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THE DENSITY AND DISTRIBUTION OF BROWN-HEADED COWBIRDS: THE CENTRAL COASTAL CALIFORNIA ENIGMA

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Abstract. I examined the density and distribution of Brown-headed Cowbirds (*Molothrus ater*) in Central Coastal California. I focused on Vandenberg Air Force Base, which contains some of the most extensive riparian vegetation along the 550 km Central Coast. Cowbirds were found only in riparian vegetation during morning point count surveys. All detected parasitization events occurred in riparian vegetation. The mean density of cowbirds on Vandenberg was 0.14 cowbird/point count in 1996 (N = 83 point counts) and 0.12 cowbird/point count in 1997 (N = 84), extremely low values compared to other regions. Breeding Bird Survey data also showed a low density of cowbirds in the vicinity of Vandenberg ($\bar{x}$ = 0.47 cowbird/route), and within the entire Central Coast ($\bar{x}$ = 1.79 cowbirds/route) when compared to other areas of California. While the causes for the low density of cowbirds along the Central Coast are unclear, this pattern shows that not all riparian zones are heavily used by cowbirds, with the subsequent parasitization risk for hosts.

Key Words: Breeding Bird Survey, Brown-headed Cowbird, *Molothrus ater*, riparian vegetation.

The need to understand the factors underlying the distribution of the Brown-headed Cowbird (*Molothrus ater*) is particularly acute due to its impact on endangered and sensitive species. Cowbird parasitization has been implicated as a cause in the decline of many passerine species (Gaines 1974, Mayfield 1977, Walkinshaw 1983, Brittingham and Temple 1983, Laymon 1987, Robinson and Wilcove 1994, Robinson et al. 1995a, Averill et al. *this volume*, Halterman and Laymon *this volume*). The impact of cowbirds on the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Unitt 1987, Whitfield 1990) and the Least Bell's Vireo (*Vireo bellii pusillus*) (Franzreb 1989a) in California has been of particular concern. Because of impacts on these Federally Endangered species there have been many management plans and control efforts targeting cowbirds, aimed at protecting these vulnerable hosts. These programs frequently view cowbirds as a threat that needs to be eliminated as quickly as possible. Understanding the causes of the distribution of cowbirds could lead to the implementation of more effective host conservation efforts. There is also the possibility that understanding the factors behind the distribution of cowbirds could generate landscape-based management alternatives to cowbird trapping.

Brown-headed Cowbirds favor riparian vegetation for breeding in the western United States, presumably due to the high density of potential hosts in this vegetation type (Grinnell and Miller 1944, Rothstein et al. 1980, Verner and Ritter 1983, Lowther 1993). However, research presented in these proceedings makes the important point that cowbirds are not limited to using riparian vegetation in the West (Ellison *this volume*, Vander Haegen and Walker *this volume*).

My study investigated two basic questions concerning cowbird ecology. The first was, do cowbirds show a preference for riparian vegetation in Central Coastal California? I compared the density of cowbirds on point counts in riparian versus non-riparian vegetation on Vandenberg Air Force Base. The second question was, what is the density of cowbirds within this region, and how does it compare to other areas of California? I examined this question on a local scale by comparing point counts from Vandenberg with other counts I conducted along the Central Coast. I also used Breeding Bird Survey data to compare the densities of this region to other areas of California.

METHODS

STUDY SITE

Vandenberg Air Force Base (VAFB) covers 39,838 ha, and extends along more than 56 km of coastline in northern Santa Barbara County, California, from 34°30′–34°56′N at 120°35′W. There are five perennial watersheds on VAFB: Honda Creek, Bear Creek, the Santa Ynez River, San Antonio Creek, and Shuman Creek. The first two are on South Vandenberg Air Force Base (SVAFB), while the other three are on North Vandenberg Air Force Base (NVAFB). Because cowbirds have only been found breeding on NVAFB (Farmer 1998, unpubl. report to Vandenberg Air Force Base), the halves of VAFB are treated separately in the examination of the distribution and abundance of cowbirds. VAFB supports large, contiguous areas of native vegetation that were once much more common in this region, with approximately 80% of the Base retained in an essentially wild state (Ferren and Collins 1997, unpubl. report to Vandenberg Air Force Base).

The three dominant plant communities found on VAFB are grasslands (native or exotic grasses), coastal sage chaparral (*Baccharis* spp. or *Artemisia* spp.), and Burton Mesa chaparral (*Arctostaphylos* spp.). Riparian vegetation comprises approximately 7% of VAFB's area (Farmer 1998, unpubl. report to Vandenberg Air Force Base). The dominant riparian vegetation on-Base is arroyo willow (*Salix lasiolepis*) with an understory of blackberry (*Rubus ursinus*), poison oak (*Toxicodendron diversilobum*), stinging nettles (*Urtica dioica*), and bulrushes (*Scirpus* spp.) (Farmer 1998, unpubl. report to Vandenberg Air Force Base).

Field Surveys

The number and identity of each avian species was recorded during a 5 min, unlimited distance point count at a site (Ralph et al. 1994). Point counts were conducted from 0400–0900 PST, between 1 May–30 June, 1996–1997. Because cowbirds are known to be highly mobile in the mornings (Rothstein et al. 1984), all counts were separated by 400 m to avoid recounting the same individual birds. The majority of riparian and palustrine regions on-Base were surveyed, but some sites could not be reached before 0900. The survey route followed the watercourse or shoreline. There were 83 riparian point counts conducted in 1996 and 84 riparian counts in 1997, of which 76 counts were replicated between years. Because the replicated counts were done at the same location each year, they are not independent. Therefore, the data were not pooled across years to avoid inflating any confound from landscape factors associated with a site (e.g., distance to feeding stations).

Additional point counts were conducted at two geographical scales to investigate cowbird density across the landscape. The first was a series of local surveys conducted in the riparian vegetation adjacent to VAFB outside the Base's boundary, upstream of the five major drainages. These counts were within 1 km of VAFB's boundary, except for those conducted along the Santa Ynez River. The riparian corridor is eliminated by agricultural lands within 1 km for all the drainages except the Santa Ynez River, where the riparian vegetation continues far beyond VAFB. The river was surveyed from VAFB to the town of Buelton (34°37′N, 120°12′W), a distance of 34 km. The majority of these local surveys were within the town of Lompoc, and these counts are referred to as LOMP hereafter. There were 24 counts in 1996 and 22 counts in 1997, with 20 counts replicated between years. The second series of comparative surveys was conducted on a regional scale and was composed of sections to the north and southeast of VAFB. The southeastern riparian vegetation (SRIP) section extended from Gaviota (34°28′N, 120°14′W) to Santa Barbara (34°25′N, 119°40′W) (8–80 km southeast of VAFB), with the same eight counts performed in 1996 and 1997. The northern riparian vegetation (NRIP) section extended from Orcutt (34°52′N, 120°27′W) to Cayucus (35°28′N, 120°55′W) (2.5–88 km north of VAFB). There were 22 counts conducted in 1996 and 34 counts in 1997, with 19 of these counts replicated between years. Across both the local and regional scale, there were 137 total point counts done in 1996 and 148 total counts done in 1997.

All point counts were on the west or south of the coastal mountain ranges, and below 500 m elevation to minimize differences in vegetation. All publicly accessible rivers, streams, lakes, and ponds between Santa Barbara and Cayucus meeting these criteria were examined, and those locations with the most extensive riparian vegetation censused. I used this selection criteria to make the comparative points more similar to those on VAFB. However, compared to the on-Base vegetation, the off-Base riparian corridor appeared much narrower with less understory and associated breeding habitat for hosts (Gates and Gysel 1978, Chasko and Gates 1982). To measure this quantitatively, aerial photos of the entire study region were examined and the width of the riparian corridor at each count was compared. The photos were from the 1994 National Aerial Photography Program (1: 40,000).

A separate series of 41 point counts was done in non-riparian vegetation on VAFB in 1997. The survey protocol for these counts was the same for the riparian counts. They were conducted in the three predominant vegetation types found on VAFB. There were 10 counts in grasslands, 12 in coastal sage chaparral, and 19 in Burton Mesa chaparral. The non-riparian surveys were all done on NVAFB, and were compared with the NVAFB subset of the 1997 riparian counts ($N = 61$). Because past cowbird research showed a preference for riparian vegetation, I used a one-tailed Mann Whitney U test to examine habitat use.

Transects of the riparian vegetation were used to independently compare the distributional pattern of cowbirds with that determined from the point count data. Each drainage or lake shore was partitioned into 500-m sections and censused between 14 April and 18 July, 1996. A transect consisted of the surveyor walking 500 m along the waterway, and noting the species and abundance of all birds detected. Only those transects completed within 15–60 min and initiated between 0400–0900 PST were used for my analysis. There were 108 transects which met these

standards, and this dataset is denoted STREAM hereafter. Because this survey effort was not as rigorously controlled as the point counts, statistical analysis is problematic. However, the stream transects covered the entire length of the five major drainages on VAFB, and extended to areas that were not covered by the point count surveys. The stream transects also included data from off-Base locations for comparative purposes.

The field notes from another extensive avifaunal study that occurred on VAFB between 1995–1997 were examined for any opportunistic detections of cowbirds (Holmgren and Collins 1998, unpubl. report to Vandenberg Air Force Base). This study was concentrated in grasslands, Burton Mesa chaparral, and coastal sage chaparral. These data were not rigorous, but were used to confirm the distributional patterns of cowbirds. Only observations in non-feeding habitat were considered. Feeding sites were defined as areas with horses or cattle, or short grass lawns, where numerous Red-winged Blackbirds (*Agelaius phoeniceus*), Brewer's Blackbirds (*Euphagus cyanocephalus*), Tricolored Blackbirds (*Agelaius tricolor*), and European Starlings (*Sturnus vulgaris*) tended to feed communally (Friedmann 1929, Rothstein et al. 1987, Lowther 1993, Thompson 1994). When cowbirds were detected at such sites, they were not searching for nests, and were observed actively foraging (Farmer 1998, unpubl. report to Vandenberg Air Force Base).

Breeding Bird Surveys

The Breeding Bird Survey (BBS) provides data for examining cowbird populations at large geographical scales. I used data from the BBS World Wide Web site to compare cowbird densities between routes from selected areas (Sauer et al. 1997). The BBS has partitioned North America into 99 strata, based on vegetative and physiographic characteristics. VAFB is in the California Foothills stratum, which is immense and contains a large array of vegetation types. It ranges from Mexico to Redding, California (34°52′N, 122°00′W), a distance of 1007 km, and encircles the Central Valley, going from the Pacific Ocean to the Sierra Nevada. Because of this, an analysis between a subset of individual routes from this stratum seemed more appropriate than the normal comparison between strata. Each route is 39.7 km long with 3 min point counts done every 0.81 km, and is conducted along secondary roads (Sauer et al. 1997). I only used routes that had been run three or more times over the most recent ten years of the BBS data. Each route's data point for my analysis was the mean of all performances of that route from 1987–1996. While some routes were conducted by the same observer over these ten years, the majority had multiple observers. Inter-observer variability, combined with the range of environmental conditions over the ten years, could introduce some variability in the results (Verner 1985).

I compared four areas using the BBS data. The Central California Coast region contained eight BBS routes, and ranged from Ventura (34°20′N, 119°15′W) to 47 km north of Highway 46 (35°50′N, 121°05′W). These are all the routes within 50 km of my entire study region. The Northern California Coast contained 17 BBS routes, and ranged from San Francisco (37°40′N, 122°30′W) to Oregon (42°00′N, 124°15′W). The Southern California Coast contained five BBS routes, and ranged from Los Angeles (34°10′N, 118°15′W) to Mexico (32°33′N, 117°00′W). The routes in each coastal region were within 70 km of the Pacific Ocean. The fourth region was California's Central Valley, which adjoins the Central Coast to the northeast and contained 16 BBS routes and ranged from Bakersfield (35°15′N, 119°00′W) to Stockton (38°00′N, 121°19′W). All routes in this region were between the coastal mountain ranges and the Sierra Nevada, and lower than 500 m elevation.

Additional insight concerning the local density of cowbirds in the vicinity of VAFB can be gained through comparing the BBS routes nearest VAFB with the adjacent regions described above. There are three BBS routes within 50 km of VAFB, and these local measures of the cowbird density near my intensive surveys serve as an index relating my work to the BBS routes. Due to the scant number of routes, the statistical power is limited and only qualitative patterns are presented.

Nest Searches

There are 34 cowbird hosts known to breed on VAFB (Farmer 1998, unpubl. report to Vandenberg Air Force Base). Intensive nest searching for all possible hosts was conducted from 15 April–31 July, 1995–1997 in the riparian vegetation on-Base. Searches were conducted by attempting to find the nests of birds exhibiting nest building or other nesting behaviors. In the latter part of the breeding season surveyors attempted to discover family groups, and received additional training to detect the loud, distinctive begging call of juvenile cowbirds. Concurrent projects studying the breeding biology of all avifauna on VAFB covered the major plant communities in 1995–1997, and most likely would have discovered any cowbird breeding if it was occurring in these areas (Holmgren and Collins

TABLE 1. MEAN (± SD) AND MEDIAN COWBIRD NUMBERS DETECTED DURING RIPARIAN SURVEYS CONDUCTED EACH YEAR FOR THE VARIOUS STUDY REGIONS IN CENTRAL COASTAL CALIFORNIA

Region	N	$\bar{x}$ ± SD	Median
Point counts, 1996 (n = 137)			
SVAFB	22	0.00 ± 0.00	0.00
NVAFB	61	0.20 ± 0.51	0.00
NRIP	22	0.36 ± 0.85	0.00
LOMP	24	0.58 ± 0.82	0.00
SRIP	8	0.63 ± 0.74	0.50
Point counts, 1997 (n = 148)			
SVAFB	23	0.00 ± 0.00	0.00
NVAFB	61	0.16 ± 0.49	0.00
SRIP	8	0.25 ± 0.46	0.00
NRIP	34	0.35 ± 0.73	0.00
LOMP	22	0.41 ± 0.59	0.00
Stream transects, 1996 (n = 108)			
SVAFB	23	0.00 ± 0.00	0.00
NVAFB	58	1.09 ± 1.37	1.00
LOMP	27	1.48 ± 2.62	0.00

1998, unpubl. report to Vandenberg Air Force Base; Holmgren and Gallo 1998, unpubl. report to Vandenberg Air Force Base).

RESULTS

HABITAT USE

The comparison of the 41 non-riparian point counts with the 61 riparian counts, all 102 of which were conducted on North VAFB in 1997, showed a strong preferential use of riparian vegetation by cowbirds. Cowbirds were detected on 8 of 61 (13.1%) riparian counts and 0 of 41 non-riparian counts (Mann Whitney U = 1086.5, P = 0.008). Further support for a differential use of riparian vegetation came from the opportunistic detections of cowbirds over the three years of the study, with 189 of 207 (91.3%) non-feeding site detections before 0900 PST occurring in riparian vegetation. Nesting and fledgling records showed that all 34 parasitization events detected from the VAFB region from 1995–1997 were in riparian vegetation.

COWBIRD DENSITY

The median number of cowbirds per point count in the riparian vegetation of VAFB was significantly less than that found in the riparian vegetation adjacent to the Base (LOMP), or in the NRIP and SRIP regions, in both 1996 and 1997 (1996: Kruskal Wallis H = 17.32, P = 0.002; 1997: Kruskal Wallis H = 12.16, P = 0.016) (Table 1). Even though cowbirds were never found on SVAFB, because of the extremely low density of cowbirds on NVAFB the difference between NVAFB and SVAFB was not quite significant in either year (Mann Whitney U test, 1996: P = 0.058, 1997: P = 0.069). Cowbirds were not concentrated at certain sites; only one cowbird was present at the majority of sites where cowbirds were detected (Fig. 1). The distributional pattern was corroborated by the STREAM dataset (Kruskal Wallis H = 19.94, P < 0.001) (Table 1). However, even with points selected to minimize differences in vegetation, the riparian zone on VAFB was wider than off-Base sites. Based on aerial photos, the mean width of the riparian vegetation at VAFB sites was 240 m with a median of 120 m, whereas

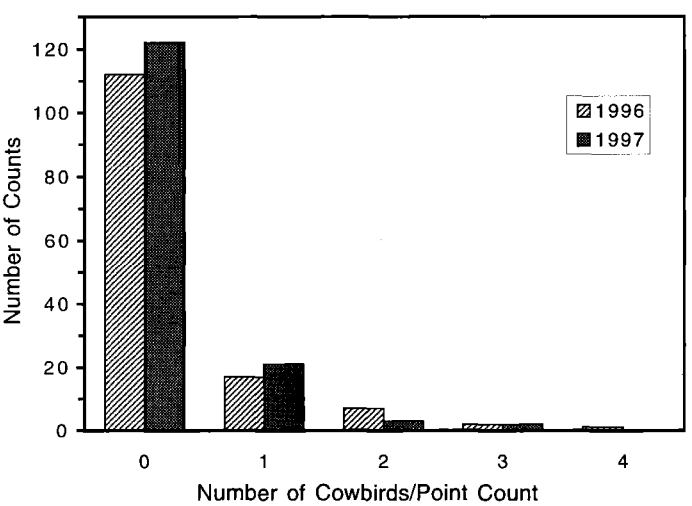

FIGURE 1. Cowbird abundance on all riparian point counts done from Santa Barbara to Cayucus, CA, 1996–1997.

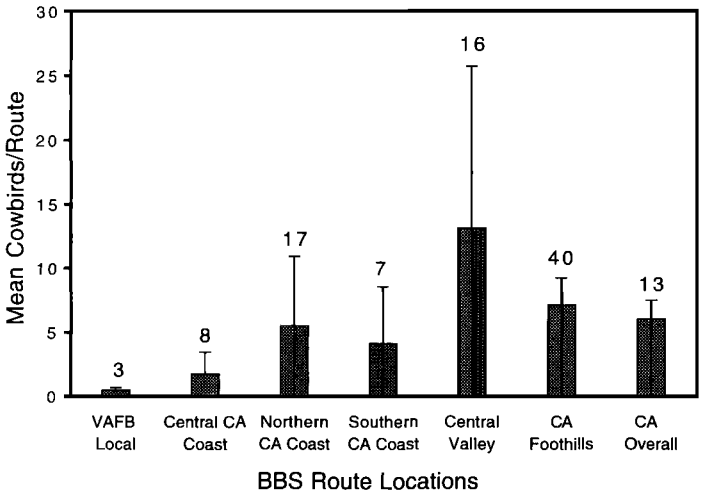

FIGURE 2. Cowbird abundance on California Breeding Bird Survey routes, mean ± SD (1987–1996). The number of routes in each region is shown above the bars.

the off-Base sites had a mean width of 78 m and a median of 60 m (Mann Whitney U = 1379.5, $P < 0.001$).

Breeding Bird Surveys

The BBS data showed a similar pattern of low cowbird density in the local Vandenberg area. The mean for the three routes closest to VAFB was 0.47 cowbird/route (Fig. 2). The cowbird density on these three local routes was an order of magnitude lower than both California overall and the California Foothills stratum, with values of 6.01 and 7.13 cowbirds/route, respectively. The more statistically rigorous analysis of the four regions defined above showed a mixed pattern. The density of cowbirds in the Central California Coast BBS routes, with a mean of 1.79 cowbirds/route and a median of 0.98 cowbird/route, was significantly lower than the routes in the Northern California Coast, which had a mean of 5.52 cowbirds/route and a median of 3.86 cowbirds/route (Mann Whitney U = 31, P = 0.031) (Fig. 2). The difference between the Central Coast and the South Coast, which had a mean of 4.13 cowbirds/route and a median of 2.67 cowbirds/route, was not significant (Mann Whitney U = 14.0, P = 0.38) (Fig. 2). BBS results from the Central Coast were significantly lower than the Central Valley, which had a mean of 13.9 cowbirds/route and a median of 11.44 (Mann Whitney U = 19.0, P = 0.006) (Fig. 2).

DISCUSSION

Brown-headed Cowbirds displayed a strongly disproportionate use of the riparian vegetation on Vandenberg Air Force Base for breeding. This followed the pattern of other studies in the West (Rothstein et al. 1980, Verner and Ritter 1983, Lowther 1993), and contrasted with studies from Maryland (Evans and Gates 1997) and Missouri (Thompson 1994), both of which found no strong preference for riparian areas.

The differences in the habitat edges of eastern and western landscapes is a possible explanation for this variation. The riparian corridors in the West tend to have sharply defined edges, with the entire corridor composed of edge habitat. The adjacent vegetation on VAFB tends to be xeric communities such as coastal sage chaparral or grasslands. The surrounding vegetation in eastern landscapes tends to be more mesic, with a less abrupt ecotone. The evidence concerning the influence of edges on cowbird distribution has been mixed, but most work has been done in the Midwest and East. Some studies have shown that cowbirds use forest edge habitats more than the interior portions of the forest (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, Gates and Griffin 1991, Thompson et al. in press), whereas other studies have found no edge effect in cowbird distribution or parasitization rates (Robinson and Wilcove 1994, Hahn and Hatfield 1995). However, no study has explicitly examined how edges influence cowbird distribution in the West.

The density of cowbirds on both North and South Vandenberg Air Force Base was lower than both the local (LOMP) and regional (NRIP, SRIP) areas. Cowbirds were most abundant where the riparian vegetation was narrower with less understory vegetation, and presumably fewer available breeding opportunities for their

hosts (Gates and Gysel 1978, Chasko and Gates 1982). The narrow riparian corridors in the LOMP, NRIP, and SRIP regions had proportionally more edge habitat than either portion of VAFB. This relationship seemed to imply that cowbirds not only favor riparian vegetation in the West, but in the Central Coast of California preferred edge habitat, with its concomitant sparse understory, as opposed to the more extensive riparian vegetation available on VAFB.

The Breeding Bird Survey results supported my intensive point count results. Whereas the density of cowbirds on the Central Coast routes was significantly lower than the Central Valley or North Coast routes, it was no different from the South Coast routes. Although adjacent to the Central Coast, the Central Valley has the highest density of cowbirds in California (Sauer et al. 1997, Peterjohn et al. in press), so this contrast was unsurprising. Although not a significant difference, the comparison between the South Coast ($\bar{x}$ = 4.13 cowbirds/route) and the Central Coast ($\bar{x}$ = 1.79 cowbirds/route), strongly suggested that the Central Coast actually does have a lower density of cowbirds than the South Coast. Not only did the Central Coast have a low density of cowbirds compared to the other regions, but within this region the three counts nearest to VAFB had a much lower density than the five remaining routes from this region ($\bar{x}$ = 0.47 and $\bar{x}$ = 2.59, respectively). These results confirmed that VAFB has a low density of cowbirds within the Central Coast, and that the Central Coast has a low density of cowbirds within the surrounding regions. The BBS results suggested that the low density of cowbirds I detected with my riparian point counts was a true distributional pattern.

These results have two important ramifications for cowbird management and endangered species protection. The first is that not all riparian vegetation in the West has high cowbird abundance, and subsequent high levels of cowbird parasitization. Whenever riparian vegetation is disturbed or destroyed, cowbird control programs are often implemented without documenting the cowbird population density or parasitization risks of the local avifauna. But if cowbirds are already at a low density, such control programs can do nothing to help the target species. The second consideration my results suggest is that when cowbird management is necessary, habitat restoration could be a highly effective means of reducing the level of cowbird parasitization in an area. Through increasing the width and extent of riparian vegetation to more resemble the VAFB landscape, habitat restoration could potentially be more effective over the long term than cowbird trapping.

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