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COMMON YELLOWTHROAT BROOD PARASITISM AND NEST SUCCESS VARY WITH HOST DENSITY AND SITE CHARACTERISTICS

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Abstract. I found significant differences in the level of Brown-headed Cowbird (*Molothrus ater*) brood parasitism and nest success of Common Yellowthroats (*Geothlypis trichas*) nesting at different densities and in different habitats on the South Fork Kern River, CA. Of 149 active nests, 16% were parasitized in 1995 and 36% in 1996. Yellowthroats responded to parasitism with an increased rate of nest desertion. Parasitized clutches were significantly smaller and produced significantly fewer fledglings, but the decrease in Mayfield nest success rate was not statistically significant. There were significant differences among sites in terms of parasitism rates, predation and Mayfield nest success. Nests in an extensive cattail marsh were rarely parasitized (4–5% of nests), experienced the lowest predation rates, and had the highest nest success. Common Yellowthroat density was significantly negatively correlated with parasitism. A forward step-wise logistic regression model developed without the marsh nests included four habitat variables. A higher level of parasitism was associated with nests built near smaller trees, and with three habitat measures in a 0.008 ha circle centered on the nest: fewer vegetation hits between 2 and 2.5 m and higher percent cover of cattails and willows.

Key Words: brood parasitism, Brown-headed Cowbird, Common Yellowthroat, *Geothlypis trichas, Moluthrus ater*, riparian habitat, riparian restoration.

The Common Yellowthroat (*Geothlypis trichas*) is one of the most widely distributed and locally abundant neotropical migrant passerines (Dunn and Garrett 1997). It is also a common host of the Brown-Headed Cowbird (*Molothrus ater*) across its range (Hofslund 1957, Brown 1994). Many other small-bodied open-cup nesters are experiencing population reductions that may be due in part to a significant reduction in nesting success associated with increases in brood parasitism by the cowbird (Laymon 1987, Marvil and Cruz 1989, Böhning-Gaese et al. 1993). Some species are particularly vulnerable and rarely fledge their own young from parasitized nests (Marvil and Cruz 1989, Harris 1991). The effects of parasitism on the Common Yellowthroat are largely unknown. One subspecies, *G. t. sinuosa,* of northern California, is experiencing a decline in population size in large part due to habitat destruction, but possibly also due to brood parasitism (Hobson et al. 1985).

One objective of this study was to describe the impact of brood parasitism on the nesting success of the Common Yellowthroat. Parasitism may trigger several responses in a host, including nest desertion, burial of eggs in nest material, egg ejection, or acceptance (Clark and Robertson 1981). If an egg is accepted, there may be a reduction in the number of host young fledging due to a reduction in clutch size (Sealy 1992), further partial predation of host eggs or of young (Arcese et al. 1996), or loss of nestlings due to starvation (Marvil and Cruz 1989). I compared the occurrence of these effects in parasitized nests with that in unparasitized nests.

A second objective concerns the examination of patterns of parasitism in yellowthroats at the landscape level. Yellowthroats breed in a wide range of marsh, riparian, and adjacent upland habitats. In this study, I compared parasitism rates and nesting success of a population found in a natural riparian area, two nearby riparian restoration sites, and a marsh.

Several hypotheses have been proposed to explain the differences in brood parasitism among habitat types or sites. I will test whether parasitism rates vary among sites due to (1) differences in cowbird density, (2) differences in host density, and (3) differences in habitat structural characteristics at the scale of the nest or of the site (Clark and Robertson 1979, Larison 1996; Barber and Martin 1997; Larison et al. 1998; G. Guepel and N. Nur, unpubl. data; S. Rothstein, unpubl. data).

STUDY SITE

The study site is located within the South Fork Kern River Preserve, in Kern Co., California, at an elevation of approximately 800 m. The preserve was purchased and restored by The Nature Conservancy and is now being managed by the Audubon Society.

Five adjacent but distinct natural forest and restoration sites were studied (Fig. 1). Riverbottom site was a mature, natural cottonwood-willow riparian forest (dominants *Populus fremontii* and *Salix laevigata*), with many trees over 100 years old. Grazing occurred here historically, but is no longer permitted. Understory dominants included mulefat (*Baccharis salicifolia*), sting-

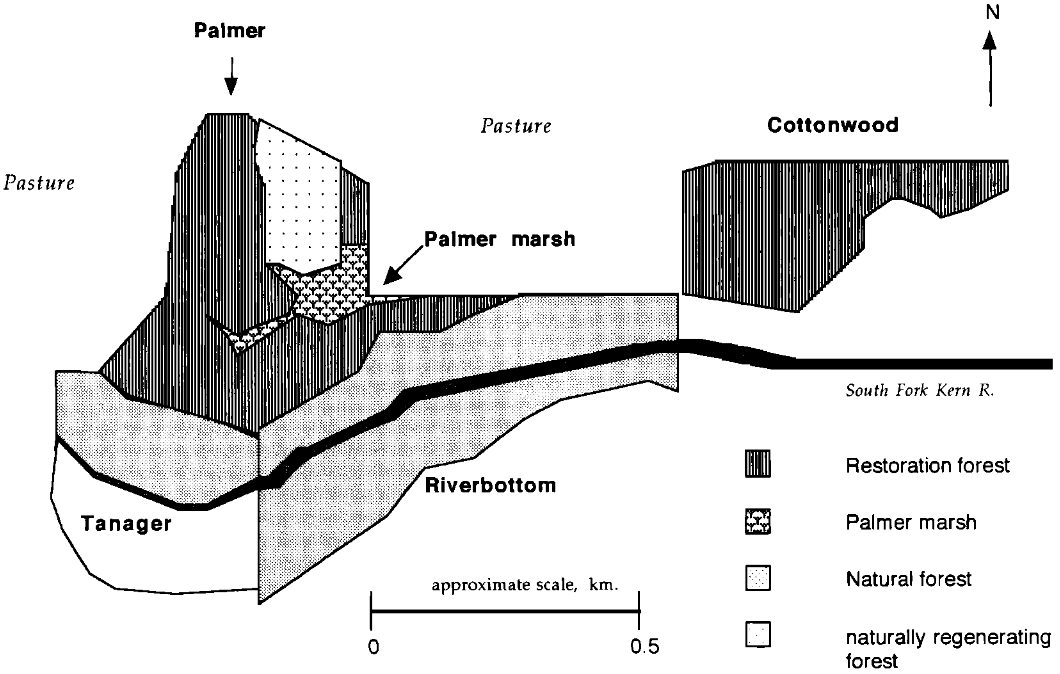

FIGURE 1. South Fork Kern River Preserve study sites, 1995–1996.

ing nettle (*Urtica dioica holosericea*), goldenrod (*Solidago spectabilis*), and patches of cattails (*Typha angustifolia*) and tules (*Scirpus acutus*). Approximately 4 ha of the site were surveyed in 1995 and 20 ha in 1996. Yellowthroats were found in cattail marsh, near the forest edge, in open areas, and in mulefat patches, but were uncommon overall in the mature forest. Other potential cowbird hosts on Riverbottom included Song Sparrow (*Melospiza melodia*), Red-winged Blackbird (*Agelaius phoeniceus*), Yellow Warbler (*Dendroica petechia*), Willow Flycatcher (*Empidonax traillii*), Lazuli Bunting (*Passerina amoena*), Blue Grosbeak (*Guiraca caerulea*), and Yellow-breasted Chat (*Icteria virens*). The most abundant host species on Riverbottom was Song Sparrow. During the study the average density of all potential cowbird hosts was 9.3 pairs per ha.

In 1996, approximately 7 ha of Tanager natural forest site were surveyed. The habitat consisted of mature cottonwood-willow forest interspersed with small patches of cattail and tule marsh. The vegetation was similar to Riverbottom, but with a wider strip of young trees on the forest edge and a more open understory due to winter cattle grazing. Yellowthroats nested in cattail marsh, near the forest edge, in open areas, and in mulefat patches, but were uncommon overall in the mature forest, as on Riverbottom. Other potential cowbird hosts included Song Sparrow, Red-winged Blackbird, Yellow Warbler, Willow Flycatcher, Lazuli Bunting, Blue Grosbeak, and Yellow-breasted Chat. The most abundant host species on Tanager was Song Sparrow. During the study the average density of all potential cowbird hosts was 11.5 pairs per ha.

Palmer restoration site, previously an irrigated pasture, was planted with Fremont cottonwoods and red willows in 1990. Fourteen hectares were surveyed in both years of the study. Habitat consisted of young trees with an understory of alkali rye (*Leymus triticoides*) and various non-native forbs. A narrow, mature riparian strip remained along a seasonal irrigation channel. Other potential cowbird hosts included Song Sparrow, Red-winged Blackbird, Yellow Warbler, Lazuli Bunting, Blue Grosbeak and Yellow-breasted Chat. Common Yellowthroat, Red-winged Blackbird, and Song Sparrow were all common on Palmer. During the study, the average density of all potential cowbird hosts was 5.2 pairs per ha.

Palmer marsh is surrounded on two sides by the Palmer restoration site and is fed by an adjacent irrigated pasture drainage. The entire 2 ha area was surveyed both years, with the exception of the center of the marsh, which was inaccessible due to high cattail density. The vegetation consisted primarily of cattails interspersed with rush (*Juncus* spp), sedge (*Carex* spp., *Eleocharis* spp.), and alkali rye in the drier patches. This marsh had the highest density of yellowthroats in both years of the study. The Red-winged Blackbird was the most common species in the marsh, while the yellowthroat was the next most abundant. The Song Sparrow was the only other potential cowbird host in the marsh, but was uncommon. During the study, the average density of all potential cowbird hosts (including red-wings) was 40 pairs per ha.

Cottonwood restoration site consisted of an overstory of cottonwood and willow planted in 1991. Prior to restoration it was irrigated pasture, and a thick understory of non-native forbs (e.g., *Lactuca* and *Cirsium* spp.) and grass (e.g., *Hordeum* spp.) remained in areas where canopy closure was not yet complete. There was no open water or marsh on the site. Approximately 12 hectares were surveyed both years. Here the Common Yellowthroat was the second most common species following the Song Sparrow. Other potential cowbird hosts included Red-winged Blackbird, Yellow Warbler, Lazuli Bunting, Blue Grosbeak and Yellow-breasted Chat. During the study the average density of all potential cowbird hosts was 5.9 pairs per ha.

METHODS

Common Yellowthroats were mist-netted and banded with USFWS numbered bands and a unique combination of three color-bands. Standard morphological measurements were taken (Ralph et al. 1993, Pyle et al. 1987). Locations of all yellowthroats seen or heard within the study sites were recorded in order to locate and track territories. Densities were based on independent spot-mapping efforts in May and June (IBCC 1970, Laymon et al. 1996, 1997). Locations were estimated with the aid of a permanent grid of 3-m tall white posts spaced 50 m apart.

An index of cowbird abundance was made using spot-mapping data (Laymon et al. 1997). Any data on cowbird population size taken over an extended time period would be imprecise because the population was always in flux due to trapping. However, here the spot-mapping data were treated as an index of habitat suitability and habitat use, although only for singing males.

Nests were located by observing pair behavior. Once a nest was located, its contents were monitored every 1–3 days. Nestlings were given USFWS numbered bands and a single color-band, and measured at approximately day 6. After the seventh day, we avoided approaching nests to minimize premature fledging (Hofslund 1959, Martin and Geupel 1993). We assumed a nest was successful if it contained at least one yellowthroat nestling at the last visit on or after day 7. If we visited the nest again between day 10 and day 14, and it was empty and damaged and we could not detect adults or young within 20 m of the nest, we assumed the nest had failed.

We manipulated some parasitized broods and did not include them in most analyses. Cowbird eggs in approximately half of the parasitized broods found during incubation were shaken or pierced to prevent hatching. These nests were included in prehatch calculations but were not included in any post-hatch calculations of nest success, fledglings per nest, brood size reduction, or predation. Cowbird eggs were allowed to hatch only in nests selected for a study of nestling growth rates (H. Spautz, unpubl. data). If a brood was parasitized, we usually removed the cowbird chick on the day the yellowthroat young were banded (approximately day 7). Because we did not observe parasitized broods for the entire nestling period, my success estimates of parasitized broods may be biased upward.

HABITAT MEASUREMENTS

Fifty-one habitat measurements were made at each nest. Each vegetation plot encompassed a 0.008 ha circle (radius 5 m) centered on the nest. Two 10-m long ropes were laid perpendicularly across the circle. To avoid bias on restoration plots, which were planted systematically in north-south rows, the direction in which the ropes were laid was varied by +5° for each subsequent plot measured. Most plots were measured in July or August, after yellowthroats had left their territories, to avoid disturbing a second nesting attempt. Nests were often built within 10 m of a previous attempt.

Nest measurements

The following measurements were made at each nest: (1) NESTHT: nest height; (2) PLSP: nest substrate species; (3) COVSP: nest cover species; (4) PLHT: height of nest plant; (5) percent concealment of a white disk placed in the nest, (a) CONAB: as viewed from directly above, at standing height, (b) CONST: as viewed 1 m away from a standing position, from each of the four directions (these figures were averaged), (c) CONLO: as viewed 0.5 m away from the ground, and from each of the four directions (these figures were averaged); (6) EDMIC: distance of the nest from the edge of the micropatch (the micropatch is the smallest area in the understory where a discontinuity between the nest plant and surrounding vegetation could be detected. If the nest was in a patch with structure distinctly different from the surrounding vegetation, the dimensions of that clump were used. If the nest plant was indistinguishable from the surrounding vegetation, as with most cattail marsh nests, the dimensions of the micropatch and macropatch were identical); (7) HTMIC: average height of the micropatch; (8) AREAMIC: area of the micropatch; (9) EDMAC: distance of the nest from the edge of the macropatch (the macropatch is the next larger area of structural discontinuity in which the micropatch was found); (10) HTMAC: average height of the macropatch; (11) AREAMAC: area of the macropatch.

Vegetation measurements

The following measurements were made within each nest-centered plot: (12) CANCLOS: percent canopy cover above the nest and 5 m from the center in each cardinal direction, using a monocular viewer engraved with a 10-square grid (Laymon 1988; these five values were averaged); (13) lateral foliage volume: the percentage of 50 squares at least one-half concealed on a 3 m high vertical cloth held 5 m from the nest, in each of the four cardinal directions, as viewed from the nest, (a) FOL1: between 0 and 1 m from the ground, (b) FOL2: between 1–2 m from ground, (c) FOL3: between 2–3 m from the ground (Noon 1981); (14) DNWV: distance from nest to the nearest tree or shrub; (15) SPNWV: species of nearest tree/shrub; (16) FOLNWV: foliage radius of nearest tree/shrub; (17) HTNWV: height of nearest tree/shrub; (18) DBHNWV: diameter at breast height of nearest tree/shrub estimated with a measure stick; (19) the percent cover of each of the following plant species or growth forms was estimated visually to the nearest 10%, and later categorized to one of 4 levels (0%, $0 \leq 10\%$, $10 < 50\%$, $\geq 50\%$); the species and percent cover of the two most common species of grass, annual forb and brush was also recorded: (a) TREE, (b) WILL: willow, (c) COTT: cottonwood, (d) GRASS, (e) FORB, (f) BRUSH: shrub (e.g., mulefat), (g) BARE: bare ground, (h) DEAD: dead forb, (i) CAT: cattail, (j) TULE; (20) HP0 to HP7: height profile, measured as the number of hits of vegetation (0 or 1) within 5 cm of a marked vertical pole, in each 0.5 m height category up to 3 m from the ground, each 1 m from 3 to 7 m, and 7 m and up; measured at the nest, and at 1 m intervals out from the nest in each of the four directions for a maximum number of hits of 21 per plot per unit height above the ground.

Other habitat measurements recorded for each plot included: (21) FORED: distance to closest forest edge (restoration or natural) or ecotone; (22) DISTWAT: distance to closest water when nest was active; (23) DISPAST: distance to closest pasture. When distances could not be measured in the field, estimates were made later using maps.

In addition, nests were classified as being in marsh habitat if they were built in marsh vegetation (e.g., cattails or tules) or above water. All others were considered upland nests.

DATA ANALYSIS

Nest success was calculated using a number of estimates including proportion of successful nests, number of fledglings per nest, and the Mayfield daily success rate (Mayfield 1961, 1975; Hensler and Nichols 1981). Mayfield values were compared with the Z test in Hensler (1985) on Excel 3.0.

Other tests included Pearson's χ^2, Fisher's exact P test, Spearman's rank correlation and Kruskal-Wallis one-way analysis of variance χ^2 (using H as an estimate of χ^2). Percentage data were arcsine transformed to approximate normality (Zar 1984). Distance data (e.g., distance to pasture) were log-transformed. Except where noted otherwise, analyses included data from only one randomly chosen nesting attempt per pair per year.

Univariate logistic regressions were performed using each habitat variable as the independent variable and presence or absence of parasitism as the dependent variable. No interaction variables were tested. A multivariate logistic regression model was then developed using a forward stepwise method. All variables with significant Wald's Z statistics (at the level of $P < 0.20$) in the univariate models were added sequentially beginning with the variable with the highest significance. A variable was then removed if its addition decreased the fit of the model (i.e., log-likelihood ratio and Pearson's χ^2 goodness of fit statistics), and if its Wald's Z statistic was not significant at $P < 0.05$ (Hosmer and Lemshow 1989). To verify the validity of the model, the process was repeated using a backward stepwise method, beginning with a model containing all variables with significant Wald's Z statistics (at $P < 0.20$) in the univariate models. Variables with the largest P-values were sequentially removed until those that remained were significant at $P < 0.05$ and the fit of the model was significant.

Analyses were performed with STATA release 5 (Stata Corporation 1997) or MINITAB release 8 (Minitab, Inc. 1991) for Macintosh.

RESULTS

EFFECTS OF PARASITISM

In 1995, 16% of all yellowthroat nests were parasitized. In 1996, in spite of increasing cowbird trapping efforts, the parasitism rate increased significantly to 36% ($\chi^2 = 7.42$, df = 1; $P = 0.006$). Although the parasitism rate was higher in 1996, the effects of parasitism were

TABLE 1. EFFECTS OF PARASITISM ON THE COMMON YELLOWTHROAT AT THE SOUTH FORK KERN RIVER STUDY SITE, 1995–1996

	Proportion unparasitized nests	N	Proportion parasitized nests	N	χ^2 (df = 1)	P
Behavioral response						
Nest deserted	0.03	102	0.12	42		0.041[a]
Eggs buried in bottom of nest	0	102	0	42	0	1.000
Reduction in clutch/brood size						
Eggs removed/partial predation clutch[b]	0.08	37	0.47	23	12.51	0.000
Host egg(s) remain unhatched	0.20	50	0.50	20	6.30	0.012
Nestlings lost/partial predation[c]	0.30	50	0.19	15	0.773	0.379
Loss of entire brood to predation	0.32	94	0.50	42	3.37	0.066

[a] Fisher's exact test.

[b] Nests found on or before 6th day of incubation.

[c] Nests found before day hatched; parasitized broods considered are only those in which a cowbird hatched.

generally not significantly different between years, so the years were pooled for all analyses, except where noted.

Yellowthroats deserted 12% of parasitized nests but only 3% of unparasitized nests, a significantly lower rate (Table 1). However, there was no evidence that this population of the species reacts to parasitism by burying cowbird eggs in the bottom of the nest as Yellow Warblers do (Clark and Robertson 1981).

Parasitism had a variety of other significant effects that contributed to an overall decrease in brood size (Table 1). Yellowthroat eggs vanished due to partial predation or removal by parents significantly more often from parasitized than unparasitized nests. The rate for parasitized nests is probably an underestimate, since it includes nests that were found up to the sixth day of incubation and some earlier removals may have been missed. Other studies indicate that cowbirds often remove a host egg for each egg laid (Sealy 1992). Significantly more yellowthroat eggs did not hatch in parasitized nests than in unparasitized nests (Table 1). Unhatched eggs were rarely removed during the nestling stage.

In only four nests (11% of parasitized nests) were cowbird eggs laid after incubation of the yellowthroat eggs had begun. None of these cowbird eggs hatched. Multiple parasitism was uncommon; only four nests were found with more than one cowbird egg or nestling.

The average size of unparasitized clutches was significantly larger in 1995 (4.0 eggs) than in 1996 (3.47; Wilcoxon rank-sum Z = 2.19. df = 33, P = 0.03). The average size of parasitized clutches was smaller in 1995 (2.8 eggs) than in 1996 (3.08), but the difference was not statistically significant (Z = 0.00, df = 18, P = 1.0). There was a large clutch reduction due to parasitism when years were considered separately, but the reduction was not statistically significant (1995: Z = 1.75, df = 20, P = 0.08; 1996: Z = 1.11, df = 30, P = 0.27). However, when years were pooled to increase the sample size, the reduction in clutch size from an average of 3.71 to 3.00 eggs per nest was significant (Z = 2.17, df = 57, P = 0.03).

After hatching, parasitized broods were no more likely to experience a reduction in size due to partial predation or nestling starvation than were unparasitized broods; in fact, fewer young disappeared from parasitized nests than from unparasitized nests (Table 1). This was unexpected. However, 50% of parasitized broods were entirely lost to predators, whereas only 32% of unparasitized broods were depredated, although the difference was marginally significant (Table 1).

All of these factors had the effect of reducing the average number of host young fledging from nests of parasitized broods. There were significantly fewer fledglings on average from successful unparasitized nests in 1996 (3.06 young) than in 1995 (3.59 young; Z = 2.285, df = 56, P = 0.022). However, there was no statistically significant difference between years for successful parasitized nests (1995: 1.67; 1996: 1.91; Z = 0.326, df = 12, P = 0.744). In 1995 an average of two fewer young fledged from parasitized broods than unparasitized broods, while in 1996 the average was only one fewer host young. In both years the reduction in the number of young fledging per successful nest due to parasitism was significant (1995: Z = 2.45, df = 20; P = 0.014; 1996: Z = 2.50, df = 40, P = 0.009).

In 1995, parasitized nests had a lower Mayfield nest success rate than unparasitized nests, but the difference was not statistically significant (Z = 1.764, df = 60, P = 0.083; Table 2). The difference in 1996 was less pronounced (Z = 1.090, df = 77, P = 0.278). The difference in success between years was low enough for un-

TABLE 2. SUCCESS OF PARASITIZED AND UNPARASITIZED COMMON YELLOWTHROAT NESTS AT THE SOUTH FORK KERN RIVER STUDY SITE, 1995–1996

		Pre-hatch daily nest survival rate[a]	N	Post-hatch daily nest survival rate[a]	N	Full nesting period success rate (SD)	N	Proportion of nests successful[c]	N
Unparasitized	1995	0.974	34	0.944	45	0.435 (0.087)	51	0.62	
	1996	0.963	36	0.960	39	0.422 (0.087)	49	0.69	
	pooled	0.968	70	0.949	84	0.423 (0.060)	100	0.65	106
Parasitized[b]	1995	0.939	9	0.875	5	0.143 (0.141)	11	0.40	
	1996	0.952	24	0.931	17	0.283 (0.094)	30	0.42	
	pooled	0.949	33	0.922	22	0.253 (0.079)	41	0.43	42

[a] Mayfield (1961, 1975); pre-hatch period: 14 days = laying (2 days) + incubation (12 days); post-hatch period: 8 days.

[b] Post-hatch includes only nests in which the cowbird hatched.

[c] Number of successful nests per all nests.

parasitized and for parasitized nests to warrant pooling across years (parasitized: Z = 0.015, df = 38, P = 0.988; unparasitized: Z = 0.103, df = 98, P = 0.917). However, when years were pooled, the difference was large but still not quite statistically significant (Z = 1.710, df = 139, P = 0.089).

Overall, failures of unparasitized nests were attributable to predation (81% of losses), abandonment (5%), and unknown factors (14%). Failures of parasitized nests were due to predation (65% of losses), loss of all host young (21%), and abandonment (13%).

HABITAT EFFECTS

In every measure of nest success, and in terms of predation and parasitism, Palmer marsh nests were always the most successful, while Cottonwood or natural forest nests were the least successful. The sites could be grouped and habitat compared in several different ways. For most analyses, sites were not grouped.

Palmer marsh had the highest Mayfield nest success rate for 1995 and 1996 pooled (Table 3). This was significantly higher than the success of restoration upland nests, including those on adjacent Palmer field (Z = 3.708, df = 110, P < 0.00). Palmer upland nests were more successful than Cottonwood nests although the difference was not statistically significant (Z = 1.022, df = 64, P = 0.311). Palmer marsh nests were also significantly more successful than those in the natural forest marsh areas (Z = 3.197, df = 41, P= 0.003). Although natural forest upland nests were slightly more successful than restoration upland nests, the difference was not significant (Z = 0.572, df = 81, P = 0.569). In the natural forest sites, upland nests were slightly more successful than marsh nests, although sample sizes were small and the difference was not significant (Z = 0.523, df = 26, P = 0.605). The difference in success between the two natural forest sites, Tanager and Riverbottom, was not statistically significant (Z = 0.752, df = 28, P = 0.458).

The differences in nest success measures between sites were due primarily to variations in parasitism and predation rates (Table 4). Parasitism rates in 1995 did not differ significantly between sites although there was a large difference between Palmer marsh and Riverbottom. In 1996, the contrast between sites was statistically significant, with Riverbottom's parasitism rate increasing to 69%. The difference in the para-

TABLE 3. COMMON YELLOWTHROAT NEST SUCCESS AT THE SOUTH FORK KERN RIVER STUDY SITE, 1995–1996

	Pre-hatch daily nest survival rate[a]	N	Post-hatch daily nest survival rate[a]	N	Mayfield full nesting period success rate (SD)	N	Proportion of nests successful[b]	N
Palmer Marsh	0.980	33	0.982	40	0.652 (0.095)	42	0.82	45
Restoration Upland-pooled	0.953	46	0.909	47	0.240 (0.059)	63	0.45	69
Palmer	0.961	19	0.929	22	0.317 (0.108)	28	0.55	19
Cottonwood	0.949	29	0.891	27	0.189 (0.064)	38	0.38	20
Natural Forest Marsh	0.952	10	0.906	8	0.229 (0.135)	12	0.50	14
Natural Forest Upland	0.950	11	0.956	13	0.339 (0.161)	16	0.60	20
Riverbottom	0.962	14	0.899	17	0.249 (0.114)	20	0.50	20
Tanager	0.938	8	1.00	6	0.411 (0.183)	10	0.60	13

[a] Mayfield (1961, 1975); pre-hatch period: 14 days = laying (2 days) + incubation (12 days); post-hatch period: 8 days.

[b] Number of successful nests per all nests.

TABLE 4. PARASITISM AND PREDATION OF COMMON YELLOWTHROAT NESTS ON THE SOUTH FORK KERN RIVER SITE, 1995–1996

	Parasitism rate[a] (N)		Predation rate[a] (N)		Predation rate of parasitized nests[a] (N)	
	1995	1996	1995	1996	Unparasitized	Parasitized
Palmer Marsh	0.05 (21)	0.04 (24)	0.14 (21)	0.08 (24)	0.12 (42)	0 (3)
Restoration Upland—Palmer	0.29 (14)	0.53 (15)	0.36 (14)	0.35 (15)	0.35 (17)	0.50 (12)
Restoration Upland—Cottonwood	0.15 (20)	0.40 (20)	0.47 (15)	0.60 (20)	0.48 (29)	0.45 (11)
Natural Forest—Riverbottom	0.25 (7)	0.69 (13)	0.43 (7)	0.46 (13)	0.33 (9)	0.54 (11)
Natural Forest—Tanager		0.38 (13)		0.15 (13)	0.25 (8)	0 (5)
Site Comparison	$\chi^2 = 2.52$ df = 3 P = 0.47	$\chi^2 = 19.46$ df = 4 P = 0.001	$\chi^2 = 3.51$ df = 3 P = 0.32	$\chi^2 = 16.98$ df = 4 P = 0.002	$\chi^2 = 9.2$ df = 4 P = 0.055	$\chi^2 = 5.43$ df = 3 P = 0.143
All sites pooled	0.16 (63)	0.36 (85)	0.29 (63)	0.33 (85)	0.32 (94)	0.50 (42)

[a] Based on proportion of all nests depredated or parasitized.

sitism rates between years was significant only for Riverbottom.

In 1995, the difference between sites in predation rates was not statistically significant (Table 4). In 1996, however, predation rates were lower in Palmer marsh and higher in Cottonwood and the difference between sites was statistically significant. Predation rates did not differ significantly between years for any site (Pearson's χ^2, df = 1, P > 0.05).

The predation rate of parasitized and unparasitized nests was compared on a site-by-site basis. For no site was there a consistent trend in the relationship between predation and parasitism (Table 4). When years were pooled there was no statistically significant difference between sites in terms of predation rate of parasitized nests ($\chi^2 = 5.43$, df = 3, P = 0.143). For unparasitized nests, the difference in predation rates across sites was almost statistically significant ($\chi^2 = 9.2$, df = 4, P = 0.055).

There was no statistically significant difference among sites in terms of fledglings per successful nest, either for parasitized or unparasitized nests (unparasitized: Kruskal-Wallis one-way ANOVA $\chi^2 = 2.03$, df = 4, P = 0.73; parasitized: Kruskal-Wallis one-way ANOVA $\chi^2 = 3.07$, df = 3, P = 0.38; there were no independent parasitized Palmer marsh nests in the sample).

TESTS OF HYPOTHESES EXPLAINING DIFFERENCES IN PARASITISM RATES

Brown-headed Cowbird density

This hypothesis predicts that there should be a higher rate of brood parasitism in areas where cowbirds are most abundant. In 1996 there were 5 datapoints while in 1995 there were only 4. Only 1996 data were used in a correlation of parasitism with cowbird density (and for the host density analysis below).

Cowbirds were most common on Tanager, which was approximately 1 km from the nearest trap (Table 5). The second highest cowbird density was in Palmer marsh, which is less than 1 km from a trap, but is adjacent to pasture. This is also the site with the lowest incidence of par-

TABLE 5. COMMON YELLOWTHROAT AND BROWN-HEADED COWBIRD DENSITY AT THE SOUTH FORK KERN RIVER SITE, 1995–1996

	Area 1996 (1995) (ha)	Common Yellowthroat density (pairs/ha)		Brown-headed Cowbird density (pairs/ha)		Ratio Yellowthroat : Cowbird	
		1995	1996	1995	1996	1995	1996
Palmer Marsh	2 (2)	10	10	0	0.25	very large	40.0
Restoration Upland—Palmer	14 (14)	1.7	1.7	0.14	0.21	12.1	8.1
Restoration Upland—Cottonwood	12 (12)	2.1	1.7	0.16	0.17	13.1	10.0
Natural Forest—Riverbottom	20 (4)	1.25	1	0.25	0.15	5.0	4.0
Natural Forest—Tanager	7	—	3	—	0.43	—	7.0

TABLE 6. LOGISTIC REGRESSION OF PROBABILITY OF PARASITISM ON NEST-SITE SCALE VEGETATION CHARACTERISTICS, COMMON YELLOWTHROAT, SOUTH FORK KERN RIVER, 1995–1996[a]

Habitat variable	Regression coefficient	Odds ratio	Wald's Z	P
Constant	0.743		1.153	0.249
Height of nearest tree or shrub	−0.232	0.792	−2.183	0.029
Measurements in 0.008 ha nest-centered plot				
number of vegetation hits 2 to 2.5 m. from ground	−0.230	0.794	−2.635	0.008
percent cover category—willows	0.751	2.120	2.750	0.006
percent cover category—cattails	1.085	2.96	2.604	0.009

Notes: Log-likelihood ratio $\chi^2 = 24.84$, df = 4, $P < 0.001$ (difference between model with and without vegetation variables). Fit: Pearsons $\chi^2 = 96.44$, df = 77, P = 0.066.

[a] Palmer marsh nests omitted

asitism. The correlation was negative, but not statistically significant (Spearman's rank correlation rho = −0.08, P = 0.10). G. Geupel and N. Nur (unpubl. data) also observed a significant negative relationship between the mean number of cowbirds detected from point counts and the incidence of parasitism in the Common Yellowthroat.

Host density

Host density was significantly negatively associated with parasitism rate (Spearman's rank correlation rho = − 0.97, P = 0.005; Table 5). Palmer marsh, which had the highest yellowthroat density, had the lowest parasitism rate. Riverbottom, which had the lowest yellowthroat density, had the highest parasitism rate.

Habitat characteristics

Habitat characteristics of parasitized nests were compared with those of unparasitized nests using univariate logistic regression. Because there were so few parasitized nests in Palmer marsh, the site "Palmer marsh" predicted the absence of parasitism perfectly. Variables with significant Wald's Z statistics ($P < 0.05$) in models including Palmer marsh nests included plant height (PLHT), species of nearest woody vegetation (SPNWV), distance to nearest woody vegetation (DNWV), height of nearest woody vegetation (HTNWV), foliage radius on nearest woody vegetation (FOLNWV), foliage density between 1–2 m (FOL2), height profile between 1–1.5 m (HP10), 1.5–2 m (HP15), and 2–2.5 m (HP20), percent cover of willows (WILL), percent cover *Juncus* (JUNC), percent cover annual forb (FORB), percent cover *Melilotus* spp. (MELO), percent cover mulefat (MULE), percent cover *Hordeum* (HOR), percent cover goldenrod (GOLD) and percent cover cattails (CAT). The analyses were then performed without Palmer marsh nest data. Significant univariate models then included the variables HTNWV, HP20, and MULE.

A final multivariate logistic model to predict parasitism based on habitat variables was developed without Palmer marsh nests (Table 6). The best fitting model contained four significant habitat variables. Coefficients associated with the height of the nearest tree or shrub (HTNWV) and the number of hits of vegetation from 2 to 2.5 m from the ground (HP20) were negative. Coefficients associated with the percent cover of willow (WILL) and cattails (CAT) were positive. This means that outside Palmer marsh, a higher rate of parasitism is associated with shorter trees close to the nest, sparser vegetation in the area around the nest between 2 and 2.5 m above the ground and a higher percent cover of cattails and willows.

DISCUSSION

It is important to note that Brown-headed Cowbirds are being trapped along the South Fork Kern River in an effort to encourage the recovery of a small population of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Whitfield and Enos 1996, Whitfield et al. *this volume*). Thus the brood parasitism patterns in this study may differ from patterns found in regions without artificial cowbird population regulation.

Hofslund (1957) found that 8% of parasitized Common Yellowthroat nests were deserted, but the rate for unparasitized nests was not given. Stewart's (1953) desertion rate was 18% overall. My data indicate that parasitism is associated with increased nest desertion rates, a common reaction to parasitism across species (e.g., Graham 1988). Sample sizes are small, however, and I have no data to indicate whether the trigger for desertion was the removal of a yellowthroat egg, the appearance of a foreign egg, a clutch size change, or disturbance by a cowbird at the nest (Hill and Sealy 1994). Most desertions were either early in the season, or involved experienced females (which I knew had bred the previous year). I found no evidence of cowbird egg burial in the 149 nests examined. Acceptance of cowbird eggs seems to be the most common reaction for the South Fork Kern River population

Clutch sizes were smaller in parasitized nests. In 1995, the reduction was approximately 1.2 eggs per nest. In 1996 however, the loss was less than 0.5 egg per nest when clutch sizes were smaller overall. This confirms that cowbirds do not always remove a host egg when they parasitize a brood (Hofslund 1957, Marvil and Cruz 1989, Sealy 1992).

In about half the parasitized nests studied, a yellowthroat egg disappeared during incubation, in addition to the egg often initially removed by a cowbird during laying. It is unknown whether these losses were due to further removal by cowbirds, by some other predator, or by the parent because they were damaged. Arcese et al. (1996) found a positive correlation between parasitism rates and rates of nest failures due to partial predation, but the success of parasitized broods was higher due to defense of laying areas by female cowbirds. On the Kern River, cowbirds are removed beginning in May (Whitfield et al. *this volume*), and this may cause a disruption in cowbird territorial defense. Thus rates of partial predation by cowbirds should theoretically be high in prime cowbird laying habitat as new females move into the area to replace those removed by trapping.

The significant reduction in the number of host young fledging from parasitized nests was expected. In both 1995 and 1996, there were approximately 1.5 fewer fledglings from successful parasitized broods than from unparasitized broods. In all cases in which a cowbird hatched, it hatched one day before the host young. In 12% of parasitized nests only a cowbird egg (3 nests) or young (2 nests) remained, due to removal of host eggs or young. The sample size is small, in part because I addled approximately half of the cowbird eggs I found, and these nests were not included in any post-hatch measures.

In terms of reduction in host productivity, brood parasitism appears to have a lower impact on Common Yellowthroats than it does on some other small hosts, e.g., vireos and flycatchers (Marvil and Cruz 1989, Briskie et al. 1990), but similar to the impact on some other warblers (Weatherhead 1989, Petit 1991). However, the average reduction in the number of fledglings by 1.5 probably has a significant impact on the population growth rate in areas with high parasitism rates (Trail and Baptista 1993). More information is needed on yellowthroat adult and juvenile mortality before the impact of parasitism on the population dynamics of the species can be fully understood.

The effect of parasitism on host fledging rates is not entirely conclusive due to the removal of cowbird nestlings by the seventh day. It is possible that a cowbird's impact on a yellowthroat nestmate is highest during the final days of the nestling period and that fewer host young fledge from parasitized nests than I have estimated. Cowbirds were allowed to fledge from only 2 nests studied, and all host young were assumed to have also fledged successfully from both.

Another factor that may contribute to the yellowthroat's ability to fledge its own young along with a cowbird is that the cowbird nestling period is longer than that of the yellowthroat. Cowbirds fledge at 10–11 days (Scott 1979) whereas yellowthroats fledge between 8–10 days (H. Spautz, pers. obs.). Assuming the cowbird hatches one day before the yellowthroats, the yellowthroat young may commonly fledge one day before the cowbird. In one nest that contained one cowbird and one yellowthroat, the yellowthroat did in fact fledge first. No other nests were observed often enough to witness this phenomenon. If yellowthroats are commonly able to fledge first, this opportunity to receive exclusive parental care from one parent may make a significant difference in their survivorship, and may lessen the impact of parasitism.

The effects of parasitism did not vary significantly across sites. The number of young fledging from parasitized nests was not significantly different among sites. Palmer marsh, which had the lowest rates of parasitism and predation, had no successful parasitized nests, and so was not included in the analysis.

I have offered several possible explanations for the large differences in parasitism rates between sites, in particular for the very low rate in Palmer marsh. In the marsh, the density of yellowthroats was highest, and nest-site characteristics were significantly different from other sites. I have shown that there was a strong negative correlation between yellowthroat density and parasitism. Two habitat factors associated with marsh nests (i.e., taller trees and more vegetation hits between 2 and 2.5 m) were associated with low rates of parasitism outside Palmer marsh. A high percent cover of cattails was also characteristic of Palmer marsh nests but was associated with higher parasitism rates outside the marsh. This latter point may indicate that cowbirds actually use this habitat characteristic as a cue, but that in a large contiguous marsh like Palmer, other factors may prevent or discourage parasitism.

If cowbirds parasitize yellowthroats less often in the marsh due to the higher population density, several explanations are possible. At high host densities, there may be a swamping effect

(S. Rothstein, unpubl. data; Freeman et al. 1990). In some other systems, parasitism rates are highest where densities of all potential hosts are highest (Barber and Martin 1997). Most first nesting attempts in Palmer marsh occurred within a two-week time span in 1996 (April 23 to May 5), and during a later three-week span on Cottonwood and Riverbottom (May 1 and May 21; H. Spautz, unpubl. data). The earliest first egg dates were in Palmer marsh because most of the first territories to be occupied when the first birds arrive in spring are there. The early nesting in Palmer marsh coincided with the start of Red-winged Blackbird nesting in 1995 and 1996. However, marsh pairs usually had two successful broods, and the second usually began after the red-wings had finished breeding. Second nests were not parasitized any more often than first attempts.

At higher densities, yellowthroats may be more likely to hear neighbors' warning calls when cowbirds are present, and they may be less likely to reveal nest locations. Notoriously well-concealed yellowthroat nests are difficult for humans to find in dense homogeneous cattail stands, although there is no evidence that cowbirds are deterred. This may also be an explanation for the reduced predation rate in the marsh. Red-winged Blackbirds densities are also higher in Palmer marsh than in any of the other sites. Clark and Robertson (1979) showed that Yellow Warbler parasitism rates are lowest in high density red-wing habitat. It is likely that the red-wings in the South Fork Kern River area offer the same benefits to yellowthroats. Although elsewhere red-wings are common cowbird hosts, no parasitized red-wing nests have been discovered in the study area either in marsh or sparsely populated upland habitat (S. Laymon, pers. comm.). Red-wing nests have not yet been systematically studied in the area but others in the Southwest have found that they are often not preferred hosts (S. Rothstein, pers. comm.). Thus cowbirds may be deterred from entering the marsh by blackbirds more than in other regions where blackbirds are preferred hosts.

The Song Sparrow is the most abundant species in most parts of the riparian forest along the river, and in restoration sites, and it is probably the most common and preferred cowbird host. Sparrow densities are lowest in Palmer marsh (Laymon et al. 1996, 1997). In 1996, 16% of Song Sparrow nests in Cottonwood and 15% in Riverbottom were parasitized (sparrows were not studied in Tanager or in Palmer marsh or upland areas; C. Strong, unpubl. data). These rates were lower than the rates I report here for yellowthroats during 1996. The highest parasitism rates I found were in Riverbottom and Cottonwood. The highest density of all potential cowbird host species combined (primarily the Song Sparrow) was 11.5 pairs per ha on Tanager and 9.3 pairs per ha on Riverbottom in 1996 (Laymon et al. 1996). Cottonwood's density was 5.9 pairs per ha. The densities were similar both years. A positive relationship between Song Sparrow density and parasitism rates for all hosts would be expected. Further study is needed to determine the relationship between parasitism and host density at the community level on the South Fork Kern River.

Another alternative explanation for differences in parasitism rates among sites is the habitat hypothesis. Some structural aspect(s) of dense cattail marshes may discourage parasitism. Nest height (Hahn and Hatfield 1995, Briskie et al. 1990), nest concealment, canopy cover, vegetation density (Larison 1996, 1997), and distance to forest edge (Gates and Gysel 1978) have been found (or predicted) to be related to high parasitism rates. Other studies have found no significant differences in habitat variables between parasitized and unparasitized nests (Barber and Martin 1997).

In this study, Palmer marsh nests, which were almost exclusively built in cattails, were parasitized so seldom that the dummy variable associated with the site predicted the absence of parasitism perfectly in a univariate logistic regression analysis. The multivariate logistic regression model developed without these marsh nests contains several non-intuitive relationships. The negative relationship between parasitism and vegetation hits in the 2 to 2.5 m height range is expected and echoes Larison's (1996, 1997) results. Since yellowthroat nests are usually built no higher than 0.5 m above the ground and are usually well-concealed, the cowbird search strategy probably works best in areas which are relatively open around the nest.

There was also a negative relationship between the height of the tree or shrub closest to the nest and the probability of parasitism. Smaller trees may provide more optimum perches for cowbirds. Nest plots with a higher percent cover of willows also had a higher predicted parasitism rate. The absence of willows or any other tree may make nest observation by cowbirds difficult (Freeman et al. 1990). The positive relationship between percent cover of cattails and the probability of parasitism was unexpected. This calls into question the hypothesis that cowbirds are deterred from parasitizing yellowthroat nests in the cattail marsh due to the structure of cattails alone. There were few very dense cattails stands in the natural forest, however. Most of the stands are small, sparse, and surrounded by or completely under the canopy of ancient trees. The nests found in most of these stands were often poorly concealed. That factor, combined with the abundance of other potential hosts and the fact that red-wing densities are very low in the natural forest, may combine to make yellowthroats in the smaller, natural marsh areas prime hosts.

The explanation for the low parasitism and predation rates on Palmer marsh nests is probably a combination of several factors. Habitat structural characteristics and high densities of both yellowthroats and Red-winged Blackbirds may deter cowbirds (and predators) from searching for yellowthroat nests. An ideal extension of this study would include samples of nests from other extensive cattail marshes in the area. It is unknown if the low parasitism rate found in Palmer marsh is characteristic of other marsh sites along the South Fork Kern River or in other parts of the Common Yellowthroat's range. If it is, my recommendations for cowbird management would include maintenance of larger tracts of marsh rather than small fragmented stands. The optimum habitat for Common Yellowthroats on the South Fork Kern River appears to be extensive freshwater marsh, rather than the natural mosaic of marsh and upland that is found now in the narrow riparian zone. Of the sites studied, Palmer marsh probably contains a source subpopulation. Free from brood parasites and predation, recruitment in Palmer marsh is very high. Most of the birds banded as nestlings in 1995 and 1996 and seen the following year were hatched in the Palmer marsh.

One goal of this study was to compare the breeding success of Common Yellowthroats nesting in riparian restoration areas with those using natural habitat. Densities in the natural forest were generally very low, and sample sizes small. I cannot generalize that yellowthroats nesting in restoration sites have a different rate of nest success than those in natural sites. The Mayfield success rate of nests in natural upland sites was higher than in restoration upland sites, but not significantly so. Natural forest nests were significantly less successful than Palmer marsh, which is not a natural site. It is surrounded by pasture and the small restoration trees of Palmer upland on three sides, and a naturally regenerating forest on the fourth. The highest parasitism rate for any of the sites I studied was in Riverbottom, a natural site. Thus, I cannot make a definitive statement at this time as to the relative quality of restoration sites vs. natural forest as Common Yellowthroat habitat.

A more complete understanding of any cowbird-host relationship requires a community-level perspective (Clark and Robertson 1979, Barber and Martin 1997). Common Yellowthroats and Song Sparrows are the most abundant cowbird hosts along the South Fork Kern River. Efforts to decrease parasitism pressure on the rarer and more vulnerable host, the Southwestern Willow Flycatcher (Whitfield et al. *this volume*), may become even more effective when the community level dynamics are more completely understood.

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