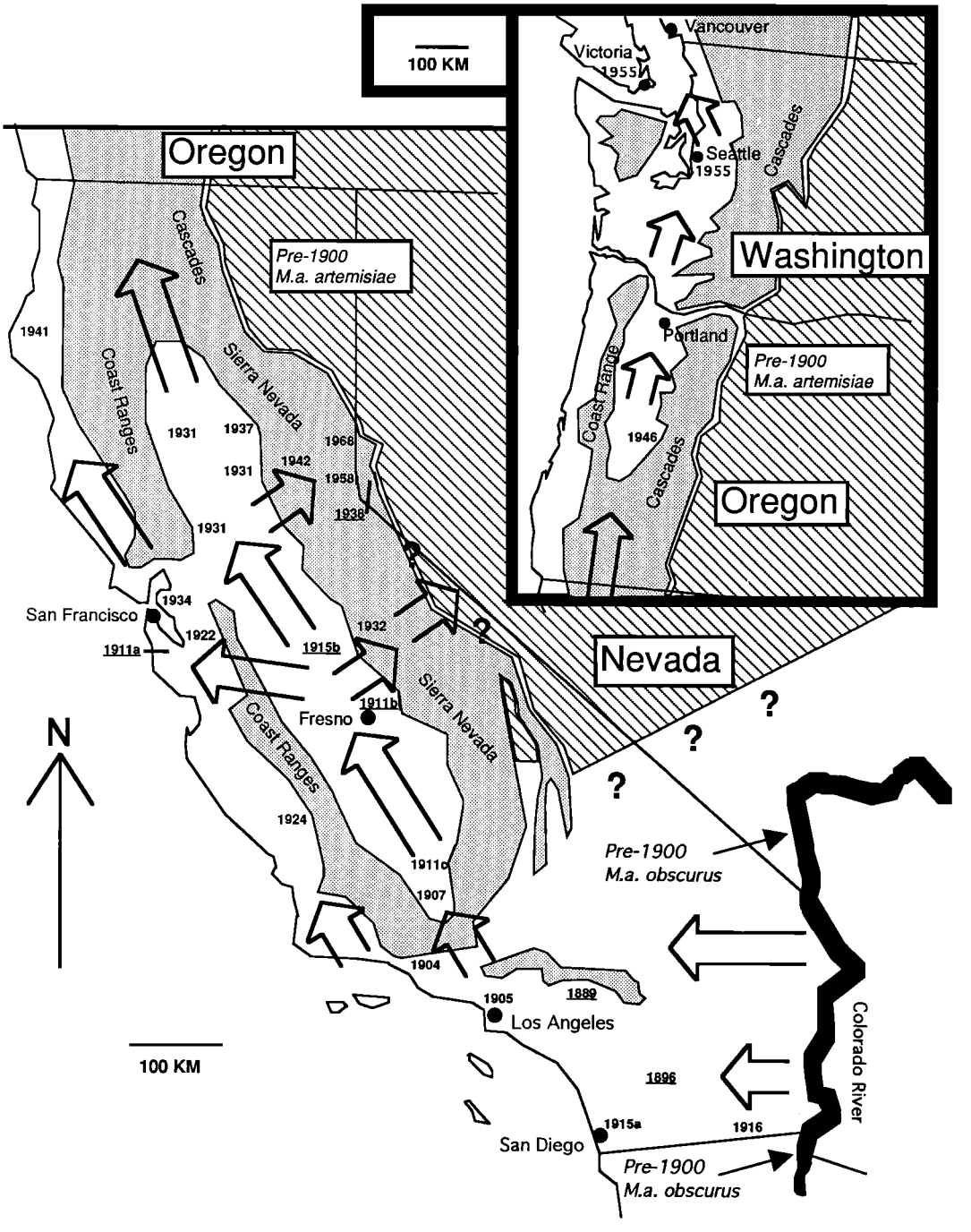

FIGURE 1. The pre-1900 distribution of *Molothrus ater artemisiae* and *M. a. obscurus*, and the subsequent spread of the latter throughout most of California and the Pacific Northwest. Shaded areas represent major mountain ranges. Question marks reflect uncertainty about the range of *artemisiae* in southern Nevada and the Eastern Sierra before 1900. Large arrows show likely movement patterns of *obscurus* and indicate the first dates that it reached various locations, most of which are mentioned in the text. Underlined years represent records that may not reflect the arrival of the advancing wave of *obscurus* because of uncertain reliability, a lack of evidence of breeding or a clear indication that a case reflects an isolated breeding episode. The locality and reference for each year are listed in Appendix I.

by H. Friedmann and his colleagues. Data from the latter are cited as "Friedmann compilations" (contact me for exact citations) unless given in major summaries (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985).

The earliest indication of breeding west of the Colorado River is Wall's (1919:209) vague reference to a cowbird egg found ". . . somewhere about thirty years ago . . ." in San Bernardino County, prompted by Hanna's (1918) claim to have found the first local breeding records in 1918. Thus cowbirds may have bred sporadically in southern California before their large scale colonization began around 1900. Similarly, two specimens collected on 30 April, 1896, at Borrego Springs, San Diego County (Unitt 1984) may have been breeders. The first wholly reliable breeding records are of single parasitized nests from Santa Paula, Ventura County, in 1904 and Los Angeles in 1905 (Willett 1912). By 1912, Willett (1912) called cowbirds "fairly common" in the lowland willow regions of Los Angeles County, but the first breeding adult was not collected until 1915 (Miller 1915). These and other records (see Willett 1933), indicate that cowbirds occurred locally in coastal California from Santa Barbara County south by 1915, although some areas were not colonized until later, e.g., Buena Park, Orange County in 1923. Rowley (1930) noted that cowbirds went from uncommon to abundant between 1920 and 1926 along the San Gabriel River and nearby areas, and Willett (1933) wrote that they were "well established" throughout southern California west of the deserts.

Cowbirds reached the southern end of the Central Valley by 1907, when Linton (1908) found their eggs in Bell's Vireo (*Vireo bellii*) nests at Buena Vista Lake. Four years later, cowbirds were common near Bakersfield, 35 km to the northeast (Swarth 1911) and one was seen farther north near Fresno (Tyler 1913). In 1915, an adult male was collected at Snelling, Merced County (Grinnell and Storer 1924), 300 km north of Buena Vista Lake.

The first records for the Bay Region were assumed to be La Jeunesse's (1923) 1922 discovery of ten cowbird eggs in nests near Irvington, Alameda County. New records for various parts of the Bay Region occurred both north and south of Irvington over the next decade (Sibley 1952), suggesting that this represented a disjunct colonization rather than an advancing wave from southern California. It is possible that this colonization originated from the Central Valley as cowbirds seemed to move northward more rapidly there than along the coast (Fig. 1, Table 2). Even as late as 1935, Miller (1935) referred to Irvington as the cowbird's center of abundance in the Bay Region. Cowbirds were not noted at Berkeley, only 50 km north of Irvington until 1934 (Benson and Russell 1934). Remarkably, the first breeding adult specimens for the Bay Region were not taken until 1934 (Grinnell 1934), despite the presence of locally active collectors from U.C. Berkeley. Curiously, a parasitized Song Sparrow (*Melospiza melodia*) clutch collected in 1911 by M. S. Ray (U.C. Berkeley, MVZ no. 12929) at Palo Alto escaped the notice of these Bay Area ornithologists (e.g., Grinnell and Wythe 1927). This may have been an isolated cowbird intrusion rather than the forerunner of the population La Jeunesse discovered 11 years later. The earliest record between southern California and the Bay Area, and outside of the Central Valley, is a parasitized Song Sparrow clutch taken in 1924 at Paso Robles (MVZ no. 11893).

The first breeding season records for the northern part of the Central Valley are from 1931, when Neff (1931) saw cowbirds at scattered localities in Yuba, Sutter and Glenn counties. Cowbirds were apparently abundant in the area by May 1937, when 99 were trapped at Oroville, Butte County (Behle 1937). Presumably, cowbirds moved rapidly northward through the Valley, which has no obstacles to dispersal and contains widespread agriculture.

Cowbirds were first noted on the west slope of the Sierra Nevada in 1932 (Friedmann compilations) and 1934 (Michael

TABLE 2. THE RATE OF NORTHWARD ADVANCE AS COWBIRDS COLONIZED AREAS WEST OF THE SIERRAN-CASCADE AXIS. DATA PRESENTED ARE THE YEARS AND DISTANCES BETWEEN THE FIRST RECORDS OF COWBIRDS DURING THE BREEDING SEASON (APRIL–JULY) FOR VARIOUS REGIONS. REFERENCES FOR EACH RECORD ARE IN THE TEXT

Site and year for each record (regions)	Years	km	km/yr
Santa Paula to Irvington, 1904–1922 (S. Coastal Calif. to Bay Region)	18	275	25
Irvington to Fernbridge, 1922–1941 (Bay Region to N. Coastal Calif.)	19	383	20
Buena Vista Lk. to Snelling, 1907–1915 (S. to mid Central Valley)	8	270	34
Fernbridge to Eugene, 1941–1946 (NW. Calif. to Oregon)	5	390	78
Eugene to Vancouver Is., 1946–1955 (Oregon to British Columbia)	9	630	70

1935) in Yosemite Valley at an elevation of 1200 m. Gaines (1988) traced their subsequent spread in the Central Sierra and showed that they reached sites as high as 2130 m by 1935. By 1961, they were "numerous" at Tuolumne Meadows at 2620 m. However, abundance may be true only for Sierran areas strongly affected by man as even in the early 1980s cowbirds were rare or absent from West Slope sites 10 km or more from human influence (Verner and Rothstein 1988). Because the colonization of the West Slope progressed from low to high elevations, the birds probably came from the Central Valley.

On the East Slope of the Sierra, parasitism records show cowbirds in Mono County at elevations above 2130 m in the early 1920s (Friedmann 1963). But they apparently largely died out by the late 1920s, as Rowley (1939) saw no adults and found only one parasitized nest from 1926 to 1939. There are additional parasitized nests from Mono County in the 1930s (Friedmann compilations). Extensive field work from 1978 to the present shows that cowbirds are now common at sites Rowley often visited (Rothstein et al. 1980, 1984). Another Eastern Sierran area that has received a relatively large amount of attention is the Tahoe Basin, where early workers found no cowbirds (Barlow 1901, Ray 1903, Bryant 1928). Orr and Moffitt (1971) give 1959 as the first year of its occurrence although G. McCaskie (pers. comm.) first noted them in 1957. In addition, N. K. Johnson (pers. comm.) noted cowbirds on rare occasions on the Nevada side of Lake Tahoe between 1948 and 1954 and they made occasional forays into the area as early as 1938, when a parasitized MacGillivray's Warbler (*Oporornis tolmiei*) nest was found (Friedmann et al. 1977). Remarkably, cowbirds did not reach the Sage Hen Valley, only 25 km north of Lake Tahoe, until 1968 after about 20 years of observations there (J. M. White, pers. comm.). Today, cowbirds occur commonly all around Lake Tahoe and in the Sage Hen Valley (pers. obs.). Cowbirds occurred nearby along the Truckee River, which drains Lake Tahoe, in the late 1800s (Baird et al. 1874) so it is not clear why it took them so long to become well established in the Tahoe area. Perhaps the dense, widespread forests of the Tahoe region retarded the cowbird's local advance.

The last major region of California to be colonized was the heavily forested northwestern corner. In 1941, Talmadge (1948) found three parasitized nests about 10 km apart in Humboldt County, and later (1947–1948) found parasitism over a much wider area. The next areas to be colonized were west of the Cascades in Oregon, Washington and British Columbia. The first breeding record for western Oregon occurred in 1946 at Eugene (Gullion 1947). In western Washington and in British Columbia, the first confirmed breeding records occurred in 1955 at Seattle and Victoria (Flahaut and Schultz 1955); by 1957, cowbirds had become "numerous" (Schultz 1957) and were still increasing in 1960 (Boggs and Boggs 1960). There are few cowbird references in *Audubon Field Notes* from 1961 to 1965, indicating that cowbirds were then widespread and common in the Pacific Northwest as confirmed by Crowell and Nehls (1971). Today, cowbirds are still common throughout western Oregon and Washington (Alcorn

TABLE 3. MALE COWBIRD WING LENGTHS. DATA FROM NORTHWESTERN NEVADA AND THE COLORADO RIVER INCLUDE NEARLY ALL SPECIMENS FROM GRINNEL (1909 AND 1914). DATA FROM THE SACRAMENTO, SAN JOAQUIN AND IMPERIAL VALLEYS INCLUDE MOST OF THE SPECIMENS CITED IN DICKEY AND VAN ROSSEM (1922) AND BEHLE (1937) AND OTHERS IN VARIOUS MUSEUMS. DATA IN THE LAST FOUR ROWS ARE FROM FLEISCHER AND ROTHSTEIN (1988)

Region, period	Adult		Yearling	
	Mean ± SE	(N)	Mean ± SE	(N)
Northwestern Nevada, 1909[1]	115.4 ± 1.00	(7)	112.3 ± 0.44	(3)
Lower Colorado River, 1910[1]	102.9 ± 0.55	(7)	100.8 ± 0.45	(23)
Sacramento Valley, pre-1940[1]	105.5 ± 0.72	(6)	102.8 ± 0.48	(11)
San Joaquin Valley, pre-1940[1]	105.4 ± 0.57	(15)	102.9 ± 0.56	(11)
Imperial Valley, pre-1940[1]	104.3 ± 0.80	(13)	—	
Western Sierra, 1981	103.7 ± 0.28	(68)	101.7 ± 0.35	(33)
Eastern Sierra—min., 1981–1985[2]	104.4 ± 0.25	(152)	102.3 ± 0.17	(264)
Eastern Sierra—max., 1981–1985[2]	105.9 ± 0.16	(283)	103.7 ± 0.17	(183)
Eastern Sierra, 1912–1922[1]	109.1 ± 0.75	(7)	104.9 ± 1.15	(4)

[1] Data for these samples are from museum specimens measured by me. Data for the remaining samples were collected in the field by my collaborators.
[2] The two Eastern Sierra, 1981–1985 samples are from the sites with the smallest and largest birds (with N's of at least 20 individuals) among five sites along a 90 km north–south transect.

1978) and at least southern coastal British Columbia (Godfrey 1986, pers. obs.). The northward range expansion proceeded at an accelerating pace when it reached Oregon and British Columbia (Table 2), "fueled" perhaps by increasing populations to the south.

WHERE DID THE COLONIZING COWBIRDS COME FROM?

The two western subspecies of the cowbird are well differentiated in areas far from potential contact zones. Grinnell's 1910 *obscurus* sample from the lower Colorado River was 11.5 to 12.5 mm smaller in male wing length than his 1909 type series for *artemisiae* from northwestern Nevada (Table 3). In addition, the rictal flanges of nestling *obscurus* are yellow whereas they are white in *artemisiae* (Rothstein 1978). The cowbirds of southern California are close in size to *obscurus* (Table 3) and have yellow flanges and evidently originated from the Colorado River, the nearest area where this subspecies bred before 1900. A Colorado River origin is also indicated by flight whistle variation. In most of California west of the Sierran crest and north of a line through the Los Angeles Basin this song type (Rothstein et al. 1988) conforms to the "coastal type" of whistle (Rothstein et al. 1986). While coastal flight whistles show dialect variation as regards certain details, they all possess a characteristic final syllable which rises gradually in frequency, then drops suddenly and ends in a brief high frequency sweep (examples in Rothstein et al. 1986, 1988). Cowbirds along the northern part of the lower Colorado River have whistles with this characteristic syllable but it is absent in dialects east of the crests of the Sierra and Cascades (Rothstein and Fleischer 1987; O'Loghlen and Rothstein 1993; SIR unpubl.). Because cowbirds south of the Los Angeles Basin in Orange and San Diego counties do not do coastal whistles, they may be *obscurus* from the southern part of the Lower Colorado River. It is unlikely that cowbirds spread from Baja California as they were found there only as wintering birds in the late 1800s (Bendire 1895).

The cowbirds of northern California west of the Sierran-Cascades axis could be the Colorado River *obscurus* continuing an advance northward, *artemisiae* from the Great Basin, or a mixture of both subspecies. The first of these possibilities is indicated by the occurrence of coastal flight whistles throughout the Central Valley and along the coast at least as far north as the Bay Region (Rothstein et al. 1986). Similarly, the chro-

nology of the colonization suggests that *artemisiae* had little or no role in it as the more northern parts of the state were colonized only after *obscurus* was established in the south (Fig. 1). Furthermore, specimens from the Bay Region, the northern Central Valley and west slope of the Sierra (Table 3; see also Grinnell 1934, Miller 1935, Grinnell and Miller 1944) are close in size to Colorado River *obscurus* and much smaller than *artemisiae*. Similarly, 95% of young cowbirds on the Sierran west slope have yellow flanges, versus 12–28% on the east slope (Fleischer and Rothstein 1988).

The only hint that *artemisiae* colonized areas west of the Sierran crest is Dickey and van Rossem's (1922) report that males from the southern end of the Central Valley were larger than typical *obscurus*. Behle (1937) reported that cowbirds from Oroville, 520 km to the north of Dickey and van Rossem's site, were closer to *obscurus* (wing lengths of 101.2 mm versus 103.5 mm) and suggested that *artemisiae* colonized the extreme southern Central Valley via the Kern River gap. I have located 14 of 15 of Behle's male specimens and 11 of 18 of Dickey and van Rossem's; 79% of the former but only 36% of the latter are yearlings, which could by itself explain the wing length difference because male cowbirds average a 2.7 mm increase in wing length between their yearling and subsequent years (Rothstein et al. 1986). My measurements of known age males from the northern and southern parts of the Central Valley show that wing lengths were virtually identical before 1940 (Table 3) and negate Behle's *artemisiae*-Kern River gap hypothesis.

The most surprising aspect of the wing length data (Table 3) is the similarity between birds from the west slope of the Sierra at Dinkey Creek and from southern California. The former are only 65 km from known populations of *artemisiae*, whereas the latter are 320–500 km away. Analyses of body size, colorimetric characters and mitochondrial DNA (Fleischer and Rothstein 1988, Fleischer et al. 1991) show that there has been recent and extensive gene flow eastwards across the Sierran crest from *obscurus* to *artemisiae* in the Mammoth Lakes area of Mono County. The wing length data (Table 3) indicate that there has been little or no gene flow in the reverse direction. The trans-Sierran gene flow could not have occurred prior to the 1930s–1940s because there were no cowbirds on the west slope before then. But it has proceeded at such a rapid rate that today's cowbirds from the eastern Sierra are closer in size to *obscurus* from the Central Valley than to eastern Sierran *artemisiae* collected between 1912–1922 (Table 3). A similar shift of cowbird populations from *artemisiae* toward *obscurus* occurred in northern Arizona sometime after 1935 (Phillips 1968) and in north–central Colorado after 1943 (Ortega and Cruz 1992). All of these data indicate that *obscurus* is more vagile or outcompetes *artemisiae* and that the latter is undergoing a general decline in size.

There are too few wing length data available to indicate the origin and subspecies status of the cowbirds that colonized western Oregon, Washington and British Columbia in the 1940s and 1950s, but this area's northern location apparently led workers to assume that the colonizers were *artemisiae* (AOU 1957). However, the timing of critical events (i.e., colonization of the Bay Area of California by 1922, coastal northwestern California by 1941, western Oregon by 1946 and western Washington in 1955) suggests that these birds are *obscurus* continuing their advance up the Pacific Coast.

The characteristics of cowbirds currently breeding west of the Cascades all but confirm that these birds are comprised mostly or exclusively of the *obscurus* stock that originated along the Colorado River. The "coastal" flight whistle that is widespread in California west of the Sierra occurs west of the Cascades in Oregon and Washington (pers. obs.). There are occasional pockets of differently structured flight whistles in this region, but this is also the case in California

where this flight whistle type occurs. The coastal form of the flight whistle is unlikely to have come from *artemisiae* populations east of the Cascades because cowbirds there have numerous highly divergent local flight whistle dialects, all different from the coastal type, as in the eastern Sierra (Rothstein and Fleischer 1987). In addition, each of 15 nestling cowbirds from Mandarte Island in southwestern British Columbia had yellow flanges (J. N. M. Smith, pers. comm.), whereas only four of 23 had yellow flanges east of the Cascades in Adams and Grant counties, Washington (E. Stevens, pers. comm.).

Unlike the present birds in the coastal Northwest, those that occasionally occurred there early in this century were probably *artemisiae,* as the nearest *obscurus* were then at least 1000 km to the south. A June 1922 adult male specimen from Clallam County on the Olympic Peninsula (Jewett et al. 1953) (UCLA no. 22-271) has a wing length of 108 mm, which is much closer to the mean size of *artemisiae* than of *obscurus* (Table 3). The small numbers of cowbirds that have occurred regularly during the breeding season in southeastern Alaska since the 1940s (Kessell and Gibson 1978) are probably a westward extension of *artemisiae* because this subspecies ranged that far north in inland Canada even in the 1920s (Friedmann 1929).

WHY DID THE COLONIZATION OCCUR?

The cowbird range extensions in the far west since 1900 are due largely or completely to a very rapid colonization by *obscurus* that originated along the Colorado River around 1900 and reached western Washington and British Columbia, 1600 km to the north, by 1955. It occurred because most anthropogenic changes (except for outright urbanization), improved or created feeding, and to lesser extent breeding habitat, for cowbirds. These changes involve irrigation and agriculture in the Southwest and forest clearing in the Sierra Nevada, Cascades and the Pacific Northwest. The ever growing suburban areas of the west also provide prime habitat. Even in the inland Northwest, increased agriculture may explain the increase that *artemisiae* underwent in the late 1800s (Dawson 1909).

But human activity does not explain all of this increase. In particular, the Central Valley of California had vast marshes and riparian zones in its pristine state which would have provided numerous hosts (Gaines 1974). It also had extensive grasslands, and the widespread tule elk (*Cervus nannodes*) would have provided a mammalian foraging associate. If cowbirds had long been present along the Colorado River, the dispersal abilities shown since 1900 suggest that they could have colonized the Valley centuries ago. That they did not do so indicates that *obscurus* may be a relative newcomer to the Colorado River. If *artemisiae* is similarly a newcomer to areas between the Sierra-Cascade axis and the Rocky Mountains (above), both subspecies may have colonized areas west of the Great Plains in the last several hundred years, with *artemisiae* coming from the north and *obscurus* from the south. The former possibility is supported by Bendire's (1895) observation that cowbirds were abundant in Saskatchewan and Alberta in 1894 whereas he and others found them to be rare in the late 1800s farther to the south in areas such as the Great Basin and eastern Washington.

IMPACT OF THE COWBIRD'S WESTERN INCREASE ON HOST SPECIES

Given its abundance and fecundity, the cowbird has a potential to lower the recruitment rate of host species. At least 10 songbird species have declined since the cowbird's spread in California and it is often suggested that these declines are due partly or mainly to parasitism (e.g., Gaines 1974, Garrett and Dunn 1981). Below, I discuss two case species (see also Rothstein and Robinson 1994).

Least Bell's Vireo
*(*Vireo bellii pusillus*)*

The Least Bell's Vireo was initially common in riparian woodland primarily in the Central Valley and coastal slopes of southern California. A decline was noticed by 1930 (Grinnell and Miller 1944), and it was extirpated from the Central Valley by the early 1970s (Goldwasser et al. 1980). It was designated as an endangered species by the U.S. Fish and Wildlife Service in 1982 (Franzreb 1989). In 1987, about 440 territorial males remained in the United States in southern California counties from Santa Barbara to San Diego.

The vireo's decline occurred within 20 to 30 years of the cowbird's invasion of California and many of the earliest cowbird records consisted of parasitized vireo nests. Within a decade or two of the cowbird's arrival most nests in southern California seemed to be parasitized (Franzreb 1989). When studies of the remnant vireo populations began in the late 1970s, most had parasitism rates of about 50% (Goldwasser et al. 1980, Franzreb 1989). Because Bell's Vireos that accept cowbird eggs generally raise only a cowbird (Pitelka and Koestner 1942, Mumford 1952), it is obvious that cowbirds can have an enormous effect on vireo recruitment. Vireos may have persisted in Southern California but not in the Central Valley because they begin to breed earlier in the former region thereby enabling many early nests there to escape parasitism.

However, parasitism is not the only factor in the vireo's decline. The Central Valley has lost 95% of its riparian vegetation in this century (Smith 1977) and the loss in southern California's has also been massive. Even where riparian habitat remains, flood control programs may keep it from regenerating seral stages that are optimal for vireos (Rosenberg et al. 1991). Thus, habitat loss is at least as important as cowbird parasitism in the vireo's near extinction. Nevertheless, it is likely that parasitism will cause the current remnant populations to go extinct without human intervention (Laymon 1987a). Removal of cowbirds (Beezely and Rieger 1987) from vireo habitat has greatly increased productivity (Franzreb 1989) and the Least Bell's Vireo is much more numerous now than when its near extinction was first recognized in the late 1970s.

Willow Flycatcher
*(*Empidonax traillii*)*

Although Grinnell and Miller (1944) described the Willow Flycatcher as common in lowland parts of California and sporadic in montane localities up to 2440 m, the entire California population had less than 150 pairs in the mid-1980s (Harris et al. 1987). Unitt (1987) reported that the Southwestern Willow Flycatcher (*E. t. extimus*) was absent from numerous southern California to western Texas sites where it once occurred and suggested that no more than 500 pairs were left. Many early California records of cowbirds were of parasitized Willow Flycatcher nests, so parasitism was a likely factor in this species' decline. But as with Bell's Vireo, both cowbird parasitism and habitat destruction appear to be the major problems.

The California Fish and Game Commission listed the Willow Flycatcher as endangered in 1990. This listing includes *extimus* and the two other subspecies in California, *brewsteri* and *adastus*. The latter two subspecies have also been virtually extirpated from California but may be maintaining reasonable healthy populations farther north from Oregon and British Columbia and east to the Rocky Mountains. Flycatcher populations west of the Cascades in Oregon to British Columbia should be closely monitored. Unlike California, this mesic region has widespread suitable habitat, so if Willow Flycatchers decline there, it may be due largely to cowbird parasitism.

The overall effect of parasitism on the Southwestern Willow Flycatcher is unclear. Cowbirds have been present in the eastern part of this bird's range throughout recorded history and some samples show little parasitism there (data in Unitt 1987, but see also Brown 1988). Although it is likely that both habitat destruction and cowbird par-

asitism are factors, it is probable that the latter will cause the extirpation of many remnant populations if left unchecked. A cowbird control program was initiated in 1993 along the South Fork of the Kern River where the largest California population of *extimus* experiences about a 50% rate of parasitism (Whitfield 1990). However, a cowbird control program to aid Least Bell's Vireos along the Santa Margarita River in San Diego County may explain an increase from five territorial flycatchers in 1981 to 17 in 1986 (Unitt 1987).

Parasitism at elevations above 1000–1500 m, where the race *brewsteri* still breeds in California, is absent to slight, even where cowbirds occur (Stafford and Valentine 1985, Flett and Sanders 1987). Suitable montane habitat was probably always limited, occurring in patchily distributed moist meadows and streams with stands of willows surrounded by forest or sagebrush. These moist areas are heavily used by range cattle which knock over nests and degrade the habitat by consuming the lower foliage of willows. Limiting cattle grazing is effective in boosting flycatcher productivity (Valentine et al. 1988). Although cowbird parasitism may not now be a major factor in high elevation parts of California, the situation may be different in the Rocky Mountains (Sedgwick and Knopf 1988). Furthermore, cowbird parasitism is the most likely cause of the flycatcher's complete extirpation from Yosemite Valley (Gaines 1988), which is at an intermediate elevation of 1200 m.

A key difference between the vireo and flycatcher is the late breeding of the latter, which usually begins about 1 June and peaks in mid-June even in the warm climate of lowland southern California (Unitt 1987). Although cowbird activity in California begins to decline by late June (Payne 1973), cowbirds show signs of breeding, such as courtship and male-male aggression, until mid- to late July (pers. obs.). This complete overlap in the breeding seasons of the cowbird and flycatcher may explain why the latter has declined even more drastically than the vireo, some of whose early nests escape parasitism.

IS COWBIRD PARASITISM THE PRIMARY REASON FOR THE DECLINE OF ANY WESTERN BIRD SPECIES?

The two hosts profiled above are obligate riparian breeders in much or all of their range, as are most of the other land birds that have declined seriously in the west (De Sante and George 1994, Ohmart 1994). While cowbirds are implicated in some changes, they are not the only factor. The Yellow-billed Cuckoo (*Coccyzus americanus*) has declined to a greater extent than any other riparian species (Laymon 1987b), yet experiences virtually no cowbird parasitism (Friedmann et al. 1977). I suggest that most or all of the cowbird hosts that have declined to near extirpation would have maintained self-sustaining populations had large expanses of riparian habitat remained.

Bell's Vireos (*V. b. arizonae*) experienced heavy parasitism along the Colorado River at least as early as 1900, yet did not decline until the 1950s when dam construction made it worthwhile to convert large riparian tracts to agriculture (Rosenberg et al. 1991). Today, they are virtually gone from this region. Another heavily-used host, the Yellow Warbler (*Dendroica petechia*), also did not begin to decline along the Colorado until the 1950s. Both Bell's Vireos and cowbirds bred in the Owens Valley early in this century and the former's disappearance (Goldwasser et al. 1980) seems wholly due to the loss of riparian habitat. Some of the largest extant populations of the Southwestern Willow Flycatcher occur in the eastern parts of its range, where it has been sympatric with cowbirds longer than in California, but where more riparian habitat remains (Unitt 1987). In addition, these and other riparian species that have declined in the west breed in the east and Midwest, where they have survived cowbird parasitism for at least hundreds of years. The key difference is that in these latter regions mesic habitats are

widespread and not limited to watercourses. Although cowbirds may be involved in recent declines of these species in the east and Midwest, which are moderate to slight compared to those in the west, habitat destruction in North America and in the Neotropics may be far more important.

Thus habitat destruction and not cowbird parasitism seems to be the primary cause of host declines in the west. This conclusion does not mean that cowbirds are blameless: it is probably no coincidence that these two species—the only once widespread riparian hosts in California that are virtually extirpated—are ones in which acceptance of a cowbird egg nearly always results in the loss of the host's entire brood. I suggest, however, that if extensive riparian habitat were still widespread, these hosts would be able to survive in the presence of cowbirds. Such habitat needs to be as broad as possible because there is often an edge effect, with cowbird parasitism dropping off towards the interior of densely wooded habitat (Gates and Gysel 1978, Brittingham and Temple 1983). An edge effect may explain why vireos and flycatchers in California and along the Colorado River persisted so long after early workers (Brown 1903, Friedmann compilations) remarked that nearly all of their nests were parasitized. Had this really been the case, these two birds would have been extirpated in only a few years. Perhaps these early rates of nearly 100% parasitism applied mainly to the nests most easily found, i.e., on the edge of dense riparian growth.

Cowbird control programs are needed to sustain the few vireos and flycatchers that remain in California. However, undue emphasis on this open-ended management technique should not deter recovery efforts from concentrating on the more long term but more difficult solution of restoration of riparian habitat.

ACKNOWLEDGMENTS

I thank J. R. Jehl, Jr. and N. K. Johnson for their numerous constructive comments, which greatly improved this paper. Preparation of this manuscript was supported by UCSB Faculty Research and Intercampus Travel Grants. NSF grants BNS 82-16778 and BNS 86-16922 supported the work, much of it done jointly with R. C. Fleischer, on cowbird vocalizations, morphological variation and distribution. Any overview of cowbird biology and host impacts, such as mine, rests on the remarkable foundation of information and insights arising from the nearly 70 years of cowbird research by the late H. Friedmann.

LITERATURE CITED

ALCORN, G. D. 1978. Northwest birds, distribution and eggs. Western Media, Tacoma, WA.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. Fifth ed. American Ornithologists' Union, Baltimore, MD.

BAIRD, S. F., T. M. BREWER, AND R. RIDGWAY. 1874. A history of North American birds. Little, Brown and Company, Boston, MA.

BAIRD, J., R. I. EMERY, AND R. EMERY. 1957. Northeastern Maritime Region. Audubon Field Notes 11: 387–390.

BARLOW, C. 1901. A list of the land birds of the Placerville-Lake Tahoe stage road. Condor 3:151–184.

BEEZLEY, J. A., AND J. P. RIEGER. 1987. Least Bell's Vireo management by cowbird trapping. Western Birds 18:55–61.

BEHLE, W. H. 1937. The cowbirds of the Sacramento Valley, California. Condor 39:227–228.

BENDIRE, C. 1877. Notes on some birds found in southeastern Oregon. Proceedings Boston Society Natural History 19:109–141.

BENDIRE, C. 1895. The cowbirds. Report of the U.S. National Museum for the year ending June 30, 1893, pp. 589–624.

BENSON, S. B., AND W. C. RUSSELL. 1934. The cowbird breeds in Berkeley. Condor 36:219.

BISHOP, L. B. 1910. Two new subspecies of North American birds. Auk 27:59–63.

BOGGS, B., AND E. BOGGS. 1960. Northern Pacific Coast Region. Audubon Field Notes 14:472–474.

BRISKIE, J. V., S. G. SEALY, AND K. A. HOBSON. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46:334–340.

BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

BROOKS, A., AND H. S. SWARTH. 1925. A distributional list of the birds of British Columbia. Pacific Coast Avifauna No. 17.

BROWN, B. T. 1988. Breeding ecology of a Willow Flycatcher population in Grand Canyon, Arizona. Western Birds 19:25–33.

BROWN, H. 1903. Arizona bird notes. Auk 20:43–50.

BRYANT, C. A. 1928. Some bird notes from Boca. Gull 10:10–11.

COOPER, J. G. 1874. Animal life of the Cuyamaca Mountains. American Naturalist 8:14–18.

COOPER, J. G. 1974. Ornithology, Volume 1, Land birds. Arno Press, New York, NY.

COUES, E. 1874. Birds of the Northwest: a hand-book of the ornithology of the region drained by the Missouri River and its tributaries. Government Printing Office, Washington, DC.

CROWELL, J. B., JR., AND H. B. NEHLS. 1971. North-

ern Pacific Coast Region. American Birds 25:787–793.

DAWSON, W. L. 1909. The birds of Washington. Occidental Publishing, Seattle, WA.

DAWSON, W. L. 1923. The birds of California, Vol. 1. South Moulton, Co., San Diego, CA.

DE SANTE, D. F., AND T. L. GEORGE. 1994. Population trends in the landbirds of western North America. Pp. 173–190 *in* J. R. Jehl and N. K. Johnson (eds.), A century of avifaunal change in western North America. Studies in Avian Biology No. 15.

DICKEY, D. R., AND A. J. VAN ROSSEM. 1922. Distribution of *Molothrus ater* in California with the description of a new race. Condor 24:206–210.

DUFTY, A. M., JR. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99: 316–327.

FLAHAUT, M. R., AND Z. M. SCULTZ. 1955. Northern Pacific Coast Region. Audubon Field Notes 9:395–397.

FLEISCHER, R. C., AND S. I. ROTHSTEIN. 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the Brown-headed Cowbird. Evolution 42:1146–1158.

FLEISCHER, R. C., S. I. ROTHSTEIN, AND L. S. MILLER. 1991. Mitochondrial DNA variation indicates gene flow across a zone of known secondary contact between two subspecies of the Brown-headed Cowbird. Condor 93:185–189.

FLETT, M. A., AND S. D. SANDERS. 1987. Ecology of a Sierra Nevada population of Willow Flycatchers. Western Birds 18:37–42.

FRANZREB, K. E. 1989. Ecology and conservation of the endangered Least Bell's Vireo. U.S. Fish Wildlife Service, Biological Report 89(1).

FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. C. C. Thomas, Springfield, IL.

FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. US National Museum Bulletin No. 233.

FRIEDMANN, H., AND L. F. KIFF. 1985. The parasitic cowbirds and their hosts. Proceedings Western Foundation Vertebrate Zoology 2:225–304.

FRIEDMANN, H., L. F. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions Zoology No. 235.

GABRIELSON, I. N., AND S. G. JEWETT. 1940. Birds of Oregon. Oregon State College, Corvallis, OR.

GAINES, D. 1974. A new look at the nesting riparian avifauna of the Sacramento Valley, California. Western Birds 5:61–80.

GAINES, D. 1988. Birds of Yosemite and the east slope. Artemisia Press, Lee Vining, CA.

GARRETT, K., AND J. DUNN. 1981. Birds of southern California. Los Angeles Audubon Society, Los Angeles, CA.

GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

GODFREY, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa.

GOLDWASSER, S., D. GAINES, AND S. R. WILBUR. 1980. The Least Bell's Vireo in California: a de facto endangered race. American Birds 34:742–745.

GRINNELL, J. 1909. A new cowbird of the genus *Molothrus*. University California Publications in Zoology 5:275–281.

GRINNELL, J. 1914. An account of the mammals and birds of the Lower Colorado Valley. University California Publications in Zoology 12:51–294.

GRINNELL, J. 1934. The race of cowbird in the San Francisco Bay region. Condor 36:218–219.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27.

GRINNELL, J., AND M. W. WYTHE. 1927. Directory to the bird-life of the San Francisco Bay region. Pacific Coast Avifauna No. 18.

GRINNELL, J., AND T. I. STORER. 1924. Animal life in the Yosemite. University California Press, Berkeley.

GULLION, G. W. 1947. Cowbird young in western Oregon. Condor 64:145.

HANNA, W. C. 1918. First occurrence of the Dwarf Cowbird in the San Bernardino Valley, California. Condor 20:211–212.

HARRIS, J. H., S. D. SAUNDERS, AND M. A. FLETT. 1987. Willow Flycatcher surveys in the Sierra Nevada. Western Birds 18:27–36.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH. 1953. Birds of Washington State. University Washington Press, Seattle, WA.

KESSELL, B., AND D. D. GIBSON. 1978. Status and distribution of Alaskan birds. Studies in Avian Biology No. 1.

KERMODE, F. 1904. British Columbia birds. Provincial Museum, Victoria.

LA JEUNESSE, H. V. 1923. Dwarf Cowbird nesting in Alameda County, California. Condor 25:31–32.

LAYMON, S. A. 1987a. Brown-headed Cowbirds in California: historical perspectives and management opportunities in riparian habitats. Western Birds 18: 63–70.

LAYMON, S. A. 1987b. Can the western subspecies of the Yellow-billed Cuckoo be saved from extinction? Western Birds 18:19–25.

LINTON, C. B. 1908. Notes from Buena Vista Lake, May 20 to June 16, 1907. Condor 10:196–198.

LITTLEFIELD, C. D. 1990. Birds of Malheur National Wildlife Refuge, Oregon. Oregon State University Press, Corvallis, OR.

MAYFIELD, H. 1965. The Brown-headed Cowbird with old and new hosts. Living Bird 4:13–28.

MAYFIELD, H. 1977. Brown-headed Cowbird: agent of extermination? American Birds 31:107–113.

MICHAEL, C. W. 1935. Cowbirds appear in Yosemite. Condor 37:178.

MILLER, A. H. 1935. Further comments on the cowbirds of the San Francisco Bay region. Condor 37: 217–218.

MILLER, L. H. 1915. Dwarf Cowbird in the San Diegan region. Condor 17:165.

MUMFORD, R. 1952. Bell's Vireo in Indiana. Wilson Bulletin 64:224–233.

NEFF, J. A. 1931. Cowbirds in the Sacramento Valley. Condor 33:250–252.

O'LOGHLEN, A. L., AND S. I. ROTHSTEIN. 1993. An extreme example of delayed vocal development: song learning in a population of wild Brown-headed Cowbirds. Animal Behaviour 46:293–304.

OHMART, R. D. 1994. The effects of human-induced

changes on the avifauna of western riparian habitats. Pp. 273–285 *in* J. R. Jehl, Jr. and N. K. Johnson (eds.), A century of avifaunal change in western North America. Studies in Avian Biology No. 15.

ORR, R. T., AND J. MOFFITT. 1971. Birds of the Lake Tahoe region. California Academy of Sciences, San Francisco, CA.

ORTEGA, C. P., AND A. CRUZ. 1992. Gene flow of the *obscurus* race into the north-central Colorado population of Brown-headed Cowbirds. Journal Field Ornithology 63:311–317.

PAYNE, R. B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird, in central California. Condor 75:80–99.

PHILLIPS, A. R. 1968. The instability of the distribution of land birds in the Southwest. Pp. 129–162 *in* A. H. Schroeder (ed.), Collected papers in honor of Lyndon Lane Hargrave. Archaeological Society New Mexico, Santa Fe, NM.

PITELKA, F. A., AND E. J. KOESTNER. 1942. Breeding behavior of Bell's Vireo in Illinois. Wilson Bulletin 54:97–106.

RAY, M. S. 1903. A list of the land birds of Lake Valley, Central Sierra Nevada mountains, California. Auk 20:180–193.

ROSENBERG, K. V., R. D. OHMART, W. C. HUNTER, AND B. W. ANDERSON. 1991. Birds of the Lower Colorado River Valley. University Arizona Press, Tucson, AZ.

ROTHSTEIN, S. I. 1978. Geographical variation in the nestling coloration of parasitic cowbirds. Auk 95: 152–160.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review Ecology and Systematics 21:481–508.

ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. Condor 89: 1–23.

ROTHSTEIN, S. I., AND S. K. ROBINSON. 1994. Conservation and coevolutionary implications of brood parasitism by cowbirds. Trends in Ecology and Evolution 9.

ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253–267.

ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77–88.

ROTHSTEIN, S. I., J. VERNER, E. STEVENS, AND L. V. RITTER. 1987. Behavioral differences among sex and age classes of the Brown-headed Cowbird and their relation to the efficacy of a control program. Wilson Bulletin 99:322–337.

ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. Current Ornithology 3:127–185.

ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1988. The agonistic and sexual functions of vocalizations of male Brown-headed Cowbirds, *Molothrus ater*. Animal Behaviour 36:73–86.

ROWLEY, J. S. 1930. Observations on the Dwarf Cowbird. Condor 32:130–131.

ROWLEY, J. S. 1939. Breeding birds of Mono County, California. Condor 41:247–254.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 58:636–643.

SCHULTZ, Z. M. 1957. Northern Pacific Coast Region. Audubon Field Notes 11:372–373.

SEDGWICK, J. A., AND F. L. KNOPF. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90:253–256.

SIBLEY, C. G. 1952. The birds of the South San Francisco Bay region. Unpubl. ms in collections of The Western Foundation of Vertebrate Zoology, Camarillo, CA.

SMITH, F. 1977. A short review of the status of riparian forests in California. Pp. 1–2 *in* A. Sands (ed.), Riparian forests in California: their ecology and conservation. Institute Ecology Publications No. 15.

STAFFORD, M. D., AND B. E. VALENTINE. 1985. A preliminary report on the biology of the Willow Flycatcher in the central Sierra Nevada. Cal-Neva Wildlife Transaction 1985:66–77.

SWARTH, H. S. 1911. Field notes from south-central California. Condor 8:160–163.

TALMADGE, R. R. 1948. The cowbird moves northward in California. Condor 50:273–274.

TYLER, J. G. 1913. Some birds of the Fresno District, California. Pacific Coast Avifauna No. 9.

UNITT, P. 1984. The birds of San Diego County. San Diego Society Natural History, San Diego, CA.

UNITT, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. Western Birds 18:137–162.

VALENTINE, B. E., T. A. ROBERTS, S. P. BOLAND, AND A. P. WOODMAN. 1988. Livestock management and productivity of Willow Flycatchers in the central Sierra Nevada. Transactions Western Section Wildlife Society 24:105–114.

VERNER, J., AND S. I. ROTHSTEIN. 1988. Implications of range expansion into the Sierra Nevada by the parasitic Brown-headed Cowbird. Pp. 92–98 *in* D. Bradley (ed.), Proceedings, State of the Sierra Symposium 1985–86. Pacific Publications Co., San Francisco, CA.

WALL, E. 1919. The Wilson Snipe nesting in southern California. Condor 21:207–209.

WHEELOCK, I. G. 1904. Birds of California. A. C. McClury, Chicago, IL.

WHITFIELD, M. J. 1990. Willow Flycatcher reproductive response to Brown-headed Cowbird parasitism. Master's thesis. California State University, Chico, CA.

WESTON, F. M. 1965. A survey of the bird life of northwestern Florida. Bulletin Tall Timbers Research Station 5:1–147.

WILLETT, G. 1912. Birds of the Pacific Slope of Southern California. Pacific Coast Avifauna No. 7.

WILLETT, G. 1933. A revised list of the birds of southwestern California. Pacific Coast Avifauna No. 21.

WILLETT, G. 1919. Bird notes from southeastern Oregon and northeastern California. Condor 21:194–205.

WOODCOCK, A. R. 1902. Annotated list of the birds of Oregon. Bulletin No. 68, Oregon Agricultural Experiment Station, Corvallis, OR.

APPENDIX I. Localities and references for each year listed in Figure 1. 1889—Colton-San Bernardino area (Wall 1919); 1896—Borrego Springs (Unitt 1984); 1904—Santa Paula and 1905—Los Angeles (Willett 1912); 1907—Buena Vista Lake (Linton 1908); 1911a—Palo Alto (MVZ no.12929); 1911b—Fresno (Tyler 1913); 1911c—Bakersfield (Swarth 1911); 1915a—San Diego (Unitt 1984); 1915b—Snelling (Grinnell and Storer 1924); 1916—Calexico (Friedmann compilations); 1922—Irvington (La Jeunesse 1923); 1924—Paso Robles (MVZ no. 11893); 1931—Yuba, Sutter and Glenn counties (Neff 1931); 1932—Yosemite Valley (Friedmann compilations); 1934—Berkeley (Benson and Russell 1934); 1937—Oroville (Behle 1937); 1938—Lake Tahoe (Friedmann et al. 1977); 1941—Humboldt County (Talmadge 1948); 1942—Nevada City (Friedmann compilations); 1946—Eugene (Gullion 1947); 1955—Seattle and Victoria (Flahaut and Schultz 1955); 1958—Lake Tahoe (G. McCaskie, pers. comm.); 1968—Sage Hen Valley (J. M. White, pers. comm.).