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Research Paper

Use of alternate upland nesting habitat reduces brood parasitism in an endangered bird

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ABSTRACT. The Least Bell's Vireo (*Vireo bellii pusillus*) is a federally endangered songbird restricted to Southern California, USA, and Baja California, Mexico. Historically abundant, it suffered a catastrophic population decline during the twentieth century due to widespread habitat destruction and the arrival of Brown-headed Cowbirds (*Molothrus ater*) within its breeding range. We monitored Least Bell's Vireo nests and conducted cowbird removals for over 13 years in a protected natural area along the Otay River in San Diego County, California. We evaluated the effects of lay date (day of the first egg laid in each nest), nest habitat (river channel versus adjacent upland terrace), and cowbird removals on Least Bell's Vireo brood parasitism rates and nest success. Least Bell's Vireos nested in 11 different host plant species, but over half of vireo nests were found in the upland shrub laurel sumac (*Malosma laurina*). We located and monitored 177 Least Bell's Vireo nests, of which 20% were parasitized. The rate of parasitized nests was strongly associated with whether cowbird removals had occurred that season (9%) or had not (35%), despite the low number of female cowbirds removed annually (1–4 females per year). We also found that nests located in the upland terrace had a lower parasitism rate compared to the river channel (12% vs. 29%), with this difference more pronounced in years without cowbird removals. These differences in parasitism rates also drove differences in nest success; only 29% of channel nests were successful versus 48% of nests on the terrace. The best model predicting cowbird brood parasitism included lay date, cowbird removals, and nest habitat (river channel versus upland terrace). Thus, recovering populations of Least Bell's Vireos may benefit by nesting outside of riparian habitats in adjacent upland habitat due to reduced cowbird parasitism rates. Conservation and restoration of upland habitats adjacent to riparian areas may provide refugia from cowbird parasitism, allowing for continued population increases in areas with limited funding for cowbird management. Conservation of upland habitats will also increase habitat available to Least Bell's Vireos under future drier climate scenarios.

La réduction du parasitisme des couvées chez un oiseau menacé d'extinction par l'utilisation d'un habitat de nidification alternatif dans les hautes terres

RÉSUMÉ. Le Viréo de Bell (*Vireo bellii pusillus*) est un oiseau chanteur menacé d'extinction au niveau fédéral, limité à la Californie du Sud (États-Unis) et à la Basse-Californie (Mexique). Historiquement abondant, sa population a connu un déclin catastrophique au cours du 20e siècle en raison de la destruction généralisée de son habitat et de l'arrivée du Vacher à tête brune (*Molothrus ater*) dans son aire de reproduction. Nous avons surveillé les nids du Viréo de Bell et nous avons procédé à l'élimination des vachers pendant plus de 13 ans dans une zone naturelle protégée le long de la rivière Otay, dans le comté de San Diego, en Californie. Nous avons évalué les effets de la date de ponte (jour du premier œuf pondu dans chaque nid), de l'habitat du nid (chenal de la rivière contre une terrasse adjacente en terres hautes) et de l'élimination des vachers sur les taux de parasitisme de la couvée du Viréo de Bell et sur le succès de sa nidification. Le Viréo de Bell a niché dans 11 espèces de plantes hôtes différentes, mais plus de la moitié de ses nids se trouvaient dans le *Malosma laurina*, un arbuste des hautes terres. Nous avons localisé et surveillé 177 nids du Viréo de Bell, dont 20 % étaient parasités. Le taux de nids parasités était fortement associé à l'élimination ou pas des vachers cette saison-là (9 % c. 35 %, respectivement), malgré le faible nombre de femelles vachers éliminées chaque année (1 à 4 femelles par an). Nous avons également constaté que les nids situés sur la terrasse dans les hautes terres affichaient un taux de parasitisme plus faible que ceux situés dans le chenal de la rivière (12 % c. 29 %), cette différence étant plus prononcée les années sans élimination de vachers. Ces différences dans les taux de parasitisme ont également entraîné des variations dans le succès de la nidification : seuls 29 % des nids dans le chenal ont réussi contre 48 % des nids sur la terrasse. Le meilleur modèle prédisant le parasitisme des couvées de vachers incluait la date de ponte, les prélèvements de vachers et l'habitat du nid (chenal de la rivière c. terrasse dans les hautes terres). Ainsi, les populations du Viréo de Bell qui se rétablissent affichent un taux moindre de parasitisme des vachers en nichant dans les zones adjacentes aux habitats riverains, dans les hautes terres. La conservation et la restauration des habitats des hautes terres adjacents aux zones riveraines offrent un refuge potentiel contre le parasitisme des vachers, ce qui permet d'augmenter les populations du Viréo de Bell dans les régions où le financement du contrôle des vachers s'avère limité. La conservation des habitats en hautes terres augmentera également l'habitat disponible pour le Viréo de Bell pusillus dans des scénarios climatiques plus secs à l'avenir.

Key Words: *brood parasitism; Brown-headed Cowbird; conservation; habitat; Least Bell's Vireo; productivity; riparian*

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INTRODUCTION

The conservation and recovery of endangered species typically requires protection and restoration of key habitats for their survival and reproduction. Identifying these habitats can often be difficult, especially when remnant populations may be occurring in a subset of habitats than were used historically. As populations recover, the use of different habitats can often confer different selective pressures driven by the varying densities of other species, such as potential competitors, predators, and parasites.

While a robust literature exists on habitat selection of bird species among potential competitors and predators (refer to reviews in Martin 1993, Jones 2001), the influence of a brood parasite on habitat selection of potential hosts has been established more recently (Forsman and Martin 2009). In sites where the brood parasite exhibits significant influence on breeding productivity, choosing habitats outside of primary parasite occurrence areas would seemingly increase the chances of successful reproduction.

The Least Bell's Vireo (*Vireo bellii pusillus*; hereafter vireo) is a federally endangered songbird restricted to central and Southern California, USA, and Baja California, Mexico. Historically abundant in riparian habitats, the subspecies suffered a catastrophic population decline and range retraction during the twentieth century due to widespread habitat destruction and the arrival of Brown-headed Cowbirds (*Molothrus ater*; hereafter cowbird) within its breeding range (Goldwasser et al. 1980, Hanna 1918, Linton 1908). By the 1980s, this subspecies was restricted to fewer than 300 pairs within its U.S. range and was listed as endangered by the U.S. Fish and Wildlife Service in 1986 (Franzreb 1989). Significant investment in habitat protection and restoration, in conjunction with continued cowbird management at breeding sites, has resulted in a recovery to an estimated 3000 pairs, with a concomitant expansion of its range back into historical areas (USFWS 2006).

Although it has long been understood that Least Bell's Vireos use habitats adjacent to riparian areas for foraging (e.g., Kus and Miner 1989), these habitats have often been considered peripheral or edge habitats and have not been a focus of conservation or restoration activities for the vireo. Habitats adjacent to riparian vegetation within the vireo's range are commonly shrublands with a diversity of shrub species (Rundel 2007). Laurel sumac (*Malosma laurina*) is a common shrub of upland areas within the vireo's breeding range. It is a large, 2–5 m tall, densely foliaged shrub, with long, folded leaves (Turner et al. 1995). Because Least Bell's Vireos characteristically place their pensile nests in Y-shaped splits of slender horizontal branches (Unitt 2004), laurel sumac is structurally very similar to willow species (*Salix* spp.) and a highly attractive plant for nest placement.

Least Bell's Vireos may have used upland habitats more extensively prior to their population crash. While Grinnell and Miller (1944:385) stated that in California the species was typically found in willow, they also noted them less commonly in "oak, wild grape, poison oak, and sumac in the margins of water courses." Dawson (1923:588) described the species' association with stream-side vegetation, continuing "yet I have seen the bird, in mid-May, in the cactus and chaparral belt." A Least Bell's Vireo nest collected near San Diego on 28 May 1912 was found "under large shumack (sic) bush near creek bottom about 3 ft. above ground." (Western Foundation Vertebrate Zoology #EN-72366). Numerous other historical nests (e.g., WFVZ #EN-6692, EN-9609, EN-9944, EN-35571) were also collected in wild rose (*Rosa californica*), an upland shrub often forming thorny brambles and thickets that would potentially confer some defense against predation.

These upland habitats adjacent to riparian vegetation have often been lost in the course of development within the range of the Least Bell's Vireo. Numerous watercourses are now defined by soft bottom channels edged by rip-rap (i.e., large rock substrates) or concrete flood protection barriers that form a hard edge between remnant willow-dominated vegetation left in the channel and upland areas either converted to human uses or left as xeric scrub with no transition or connection to the riparian system. Dense stands of riparian scrub or transitional vegetation including species such as laurel sumac and wild rose are often removed and lost in these areas.

Least Bell's Vireos typically place their nests on thin branches suspended over the substrate, often just 0.5–1 m above the ground. These nests are often visually very evident, though placed in a situation that would be difficult for approach by snakes. Snakes are major nest predators of ground- and shrub-nesting birds in Southern California and use predominantly chemical, but possibly also visual, cues in hunting for nests (Clark 2009, Morrison and Bolger 2002, Patten and Bolger 2003). Nest placement in open situations to avoid a dominant nest predator proved maladaptive upon the arrival of a brood parasite that relies primarily on visual cues for finding nests. Besides providing habitats with high densities of suitable hosts, riparian vegetation in western xeric regions offers abundant perches, such as trees, from which female cowbirds can search for suitable nests. Multiple studies have found that proximity to perches such as trees significantly influenced parasitism rates (Averill-Murray et al. 1999, Clotfelter 1998, Sharp and Kus 2006).

The costs and benefits of cowbird management to conserve endangered species has been debated extensively. However, in the case of the Least Bell's Vireo, cowbird control at breeding sites has proven effective in raising reproductive rates from critically low levels (Kus 1999). While some larger host species may fledge mixed broods of cowbirds and host young, less than 5% of vireo nests with cowbird eggs that are not rescued will fledge vireo young (Ferree 2002). Additionally, vireos in California primarily nest in and adjacent to watercourses, while Brown-headed Cowbirds have been widely documented to favor nest searching in riparian habitat over scrub habitats in western North America (e.g., Farmer 1999, Tewksbury et al. 1999). Therefore, the vireo's visually evident nest placement tendencies, small body size of the chicks, and preferences for riparian habitats for breeding all conspire to make this species particularly vulnerable to reduced productivity from cowbird brood parasitism. Thus, any ability of vireos to evade cowbird parasitism pressure by nesting outside primary cowbird breeding areas may increase the species' overall productivity.

Brown-headed Cowbirds begin laying later in the season than some of their hosts (Lowther 2020). In Southern California, Least Bell's Vireos may begin laying as early as thirty days before the earliest cowbird laying occurs (Unitt 2004). Therefore, we predicted that Least Bell's Vireo nests initiated later in the season would have a higher probability of brood parasitism than nests earlier in the season.

We compared parasitism rates of Least Bell's Vireos nesting in both a riparian river channel and adjacent upland terrace from a long-term study in a protected natural area. In years with available funding, cowbird management was also performed (including targeted mist-netting or cowbird trapping; hereafter cowbird removals). The uneven funding allowed us to compare years with and without cowbird management at a site with a population of 14–17 breeding vireo pairs. We predicted that (1) brood parasitism would be lower in years with cowbird removals; (2) brood parasitism would be higher in the river channel compared to the upland terrace due to cowbird preferences for nest searching in riparian habitat; (3) brood parasitism would increase with lay date; and (4) nest success would be lower in years without cowbird removals, particularly in the river channel where cowbirds were more likely to search for nests. These predictions were tested using a long-term data set from a protected area.

METHODS

Study area

We conducted our study in the Otay Ranch Preserve, within and adjacent to the Otay River, in Chula Vista, San Diego County, California. The study area is located southwest of Lower Otay Lake, ranging in elevation from approximately 73–164 m above mean sea level. The drainage is defined by the main course of the Otay River, bordered by a steep bank of several meters, above which is a flat terrace, 50–200 m in width. In the river channel, several willow species (*Salix goodingii*, *S. lasiolepis*, and *S. exigua*) dominated, interspersed with dense stands of arrow weed (*Pluchea sericea*), mule fat (*Baccharis salicifolia*), and tamarisk (*Tamarix* sp.). The upland terrace consisted of dense laurel sumac stands and smaller scrub species such as California sagebrush (*Artemisia californica*) and flat-topped buckwheat (*Eriogonum fasciculatum*). The habitat is further described in Clark et al. (2014).

Nest monitoring

We located and monitored Least Bell's Vireo nests from 2011–2023, excluding 2015 when funding was unavailable, using standard survey techniques recommended for the species (USFWS 2001). We searched for nests both in the river channel and in adjacent upland terraces. We typically visited nests every five to seven days (mean = 5.7 days, range = 1–9 days), with more frequent visits during building and egg-laying stages to confirm whether eggs were laid and to check for cowbird eggs. We found most nests (> 90%) during building, laying, or incubation stages. Presence of cowbird eggs was noted, and if present, cowbird eggs and/or chicks were removed. We considered a nest to be parasitized if we observed at least one cowbird egg or nestling during a nest visit. Some nests (n = 9, 5% of total) failed before it was determined whether eggs had been laid; these nests were included in analyses and grouped with unparasitized nests. Vireo nest success was determined through direct observation of fledglings in the territory. At the end of the breeding season, after nests had either fledged or failed, we returned to measure characteristics associated with nest placement. We recorded the shrub or tree species supporting each nest (nest substrate), nest height above ground, and nest substrate height. Surveys and nest monitoring were conducted under USFWS section 10(a)(1)(A) permits (TE-117947; TE-122632).

Brown-headed Cowbird management

Cowbirds were trapped at the Otay Ranch Preserve from 2012–2014. One to two traps were established, baited with live cowbirds, and checked daily from early April to early July. No funding was available for cowbird removals from 2015–2017 and 2020–2021. Targeted mist-netting for cowbirds occurred in 2018–2019 and 2022–2023. Mist net stations were established at two locations in the study area, and mist-netting occurred on a bi-weekly basis from April-June. Two female and one male decoy mounted cowbirds were placed on artificial perches in front of the net, and continuous vocalizations of both sexes were played through a remote speaker placed under the net. Nets were monitored continuously, and captured females were humanely removed while males were banded and released.

Statistical analysis

Chi-square analyses were used to test for associations between brood parasitism and nest habitat (river channel versus upland terrace), cowbird removals (years with cowbird removals, years without cowbird removals), and nest substrate. We also examined the association between brood parasitism and nest habitat during years with and without cowbird removals using two 2x2 contingency tables. Each nest was considered independent because territories were large and heterogeneous. We excluded nests that were not completed. Small sample sizes prevented us from evaluating all nest substrate species individually; therefore, we performed a chi-square analysis using the three most frequently used plants (laurel sumac, mule fat, and tamarisk) and combined the remaining plants into one group.

To evaluate the effects of cowbird management on Least Bell's Vireos, we conducted a chi-square analysis to examine the association between nest success and nest habitat (river channel versus upland terrace). Nests that had cowbird eggs removed and were ultimately successful were considered "rescued nests" and classified as failed nests, as these would have failed without intervention (Ferree 2002).

We used logistic regression to evaluate the effects of lay date, nest habitat, and cowbird removals on the probability of brood parasitism of Least Bell's Vireo. Variables significant in chi-square analyses were included. The response variable was binomial: parasitized nests were classified as "1" and unparasitized as "0". Lay date (day of the first egg laid in each nest) was treated as a continuous variable expressed in day-of-year format, while nest habitat and cowbird removals (years with cowbird removals, years without cowbird removals) were categorical variables. Models were compared using Akaike's Information Criterion adjusted for sample sizes (AICc) and model weight (w_i) representing evidence in support of a particular model (Burnham and Anderson 2002). Five models were compared including (1) lay date only, (2) lay date and nest habitat, (3) lay date and cowbird removals, (4) lay date, nest habitat, and cowbird removals, and (5) an intercept-only model including only random effects, i.e., brood parasitism is independent of lay date, nest habitat, or cowbird removals. Model(s) with delta AICc < 2 and highest weights were considered best-fitting to explain effects of an independent variable or combination of variables on the probability of parasitism. Analyses were performed in R v.4.3.1 (R Core Team 2022) using AICcmodavg (Mazerolle 2023) and ggplot2 (Wickham 2016).

Table 1. Results from chi-square analyses testing for the association between 1) parasitism of nests in the river channel versus upland terrace habitat, 2) parasitism of nests during years with and without cowbird removals, 3) parasitism of nests in the channel versus terrace during years without cowbird removals, and 4) parasitism of nests in the channel versus terrace during years with cowbird removals for Least Bell's Vireos (*Vireo bellii pusillus*) at Otay Ranch Preserve, California, USA, 2011–2023.

Chi-square analysis	Nest habitat	Cowbird removals	Total # parasitized nests	Total # nests	Parasitism rate (%)	χ^2	df	P
1	Channel	--	23	80	29	7.4	1	0.01
	Terrace	--	12	97	12			
2	--	No	25	71	35	17.8	1	< 0.001
	--	Yes	10	106	9			
3	Channel	No	16	34	47	4.0	1	0.05
	Terrace	No	9	37	24			
4	Channel	Yes	7	46	15	3.2	1	0.07
	Terrace	Yes	3	60	5			

RESULTS

We located and monitored 177 Least Bell's Vireo nests, of which 20% (35/177) were parasitized during 2011–2023. Three nests with unknown lay dates were excluded from logistic regression analysis, and one nest with an unknown fate was excluded from further analysis. Vireo lay dates ranged from 4 April and 7 July across all years, while cowbird lay dates ranged from 1 May and 6 July.

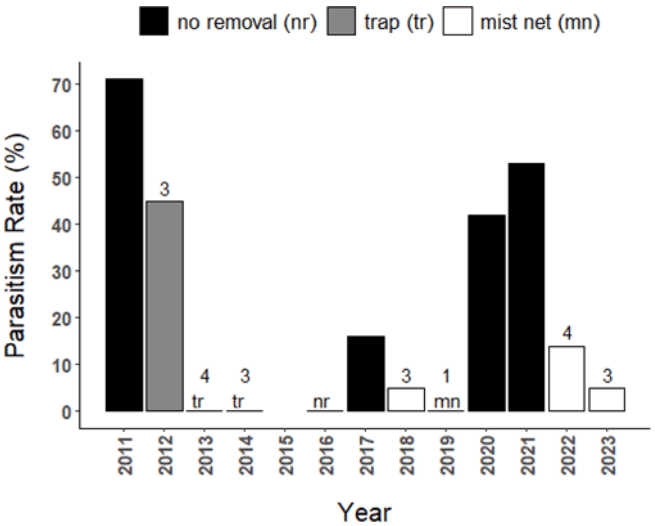
Least Bell's Vireos placed their nests in 11 different plant species in the study area. Laurel sumac was the most commonly used nest substrate, supporting 52% (92/177) of all nests. Mule fat accounted for 21%, tamarisk 7%, and the remaining eight plant species collectively supported less than 5% of the nests found over the study period. Nest substrate was not associated with parasitism (χ^2 = 2.8, df = 3, P = 0.43) and was excluded from further analysis.

The brood parasitism rate was strongly associated with nest location, with nests placed in the river channel suffering a higher parasitism rate than nests placed in the upland terrace (29% versus 12%; Table 1). The brood parasitism rate was also strongly affected by cowbird management activities (Table 1). Parasitism rates were higher in years without cowbird removals compared to years with cowbird removals (35% versus 9%). The difference in parasitism between river channel and upland terrace nests was more pronounced in years without cowbird removals; 47% of nests in the channel were parasitized compared to 24% in the terrace (Table 1). In years with cowbird removals (i.e., when fewer cowbirds were in the area) the difference between sites was less pronounced, but still suggestive that channel nests were parasitized at a higher rate than terrace nests (Table 1).

Differences in parasitism rates between river channel and upland terrace habitats also drove differences in nest success. Assuming parasitized and then rescued nests would have failed without intervention, only 29% (23/79) of channel nests were successful versus 48% [47/97] of terrace nests (χ^2 = 6.8, df = 1, P = 0.01).

We found that even removing small numbers of cowbirds from the study area had measurable impacts on parasitism rates (Fig. 1). For instance, removals of three females in 2018 and one female in 2019 maintained a parasitism rate of 5% in 2018 and 0% in 2019. Following two years without cowbird removals in 2020 and 2021, parasitism rates increased to 42% in 2020 and 53% in 2021. In 2022, four female cowbirds were removed and the rate dropped to 14%. Thus, in this system, the reproductive potential of 14–17 Least Bell's Vireo pairs can be strongly affected by only one to four female cowbirds inhabiting the area.

Fig. 1. Brown-headed Cowbird (*Molothrus ater*) brood parasitism rate of Least Bell's Vireo (*Vireo bellii pusillus*) nests by year over the course of the study period at Otay Preserve, California, USA. Rates varied widely each year and were affected by whether no cowbird removals occurred or whether cowbird trapping or targeted mist-netting was implemented. In years with a parasitism rate of 0%, the treatment type is represented by a two-letter code. Numbers above the bars indicate the total number of female cowbirds removed each year (1–4 females). Nest monitoring was not conducted in 2015.



Predation rates were higher in the river channel (35/69; 51%) than in the terrace (33/84; 39%), but this difference was not significant (χ^2 = 2.0, df = 1, P = 0.16).

The best model predicting cowbird brood parasitism included lay date, cowbird removals, and nest habitat, with a summed AICc weight of 0.95, indicating strong support for these effects (Table 2, Fig. 2). Confidence intervals for parameter estimates did not overlap zero, thus providing additional evidence of the strength

Table 2. Rankings of models from logistic regression analysis by AICc predicting Brown-headed Cowbird (*Molothrus ater*) parasitism of Least Bell's Vireo (*Vireo bellii pusillus*) nests (n = 174) as a function of lay date, cowbird removals, and nest habitat at Otay Ranch Preserve, California, USA, 2011–2023.

Model	K[†]	AICc[‡]	ΔAICc[§]	Model likelihood	AICc weight	Log-likelihood[|]
Lay Date + Cowbird removals + Nest habitat	4	139.04	0.00	1.00	0.95	-65.40
Cowbird removals + Lay Date	3	144.93	5.89	0.05	0.05	-69.39
Nest habitat + Lay Date	3	152.94	13.90	0.00	0.00	-73.40
Lay Date	2	159.68	20.64	0.00	0.00	-77.80
Intercept-only	1	178.05	39.01	0.00	0.00	-88.01

[†] Number of parameters in the model.
[‡] Akaike's information criterion corrected for small sample sizes.
[§] Change in AICc value between other candidate models and the top model.
[|] Log-likelihood of each model if $\hat{c} = 1$ and parameters are estimated by maximum likelihood.

of these effects (Table 3). The probability of brood parasitism increased as the breeding season progressed; nests with earlier lay dates were less likely to be parasitized than nests that were initiated later in the breeding season (Fig. 2). Nests in the river channel were more likely to be parasitized than those in the upland terrace, with the difference more pronounced in years without cowbird removals. These results underscore the additive effect of nest habitat in predicting brood parasitism.

DISCUSSION

This study demonstrates that recovering populations of Least Bell's Vireos nesting outside of riparian habitats in adjacent upland scrub habitats, experience reduced cowbird parasitism rates and increased nest success at our study site. Brown-headed Cowbirds target riparian areas for nest searching in western North America (Farmer 1999, Tewksbury et al. 1999). Surrounding scrub habitats can exhibit varying levels of cowbird parasitism, but in Southern California are often characterized by low rates (Ellison 1999, Morrison and Bolger 2002). The ability of Least Bell's Vireo to successfully breed outside of high-target areas for cowbird egg-laying will greatly increase the possibility of successful recovery despite continued high cowbird numbers in the region.

Other advantages to nesting in upland terrace habitats may include altered nest predator communities. A primary nest predator in Southern California is the California kingsnake (*Lampropeltis californiae*; Clark 2009), which, while a habitat generalist, in arid regions of its range is typically found "especially near water" (Lemm 2006). The California kingsnake has long been recognized as an important predator of bird nests in riparian habitats in the region, including Least Bell's Vireos (Clark 2009, Patten and Bolger 2003, Pemberton and Carriger 1916). Morrison and Bolger (2002) reported that seven of ten documented nest predation events in their study in Southern California involved the California kingsnake. While we found higher rates of nest predation in the river channel (51%) versus the terrace (39%), this difference was not statistically significant. Furthermore, we did not identify the species of nest predators in either area. Further research into the effects of snake predation on vireo reproduction, and differences in predator communities between upland and riparian habitats in this region, is worthwhile (Weatherhead and Blouin-Demers 2004).

We also found that laurel sumac is an important shrub for nest placement, supporting 52% of nests. The size, branching pattern, and foliage density of this upland shrub resembles several willow species, which may make it attractive to nesting Least Bell's Vireos. This shrub has not previously been identified as an important nesting substrate for the vireo (e.g., Kus et al. 2022), and should be considered in restoration projects adjacent to riparian areas within its range, especially in more xeric sites that may be too dry for willows or other mesic species to persist. The dense foliage of this shrub may also confer some advantage against cowbird parasitism. Sharp and Kus (2006) found that Least Bell's Vireo nests with high vegetative cover values close to the nest suffered

Fig. 2. Predicted probability with 95% confidence intervals of Brown-headed Cowbird (*Molothrus ater*) parasitism of Least Bell's Vireo (*Vireo bellii pusillus*) as a function of lay date, cowbird removals, and nest habitat (river channel versus upland terrace) at Otay Ranch Preserve, California, USA, 2011–2023.

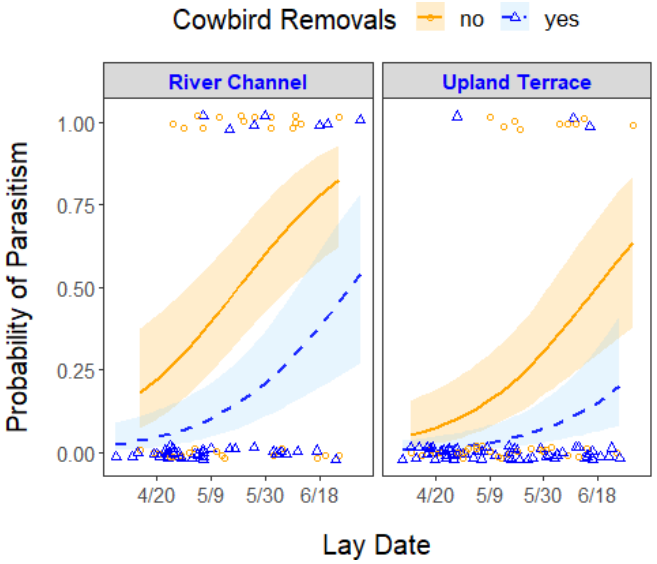


Table 3. Parameter estimates with standard error (SE) and 95% confidence intervals from the top-ranked model from logistic regression analysis predicting Brown-headed Cowbird (*Molothrus ater*) parasitism of Least Bell's Vireo (*Vireo bellii pusillus*) nests (n = 174) as a function of nest habitat, cowbird removals, and lay date at Otay Ranch Preserve, California, USA, 2011–2023.

Coefficients	Estimate	SE	95% LCL	95% UCL
Intercept	-5.88	1.53	-9.06	-3.00
Nest habitat	-1.24	0.45	-2.17	-0.37
Cowbird removals	-1.73	0.46	-2.68	-0.87
Lay date	0.04	0.01	0.02	0.06

lower parasitism rates than nests in more open situations. The upland terraces adjacent to the river channel in our study area often supported dense stands of laurel sumac up to four meters tall, and this high foliage density, combined with fewer tall perches than in the adjacent riparian, may allow vireos to hide their nests from cowbirds with greater success. Budnik et al. (2002) also found a relationship with increasing vegetation density around Bell's Vireo nests and decreasing brood parasitism by the cowbird in their Midwestern USA study site.

We found that Least Bell's Vireos initiate egg-laying as early as 25 days before Brown-headed Cowbirds in our study area (earliest dates: 4 April for vireos versus 1 May for cowbirds). This confers an advantage to early nesting vireos, and should an early nest be lost, pushes many second nest attempts into the period when cowbirds are actively laying. Therefore, early season nest predation events may be particularly costly for the vireo in the region, and hiding nests from predators becomes even more important. Further study on the suite of nest predators affecting the vireo, and the confounding effects of nest predation and brood parasitism, would be informative.

In our study, low numbers of cowbirds still had profound effects on vireo reproduction rates. This cautions against using cowbird density estimates, such as point counts or other methods, as proxies for determining parasitism threats to species of conservation concern. The relationship between overall cowbird numbers at a site and brood parasitism rates of particular species is very likely confounded by a number of factors, including host vulnerability to parasitism, vegetation density, and availability of alternate hosts (e.g., Averill-Murray et al. 1999, Budnik et al. 2002, Campomizzi et al. 2013, Sharp and Kus 2006). Therefore, we recommend that brood parasitism rates be directly measured for species of conservation concern, rather than using cowbird densities as a proxy.

We also found that cowbird parasitism rates rose and fell dramatically depending on whether cowbird removals occurred, and despite the small numbers of female cowbirds removed from the area (1–4 females per year). Other studies have found variable lag effects of cowbird control, likely related to the total cowbird population in the area and the population size of available hosts (Parker et al. 2022). Our results demonstrate that modest-sized vireo populations are highly susceptible to reduced productivity with even small numbers of cowbirds in the area.

This study also demonstrates the value of even periodic cowbird removals in reducing parasitism rates for the vireo. The uneven funding available for management, not unusual in many managed natural preserves, allowed for comparisons between years without cowbird management and years when cowbird removals were conducted. In our study, parasitism rates were maintained at low levels in years of cowbird management. As Brown-headed Cowbirds parasitize a wide range of host species (Lowther 2020), targeted management to benefit the vireo provides ancillary benefit to a variety of other species nesting in the study area (e.g., Yellow Warbler [*Setophaga petechia*] and Yellow-breasted Chat [*Icteria virens*] both California Bird Species of Special Concern [Shuford and Gardali 2008], and the federally listed California Gnatcatcher [*Polioptila californica*]).

Development patterns in Southern California have led to the channelization of riparian systems, with adjacent upland vegetation removed for urban uses. This has removed the upland habitat available for breeding and foraging for species that benefit from these habitats. Conservation of upland transitional habitats adjacent to riparian zones would provide expanded nesting areas for recovering populations of Least Bell's Vireo. A number of other rare and sensitive species in the region use both riparian and upland habitats at differing stages of their life cycle and would receive benefit from added efforts to conserve these habitats (e.g., western pond turtle [*Actinemys marmorata*], arroyo toad [*Anaxyrus californicus*], Yellow-breasted Chat).

Climate change is predicted to shift rainfall patterns in California, with increased heating potentially causing a drying out of the landscape resulting in reduced runoff and reduced riparian habitat (Kalansky et al. 2018, Thorne et al. 2016). Drought also delays nest initiation for many birds in the southwestern USA (McCreedy and van Riper 2015), which in the case of the vireo may cause more overlap with the laying period of the cowbird. Cowbird nest initiation may be more resistant to drought as they are often subsidized by anthropomorphic food sources (Lowther 2020). Therefore, a future drier climate may shorten the length of the earlier nesting period, reduce the frequency of nests, and ultimately result in a decline in vireo nesting productivity.

Conversely, the ability of Least Bell's Vireos to successfully reproduce in upland habitats presents a potential adaptation to a future drier landscape. Preserving connectivity between riparian systems and adjacent upland habitats will be crucial for riparian species to move and adapt to this rapidly changing environment.

Author Contributions:

Kevin Clark contributed to study conceptualization; field data collection; data curation; funding acquisition; writing of the original draft; and manuscript review and editing. Kimberly Ferree contributed to study conceptualization; field data collection; data curation; formal analysis; writing of the original draft; and manuscript review and editing.

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