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ABUNDANCE AND RATES OF BROOD PARASITISM BY BROWN-HEADED COWBIRDS OVER AN ELEVATIONAL GRADIENT IN THE SOUTHERN SIERRA NEVADA

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Abstract. We studied Brown-headed Cowbird (*Molothrus ater*) parasitism rates in four forest types (ponderosa pine, mixed conifer, true fir, and lodgepole pine) over an elevational gradient in the southern Sierra Nevada. Cowbirds were most abundant and parasitism rates were highest at the lowest sites. All but one of 17 parasitized nests were found in the ponderosa pine type and cowbirds were detected only in ponderosa pine and mixed-conifer forest types. A hypothesis that cowbird breeding and egg-laying are limited by late release of livestock at higher elevations was not rejected. Data also supported a second hypothesis—that host abundance and richness influence cowbird abundance and parasitism rates. Bird species richness was a better predictor of cowbird abundance than abundance (total count per plot per year, pooled across species), and models including all passerines were better predictors than models with only host species. Brood parasitism rates were low overall, although rates for Warbling Vireos (*Vireo gilvus*), Cassin's Vireos (*Vireo cassinii*), and Black-throated Gray Warblers (*Dendroica nigrescens*) were high enough to warrant some concern. We recommend continued monitoring of cowbird parasitism rates for these three species in the Sierra Nevada.

Key Words: Black-throated Gray Warbler, brood parasitism, Brown-headed Cowbird, bird species richness, Cassin's Vireo, *Dendroica nigrescens*, elevation, *Molothrus ater*, ponderosa pine, Sierra Nevada, *Vireo cassinii.*

The Brown-headed Cowbird (*Molothrus ater*) is a fairly recent addition to the avifauna of the west slope of the Sierra Nevada, having invaded the region only within the last 60 to 70 years (Rothstein et al. 1980). This raises a concern about potential impacts on endemic populations of host species that have only recently been exposed to cowbird parasitism. Twenty-seven species have been confirmed as hosts of Brown-headed Cowbirds in the Sierra Nevada (Table 1), and populations of these species may be particularly vulnerable to the loss of productivity associated with brood parasitism.

As part of an ongoing study of productivity of forest birds in four forest types, we accumulated data on relative abundance of cowbirds and rates of brood parasitism over an elevational gradient in the Sierra National Forest. Our objectives were to examine patterns of abundance of cowbirds, patterns and rates of brood parasitism, and their potential effects on host species.

Although Verner and Ritter (1983) found cowbirds at all elevations when pack stations and other anthropogenic food sources were nearby, we observed in the present study that cowbird abundance and parasitism rates decreased with increasing elevation. To investigate the observed pattern of higher parasitism rates at lower elevations, we examined two hypotheses. First, because cowbirds in the Sierra seem to depend on supplemental food sources related to various sorts of human activity, especially those connected to livestock, breeding and egg-laying by cowbirds may depend on the timing of livestock release ("cattle on-dates") into the mountains. This hypothesis predicts that cattle on-dates at the higher elevations were later in relation to the arrival and laying dates of the host species. Second, because host abundance and richness tend to be greater at lower elevations, one or both of these variables could influence cowbird abundance.

METHODS

From 1995–1997, we censused birds and monitored nests of all bird species in four forest types over an elevational gradient on the Kings River Ranger District of the Sierra National Forest on the western slope of the southern Sierra Nevada—ponderosa pine (*Pinus ponderosa*; four sites, 1024–1372 m), mixed-conifer (six sites, 1707–2012 m), true fir (four sites, 2170–2347 m), and lodgepole pine (*Pinus contorta*; four sites, 2469–2774 m). All sites consisted of at least 60 ha of mature forest with relatively high canopy cover. Within the 60-ha sites, 40-ha gridded plots were established to allow censusing and facilitate mapping and relocation of nests. The sites tended to be heterogeneous—most included small meadows, creeks, and open, rocky areas. Only the mixed-conifer sites were close to large campgrounds and pack stations. We are not aware that bird feeders play a role in cowbird abundance in any of our study areas. In addition, the ponderosa pine sites were relatively remote and inaccessible, particularly early in the nesting season. All sites were protected from major disturbances, including timber harvest, road construction, and major fuel breaks.

TABLE 1. PERCENTAGE OF BROODS OF PASSERINE SPECIES PARASITIZED BY BROWN-HEADED COWBIRDS (TOTAL NUMBER OF NESTS FOUND[a]) IN FOUR FOREST TYPES, 1995–1997, AND REFERENCES FOR CONFIRMED HOSTS (*) IN THE SIERRA NEVADA

Species	Ponderosa pine	Mixed conifer	True fir	Lodgepole pine	References[b]
Olive-sided Flycatcher (*Contopus cooperi*)*	0 (1)				D
Western Wood-Pewee (*Contopus sordidulus*)*	0 (17)	0 (4)	0 (1)		D, J
Black Phoebe (*Sayornis nigricans*)	0 (1)				
Hammond's Flycatcher (*Empidonax hammondii*)*	0 (4)	0 (15)	0 (2)		D
Dusky Flycatcher (*Empidonax oberholseri*)*		0 (65)	0 (25)	0 (21)	D, J
Pacific-slope Flycatcher (*Empidonax difficilis*)	0 (12)	0 (2)			
Cassin's Vireo (*Vireo cassinii*)*	25 (20)	10 (10)	0 (1)		D, E, I, J, L, N
Hutton's Vireo (*Vireo huttoni*)*	9 (23)				N
Warbling Vireo (*Vireo gilvus*)*	67 (3)	0 (24)	0 (3)	0 (1)	H, I, J, M, N
Steller's Jay (*Cyanocitta stelleri*)	0 (8)	0 (5)	0 (1)		
Mountain Chickadee (*Poecile gambeli*)	0 (1)	0 (19)	0 (39)	0 (19)	
Bushtit (*Psaltriparus minimus*)	0 (6)				
Red-breasted Nuthatch (*Sitta canadensis*)	0 (6)	0 (10)	0 (4)		
Brown Creeper (*Certhia americana*)	0 (10)	0 (10)	0 (5)	0 (14)	
House Wren (*Troglodytes aedon*)		0 (1)			
Winter Wren (*Troglodytes troglodytes*)		0 (1)			
Golden-crowned Kinglet (*Regulus satrapa*)*		0 (1)	0 (1)		J
Ruby-crowned Kinglet (*Regulus calendula*)*					D, E
Blue-gray Gnatcatcher (*Polioptila caerulea*)	0 (4)				
Townsend's Solitaire (*Myadestes townsendi*)		0 (2)	0 (5)		
Hermit Thrush (*Catharus guttatus*)*		0 (6)	0 (5)	0 (10)	D
American Robin (*Turdus migratorius*)	0 (25)	0 (14)	0 (15)	0 (10)	
Wrentit (*Chamaea fasciata*)	0 (3)				
Nashville Warbler (*Vermivora ruficapilla*)*	17 (6)	0 (2)			N
Yellow Warbler (*Dendroica petechia*)*		0 (2)			H, I, J, L
Yellow-rumped Warbler (*Dendroica coronata*)*	0 (1)	0 (9)	0 (2)	0 (12)	D, J, L
Black-throated Gray Warbler (*Dendroica nigrescens*)*	29 (14)				E, I, M, N
Hermit Warbler (*Dendroica occidentalis*)*	0 (2)	0 (2)			A, E, J, M
MacGillivray's Warbler (*Oporornis tolmiei*)*		0 (12)	0 (1)		D, I, J, L, M
Wilson's Warbler (*Wilsonia pusilla*)*					D, E, F
Western Tanager (*Piranga ludoviciana*)*	9 (11)	0 (14)	0 (4)		D, L, N
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0 (41)				
Green-tailed Towhee (*Pipilo chlorurus*)*		0 (4)			D, H, K
Spotted Towhee (*Pipilo maculatus*)	0 (48)	0 (4)			
California Towhee (*Pipilo crissalis*)*					D, M
Chipping Sparrow (*Spizella passerina*)*	0 (10)	0 (2)			L
Fox Sparrow (*Passerella iliaca*)*		0 (8)	0 (4)		D, L
Song Sparrow (*Melospiza melodia*)*					D, H, I, M
Lincoln's Sparrow (*Melospiza lincolnii*)*		0 (1)	0 (1)		D, G, M
White-crowned Sparrow (*Zonotrichia leucophrys*)*					M
Dark-eyed Junco (*Junco hyemalis*)*	4 (51)	0 (76)	0 (55)	0 (46)	B, C, D, E, H, J, L, N
Pine Grosbeak (*Pinicola enucleator*)				0 (2)	
Gray-crowned Rosy-finch (*Leucosticte tephrocotis*)*					M
Purple Finch (*Carpodacus purpureus*)	0 (12)	0 (1)			
Cassin's Finch (*Carpodacus cassinii*)		0 (1)	0 (2)	0 (3)	
Pine Siskin (*Carduelis pinus*)				0 (1)	
Lesser Goldfinch (*Carduelis psaltria*)	0 (1)				
Evening Grosbeak (*Coccothraustes vespertinus*)			0 (1)		

[a] Number of nests we could look into to confirm parasitism.

[b] References (chronologically): A—Friedmann 1963, B—Orr and Moffitt 1971, C—White 1973, D—Friedmann et al. 1977, E—Gaines 1977, F—Stewart et al. 1977, G—Rothstein 1978, H—Rothstein et al. 1980, I—Gaines (in Rothstein et al. 1980), J—Verner and Ritter 1983, K—Friedmann and Kiff 1985, L—Airola 1986, M—Gaines 1988, N—this study.

We censused 8 (1995) or 16 (1996–97) plots each year, using a timed transect method. Transects were 1000 m in length and observers walked at a rate of 50 m per 3 minutes. We recorded birds <50 and >50 m from the transect line. Observers received training in bird vocalizations at the beginning of the season and before moving up to a new elevational band. Each transect was counted six times during the breeding season, with two visits by each of three observers. All censuses were completed by 0930 PDT.

We searched for nests of all bird species and monitored nests every 3 to 4 days. Open nests were checked directly where possible, or with a mirror on a pole. Cavity nests were checked with a fiberscope (Purcell 1997). When nests were too high to reach from the ground, and nest substrates were sturdy, we climbed to nests using a variety of climbing techniques. Laying dates were determined by backdating, assuming one egg laid per day.

Personnel from the Kings River Ranger District provided data on dates when cattle were released onto grazing allotments each year. All livestock permitted for a given allotment were released annually on the date each was open to grazing and generally the cattle had dispersed over the full allotment within a couple of days. Most allotments in a particular forest type had the same on-date. Livestock release preceded the presence of horses at pack stations, and the study sites were not in locations where we would expect cowbirds to occur because of pack stations. Radio-tagged cowbirds on the eastern slope of the Sierra Nevada traveled up to 7 km between feeding and breeding sites (Rothstein et al. 1984). We assume here that cowbirds could have traveled up to 7 km from feeding sites (cattle allotments) to breeding sites (our study sites), although they traveled a maximum of only 4.5 km in an earlier radio-tracking study in the same watersheds as the present study (J. Verner, unpubl. data).

Host abundance and richness were analyzed for correlations with cowbird abundance. Our measure of abundance was the total number of individuals detected per plot per year. Richness was the total number of species detected per plot per year. Two groups of species were used in analyses of host abundance and richness: (1) the 14 species identified as cowbird hosts in the combined results of this study and Verner and Ritter (1983), also done in the Sierra National Forest; and (2) all confirmed Sierran host species (Table 1). Common Ravens (scientific names listed in Table 1) were omitted from analyses. We used Poisson regression to model cowbird abundance because the errors in count data generally are non-normally distributed. The regression parameters were estimated using SAS (SAS Institute 1997). Because count data are typically overdispersed (the variance is greater than the mean), we used a scaled deviance formula to accommodate the assumption of a Poisson distribution (Littell et al. 1996). Plots of deviance residuals showed homogeneity of variance, indicating that this was an appropriate approach. We included a year term in all models to control for year effects.

RESULTS

We monitored 300 nests of 31 passerine species in 1995 for which we were able to confirm the presence or lack of parasitism, 323 nests of 35 species in 1996, and 360 nests of 36 species in 1997. During the three years, all but one of the 17 parasitized nests were found in ponderosa pine habitat (Table 1). Brown-headed Cowbirds were most abundant and parasitism rates were highest in the ponderosa pine forest type, i.e., sites at the lowest elevations. Cowbirds were never detected in our true fir or lodgepole pine sites (Table 2, Fig. 1), nor was brood parasitism. This study added two new species to the list of confirmed hosts in the Sierra Nevada: Hutton's Vireo and Nashville Warbler. Overall rates of cowbird parasitism were low—1.4% of all passerine nests and 3.8% of all passerine nests in ponderosa pine sites. Considering only nests in the ponderosa pine sites, parasitism rates of some individual species were high (Table 1), although sample sizes were small for many species.

Our first hypothesis, that timing of livestock release may influence the timing of cowbird breeding and egg laying, was not rejected. Grazing allotments on the lodgepole pine sites were rested or vacant during the study, except for 10 cow/calf pairs released on 1 July (Julian date = 182) in 1997 within 7 km of 2 plots, and cowbirds were not detected in these sites. In the ponderosa pine sites, cattle were released prior to the first egg dates of nearly all nests, whereas cattle did not arrive in the mixed-conifer and true fir sites until about the middle of the laying period (Fig. 2). Cowbirds arrived only after livestock release in the ponderosa pine sites, and did not begin laying until about two weeks later (Fig. 2a). In the mixed conifer sites, cowbirds arrived just prior to livestock release, and the only parasitized brood was coincident with livestock release (Fig. 2b.). While there does not appear to be a close connection between cattle on-date and cowbird laying date, cowbirds are rare and do not regularly breed in areas where food sources (associated with cattle) are not available until late in the breeding season.

The second hypothesis, that host abundance

TABLE 2. BROWN-HEADED COWBIRD ABUNDANCE, HOST SPECIES RICHNESS, AND HOST ABUNDANCE (SE) IN FOUR FOREST TYPES

	Ponderosa pine	Mixed conifer	True fir	Lodgepole pine
Cowbird abundance	7.3 (0.8)	0.9 (0.3)	0	0
Species richness				
14 Sierran hosts	10.1 (0.5)	11.0 (0.2)	7.8 (0.2)	4.9 (0.4)
All Sierran hosts	12.1 (0.9)	13.6 (0.3)	9.9 (0.3)	6.2 (0.5)
All passerines	28.6 (1.4)	26.6 (1.1)	22.0 (0.9)	17.2 (0.6)
Host Abundance[a]				
14 Sierran hosts	212.7 (16.5)	261.0 (16.1)	211.8 (11.5)	151.7 (13.1)
All Sierran hosts	220.5 (17.6)	292.0 (20.0)	227.2 (14.3)	159.7 (14.0)
All passerines	396.9 (26.8)	387.8 (27.5)	327.6 (23.8)	263.8 (20.9)

Notes: The 14 Sierran hosts include species parasitized by cowbirds in this study and the study by Verner and Ritter (1983). "All Sierran hosts" included all confirmed Sierran host species (Table 1). Common Ravens were excluded from the passerine group.

[a] Mean total count per site per year, N = 12 (3 years × 4 sites).

and richness influenced cowbird abundance, was also supported by the data. Host abundances and richness across the four forest types are given in Table 2. Species richness was a better predictor of cowbird abundance than summed species abundance (Table 3), and adding abundance did not significantly improve the model. Models including all passerine species were better predictors of cowbird abundance than models including only known host species (Table 3). The best model, in terms of goodness of fit and significance, included richness of all passerine species and year (Table 3; Fig. 3). Outliers from that model reveal that richness of all passerines tended to underestimate cowbird abundance at lower elevations and to overestimate it at higher elevations (Fig 3), providing further evidence for an elevation effect. (Estimated equations available from K. Purcell)

DISCUSSION

Cowbird abundance was related to both the timing of livestock release and the number of passerine species. These hypotheses are not mutually exclusive and both may be important influences on the observed patterns of higher abundance of cowbirds and higher rates of brood parasitism at lower elevations. Of course, even a highly significant statistical model cannot imply cause and effect, and we do not rule out the possibility that other factors may contribute to the observed patterns.

Other studies have found that cowbird abundance or parasitism rates were related to host densities (Barber and Martin 1997, Evans and Gates 1997, Tewksbury et al. *this volume*). Donovan et al. (1997) found that cowbird abundance was positively associated with host abundance

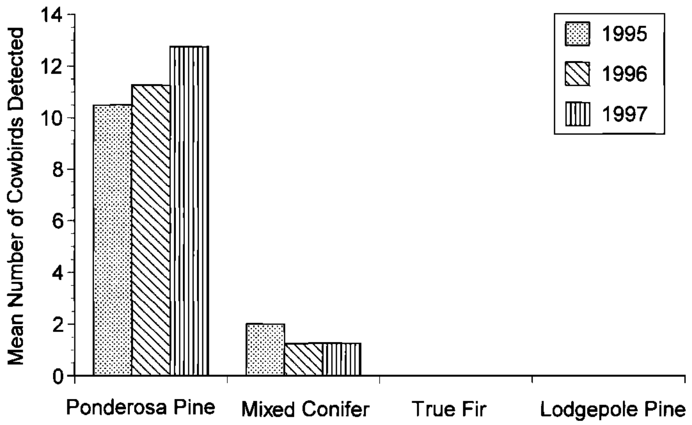

FIGURE 1. Mean number of Brown-headed Cowbirds detected per plot (unlimited distance) in four forest types from 1995–1997. N = 8 plots in 1995 and 16 in 1996 and 1997.

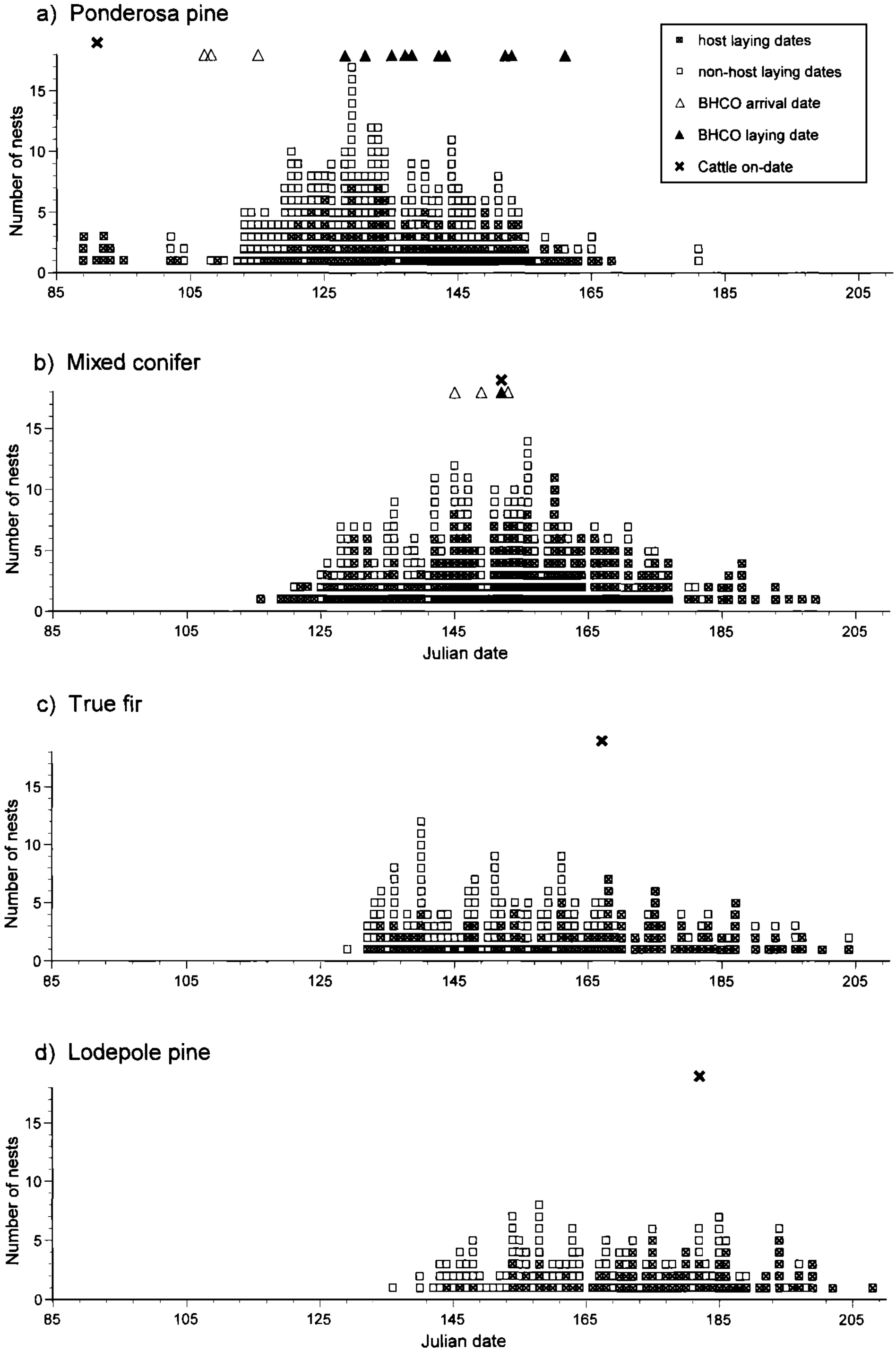

FIGURE 2. Host (all confirmed Sierran hosts) and other passerine laying dates (non hosts), cowbird arrival and laying dates, and cattle on-dates for the four forest types from 1995–1997. Laying dates for hosts, other passerines, and cowbirds represent specific nests and represent all attempts. Cowbird arrival dates are the earliest date cowbirds were recorded in a forest type each year. Cattle on-dates are the date that cows are released onto grazing allotments annually. The cattle on-date for the lodgepole pine sites represents 10 cow/calf pairs released on 1 July (Julian date = 182) within 7 km of two of the four plots only in 1997.

TABLE 3. POISSON REGRESSION ANALYSIS OF BIRD SPECIES RICHNESS AND ABUNDANCE ON BROWN-HEADED COWBIRD ABUNDANCE

		dev/df[a]	Chi-square	P
Species richness				
14 Sierran hosts	richness	3.96	12.19	0.001
	year		7.15	0.067
All Sierran hosts	richness	4.39	7.59	0.006
	year		4.17	0.244
All passerines	richness	2.24	49.54	0.000
	year		39.34	0.000
Abundance[b]				
14 Sierran hosts	abundance	5.22	0.60	0.438
	year		0.82	0.845
All Sierran hosts	abundance	5.30	0.07	0.798
	year		0.93	0.818
All passerines	abundance	3.23	23.18	0.000
	year		19.30	0.000

[a] Deviance/df ratio is the dispersion parameter. This value indicates the goodness of fit of the model and should be close to 1.
[b] Total count per plot per year.

in core habitats but negatively associated with host abundance in edge habitats. S. Rothstein (pers. comm.) argues that parasitism rates should be more closely related to richness because individual species have a distinct breeding "pulse," resulting in more pulses and a longer period of high availability of host nests for cowbirds when many potential species are present. In eastern Sierran sites, S. Rothstein (pers. comm.) also found that richness of passerine species predicted cowbird abundance better than the number of individuals.

Elevation, per se, is not an impediment to cowbirds if they have supplemental food sources. Rothstein et al. (1980) reported that cowbirds were ubiquitous over most or all of the Sierra Nevada, but most of their study sites were close to human influences such as roads, towns, campgrounds, and pack stations. Verner and Ritter (1983) found that cowbird abundance in the

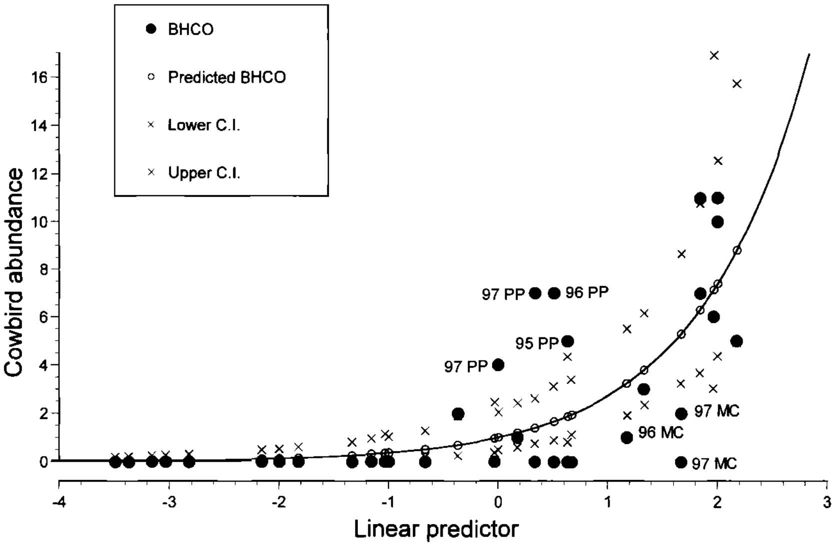

FIGURE 3. Plot of cowbird abundance (BHCO), predicted cowbird abundance (predicted BHCO), and upper and lower confidence limits on the linear predictor for the Poisson regression of cowbird abundance on richness of all passerine species. Outliers are labeled by forest type (PP = ponderosa pine, MC = mixed conifer) and year of census.

Sierra National Forest was positively related to proximity to human disturbance and negatively related to elevation. Sampling mountain meadows, they found that remote meadows without cattle did not have cowbirds, whereas meadows close to supplemental food sources did. Because most of their high-elevation sites were also far from pack stations and other livestock, they concluded that the negative correlation with elevation was spurious. Our high-elevation study sites were not in locations where we expected cowbirds to occur because no pack stations or livestock were nearby. Livestock at high elevations, if they occurred at all, were brought in too late for the cowbirds to use them as a focal point for foraging to promote reproduction. It thus appears that distance to food sources, timing of food sources, host species richness, and elevation are all influences on cowbird abundance in the Sierra Nevada.

Does this level of parasitism impact population viability for any species studied? Warbling Vireos, Cassin's Vireos, and Black-throated Gray Warblers had parasitism rates of 25% or greater (Table 1). Compared to parasitism rates in fragmented landscapes in the Midwest (Robinson et al. 1995b; S. Robinson, pers. comm.), the levels of cowbird parasitism we observed are not high, suggesting that parasitism is probably not a problem for these species, especially if they are double-brooded. Rothstein et al. (1980), Verner and Ritter (1983), and Verner and Rothstein (1988) suggested that Warbling Vireos might be significantly impacted by brood parasitism in certain localities. Warbling Vireos in this study had the highest parasitism rates in ponderosa pine sites, although the sample size was small (Table 1). Because they are most abundant in mixed-conifer stands, where brood parasitism rates were low, productivity of populations there is probably adequate to sustain their numbers in the Sierra Nevada, especially in areas ≥7 km from feeding sources. Cassin's Vireos are abundant in both ponderosa pine and mixed conifer forests. Parasitism rates were low in mixed-conifer forests (Table 1), suggesting that viable populations may exist in this forest type in areas free or nearly free of cowbirds. Black-throated Gray Warblers breed in ponderosa pine forests and lower-elevation oak types, but they occur only rarely above 1830 m (Verner and Boss 1980). Most populations are probably exposed to cowbird parasitism. Black-throated Gray Warblers deserve further monitoring to determine if they are significantly impacted by cowbird parasitism in the Sierra Nevada.

Although we found that cowbird parasitism rates for most species nesting in this portion of the Sierra Nevada are not high, cowbirds are still a relatively new addition to the avifauna there, and they bear continued watching as cowbird numbers have not stabilized. Based on point-count data from both the western and eastern slopes of the Sierra Nevada, cowbird numbers decreased between the late 1970s and the early 1990s (S. Rothstein, pers. comm.). The decline could have occurred at any time during that period, and may or may not be continuing. The elevational pattern for cowbird abundance and rates of parasitism that we found has not been previously reported. The proximate cues for cowbird settling appear to be related to both the timing of livestock release and species richness, although the latter could also be an ultimate factor if cowbirds are evolutionarily tied to their hosts. This does not seem to be the case, as richness of all passerine species was a better indicator of cowbird abundance than was host richness. Further research to identify the relative importance of each of these variables will need to involve the manipulation of cattle on-dates in relation to cowbird arrival and laying dates, and the laying dates of host species.

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