CHACE

THE FACTORS AFFECTING THE REPRODUCTIVE SUCCESS OF THE SOLITARY VIREO (*VIREO SOLITARIUS PLUMBEUS*) IN COLORADO

by

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The Factors Affecting the Reproductive Success of the Solitary Vireo (*Vireo solitarius plumbeus*) in Colorado.

Thesis directed by Associate Professor Ruth A. Bernstein

Solitary Vireos (*Vireo solitarius plumbeus*) nesting in the ponderosa pine (*Pinus ponderosa*) foothills west of the city of Boulder, Colorado have reduced reproductive success due to brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and nest predation. Solitary Vireos accept cowbird eggs, and 54.3% of their nests (n = 81) were parasitized. Parasitized nests had significantly lower hatching success and fledgling success than nonparasitized nests. Nests that were preyed upon (49.4%) resulted in total nest loss. The combined effect of parasitism and predation was found to have a strong negative effect on this population. Ultimately, few nests were successful, and evidence presented in this study supports Marvil and Cruz's (1989) hypothesis that this is a "sink" population that is only able to sustain itself with the immigration of vireos from other "source" populations.

Nest-site selection is crucial to avian reproductive success and Solitary Vireos choose specific locations for building their nests. Microhabitat (n = 9) and macrohabitat (n = 23) measurements of vegetation were taken at each vireo nest site (n = 81) and 15 randomly chosen sites. Univariate (Wilcoxon two-sample test) and multivariate (logistic regression and discriminant function analysis) tests were used to determine what aspects of the available environment vireos utilized for nest sites. Nest microclimate, food availability, predation, and cowbird parasitism appear to be important factors driving the selection of nest sites.

Solitary Vireos choose nest sites nonrandomly. Using 32 measurements of vegetation, six hypotheses were tested to determine the relationship between nest-site selection and parasitism and predation. Five of six hypotheses were rejected, and the edge-effect hypothesis was supported. Parasitized nests were significantly closer to edge habitat created by openings in the forest canopy, while depredated nests were significantly closer to roads and residential areas. Changes in forest landscapes due to increasing urbanization has been shown to have negative impacts on songbirds nesting in forest interiors. This study shows that species, such as the Solitary Vireo, which are nesting generalists with respect to fragmentation and often respond numerically in disturbed habitats, also are impacted by brood parasitism and nest predation in association with increasing urbanization of forested landscapes.

DEDICATION

This thesis is dedicated to my grandparents:
John Richmond Fales
and
Barbara Bolster Fales

For their love and generosity that enabled
me to begin this project.

And it is with great regret
that my grandfather will never know
that I have finished.

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SOLITARY VIREOS NESTING IN A FRAGMENTED LANDSCAPE: THE EFFECT OF BROOD PARASITISM AND NEST PREDATION ON POPULATION SIZE.

INTRODUCTION

Deforestation of tropical wintering grounds was previously believed to be the cause of declines in Neotropical migratory songbirds (Morse 1980, Terborgh 1980, Rappole and Morton 1985, Terborgh 1989). Loss of breeding ground habitat, fragmentation of habitat, and human-related disturbance are now thought to be equally detrimental to these populations (Morse 1980, Wilcove and Whitcomb 1983, Wilcove and Terborgh 1984, Hutto 1988, Askins et al. 1990, Finch 1991). This study describes and discusses the effects of predation and brood parasitism on the population dynamics of a migrant species breeding in a highly disturbed landscape.

Habitat loss by forest-breeding migrants has occurred in many areas, and has been mostly studied in the eastern U.S. The loss of habitat has reduced the nesting success and population sizes of some forest breeding migrants (Temple and Cary 1988). Where reforestation has reclaimed abandoned fields, population increases in forest breeding migrant species is further evidence for the impact of habitat loss (Sauer and Droege 1992). The important detrimental effect of habitat loss is habitat fragmentation, which decreases the patch size of intact forest and increases the ratio of edge-to-interior area. These edge effects reduce the reproductive success of forest-interior nesting migrants by increasing nest predation and brood parasitism (Brittingham and Temple 1983, Ambel and Temple 1983, Wilcove et al. 1986, Temple and Cary 1988, Yahner and Scott 1988, Robinson 1992). Gates and Gysel (1978) showed that nest predation and brood parasitism were higher in nests closer to the forest edge. Human-related disturbance in conjunction with forest fragmentation (e.g. fragmentation by roads and residential areas) increases rates of nest predation in smaller woodlots (Wilcove 1985).

Brown-headed Cowbirds (*Molothrus ater*) are brood parasites that have shown a recent range expansion with increasing forest fragmentation and livestock movement into forested areas (Mayfield 1965, Brittingham and Temple 1983, Rothstein et al. 1980, 1984). The frequency of cowbird parasitism has a strong, negative correlation with forest patch size in the midwest (Robinson 1992). Neotropical migrants typically accept cowbird eggs and are highly parasitized by cowbirds. Parasitism usually reduces host nest success as the parents usually raise only the large cowbird to the detriment of their own young (Friedmann 1963, et al. 1977, see Payne 1977). Elevated rates of cowbird parasitism and nest predation in fragmented and disturbed landscapes negatively impact the reproductive success and population dynamics of neotropical migrants breeding in temperate forests of North America.

The Solitary Vireo (*Vireo solitarius*) is a neotropical migrant that breeds in the temperate forests throughout North America (AOU 1983). A localized population (*V. s. plumbeus*) that breeds in the greenbelt surrounding the city of Boulder, Colorado, was studied by Marvil and Cruz (1989). This ponderosa pine forest is fragmented both by forest grassland openings and by openings due to human-related activities (e.g. trails, roads, residential areas). While frequency of predation has not been reported for this population, Marvil and Cruz (1989) determined that nearly 50% of the vireo nests were parasitized by Brown-headed Cowbirds, resulting in significantly reduced reproductive success. They speculated that this may be a "sink" population replaced by emigrants from some "source" population (Marvil and Cruz 1989).

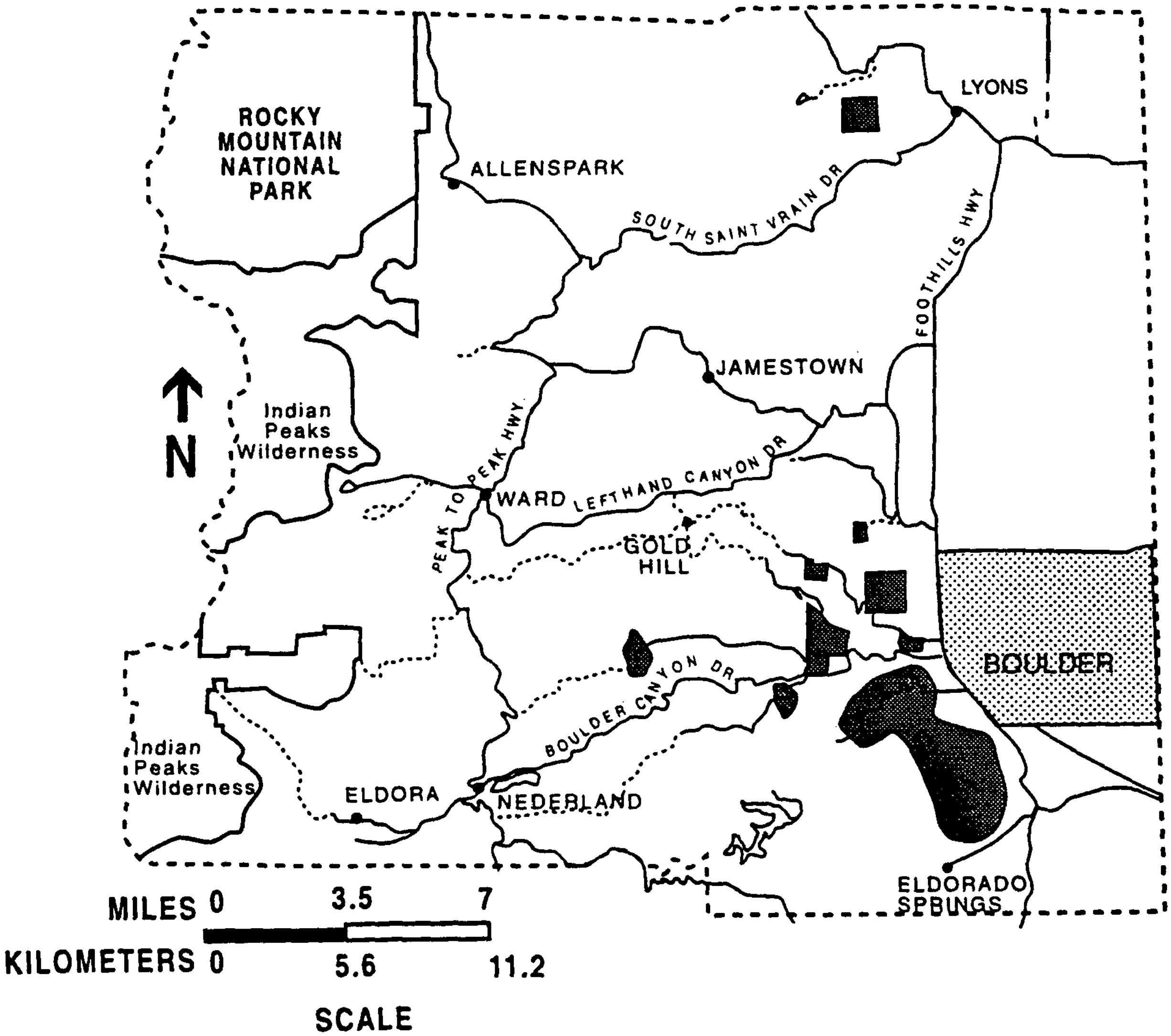
The purpose of this paper is to determine the frequency and impact of nest predation and brood parasitism in relation to the reproductive success of Solitary Vireos breeding in the foothills of Boulder, Colorado. The effects of parasitism and predation are estimated in relation to population dynamics, and the "sink" population hypothesis proposed by Marvil and Cruz (1989) is tested.

METHODS

This study was conducted during the summers of 1993 and 1994 in the foothills of central Boulder County, Colorado. Study sites were on City of Boulder Mountain Parks and Open Space, Boulder County Open Space, and Roosevelt National Forest; they ranged in elevation from 1,800 m to 2,400 m (Fig. 1). The vegetation of the field sites was dominated by an overstory of ponderosa pine (*Pinus ponderosa*) interspersed with Douglas fir (*Psuedotsuga menziesii*) (common and latin names after Weber 1990). The understory was dominated by chokecherry (*Prunus virginiana*), wax currant (*Ribes cereum*), skunkbrush (*Rhus aromatica*), small ninebark (*Physocarpus monogynus*), Oregon grape (*Mahonia repens*), and various grasses (*Agropyron, Anisantha, Bouteloua, Bromus,* and *Koeleria*).

Vireo nests were found during all stages of the nesting cycle and subsequently visited at least once every four days. Care was taken to minimize disturbance and attraction of nest predators to the nest site (Major 1990, MacIvor et al. 1990, Ralph et al. 1993). Only nests with vireo and/or cowbird eggs (active nests) were used in the analysis. The

Figure 1. Solitary Vireo study sites darkly stippled on map, Boulder County, Colorado.


ROCKY MOUNTAIN NATIONAL PARK
ALLENSPARK
LYONS
SOUTH SAINT VRAIN DR
FOOTHILLS HWY
JAMESTOWN
N
Indian Peaks Wilderness
WARD
LEFTHAND CANYON DR
PEAK TO PEAK HWY
GOLD HILL
BOULDER
BOULDER CANYON DR
Indian Peaks Wilderness
ELDORA
NEDERLAND
ELDORADO SPRINGS
MILES 0 3.5 7
KILOMETERS 0 5.6 11.2
SCALE

fate of each active nest was determined: parasitism, predation, fledging, abandonment. Nest appearance and disturbance characteristics were used to determine whether nests were preyed upon. Weight (nearest 0.1 g) was taken on 53 vireo nestlings and 9 cowbird nestlings with 30- and 50-g Pesola spring scales.

Growth rates were analyzed for 29 nestlings spanning all years of study. I used Ricklefs' (1967, also see Weatherhead 1989) method to fit logistic growth curves for each nestling based on ≥ three measurements per nestling and to calculate the rate constant (K) for each nestling's growth equation. No nestlings were chosen to represent parasitized vireos because none had > two measurements, and they all died. Nestlings chosen to represent nonparasitized vireos include 24 vireos that fledged from nine nests. Cowbirds chosen ($n = 5$) all fledged from separate nests. The rate constants were analyzed with the Student's *t*-test, and alpha was set at 0.05.

Only nests in which the final outcomes were known were included in the analysis. Nesting success was calculated using the Mayfield method (1975) to reduce the error introduced when nests observed for different lengths of time are treated equally. Alpha values for nonparametric univariate statistical analyses were set at 0.05. Wilcoxon two-sample and goodness-of-fit tests were used because most of the data were not normally distributed (Zar 1984).

RESULTS

During both field seasons 81 active Solitary Vireo nests were found. Brown-headed Cowbirds parasitized 44 (54.3%) nests and 40 (49.4%) nests were preyed upon. Frequencies of parasitism and predation were both independent of year, and therefore data for both years are combined (tables 1 and 2). Predation upon vireo nests was independent of parasitism; a nest that was parasitized did not have a greater likelihood of being preyed upon than a nonparasitized nest (Table 3).

The percentage of Solitary Vireo nests that were parasitized increased as the breeding season progressed (Fig. 2). Most cowbird eggs (67.2%, n = 61) were laid during vireo clutch initiation. Cowbird eggs hatched after about 11 days of incubation and fledged about 11 days later. Solitary Vireo eggs hatched after about 16 days of incubation and fledged about 14 days later. The majority of parasitized nests contained one cowbird egg (70.4%, n = 44), 10 nests (22.7%) contained two cowbird eggs, two nests (4.5%) contained three cowbird eggs, and one nest (2.3%) contained four cowbird eggs. Nest desertion was rare. The one deserted nest was parasitized prior to clutch initiation.

Clutch sizes of parasitized vireo nests were not significantly different from those of nonparasitized nests (Table 4). Egg removal by cowbirds was suspected in five cases where one host egg was missing following a parasitic event, and/or a broken egg was found near a parasitized nest. Parasitized nests had significantly lower hatching success, fledging success per egg, and fledglings per hatched egg than nonparasitized nests (Table 5). Nonparasitized nests fledged significantly more vireos per nest (1.51) than did parasitized nests (0.26) (Table 5).

Table 1. Frequency of cowbird parasitism on Solitary Vireo nests during years of study, Boulder County, Colorado.

	1993	1994	Total	%
Parasitized	21	23	44	54.3
Nonparasitized	25	12	37	45.7
Total Nests	46	35	81	

Parasitism is independent of year, $G = 3.2590$, $P > 0.05$.

Table 2. Predation on Solitary Vireo nests, Boulder County, Colorado, 1993-1994.

	1993	1994	Total	%
Preyed Upon	25	15	40	49.4
Not Preyed Upon	21	20	41	50.6
Total Nests	46	35	81	

Predation is independent of year, G = 1.0526, df = 1, $P > 0.25$.

Table 3. Predation on parasitized and nonparasitized Solitary Vireo nests, Boulder County, Colorado, 1993-1994.

	Parasitized	Nonparasitized	Total
Preyed Upon	21	19	40
Not Preyed Upon	23	18	41
Total	44	37	81

Predation upon Solitary Vireo nests is independent of parasitism, $G = 0.1056$, $df = 1$, $P > 0.75$.

Table 4. Clutch size of parasitized and nonparasitized Solitary Vireo nests, Boulder County, Colorado, 1993-1994.

	Clutch Size					
	1	2	3	4	5	Mean ± SE
Parasitized	0	5	15	23	1	3.45 ± 0.11
Nonparasitized	0	1	9	25	1	3.72 ± 0.10
Total	0	6	24	48	2	3.57 ± 0.07

Difference in mean clutch size between parasitized and nonparasitized nest is not significant (Wilcoxon two-sample test, $Z = 1.6291$, $P = 0.1033$).

Table 5. Reproductive success in nonparasitized and parasitized nests of Solitary Vireos, Boulder County, Colorado, 1993-1994.

	Vireo Nests			
	Nonparasitized	Parasitized	All	Cowbird
No. active nests	37	44	81	44
Total eggs	134	152	286	61
Total hatched	84	49	133	37
Total fledged	53	11	64	18
Hatching success (%)	62.7 a	32.2	46.5	60.7
Fledgling success (%)	39.5 b	7.2	22.4	29.5
Fledge/egg hatch (%)	63.1 c	22.4	48.1	48.6
Mean fledge/ active nest	1.51 d	0.26	0.82	0.41

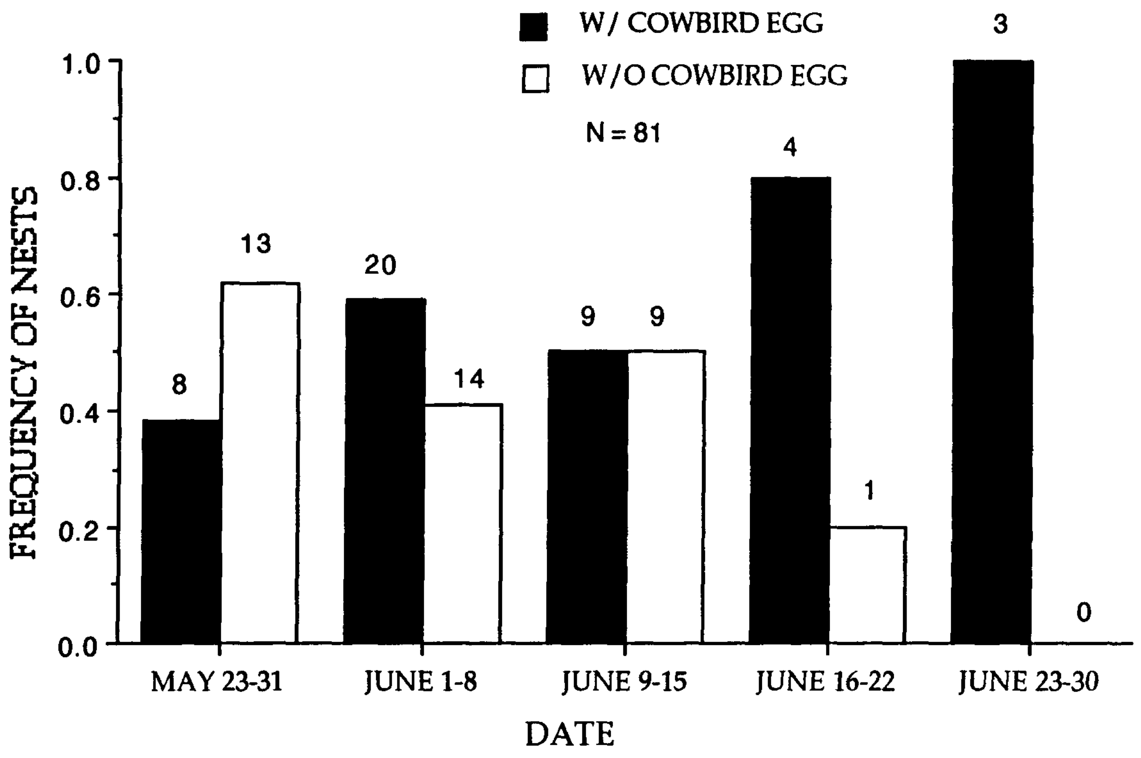
a Differences in hatching success between nonparasitized and parasitized nests are significant (G = 26.9319, df = 1, $P < 0.01$).

b Differences in fledgling success between nonparasitized and parasitized nests are significant (G = 45.2765, df = 1, $P < 0.01$).

c Differences in number fledged per egg hatched between nonparasitized and parasitized nests are significant (G = 21.3819, df = 1, $P < 0.01$).

d Differences in number fledged per active nest between nonparasitized and parasitized nests are significant (Wilcoxon two-sample test, Z = 3.4647, $P = 0.0005$).

Figure 2. Frequency of cowbird parasitism on Solitary Vireo nests by date of clutch initiation.

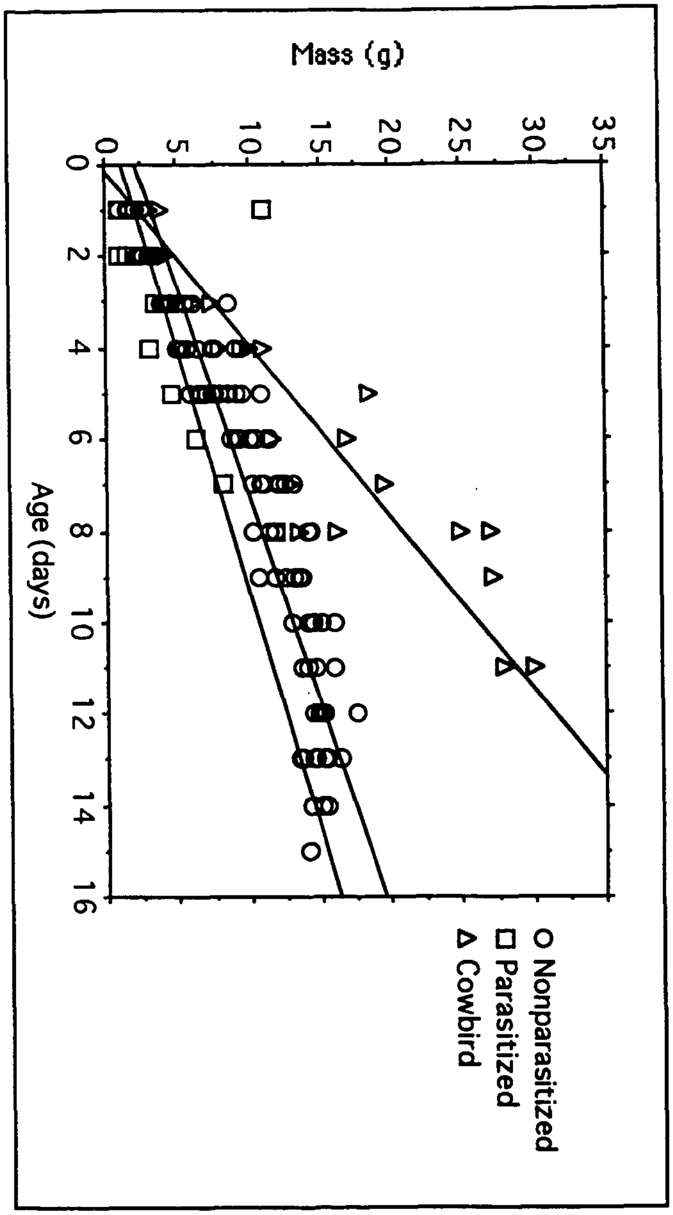

■ W/ COWBIRD EGG
□ W/O COWBIRD EGG
N = 81
FREQUENCY OF NESTS
1.0
0.8
0.6
0.4
0.2
0.0
8
13
20
14
9
9
4
1
3
0
MAY 23-31
JUNE 1-8
JUNE 9-15
JUNE 16-22
JUNE 23-30
DATE

Growth rates were analyzed for 24 vireo nestlings spanning all years of study. Development of vireo chicks in nonparasitized nests (n = 24, mean K ± SE, 0.288 ± 0.014) was significantly slower than cowbirds (n = 5, K = 0.497 ± 0.071, $t = 4.7563$, df = 27, $P < 0.001$). Differences in growth rate between vireos and cowbirds probably account for the lower fledging success of vireos in parasitized nests (Fig. 3). Cowbird-vireo competition for food provided by parents probably accounts for the differences in vireo mortality between parasitized nests (16 cases) and nonparasitized nests (zero cases). The presence of a Brown-headed Cowbird chick has a strong negative effect on the growth rate of Solitary Vireos.

The timing of cowbird parasitism greatly affected the reproductive success of the parasitized vireo nest. Parasitized nests in which cowbirds hatched two or more days ahead of the host young (n = 27) produced two fledging vireos and 16 fledging cowbirds. In nests where cowbirds were the same age or younger than vireos (n = six) no vireos and one cowbird fledged. In the latter case, success is nearly equal for cowbirds and vireos. Some cowbird eggs did not fledge because the eggs did not hatch (ten eggs), the eggs were laid too late (eight eggs), two cowbirds hatched and only one fledged (two eggs), or they were eaten by predators (23 eggs).

Nest predation reduced the reproductive success of 40 Solitary Vireo nests. In three cases, nests were partially preyed upon and two of these nests were ultimately successful in fledging at least one vireo. Potential nest predators include the Steller's Jays (*Cyanocitta stelleri*), American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*),

Figure 3. Growth rates (mass) for nestling Solitary Vireos in nonparasitized nests, parasitized nests, and for Brown-headed Cowbirds in Solitary Vireo nests. Regression of growth rates significant for each group. Nonparasitized vireos: $y = 1.087x + 2.115$, $R^2 = 0.871$, $F = 786.29$, $P = 0.0001$. Parasitized vireos: $y = 1.365x - 1.119$, $R^2 = 0.926$, $F = 125.725$, $P = 0.0001$. Brown-headed Cowbirds: $y = 2.66x - 0.478$, $R^2 = 0.868$, $F = 150.635$, $P = 0.0001$.


Mass (g)
0
5
10
15
20
25
30
35
Age (days)
0
2
4
6
8
10
12
14
16
○ Nonparasitized
□ Parasitized
△ Cowbird

Abert's squirrel (*Sciurus aberti*), least chipmunk, (*E. minimus*), Colorado chipmunk (*Eutamias quadrivittatus*), and the bull snake (*Pituophis melanoleucus*).

Nest success was not significantly different between years, therefore data for both years are combined (G= 0.1128, df =1, $P > 0.05$). The probability of a Solitary Vireo clutch surviving 28 days to fledge at least one young was 0.27, with egg success greater than nestling success (Table 6). Furthermore, parasitized nests have a significantly lower probability of success than nonparasitized nests (Table 6).

DISCUSSION

Solitary Vireos nesting in the ponderosa pine foothills along the Colorado Front Range in Boulder County in 1993 and 1994 had a relatively low probability of successfully fledging young due to nest parasitism and predation. Solitary Vireos had a 0.27 nest success probability (0.40 for nonparasitized, 0.17 for parasitized). This success is similar to other studies of parasitized host species. The probability of nest success for the Abert's Towhee was 0.31 when nonparasitized and 0.05 when parasitized (Finch 1983). The probability for the Eastern Phoebe was 0.43 to 0.61 for nonparasitized nests and 0.001 for parasitized nests (Klaas 1993). The probability of nest success for cardinals was 0.15, in a population where they were not parasitized (Filliater et al. 1994). Parasitized vireo nests have a higher probability of success than parasitized nests of other passerines. However, the success of parasitized vireo nests is significantly lower than that of nonparasitized nests. Predation on vireo nests usually results in complete brood loss. I conclude that nest predation and cowbird

Table 6. Mayfield's nesting success calculated for parasitized and nonparasitized Solitary Vireo nests, Boulder County, Colorado, 1993-1994.

	Probability of Survival		
	Egg Stage	Nestling Stage	Overall
Parasitized	0.48	0.21	0.17
Nonparasitized	0.66	0.59	0.40
Overall	0.55	0.43	0.27

Probabilities based on survival of at least one offspring for duration of 16 day incubation period and 14 day nestling period.

parasitism negatively impact the reproductive success of Solitary Vireos in Boulder County. Cowbird parasitism and nest predation are important components of Solitary Vireo population dynamics and deserve further discussion.

Cowbird Parasitism

Solitary Vireos accept cowbird eggs. Cowbird young in vireo nests reduce the reproductive success of vireos by: 1) reducing vireo clutch size, 2) reducing vireo hatching success when the cowbirds hatch earlier than vireos, and 3) outcompeting nestling vireos for food and space. Cowbirds often remove host eggs when parasitizing a nest (Sealy 1992). In the Solitary Vireo nests studied, parasitized nests had smaller clutches (0.27 fewer eggs) than nonparasitized nests and there was evidence of egg removal by cowbirds. These results indicate that female cowbirds remove host eggs from about 25% of the nests they parasitize.

Several hypotheses have been advanced to explain the removal of eggs by cowbirds. The behavior may be an attempt to deceive an egg-counting host into accepting the cowbird egg (Hamilton and Orians 1965). Cowbirds may eat the removed egg to gain supplemental calcium, which is needed given the large cowbird clutch size (Ankney and Scott 1980). Sealy (1992) showed that cowbirds often remove a host egg from Yellow Warbler (*Dendroica petechia*) nests before laying their own egg, possibly to synchronize egg-laying with early stages of host-clutch incubation (Livessey 1936, Sealy 1992). Removal of a host egg by cowbirds may reduce nestling competition (Blankespoor et al. 1982). Removal could enhance incubation efficiency if larger clutches have a higher probability of unhatched eggs (Davies and Brooke 1988). Finally, where a cowbird nestling is equivalent to more than one host nestling, it may advantageous for the cowbird to remove more than one host egg. Sealy (1992) determined that egg removal did not increase the acceptance of cowbird eggs in Yellow Warbler nests, and that warblers did not abandon nests when one or two eggs were removed. Despite these observations, it is still not clear why Brown-headed Cowbirds remove eggs from Solitary Vireo nests. However, a cowbird that ingested a host egg would gain nourishment.

Cowbirds have a shorter incubation period and hatch sooner than vireos when laid during vireo clutch initiation. Nests in which cowbirds lay eggs prior to clutch initiation are likely to be abandoned and go unstudied, and thus be underrepresented in the literature. Cowbirds grow faster and larger than vireo nestlings and outcompete their nestmates for food and space. Only 11 vireos fledged from 44 parasitized nests; of the 49 vireos that hatched, the remaining 38 died from nest predation or starvation. By the cowbird's fifth day after hatching, it usually fills the entire nest and completely covers vireo nestlings which, then, are unlikely to receive food from the adults (also see Friedmann 1963). Dead vireos found in parasitized nests were underweight for their age (Fig. 3), presumably from competition-induced starvation. When the cowbird fledges, usually before vireo nestmates, it disperses from the nest site by the second day. Usually both host parents follow the juvenile cowbird and leave any remaining vireo nestlings in the nest to starve (pers. obs.). Starvation was the primary cause of vireo nestling mortality in nests parasitized by cowbirds.

Cowbirds are successful in fledging their young in Solitary Vireo nests; nearly half the parasitized nests yielded a cowbird fledgling, whereas parasitized vireos are less successful in fledging their own young. Solitary Vireos are a good host species for Brown-headed Cowbirds in Boulder County. The nesting success of parasitized vireos is higher than other parasitized species--Abert's Towhee (Finch 1983), Eastern Phoebe (Klaas 1993), and Dickcissel (Zimmerman 1983) yet, given the mortality rates of first year passerines, parasitized nests probably do not act as net producers of young. Therefore, there must be strong selective pressure on Solitary Vireos to reduce cowbird parasitism. The question remains, why do Solitary Vireos accept cowbird eggs and raise cowbird young to the detriment of their own reproductive fitness?

Several hypotheses have been put forward to explain host acceptance of cowbird eggs. Rothstein (1975a, 1975b) speculated that hosts that have been long exposed to cowbird parasitism and do not reject cowbird eggs have not experienced the mutations necessary to evolve such a behavior. This idea is based on the observation that species exposed to cowbird eggs in their nest either completely reject or completely accept the egg; the lack of an intermediate response suggests that once the behavior has arisen, it quickly becomes fixed in the host population because of the great reproductive advantage of not being parasitized (Rothstein 1975b). Solitary Vireos in Boulder County occur within the former range of the Brown-headed Cowbird and most likely parasitism is not a novel phenomenon within this population. Therefore, according to the Rothstein hypothesis, vireos do not possess the genetic variability to evolve an anti-parasite behavior.

Alternatively, Rohwer and Spaw (1988) suggested that small hosts are unable to grasp and eject cowbird eggs, due to constraints of bill size, and do not puncture-eject the eggs because the hard shell of the cowbird egg would cause glancing blows that would damage the host's own eggs (Spaw and Rohwer 1987). Therefore, small hosts like the Solitary Vireo are forced to accept the cowbird egg, or abandon the nest and begin the entire reproductive cycle again. For the population described here the frequency of parasitism increases through the breeding season (Fig. 2), so that a renesting attempt is likely to be parasitized. Additionally, all parasitized nests did not fail completely and it is possible that the fledging of one young during one year and reserving energy for subsequent years outweighs the advantage of abandonment and the effort of renesting with each parasitic event. If the genetic information is available for the vireo to recognize the cowbird egg as foreign, then rejection may still not be feasible given the constraints of bill size.

Nest Predation

Nest predators eliminated approximately half the active vireo nests on the study sites. Similarily, Ricklefs (1969) estimated that predation accounted for 55% of egg losses and 66% of nestling losses of the six passerine species that he studied. Predation occurred on 20 (50%) of the vireo egg-stage nests and 20 (50%) of the vireo nestling-stage nests. Nest predation usually caused complete nest failure. If predation occurred early in the egg stage the adults built a new nest and initiated a new clutch. However, later nests had a greater chance of being parasitized (Fig. 2); the latest successful nest of the season was initiated on 15 June 1993 and 8 June 1994. Therefore, Solitary Vireos rarely had an opportunity to successfully raise a clutch after the nest was preyed upon.

Although the frequency of predation on Solitary Vireos in Boulder County is not different from other studies, the rate of parasitism coupled with predation had a dramatic effect on the reproductive success of Solitary Vireos in this area.

Sink Population

Marvil and Cruz (1989) proposed that the Solitary Vireo population in Boulder County was a population "sink" due to the number of reproductive failures caused by cowbird parasitism. Since predation is random with respect to parasitism and has the same impacts on both parasitized and nonparasitized nests, I calculated the maximum rate of parasitism that will allow a Solitary Vireo population to maintain the same population size from the equation

$$P_c = \{\lambda - [2\,\mu / (1 - \mu_o)]\} / (\lambda - \lambda')$$

(May and Robinson 1985, equation 4), where

λ = number of young fledged by nonparasitized female,
λ' = number of young fledged by parasitized female
μ = mortality rate of adult females, and
μ_o = mortality rate in the first year.

For the Solitary Vireos in Boulder County, the observed values for these variables are as follows: $\lambda = 1.51$ fledglings/year, $\lambda' = 0.26$ fledglings/year. I used known estimates of the adult mortality of nine warbler species (in Morse 1989), assuming that the mortality rate is the same among migratory insectivorous warblers and vireos: $\mu = 0.33$, and

I used known juvenile mortalities of Prairie Warblers (*Dendroica discolor*), again assuming a similar mortalities among migratory insectivorous warblers and vireos: $\mu_o = 0.67$ (Nolan 1978).

The value of P_c yielded by these calculations is -0.392. This value is negative because the annual mortality of females and juveniles ($[2\mu / (1 - \mu_o)]$), as estimated from other species, is greater than the number of young fledged per nonparasitized female (λ). This suggests that the present rate of brood parasitism strongly decreases the vireo population over time. The strong negative rate also suggests that predation and/or some other mortality factor has a large impact on the population because of the low number of young fledged per nonparasitized female.

Since this equation was developed for parasitism independent of other events inducing nest mortality, P_c was recalculated using only vireo nests that were not preyed upon. Nonparasitized-nondepredated nests (n = 18) fledged 3.17 vireos/nest and parasitized-nondepredated nests (n = 23) fledged 0.48 vireos/nest. The recalculation of these variables are $\lambda = 3.17$ fledglings/year and $\lambda' = 0.48$ fledglings/year, yielded a P_c of 0.435. The recalculated critical level of parasitism is lower than the observed frequency of parasitism. This suggests that when predation is removed, the Solitary Vireo population size is declining due to the can be high frequency of parasitism. As the frequency of nest predation approaches 50% the population becomes severely impacted as the number of young fledged/nest is reduced by half.

Since the critical level parasitism is largely determined by the mortailites of adults and juveniles, I determined the mortaility rate when P_c was held constant at the observed 0.543. The mortality equation ($[2\ \mu\ /\ (1 - \mu_o)]$) equals 0.83 when $\lambda = 1.51$ fledglings/year and $\lambda' = 0.26$ fledglings/year. I estimated that the adult mortality is approximately 0.10, and the juvenile mortality is 0.50, which is very different than what was extrapolated from Nolan (1978), Morse (1989), and from a breeding population of White-crowned Sparrows (*Zonotrichia leucophrys*) in California (Trail and Baptista 1993). Thus, the estimated vireo mortaility are unreasonable. This suggests that, given the levels of predation and parasitism, this population of Solitary Vireos is unable to maintain its size without emigration of individuals from some area that acts as a "source" production of young.

To further test Marvil and Cruz's (1989) population "sink" hypothesis, I constructed a vireo life history table to determine the intrinsic rate of increase (r) in the absence of parasitism. Using only nonparasitized nests, and assuming the previously mentioned mortality estimates and a fecundity of 0.75, the intrinsic rate of increase is -0.143 (Table 7). Since the life history table is dependedent on estimations of surviviorship of adults and juveniles to determine the intrisic rate of increase, I estimated the survioship when $r = 0$ in the absence of parasitism. I determined that $r = 0.04$ when surviorship of adults is 0.75 ($\mu = 0.25$) and of juveniles is 0.45 ($\mu_o = 0.55$). The estimation of juvenile surviorship is probably unrealistic. This suggests that even in the absence of parasitism the population is declining.

To further test the population "sink" hypothesis (Marvil and Cruz 1989), I used iterative means to project population growth, assuming: the above estimates of mortality, average fledglings/nest = 0.82 (Table 5), complete recruitment of females back into the population, and zero emigration. The calculated population growth of the Solitary Vireo population (n = 50 at time t) is strongly negative and the population number is reduced by half in 11 years, and is reduced to < 15 females in 20 years (Fig. 4). This shows that the net production of vireos is negative given mortality estimates. This supports the hypothesis that the population size of Solitary Vireos in Boulder County relies on emigration from other "source" areas which probably have a positive net production of young. While this is a hypothetical curve it demonstrates the strong negative impact that cowbird parasitism and nest predation can have on a neotropical migratory songbird population. Marvil and Cruz (1989) correctly proposed a population"sink" explanation for the population of Solitary Vireos in Boulder County, Colorado.

Given the frequency of nest predation and parasitism the Solitary Vireo population in Boulder County is a "sink" population which is unable to reproduce itself. The population is maintained as a vireo breeding site only because a "source" population, with lower rates of predation and parasitism, that has a high net production of young each year provides regular immigrants that breed in Boulder County. The source population of this subspecies (*S. v. plumbeus*) is probably located in a region with low frequencies of cowbird parasitism and nest predation. Such a location probably does not occur along the Colorado Front Range which is highly urbanized and within the range of the Brown-headed Cowbird. Females from the source population

Table 7. Solitary Vireo life history table for nonparasitized females. Assumptions: 1.51 fledglings/female, survivorship of adults = 0.67, survivorship of juveniles = 0.33.

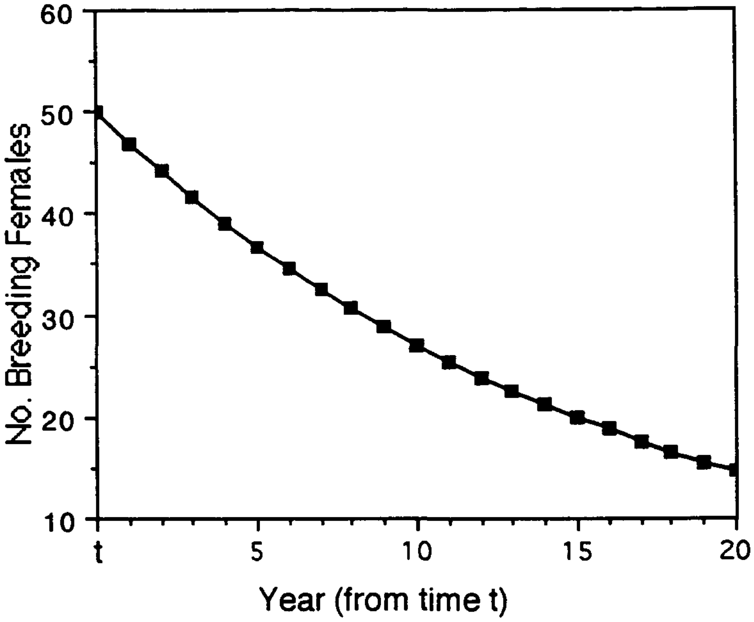
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	0	0	0
1	0.33	0.75	0.25	0.25
2	0.22	0.75	0.17	0.34
3	0.15	0.75	0.11	0.33
4	0.10	0.75	0.08	0.32
5	0.07	0.75	0.05	0.25
6	0.05	0.75	0.04	0.24

$R_o = 0.70$

generation time (T) = 2.5

intrinsic rate of population increase (r) = -0.143

Figure 4. Projected population growth curve for the Solitary Vireos in Boulder County, Colorado. Population size at time t is 50 females. The growth curve is a test of the population "sink" hypothesis in which there is no immigration or emigration, and there is complete recruitment of females back into the breeding population. The curve shows that the population is unable to maintain itself without immigration given set rates of mortality, cowbird parasitism, and nest predation.


60
50
40
30
20
10
No. Breeding Females
t
5
10
15
20
Year (from time t)

probably enter Boulder County in their first breeding season when migrating north from western Mexico in the spring.

Why is cowbird parasitism and nest predation on Solitary Vireos so high in Boulder County? The Solitary Vireo nests at low elevations in the ponderosa pine, which is in close proximity to cattle grazing on Open Space and to urbanized areas of the city of Boulder (pop. 83,312, 1990 census). Historically, Brown-headed Cowbirds have been known to be associated with bison and more recently with cattle (Mayfield 1965). Cattle grazing on Open Space may provide foraging places for cowbirds which then move to the ponderosa pine forests to search for nests (Rothstein et al. 1980, 1984). The large urban area of Boulder may provide year round foraging opportunities for corvids, which then are able to take advantage of nesting birds in the ponderosa pine forest as a food source during the breeding season.

Summary

Solitary Vireos nesting in the foothills west of Boulder, Colorado, have reduced reproductive success due to nest predation and cowbird parasitism. Frequencies of predation and parasitism are similar to those found in other migrant songbirds nesting in other regions. The difference is that the combined rates of predation and parasitism have a strong negative effect on this Solitary Vireo population. Cowbird parasitism results in almost complete nest failure for the hosts, while nearly half fledge cowbird young. Nests that are preyed upon result in total nest loss. The adults can renest, but ususally with limited success. Human-caused disturbance and fragmentation of the lower elevation ponderosa pine, where the vireos nest, may cause an increase in the frequency of parasitism and predation beyond which the population is able sustain itself. Ultimately, few nests are successful, and the population is only able to sustain itself with the immigration of vireos from other areas.

CHAPTER 2

NEST-SITE SELECTION BY SOLITARY VIREOS

INTRODUCTION

Nest-site selection is crucial to avian reproductive success, thus there is intense pressure to select an optimal nest site. Factors that determine the suitability of a particular site for laying eggs and raising nestlings include the microclimate (Calder 1973, Walsberg 1981, 1985), degree of exposure to nest predators (Nolan 1978, Best and Stauffer 1980, Murphy 1983, Peterson and Best 1985, Page et al. 1985, Marks 1986, Stauffer and Best 1986, Martin 1988, Martin and Roper 1988, Kelly 1993), and food availability (MacArthur and MacArthur 1961, Cody 1968, Holmes 1981, Weins and Rotenberry 1981, Robinson and Holmes 1984, Rotenberry 1985, Holmes et al. 1986). Microclimate, nest detection by predators, and food availability are governed by habitat structure, which largely determines the success of the nest.

The Solitary Vireo (*Vireo solitarius plumbeus*) is a common species breeding throughout the low-elevation forests of the Rocky Mountains (AOU 1983, Dobkin 1995). In Colorado, the reproductive success of Solitary Vireos is depressed by losses from both nest predators and brood parasites (Marvil and Cruz 1989, Chace et al. *in press*, Chapter 1). The objective of this paper is to determine if Solitary Vireos have nest-site preferences.

METHODS

A population of Solitary Vireos was studied during the summers of 1993 and 1994 in the ponderosa pine forest foothills west of the city of Boulder, Colorado (40° 00' N, 105° 20' W) between 1,800 m and 2,400 m. See Chapter 1 for study site locations and descriptions of vegetation (Fig. 2). After nest activity ceased, the vegetation surrounding Solitary Vireo nests and 15 random sites was measured. The analysis was designed after Noon (1981) and based on two measurement scales, microhabitat and macrohabitat. Random site coordinates were chosen using a random number table (Zar 1984) and a numbered grid over the study areas. All sites were within the home range and habitat of active Solitary Vireo nests.

Seven microhabitat variables were quantified at each nest site (Table 8). Characteristics of the nest tree (both actual and randomly chosen) were: diameter at breast height (1.4 m) (hereafter NTDBH), height (NTHT), and lowest living branch height (NTLB). Characteristics of nest position were: nest height (NHT), nest facing direction (NDIR), and distance from nest to trunk (or stem) (NTRK), distance from nest to branch tip (NTIP). Random variables for nest position were determined by using randomly chosen numbers as a percentage of the tree height and branch length. Nest facing direction was chosen randomly as well.

Most macrohabitat variables were measured within an 11.3 m radius circular plot centered on the nest (Noon 1981) (Table 8). Distances were measured to the nearest road, trail, forest canopy opening (> 400 sq. m, at least 10 m on one side, with < 15% canopy cover), riparian vegetation, town (Boulder or Lyons, Colorado), year-round occupied residence, using a 5 m and 50 m measuring tape to the nearest 0.1 m within 50 m, 1 m between 51 m and 200 m, and to the nearest 50 m when distances were > 200 m. Canopy cover of the site was estimated from 20 forest densiometer (concave) readings taken at uniform points within the circular plot. Ground cover was estimated from 20 ocular tube (James and Shuggart 1970, Noon 1981) readings

Table 8. Microhabitat and macrohabitat variables (30) measured on Solitary Vireo nests (81) and randomly chosen sites (15).

Variable	Description
Microhabitat	
NTDBH	Nest tree DBH (cm)
NTHT	Nest tree height (m)
NTLB	Height of lowest living branch (m)
NHT	Nest height (m)
NTRK	Distance of nest to trunk (m)
NTIP	Distance of nest to tip
NDIR	Nest facing direction
Macrohabitat	
SLOPE	Slope of site (degrees)
SDIR	Slope facing direction (degrees)
ELEV	Elevation of site (m)
TREES	No. of trees (> 8 cm dbh) per ha
SAPL	No. of saplings (< 8 cm dbh) per ha
BASAL	Total basal area/ha (cm2)
MBASAL	Mean basal area (m2)
MTRHT	Mean tree height (m)
MLBHT	Mean height lowest live branch (m)
SHRUB	No. shrub species
STEMS	Stems intersected/ ha
NRTRDIST	Distance to nearest tree (m)
NRTRDBH	DBH (cm) of nearest tree
NRTRHT	Height (m) of nearest tree
GROUND	Total % ground cover at 20 pts
CANOPY	Total % canopy cover at 20 pts
ROAD	Distance to nearest road (m)
TRAIL	Distance to nearest trail (m)
OPEN	Dist. to near. opening (>400sq.m) (m)
RIPAR	Distance to nearest riparian zone (m)
TOWN	Distance to nearest town (m)
RESID	Distance to nearest residence (m)
NRHUMAN	Dist. to near. human distubance (m)

taken within the circular plot from the same points as canopy cover. Heights were determined using a clinometer, and corrected by multiplying the height by the cosine of the degree of slope. Woody plants with a dbh ≥ 8 cm were called trees, and those with a dbh < 8 cm were called saplings. Woody plants with multiple stems and ≥ 40 cm in height were called shrubs. When shrubs occurred in large clumps a single shrub occupied a ground area not > 1 sq. m. Number of stems (trees and shrubs) intersected at breast height were counted on the two 22.6 m N-S, E-W axes of the circular plot (Noon 1981). All variables were continuous.

Data for the two years of study were pooled for analysis after testing for significant differences in site characteristics between years. Except where noted no differences were found between years. Random sites were selected and measured in 1994. The variables were not normally distributed, so that all statistical tests were necessarily nonparametric. Univariate statistical analyses employed median and goodness-of-fit tests. Median tests (Wilcoxon two-sample test) were used to compare shapes of frequency distributions. Means ± SE are reported for descriptive statistics. Results are reported as significant when $P < 0.05$.

Multivariate statistics were used to analyze nest-site variables in relation to cowbird parasitism and nest predation. Microhabitat and macrohabitat variables were analyzed separately (Table 8). A principal components analysis (PROC FACTOR) was employed to find key habitat factors (SAS programming). Only factors having eigenvalues > 1.0 were retained. Factors were rotated to an oblique solution (PROMAX) permitting correlations among the factors, and a logistic regression (PROC LOGIST) was used to test for differences between actual and randomly chosen nest sites. Nonparametric discriminant function analysis was used to discriminate between actual and random sites after redistribution using three nearest neighbors (PROC DISCRIM). The purpose of this exploratory study was to determine if patterns of nest-site selection exist. Therefore, the alpha value for the multivariate analysis was set at $P < 0.1$.

RESULTS

Solitary vireos nesting in the ponderosa pine forests of Boulder County, Colorado, showed specific nest placement. Vireos built 92.6% (n = 81) of their nests in ponderosa pines. The remaining nests were built in shrubs -- four nests in chokecherry (*Prunus virginiana*), one nest in American plum (*Prunus americana*), and one in western birch (*Betula fontinalis*). Nest trees were typically average in size for the site, approximately 10 m tall (Table 9). Nests were placed on the lowest branch, close to the tip, and 2.55 (± 0.12) m from the ground (Table 9). Vireo nests were oriented in a south-southwest direction and canopy cover above the nest averaged 84.17% (Table 9). The nests were located in the ponderosa pine forests, of lower elevations, typically with a slope of 16° and a southeast orientation (Table 9).

Of the 32 measurements of vegetation near each vireo nest, five (16.7%) showed significant differences between years of study (Table 10). Nests in 1994 tended to have higher low branches on nest trees and all surrounding trees (NTLB, MLBHT), higher nests (NHT), to be surrounded by larger trees (BASAL), and to have fewer shrub species

Table 9. Mean values (± SE) of microhabitat and macrohabitat variables at Solitary Vireo nest sites, 1993-1994, and randomly chosen locations within habitats occupied by Solitary Vireos, 1994. All statistical tests Wilcoxon two-sample tests.

Variables	Nest Sites (n = 81)	Random (n = 15)	*P* value
Microhabitat			
NTDBH (cm^2)	28.66 (1.73)	27.90 (2.46)	0.7969
NTHT (m)	10.71 (0.47)	9.91 (0.98)	0.4800
NTLB (m)	2.44 (0.16)	2.37 (0.50)	0.6827
NHT (m)	2.55 (0.12)	4.75 (0.96)	0.0386
NTRK (m)	2.29 (0.13)	0.64 (0.07)	0.0001
NTIP (m)	0.76 (0.28)	0.46 (0.06)	0.7733
NDIR (°)	193.60 (21.53)	166.93 (24.77)	0.7659
NCC (%)	84.17 (1.93)	--------	
NGC (%)	25.41 (3.39)	--------	
Macrohabitat			
SLOPE (°)	16.29 (0.94)	15.67 (2.51)	0.7160
SDIR (°)	146.49 (15.88)	81.67 (18.23)	0.0420
ELEV(m)	1862.64 (9.91)	1830.40 (25.31)	0.0850
TREES (#/ha)	317.90 (27.07)	181.67 32.32)	0.0195
SAPL (#/ha)	236.11 (34.15)	178.33 (79.88)	0.1795
BASAL (m^2/ha)	2023.33 (104.70)	1505.14 (268.92)	0.0844
MBASAL (m^2/ha)	8.51 (0.55)	8.40 (0.89)	0.6571
MTRHT (m)	11.69 (0.27)	15.83 (5.79)	0.1862
MLBHT (m)	3.03 (0.15)	2.57 (0.46)	0.1563
SHRUBS (#/ha)	3.04 (0.21)	3.73 (0.41)	0.2191
STEMS (#/ha)	172.84 (65.13)	86.67 (33.17)	0.6725
NRTRDIST (m)	4.77 (0.23)	4.96 (0.66)	0.7408
NRTRDBH (cm^2)	32.52 (2.00)	33.20 (3.49)	0.6669
NRTRHT (m)	11.86 (0.45)	11.62 (1.08)	0.7808
GROUND (%@20pts)	800.18 (48.48)	1362.07 (78.85)	0.0001
CANOPY (%@20pts)	1309.93 (38.82)	1044.27 (121.07)	0.0546
ROAD (m)	813.31 (60.75)	901.33 (169.86)	0.7735
TRAIL (m)	264.38 (59.47)	302.17 (123.62)	0.5686
OPEN (m)	43.80 (6.59)	18.19 (4.92)	0.0372
RIPAR (m)	283.00 (39.14)	267.36 (68.75)	0.8478
RESID (m)	1089.52 (85.05)	896.33 (171.22)	0.3299
TOWN (m)	1903.15 (149.87)	1511.33 (299.66)	0.3250
NRHUMAN (m)	162.33 (26.02)	344.96 (195.14)	0.4341

Table 10. Microhabitat and macrohabitat nest site variables which differ significantly* between Solitary Vireo nests found in 1993 (n = 46) and 1994 (n = 35), 1993-1994.

Variable	x 1993 (SE)	x 1994 (SE)	*P* - value
NTLB	2.15 (0.21) m	2.82 (0.23) m	0.0174
NHT	2.38 (0.16) m	2.78 (0.17) m	0.0224
BASAL	1772.05 (119.98) m2	2353.59 (170.30) m2	0.0030
MLBHT	2.64 (0.18) m	3.55 (0.24) m	0.0030
SHRUBS	3.63 (0.26)	2.26 (0.31)	0.0012

*Wilcoxon two-sample test.

surrounding the nest site (SHRUBS) (Table 10). These differences between years can be attributed to the differences in selection of nest tree species; five nests in 1993 (10.9%) and one nest in 1994 (2.8%) were built in shrubs. Differences were not significant, G = 2.0667, df = 1, $P >$ 0.05. The proportion of nests built in ponderosa pine did not differ significantly from the number of random nest sites (n = 13, 86.7%) (G = 0.5158 , df = 1, $P > 0.05$). Two of 15 random sites were based on Douglas fir (*Psuedotsuga menziesii*) as the nest tree.

Univariate analysis of microhabitat and macrohabitat variables revealed several significant differences between actual and randomly chosen sites. Solitary Vireo nests were built lower in nest trees and farther from the trunk than randomly chosen sites (Table 9). Actual sites had a more southerly orientation, a greater density of trees, less ground cover, and were farther from openings in the forest canopy than was typical of the surrounding habitat (Table 9).

Microhabitat

Variable NTDBH was removed from analysis because of high correlations ($r > 0.80$) with other more meaningful variables (Appendix A). Three microhabitat factors were extracted based on the scree method and eigenvalues; they accounted for 74.1% of the variance. Factor 1 (nest tree size, hereafter Size) had high salient loadings ($r > 0.6$) on NTHT and NTRK, and accounted for 35.7% of the variance (Table 11). Factor 2 (Height) had high salient loading on NTLB and NHT and accounted for 20.0% of the variance (Table 11). Factor 3 (Direction) had high salient loadings on NTIP and NDIR which accounted for 18.4% of the variance (Table 11).

Table 11. Microhabitat factor correlations for actual Solitary Vireo nests (n = 81), 1993-1994 and randomly chosen sites (n = 15), 1994.

Variable	Factor 1 Size	Factor 2 Height	Factor 3 Direction
NTHT	0.85	0.48	0.17
NTLB	0.54	0.66	0.01
NHT	0.03	0.85	0.01
NTRK	0.90	-0.09	0.04
NTIP	0.13	-0.21	0.82
NDIR	0.00	0.41	0.66

Table 12. Logistic regression for three microhabitat factors. Criteria for model fit $\chi^2 = 37.053$, df =3, P =0.0001. Of 96 nests, 90.4% were corrrectly classified as actual (n = 81) and randomly chosen (n = 15).

Variable	DF	Parameter Estimate	χ^2 Prob	Standarized Estimate
Intercept	1	-3.0520	0.0001	
Size	1	-2.1514	0.0001	-1.1861
Height	1	1.8783	0.0005	1.0355
Direction	1	-1.5593	0.1262	-0.8597

Logistic regression of the three microhabitat variables revealed a highly significant relationship with actual nest location. Regression correctly classified 90.4% of 96 sites as actual or randomly chosen (Table 12). Factors Size and Height were the most important in discriminating actual from randomly chosen sites. Nonparametric discriminant function analysis correctly classified 90.1% (n = 81) of actual sites and 100% (n = 15) of the randomly chosen sites, which is significantly different than expected by chance ($([(81/96)^2 + (15/96)^2] \times 100]$) (see Bekoff et al. 1987), G = 67.9105, df = 1, $P < 0.001$.

Macrohabitat

One randomly chosen site had no nearest tree (variables NRTRDIST, NRTRDBH, NRTRHT) which removed the observation from analysis by statistical programing (PROC LOGIST and PROC DISCRIM), thus leaving 14 randomly chosen sites for analysis.

Eight macrohabitat factors were retained based on the scree method; all had eigenvalues > 1.0. The eight factors accounted for 71.4% of the variance. Factor 1 (hereafter Trees) accounted for 18.0% of the variance and had high salient loadings on TREES, BASAL, MLBHT, NRTRDIST, GROUND, and CANOPY (Table 13). Factor 2 (Nhuman) accounted for 12.8% of the variance and had high salient loadings on TRAIL, RESID, TOWN, and NRHUMAN (Table 13). Factor 3 (Edge) accounted for 10.3% of the variance and had high salient loadings on ROAD and RIPAR (Table 13). Factor 4 (Ntree) had high salient loadings on NRTRDBH and NRTRHT, and accounted for 9.5% of the variance (Table 13). Factor 5 (Site) accounted for 6.0% of the variance and had high salient loadings on SLOPE and ELEV (Table 13).

Table 13. Macrohabitat factor correlations for actual Solitary Vireo nests and randomly chosen sites.

Variable	Factor 1 Trees	Factor 2 Nhuman	Factor 3 Edge	Factor 4 Ntree	Factor 5 Site	Factor 6 Mtrht	Factor 7 Stems	Factor 8 Sapl
SLOPE	0.06	0.10	-0.42	-0.15	0.70	-0.23	0.19	-0.05
SDIR	-0.00	-0.02	-0.08	0.16	0.21	-0.15	-0.04	0.77
ELEV	0.23	0.18	0.27	0.02	0.76	0.06	-0.20	0.09
TREES	0.84	-0.13	-0.03	-0.32	0.29	-0.30	-0.11	-0.03
SAPL	0.25	-0.03	-0.15	0.27	0.40	-0.24	0.04	-0.65
MBASAL	-0.38	0.22	-0.16	0.52	-0.54	0.52	0.15	-0.14
BASAL	0.87	-0.11	0.02	0.06	0.05	0.18	-0.06	-0.07
MTRHT	0.13	-0.11	0.07	0.14	-0.07	0.78	-0.03	-0.01
MLBHT	0.71	-0.28	0.25	0.08	0.01	0.42	-0.28	-0.06
SHRUB	-0.08	0.18	-0.37	0.25	0.17	0.39	0.46	-0.28
STEMS	-0.01	-0.11	-0.12	-0.00	-0.10	-0.10	0.75	-0.13
NRTRDIST	-0.64	0.32	-0.35	0.27	-0.41	0.16	-0.24	-0.06
NRTRDBH	-0.24	0.18	-0.15	0.80	-0.25	0.09	0.09	-0.06
NRTRHT	0.03	-0.11	-0.01	0.84	0.03	0.31	-0.04	0.04
GROUND	-0.63	-0.05	-0.02	0.04	-0.33	0.41	0.29	-0.02
CANOPY	0.83	-0.15	0.07	-0.04	0.23	0.09	0.05	-0.17
ROAD	0.10	0.22	0.81	0.03	-0.08	0.07	-0.31	-0.05
TRAIL	-0.09	0.85	-0.16	0.07	0.133	-0.08	-0.04	-0.02
OPEN	0.22	-0.13	0.27	-0.11	0.06	-0.22	-0.51	-0.14
RIPAR	-0.11	-0.21	0.74	-0.22	0.03	-0.03	-0.04	0.13
RESID	0.11	0.62	0.58	0.15	0.18	0.16	-0.24	0.01
TOWN	-0.12	0.64	0.00	0.10	0.50	-0.20	-0.23	-0.04
NRHUMAN	-0.14	0.73	0.05	-0.09	0.05	-0.10	0.08	-0.03

Table 14. Logistic regression for eight macrohabitat factors. Criteria for model fit $\chi^2 = 15.052$, df =8, $P = 0.0581$. Of 95 sites, 80.6% were corrrectly classified as actual (n = 81) and random (n = 14).

Variable	DF	Parameter Estimate	χ^2 Prob.	Standardized Estimate
Intercept	1	-2.2790	0.0001	
Tree	1	-0.9738	0.0300	-0.5369
Nhuman	1	0.0201	0.9471	0.0111
Edge	1	0.0912	0.7899	0.0503
Ntree	1	-0.5041	0.1724	-0.2779
Site	1	0.0938	0.7858	0.0517
Mtrht	1	0.7616	0.0338	0.4199
Stem	1	0.2820	0.3644	0.1554
Sapl	1	-0.5098	0.2409	-0.2810

Factor 6 (Mtrht) accounted for 5.4% of the variance and had a high salient loading on MTRHT (Table 13). Factor 7 (Stems) accounted for 4.8% of the variance and had a high loading on STEMS (Table 13). Factor 8 (Sapl) had high loadings on the variables SDIR and SAPL and accounted for 4.6% of the total variance (Table 13). The variables MBASAL, SHRUB, and OPEN did not load highly (< 0.6) on any factor (Table 13).

When the eight macrohabitat factors -- Trees, Nhuman, Edge, Ntree, Site, Mtrht, Stems, and Sapl -- were analyzed in a logistic regression, a significant relationship was revealed ($P < 0.1$). Trees and Mtrht were the significant factors in correctly classifying 80.6% of the sites (n = 95) as actual or randomly chosen (Table 14). Nonparametric discriminant function analysis revealed a significant relationship between the habitat parameters between actual and randomly chosen sites. Analysis correctly classified 72.8% actual sites (n = 81) and 100% of randomly chosen sites (n = 14), which was significantly different from classification by chance ($G = 81.0810$, df = 1, $P < 0.001$).

DISCUSSION

Solitary Vireos do not randomly choose nest sites in the ponderosa pine forests of Boulder County. They apparently assess their surroundings in a hierarchical fashion until a suitable nesting place is found (Darlington 1975). There is probably a sequence of finer and finer choices made within preferred habitat, going from macrohabitat to microhabitat (Walsberg 1985, Bekoff et. al. 1987). These decisions appear to be based on species-specific requirements. For example, Yellow Warblers (*Dendroica petechia*) and Sage Sparrows (*Amphispiza* *belli*) choose nest sites largely on the basis of the macrohabitat (Peterson and Best 1985, Knopf and Sedgewick 1992), whereas Dusky Flycatchers (*Empidonax oberholseri*) choose nest sites largely on the basis of the microhabitat (Kelly 1993). In the study reported here, Solitary Vireos were shown to discriminate nest sites at both levels, but were more selective at microhabitat level.

Solitary Vireos choose nest sites according to tree density and build their nests in specific locations on the nest tree. Vireos select sites with higher tree density, higher basal area, closer clumping of trees, greater canopy cover, and higher lowest living branches than occur at random sites in the ponderosa pine forest. However, Solitary Vireos do not choose the young, dense stands of ponderosa pine for nesting, where tree density and canopy cover are greatest. This macrohabitat preference may be a consequence of their preference for trees of a certain height (averaging 10.71 m) and for a certain distance from the trunk (averaging 2.29 m).

Nest-Site Selection

Inclement weather and physiological constraints may influence selection of nest sites by Solitary Vireos (Calder 1973, Nolan 1978, Walsberg 1981, 1985). These birds choose sites with dense trees and a high percentage of canopy cover, both of which could protect the nest from the elements. However, in the summer in Boulder County inclement weather is rare and it is possible that Solitary Vireos, like Warbling Vireos (*Vireo gilvus,* Walsberg 1985), select for the shading provided by canopy cover. Increased canopy cover may also reduce nocturnal heat radiation (Walsberg 1985). North slopes would provide maximum shading, however vireos rarely nest on north-facing slopes, which are usually dominated by Douglas fir and not a typical nesting habitat for Solitary Vireos in Boulder County (Marvil and Cruz 1989, pers. obs.). Nest placement in the shade may also increase the humidity in the nest thereby reducing dehydration of the eggs (Walsberg 1985), but this factor was not examined directly. The placement of nests by these Solitary Vireos may reduce solar radiation during the day and reduce heat loss at night.

Avian communities are structured by competition when food is limited. Food availability has been shown also to be important in nest-site selection (MacArthur and MacArthur 1961, Cody 1968, Holmes 1981, Weins and Rotenberry 1981, Robinson and Holmes 1984, Rotenberry 1985, Holmes et al. 1986, Martin 1987). For some birds, however, food seems to be abundant and competition for food non-existent during the breeding season (Weins 1977, Rotenberry 1980, Anderson et al. 1982, Rosenberg et al. 1982). Regardless of whether or not food availability structures the community, one would expect insectivorous birds to choose macrohabitats surrounding nest sites that ensure a consistent supply of insect larvae in order to maximize foraging efficiency when raising a brood. In the vireos of this study, breeding territories were uniformly spaced and nest-site macrohabitats had significantly more foraging surface area than found at random throughout the forest. Assuming that a greater canopy cover and a larger total basal area of the site yields increased abundance of insect larvae, Solitary Vireos maximize foraging opportunities by macrohabitat selection. A quantitative comparison of insect larvae abundance between actual and randomly chosen sites needs to be conducted.

Predation has a substantial influence on species-specific selection of nest sites (Martin 1988a, 1988b, Martin and Roper 1988, Martin 1993). Solitary Vireos choose nest sites with greater overall canopy cover, which may hide low nests from aerial predators. If ground dwelling predators had a significant long-term impact on reproductive success, then nests would be expected to be higher in the tree or in sites with greater ground cover (Bowman and Harris 1980, Yahner and Cypher 1987, Martin 1991, Leimgruber et al. 1994). Further, nests were placed in the most abundant tree species, which may increase the searching time by predators (Martin and Roper 1988). Vireos place their nests far from the trunk on small branches, which would be an advantageous strategy to avoid nest predation by large mammal (e.g. feral cats). Additionaly, reduced ground cover may reveal ground predators within the area surrounding the nest.

Like predation, cowbird parasitism has a negative effect on the reproductive success of Solitary Vireos (Marvil and Cruz 1989, Chapter 1) and probably is a selection pressure for nest-site preferences in these vireos. Cowbirds searching for nests from the air may not detect vireo nests beneath an almost closed canopy. Results from this study suggest that if cowbird parasitism is an important factor in nest-site selection, then cowbirds are more likely to locate nests from the air than from the ground.

Both nest predators and cowbirds may find nests by parental activity, which would depend on habitat variables that conceal parental activity at the nest site. Habitat variables of nest concealment and proximity of available food would reduce detection of parental movement and nest failure due to predation and parasitism.

Conclusion

Solitary Vireos choose certain sites for building their nests in the ponderosa pine forests of Boulder County. Nest microclimate, food availability, predation and cowbird parasitism appear to be important factors driving the selection of nest sites. These selection pressures are probably combined such that vireos must make trade-offs between these factors when selecting a nesting macrohabitat and microhabitat (Filliater et al. 1994).

CHAPTER 3

COWBIRD PARASITISM AND NEST PREDATION ON SOLITARY VIREO NESTS: DOES THE NEST SITE MAKE A DIFFERENCE?

INTRODUCTION

Selection of a nest site may be crucial to the reproductive success of birds. Many birds hide their nests or build them in inaccessible sites (Collias and Collias 1984), and the behavior of parents visiting the nest has been described as stealthy (Skutch 1976, Breitwisch et al. 1989). Nearly all species show some degree of intraspecific variation in nest site selection. Some studies have revealed that nest-site selection is related to the probability of nest success (Martin and Roper 1988, Kelly 1993), but others have not (Morton et al. 1993, Filliater et al. 1994). Appropriate selection of a nest site may reduce the probability of nest detection by predators and cowbirds.

Nest predation is a major factor that reduces reproductive success in open-nesting passerine birds (Ricklefs 1969, Martin 1991, Chapter 1). Moreover, high rates of predation have been shown to cause fluctuations in bird populations (Angelstram 1986, Sherry and Holmes 1991). Predation is considered to be the most important factor in the decline of North American insectivorous passerine populations (Bohning-Gaese et al. 1993). Therefore, there is selection pressure for songbirds to choose nest sites that are safe from predators.

Brown-headed Cowbirds (*Molothrus ater*) lay their eggs in the nests of over 220 species of passerines in North America (Friedmann et al. 1977, Friedmann and Kiff 1985, Chace and Cruz *in review*). Like predation, cowbird brood parasitism also has significant impacts on populations of open-nesting migratory passerines (Mayfield 1965, Brittingham and Temple 1983, Marvil and Cruz 1989, Trail and Baptista 1993, Chapter 1). Cowbirds often find host nests during nest building, and cowbirds search for nests in forested habitats from high perches, from the ground, and by actively trying to flush hosts from the nest (Norman and Robertson 1975, Thompson and Gottfried 1976, 1981). Therefore, there is selection pressure for songbirds prone to being parasitized to choose nest sites that are less detectable by cowbirds.

The purpose of this paper is to test several hypotheses about the relationship between nest-site selection and nest success for the Solitary Vireo (*Vireo solitarius plumbeus*). Solitary Vireos, in Boulder County, Colorado, choose their nest sites nonrandomly (Chapter 2) and are negatively impacted by both cowbird parasitism and nest predation (Marvil and Cruz 1989, Chace et al. *in press*, Chapter 1). Clearly there is strong selection pressure on birds in this population to select nest sites that will not be found by predators or brood parasites. The purpose of this paper will be to test several hypotheses regarding nest-site selection and the probability of nest predation or brood parasitism. The six hypotheses--nest-site behavior hypothesis, edge effect hypothesis, nest canopy cover hypothesis, rare site hypothesis, nest-site microhabitat hypothesis, nest-site macrohabitat hypothesis -- are described below.

The nest-site behavior hypothesis predicts that nests with greater activity will have a greater probability of being noticed and preyed upon (Ricklefs 1969). While evidence of nest-site activity was not directly determined in this study, based on this hypothesis the incubation stage should have lower rates of predation than the nestling stage, when parents deliver food to begging young. Tests of this hypothesis with regard to parasitism were not conducted because cowbird eggs must be laid during host clutch initiation to effectively have a cowbird fledge from a vireo nest (Marvil and Cruz 1989, Chapter 1).

The edge effect hypothesis (Gates and Gysel 1978) states that nest predation and parasitism are caused by animals that frequently occur along edges. It predicts a decrease in predation and parasitism with increasing distance from edges (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Wilcove et al. 1986, Temple and Cary 1988, Gates and Giffen 1991). There is strong evidence that in some cases nest predators and cowbirds occur in greater abundances along natural and human-induced forest edges. Also, greater abundance of nest predators is correlated with a greater proportion of nests depredated (Angelstram 1986, Audren 1992). Additionally, cowbird abundance has been shown to be related to forest edges, forest interior openings, and human related activities (O'Conner and Faaborg 1992, Robinson et al. 1992).

The nest canopy cover hypothesis states that forest canopy cover conceals nests from predators and brood parasites. It predicts that increased canopy cover reduces rates of nest parasitism and predation. Many studies have shown that nest concealment is critical to the avoidance of predation (Martin 1991, Leimgruber et al. 1994), and similar studies have been conducted in relation to cowbird parasitism (Wiley 1982). Solitary Vireo nests are not concealed within the surrounding vegetation like the nests of other species (Best and Stauffer 1980, Martin and Roper 1988). In Boulder County the vireo nest is built on the extreme distal portion of the lowest living limb of a ponderosa pine, usually 2-3 m above the ground (pers. obs.). Therefore, the typical nest concealment classifications used for other species cannot be applied to the Solitary Vireo nests in this study. However, canopy cover may be important in concealing nests from visuallyoriented aerial predators and parasites which often search for nests from the tops of trees (Norman and Robertson 1975).

The rare site hypothesis (Martin and Roper 1988) states that predators find more prey in less abundant substrates because they have fewer places to search. It predicts that birds nesting in less abundant plant species will suffer higher rates of predation than birds nesting in the most common plant species in the habitat. Specifically, this hypothesis predicts that Solitary Vireos nesting in ponderosa pine trees, the most common plant species on the study sites, will be more successful than vireo nests placed in other, less abundant, vegetation.

The canopy cover and rare site hypotheses require characterization of the vegetation. Many variables define the vegetative characteristics of nest sites; it is problematic to conduct an analysis of many correlated independent variables using univariate statistical techniques (Tabachnick and Fidell 1989). This is especially true when trying to separate successful from unsuccessful nests. Studies using multivariate statistics have shown that birds choose nest sites nonrandomly among a suite of variables (Bekoff et al. 1987, Martin and Roper 1988), and this has been described for the Solitary Vireo (Chapter 2). Multivariate analysis can also determine which nest-site characteristics are reliable predictors of predation and cowbird parasitism. In this study, measurements of vegetation are divided into two scales, microhabitat and macrohabitat (Chapter 2). Microhabitat and macrohabitat characteristics of vegetation are predicted to determine the probability of nest success, thus driving species-specific selection of nest sites (Martin 1988). The microhabitat hypothesis predicts that nest predators and parasites find nests based on the parameters of nest placement (e.g. nest height). The macrohabitat hypothesis predicts that nest predators and parasites find nests based on parameters of vegetation surrounding the nest site (e.g. tree density). This paper describes the habitat correlates of parasitism and predation.

METHODS

A population of Solitary Vireos was studied from 1993-1994 in the ponderosa pine forests of the foothills west of the city of Boulder, Colorado (40° 00' N, 105° 20' W) between 1,800 m and 2,400 m. For study site location and vegetation see Chapter 1 (Fig. 2). Each of 81 vireo nests was observed at least once every three days until it succeeded (fledged at least one young) or failed. Cowbird parasitism, nest predation, and abandonment were determined for each nest. Predation was defined as the loss of at least one egg or nestling from a nest within the normal time of development (14 day incubation, 16 day nestling). Potential nest predators include the Steller's Jay (*Cyanocitta stelleri*), American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), Abert's squirrel (*Sciurus aberti*), least chipmunk (*Eutamias minimus*), Colorado chipmunk (*E. quadrivittatus*), and the bull snake (*Pituophis melanoleucus*). Nesting success for both the egg stage and nestling stage was determined using the Mayfield Method (Mayfield 1975). Statistical differences were tested by using the goodness-of-fit test (G-test), with alpha set at 0.05.

Following the termination of nest-site activity measurements of vegetation were taken. Nine microhabitat variables were quantified at each nest site (Table 15). Characteristics of the nest tree (both actual and randomly chosen) were: diameter at breast height (1.4 m) (hereafter

Table 15. Microhabitat and macrohabitat variables (32) measured on 81 Solitary Vireo nests, 1993-1994.

Variable	Description
Microhabitat	
NTDBH	Nest tree DBH (cm)
NTHT	Nest tree height (m)
NTLB	Height of lowest living branch (m)
NHT	Nest height (m)
NTRK	Distance of nest to trunk (m)
NTIP	Distance of nest to tip
NDIR	Nest facing direction
NCC	Canopy cover at nest (%)
NGC	Ground cover at nest (%)
Macrohabitat	
SLOPE	Slope of site (degrees)
SDIR	Slope facing direction (degrees)
ELEV	Elevation of site (m)
TREES	No. of trees (> 8 cm dbh) per ha
SAPL	No. of saplings (< 8 cm dbh) per ha
BASAL	Total basal area/ha (cm2)
MBASAL	Mean basal area (m2)
MTRHT	Mean tree height (m)
MLBHT	Mean height lowest live branch (m)
SHRUB	No. shrub species
STEMS	Stems intersected/ ha
NRTRDIST	Distance to nearest tree (m)
NRTRDBH	DBH (cm) of nearest tree
NRTRHT	Height (m) of nearest tree
GROUND	Total % ground cover at 20 pts
CANOPY	Total % canopy cover at 20 pts
ROAD	Distance to nearest road (m)
TRAIL	Distance to nearest trail (m)
OPEN	Dist. to near. opening (>400sq.m) (m)
RIPAR	Distance to nearest riparian zone (m)
TOWN	Distance to nearest town (m)
RESID	Distance to nearest residence (m)
NRHUMAN	Dist. to near. human distubance (m)

NTDBH), height (NTHT), and lowest living-branch height (NTLB). Characteristics of nest position were: nest height (NHT), nest facing direction (NDIR), distance from nest to trunk (or stem) (NTRK), and distance from nest to branch tip (NTIP). Random variables for nest position were determined by using randomly chosen numbers as a percentage of the tree height and branch length, as well as for nest direction.

Most macrohabitat variables were measured within a circular plot, with a radius of 11.3 m centered on the nest (Noon 1981) (Table 15). Distances were measured to the nearest road, trail, forest canopy opening (> 400 sq. m, at least 10 m on one side, with < 15% canopy cover), riparian vegetation, town (Boulder or Lyons, Colorado), year-round occupied residence, using a 5 m and 50 m measuring tape to the nearest 0.1 m within 50 m, 1 m between 51 m and 200 m, and to the nearest 50 m when distances were > 200 m. Canopy cover of the site was estimated from 20 forest densiometer (concave) readings taken at uniform points within the circular plot. Ground cover was estimated from 20 ocular tube (James and Shuggart 1970, Noon 1981) readings taken within the circular plot from the same points as canopy cover. Heights were determined using a clinometer, and corrected by multiplying the height by the cosine of the degree of slope. Woody plants with a dbh ≥ 8 cm were called trees, and those with a dbh < 8 cm were called saplings. Woody plants with multiple stems and ≥ 40 cm in height were called shrubs. When shrubs occurred in large clumps a single shrub occupied a ground area not > 1 sq. m. Number of stems (trees and shrubs) intersected at breast height were counted on the two

22.6 m N-S, E-W axes of the circular plot (Noon 1981). All variables were continuous.

Data for the two years of study were pooled for analysis after testing for significant differences in site characteristics between years. Except where noted no differences were found between years. The variables were not normally distributed, so all statistical tests were necessarily nonparametric. Univariate statistical analyses employed median and goodness-of-fit tests. Median tests (Wilcoxon two-sample test) were used to compare shapes of frequency distributions. Means ± SE are reported for descriptive statistics. Results are reported as significant when $P < 0.05$.

Multivariate statistics were used to analyze nest-site variables in relation to cowbird parasitism and nest predation. Microhabitat and macrohabitat variables were analyzed separately. A principal components analysis (PROC FACTOR) was employed to find key habitat factors (SAS programming). Only factors having eigenvalues > 1.0 were retained. Factors were rotated to an oblique solution (PROMAX) permitting correlations among the factors, and a logistic regression (PROC LOGIST) was used to seperate parasitized from nonparasitized nests, and nests not preyed upon from those that were preyed upon, based on nest site characteristics. Nonparametric discriminant function analysis was used to discriminate between parasitized/nonparasitized and predation/no predation after redistribution using three nearest neighbors (PROC DISCRIM). The purpose of this exploratory study was to determine if nest-site characteristics could predict patterns of parasitism and predation.

Therefore, the alpha value for the multivariate analysis was set at $P < 0.1$.

RESULTS

Brown-headed Cowbirds parasitized 54.3% of 81 Solitary Vireo nests (Table 1) and predation occurred at 49.4% of Solitary Vireo nest sites (Table 2). Predation was independent of parasitism (Table 3). Parasitism and predation on Solitary Vireo nests have a significant negative impact on the reproductive success of the vireo population in Boulder County (Chapter 1).

Of 32 measurements taken on the vegetation at each vireo nest, five (15.6%) showed significant differences between years of study (Table 10). Nests were higher (NHT) in 1994, and nest trees tended to have higher lowest living branches (NTLB) in 1994. Trees surrounding nest-sites had higher lowest branches (MLBHT), were surrounded by larger trees (BASAL), and had fewer shrub species surrounding the nest site (SHRUBS) (Table 10) in 1994. These differences between years can be attributed to differences in selection of nest tree species: 92.6% of Solitary Vireo nests were built in ponderosa pine trees, while five nests in 1993 (10.9%) and one nest in 1994 (2.8%) were built in shrubs. Differences were not significant ($G = 2.0667$, $df = 1$, $P > 0.05$).

NEST-SITE BEHAVIOR HYPOTHESIS

I tested for an association between nest-site activity and nest failure. The overall daily nest mortality per nest was 0.0431. There were 906 incubation stage days with 33 nests lost, and 392 nestling stage days with 23 nests lost. Differences in nest success between egg and nestling stage were not significant, G = 2.8397, df = 1, $P > 0.05$. Thus, the nest-site behavior hypothesis was rejected: increased nest activity did not increase nest detection by predators.

Solitary Vireos actively chased Steller's Jays and Brown-headed Cowbirds from the nest area. Whether active defense eventually results in higher predation/parasitism was not determined.

EDGE EFFECT HYPOTHESIS

Differences in predation and parasitism were tested for in relation to natural and artificial edges. The mean distance of Solitary Vireo nests from a trail was 264.38 ± 59.47 m, from a road was 813.81 ± 60.78 m, from a residence was 1089.52 ± 85.05 m, from a town was 1903.15 ± 149.87 m, from the nearest human disturbance was 162.33 ± 26.02 m, from a riparian zone was 283.00 ± 39.14 m, and from a canopy opening was 43.80 ± 6.59 m. Nests preyed upon were significantly closer to roads and residences (Table 16). Parasitized nests were significantly closer to openings in the forest canopy (Table 17). Openings created naturally in the canopy of the ponderosa pine forest and openings created by roads, residences, towns, and occasionally trails were not separated in this analysis.

NEST CANOPY COVER HYPOTHESIS

Mean canopy cover above the Solitary Vireo nests was 84.17 ± 1.93%. Differences in canopy cover at nests preyed upon (84.88 ± 2.48%) and not preyed upon (83.45 ± 3.00%) were not significant (Table 16). Canopy cover at parasitized nests (82.04 ± 3.06%) and nonparasitized

Table 16. Mean values (± SE) of microhabitat and macrohabitat variables atnondepredated (n = 40) and depredated (n = 41) Solitary Vireo nest sites, 1993-1994. All statistical tests Wilcoxon two-sample tests.

Variables	No Predation	Predation	*P* value
Microhabitat			
NTDBH (cm^2)	30.28 (2.40)	27.07 (2.49)	0.2670
NTHT (m)	10.45 (0.60)	10.96 (0.73)	0.3212
NTLB (m)	2.42 (0.20)	2.47 (0.25)	0.8464
NHT (m)	2.50 (0.15)	2.61 (0.19)	0.8501
NTRK (m)	2.46 (0.18)	2.13 (0.17)	0.2649
NTIP (m)	1.01 (0.56)	0.51 (0.05)	0.6909
NDIR (^{o})	164.97 (18.78)	221.54 (38.16)	0.2752
NCC (%)	83.45 (3.00)	84.88 (2.48)	0.9887
NGC (%)	27.35 (5.48)	23.51 (4.10)	0.9466
Macrohabitat			
SLOPE (^{o})	14.73 (1.31)	17.82 (1.31)	0.0851
SDIR (^{o})	152.00 (28.10)	141.12 (15.61)	0.7660
ELEV(m)	1858.65 (12.46)	1866.54 (15.48)	0.5704
TREES (#/ha)	338.12 (44.11)	298.17 (32.00)	0.6980
SAPL (#/ha)	238.75 (38.97)	233.54 (56.25)	0.3151
BASAL (m^2/ha)	2077.25 (169.99)	1970.73 (125.25)	0.7950
MBASAL (m^2/ha)	874.38 (0.88)	8.28 (0.63)	0.6536
MTRHT (m)	11.31 (0.36)	12.06 (0.40)	0.3595
MLBHT (m)	2.93 (0.22)	3.13 (0.21)	0.4085
SHRUBS (#/ha)	3.05 (0.32)	3.02 (0.28)	0.8442
STEMS (#/ha)	165.00 (77.89)	180.49 (104.83)	0.9661
NRTRDIST (m)	4.86 (0.34)	4.67 (0.31)	0.7987
NRTRDBH (cm^2)	31.31 (2.62)	33.70 (3.03)	0.4138
NRTRHT (m)	11.55 (0.57)	12.16 (0.70)	0.3874
GROUND (%@20pts)	705.25 (69.99)	892.80 (64.76)	0.0377
CANOPY (%@20pts)	1320.32 (58.66)	1299.78 (51.72)	0.7161
ROAD (m)	924.92 (77.84)	704.42 (90.65)	0.0384
TRAIL (m)	347.30 (107.39)	183.49 (51.70)	0.5612
OPEN (m)	49.29 (11.13)	38.44 (7.22)	0.7302
RIPAR (m)	249.20 (32.59)	315.98 (70.64)	0.7803
RESID (m)	1289.00 (136.22)	894.90 (94.95)	0.0371
TOWN (m)	2069.62 (240.71)	1740.73 (179.72)	0.5358
NRHUMAN (m)	214.80 (46.07)	111.14 (22.90)	0.3143

Table 17. Mean values (± SE) of microhabitat and macrohabitat variables at nonparasitized (n = 37) and parasitized (n = 44) Solitary Vireo nest sites, 1993-1994. All statistical tests Wilcoxon two-sample tests.

Variables	Nonparasitized	Parasitized	*P* value
Microhabitat			
NTDBH (cm^2)	27.85 (2.63)	29.33 (2.32)	0.4121
NTHT (m)	10.95 (0.75)	10.50 (0.61)	0.7544
NTLB (m)	2.67 (0.26)	2.25 (0.19)	0.4257
NHT (m)	2.52 (0.20)	2.58 (0.14)	0.4230
NTRK (m)	2.37 (0.19)	2.22 (0.17)	0.5376
NTIP (m)	1.05 (0.61)	0.51 (0.04)	0.2767
NDIR (°)	181.73 (19.23)	203.59 (36.36)	0.7943
NCC (%)	86.70 (2.12)	82.04 (3.06)	0.6689
NGC (%)	25.27 (4.70)	25.52 (4.89)	0.8400
Macrohabitat			
SLOPE (°)	15.45 (1.25)	17.00 (1.37)	0.4503
SDIR (°)	125.89 (14.62)	163.82 (26.41)	0.6020
ELEV(m)	1873.89 (12.32)	1853.18 (15.00)	0.3076
TREES (#/ha)	347.30 (35.29)	293.18 (40.01)	0.0562
SAPL (#/ha)	249.32 (60.75)	225.00 (37.29)	0.6826
BASAL (m^2/ha)	2207.27 (164.14)	1868.66 (131.76)	0.1188
MBASAL (m^2/ha)	7.45 (0.55)	9.40 (0.86)	0.2267
MTRHT (m)	12.01 (0.40)	11.42 (0.37)	0.3627
MLBHT (m)	3.32 (0.24)	2.79 (19)	0.1211
SHRUBS (#/ha)	2.89 (0.28)	3.16 (0.31)	0.8099
STEMS (#/ha)	167.57 (116.09)	177.27 (71.00)	0.2497
NRTRDIST (m)	4.70 (0.32)	4.82 (0.33)	0.7257
NRTRDBH (cm^2)	28.79 (1.76)	35.66 (3.31)	0.1782
NRTRHT (m)	12.11 (0.71)	11.64 (0.58)	0.8163
GROUND (%@20pts)	747.27 (63.86)	844.68 (71.26)	0.4829
CANOPY (%@20pts)	1379.68 (51.48)	1251.27 (55.85)	0.1101
ROAD (m)	903.95 (87.99)	737.10 (83.02)	0.1414
TRAIL (m)	250.74 (81.03)	275.86 (86.51)	0.6253
OPEN (m)	60.28 (12.64)	29.94 (5.13)	0.0166
RIPAR (m)	343.53 (62.19)	232.09 (48.92)	0.0547
RESID (m)	1109.73 (112.75)	1072.52 (125.75)	0.4945
TOWN (m)	2016.89 (218.53)	1807.50 (206.99)	0.4228
NRHUMAN (m)	168.89 (38.70)	156.81 (35.55)	0.7724

nests (86.70 ± 2.12%) were not significantly different (Table 17). The nest canopy cover hypothesis was rejected.

RARE SITE HYPOTHESIS

This hypothesis cannot be tested directly because I did not determine the searching strategies of all possible avian, mammalian, and reptilian predators. Further, I did not determine how cowbirds search for nests to parasitize. I tested this hypothesis indirectly by comparing the frequency of predation and parasitism on Solitary Vireo nests in the most common plant species, ponderosa pine, with all other plant species. Most Solitary Vireos (92.5%, n = 81) nested in ponderosa pine. Four (4.9%) nested in chokecherry (*Prunus virginiana*), one (1.2%) nested in wild plum (*Prunus americana*), and one nested in western birch (*Betula fontinalis*). The probability of parasitism was not significantly different between nests in ponderosa pine trees and nests in other species, $G = 0.0486$, $df = 1$, $P > 0.05$. Likewise, predation was not significantly related to the relative abundance of the nesting substrate, $G = 3.2323$, $df = 1$, $P > 0.05$. Thus, the rare site hypothesis was rejected.

Multivariate Analysis of Microhabitat and Macrohabitat Variables

Univariate analysis of microhabitat and macrohabitat variables revealed several significant relationships with parasitism and predation. Vireo nests in sites with greater ground cover, and closer to roads and residences had a significantly greater chance of being preyed upon (Table 16). Parasitism on Solitary Vireo nests was significantly higher on nests closer to openings in the canopy (Table 17). Nests in sites with fewer trees and closer to residential areas typically experienced more parasitism, although the difference was not significant (Table 17).

MICROHABITAT HYPOTHESIS

Variables NTDBH and NRHUMAN were removed from analysis because of high correlations ($r > 0.80$) with other, more meaningful variables (Appendix B). Three microhabitat factors were extracted based on the scree method and eigenvalues; the three factors accounted for 66.5% of the variance. Factor 1 (Nest Tree Size, hereafter NTSize) had high salient loadings ($r > 0.6$) on NTHT, NTRK, and NCC and accounted for 32.8% of the variance (Table 18). Factor 2 (Position I) had high salient loadings on NTLB, NHT, NDIR and accounted for 18.7% of the variance (Table 18). Factor 3 (Position II) had high salient loadings on NTIP and NGC and accounted for 15.0% of the variance (Table 18).

Logistic regression of the three microhabitat variables revealed no significant relationships with parasitism or predation. The regression correctly classified 52.9% ($n = 81$) of vireo nests as parasitized and nonparasitized, and 54.6% of the nests were correctly classified as preyed upon and not preyed upon (tables 19 and 20). Microhabitat variables are not significant indicators for the likelihood of nests disturbance by predators or cowbirds. Discriminant function analysis correctly classified 86.4% ($n = 44$) of nests parasitized and 59.5% ($n = 37$) of the nest not parasitized, which is not significantly different from those expected by chance ($[(37/81)^2 + (44/81)^2] \times 100]$) (see Bekoff et al. 1987), $G = 0.006$, $df = 1$, $P > 0.05$. Discriminant function analysis

Table 18. Microhabitat factor correlations for Solitary Vireo nests, 1993-1994.

Variable	Factor 1 NT Size	Factor 2 Position I	Factor 3 Position II
NTHT	0.85	0.43	0.16
NTLB	0.44	0.63	-0.25
NHT	0.36	0.69	-0.14
NTRK	0.87	0.09	0.15
NTIP	-0.02	0.05	0.82
NDIR	-0.09	0.74	0.23
NCC	-0.59	-0.05	0.30
NGC	0.43	-0.42	0.60

Table 19. Logistic regression for three microhabitat factors. Criteria for model fit $\chi^2 = 0.631$, df = 3, $P = 0.8893$. 52.9% of 81 nests corrrectly classified as parasitized or nonparasitized.

Variable	DF	Parameter Estimate	χ^2 Prob.	Standardized Estimate
Intercept	1	0.1729	0.4402	
Tree	1	-0.0349	0.8780	-0.0192
Postion I	1	-0.0745	0.7450	-0.0410
Position II	1	-0.1670	0.4931	-0.0921

Table 20. Logistic regression for three microhabitat factors. Criteria for model fit $\chi^2 = 2.213$, df = 3, $P = 0.5294$. 54.6% of 81 nests corrrectly classified as preyed upon or not preyed upon.

Variable	DF	Parameter Estimate	χ^2 Prob.	Standardized Estimate
Intercept	1	0.0264	0.9069	
Tree	1	-0.1857	0.4201	-0.1024
Postion I	1	-0.2918	0.2417	0.1609
Position II	1	-0.0774	0.7381	-0.0426

correctly classified 70.7% (n = 41) of nests preyed upon and 77.5% (n = 40) of nests not preyed upon, which was not significantly different from nests classified by chance, G = 0.02, df = 1, $P > 0.05$.

Microhabitat variables of Solitary Vireo nest sites are not good predictors of cowbird parasitism or nest predation, and therefore the microhabitat hypothesis was rejected.

MACROHABITAT HYPOTHESIS

Eight macrohabitat factors were retained based on the scree method and all factors had eigenvalues > 1.0; the eight factors accounted for 75.0% of the variance (Table 21). Factor 1 (hereafter Trees) accounted for 18.7% of the variance and had high salient loadings ($r > 0.60$) on TREES, BASAL, MLBHT, NRTRDIST, GROUND, and CANOPY. Factor 2 (Edge) accounted for 12.7% of the variance and had high salient loadings on SLOPE, ROAD, and RIPAR. Factor 3 (Tsize) accounted for 11.8% of the variance and had high salient loadings on MBASAL and MTRHT. Factor 4 (Nhuman) had high salient loadings on TRAIL, RESID, and TOWN, and accounted for 10.3% of the variance. Factor 5 (Ntree) accounted for 6.9% of the variance and had high loadings on NRTRDBH and NRTRHT. Factor 6 (Elev) accounted for 5.3% of the variance and had high salient loadings on ELEV. Factor 7 (Shrub) accounted for 5.1% of the variance and had high salient loadings on SHRUBS and STEMS. Factor 8 (Sapl) had high salient loadings on the variables SDIR and SAPL and accounted for 4.9% of the total variance. The variable OPEN did not load highly (< 0.6) on any factor.

Table 21. Macrohabitat factor correlations for actual Solitary Vireo nests, 1993-1994.

Variable	Factor 1 Trees	Factor 2 Edge	Factor 3 Tsize	Factor 4 Nhuman	Factor 5 Ntree	Factor 6 Elev	Factor 7 Shrub	Factor 8 Sapl
SLOPE	0.07	-0.67	-0.30	0.12	-0.03	0.46	0.21	0.22
SDIR	-0.02	-0.11	-0.26	-0.02	0.42	0.24	-0.02	-0.61
ELEV	0.16	0.05	-0.06	0.22	0.02	0.85	-0.10	0.08
TREES	0.82	-0.13	-0.44	-0.11	-0.24	0.17	-0.12	0.16
SAPL	0.19	-0.19	-0.23	0.08	0.21	0.23	0.15	0.72
MBASAL	-0.41	-0.06	0.79	0.21	0.18	-0.45	0.17	-0.18
BASAL	0.88	-0.04	0.17	-0.11	-0.06	0.07	-0.04	-0.00
MTRHT	0.10	0.10	0.88	-0.13	0.27	0.05	0.02	-0.06
MLBHT	0.71	0.23	0.37	-0.36	-0.01	0.19	-0.26	0.11
SHRUBS	-0.07	-0.36	0.24	0.20	0.18	0.14	0.62	0.16
STEMS	-0.02	-0.10	-0.03	-0.15	-0.02	-0.18	0.73	0.03
NRTRDIST	-0.68	-0.25	0.38	0.29	0.12	-0.38	-0.24	-0.04
NRTRDBH	-0.26	-0.10	0.25	0.24	0.75	-0.36	0.10	-0.03
NRTRHT	-0.06	-0.03	0.35	-0.13	0.86	0.09	0.01	-0.06
GROUND	-0.61	0.05	0.34	-0.12	-0.08	-0.19	0.25	-0.28
CANOPY	0.81	-0.04	-0.05	-0.14	-0.09	0.23	0.11	0.20
ROAD	0.01	0.83	0.07	0.12	-0.07	-0.01	-0.32	0.06
TRAIL	-0.07	-0.15	-0.08	0.90	0.00	0.05	0.03	0.05
OPEN	0.12	0.27	-0.19	-0.20	-0.08	0.18	-0.45	0.42
RIPAR	-0.07	0.76	-0.04	-0.20	-0.15	0.15	-0.06	-0.04
RESID	0.02	0.52	0.18	0.62	0.00	0.27	-0.13	-0.01
TOWN	-0.17	-0.1	-0.23	0.67	0.10	0.42	-0.12	0.21

Table 22. Logistic regression for eight macrohabitat factors. Criteria for model fit $\chi^2 = 10.848$, df = 8, $P = 0.2105$. Of 81 nests, 70.9% were corrrectly classified as parasitized or nonparasitized.

Variable	DF	Parameter Estimate	χ^2 Prob.	Standardized Estimate
Intercept	1	0.1942	0.4178	
Tree	1	-0.2238	0.3830	-0.1234
Edge	1	-0.2950	0.2594	-0.1627
Tsize	1	-0.1946	0.4538	-0.1073
Nhuman	1	0.1458	0.5703	0.0804
Ntree	1	0.1229	0.6360	0.0678
Elev	1	-0.2913	0.2751	-0.1606
Shrub	1	0.2551	0.3409	0.1407
Sapl	1	-0.4301	0.1179	-0.2371

Table 23. Logistic regression for eight macrohabitat factors. Criteria for model fit $\chi^2 = 11.901$, df = 8, $P = 0.1557$. Of 81 nests, 72.3% were corrrectly classified as preyed upon or not preyed upon.

Variable	DF	Parameter Estimate	χ^2 Prob.	Standardized Estimate
Intercept	1	-0.0398	0.8723	
Tree	1	-0.3455	0.1852	-0.1905
Edge	1	-0.3283	0.1934	-0.1810
Tsize	1	0.2120	0.4056	0.1169
Nhuman	1	-0.9179	0.0346	-0.5061
Ntree	1	-0.0490	0.8481	-0.0270
Elev	1	0.3925	0.1613	0.2164
Shrub	1	0.0839	0.7430	0.0463
Sapl	1	-0.0108	0.9644	-0.0060

When the eight macrohabitat factors -- Tree, Edge, Tsize, Nhuman, Ntree, Elev, Shrub and Sapl -- were analyzed in a logistic regression 70.9% of the vireo nests (n = 81) were correctly classified as parasitized or nonparasitized (Table 22), and 72.3% were correctly classified as preyed upon and not preyed (Table 23). Nonparametric discriminant function analysis also revealed no significant relationships between habitat parameters and predation and/or parasitism. A discriminant function analysis correctly classified 70.4% of nests parasitized (n = 44) and 75.7% of nests not parasitized (n = 37), which was not significantly different from nests classified by chance, G = 1.6171, df = 1, $P > 0.05$. 58.5% of nests preyed upon (n = 40) and 75.0% of nests not preyed upon (n = 41) were correctly classified in a discriminant function analysis, which was not significantly different from nests classified by chance, G = 0.8, df = 1, $P > 0.05$.

Macrohabitat variables of Solitary Vireo nest-sites are not good predictors of cowbird parasitism or nest predation, and therefore the macrohabitat hypothesis was rejected.

DISCUSSION

Five of six hypotheses tested to determine the relationship between Solitary Vireo nest-site selection and cowbird parasitism and nest predation were rejected. Increased activity at the nest site did not significantly increase rates of predation. There was not a significant relationship between vireo nest canopy cover and predation or parasitism. Nesting in rare plant substrate did not increase the probability of parasitism or predation in this population. Analysis of 32 nest-site variables in a multivariate analysis revealed no significant associations between characteristics of vegetation near the nest site and parasitism or predation.

The fact that most nests were built low in ponderosa pine trees suggests the importance of aerial predation over ground predator pressure on this population (Nolan 1978, Martin and Roper 1988, Filliater et al. 1994). Arboreal nests subject to high rates of ground predation would be expected to be found higher in trees reducing detection from the ground, while nests subject to high aerial predation would be expected to be found lower in the tree taking advantage of increased canopy cover. However, canopy cover decreases with increasing distance from the trunk, so vireos may nest on distal branch tips to avoid ground predation by large mammals. Based on nest-placement in the nest tree, Solitary Vireos probably make trade-offs by placing nests low avoid aerial predation and high enough and far from the trunk to avoid large ground predators from disturbing the nest.

Distance from edges was found to be significantly related with parasitism and predation, and the edge effect hypothesis was supported. Interestingly, predation was related to human-induced edges, whereas cowbird parasitism was related to both natural and human-induced openings in the ponderosa pine forests.

Edges have received a great deal of attention in recent years although the verdict of under what conditions edge effects occur is still being debated (Paton 1994). Many studies have shown that nest predation and brood parasitism are greater where forests border grasslands and riparian zones (Gates and Gysel 1978, Temple and Carey 1983, Andren 1985, Wilcove et al. 1986, Andren and Angelstram 1988, Gates and Giffen 1991, Andren 1992). Greater levels of predation at these ecotones is due largely to avian predators (corvids) (Angelstram et al. 1985, Andren et al. 1985, Andren 1992, Nour et al. 1993). As the relative abundance of nest predators increases so also do the proportion of nests depredated (Angelstram 1986, Andren 1992). Roads and urbanization create edges along which many predators travel (Burkey 1993, Engels and Saxton 1994), and it is not surprising that predation increases in these areas. Robinson et al. (1995) found that in the northern Midwest states predation increased in urbanized landscapes, and both predation and cowbird parasitism increased in agricultural landscapes. In Boulder County, Solitary Vireo nests are negatively impacted by proximity to roads and residential areas.

Cowbird abundance and parasitism have been shown to decrease with distance from the edge to the forest interior (Gates and Gysel 1978, Brittingham and Temple 1983, Temple and Cary 1988, Yahner and DeLong 1991, O'Conner and Faaborg 1992). Solitary Vireos nesting in the ponderosa pine forests of Boulder County occur in a naturally discontinuous forest landscape with large openings and consequently longer edges. Greater levels of parasitism occur in response to natural edges caused by openings in the forest canopy or breaks in the continuity of the forest, and greater levels of parasitism reduces the reproductive success of vireos placing their nests near such openings. Additionally, cowbird abundance increases in response to human activities which often create foraging opportunities from which they disperse to parasitize nests (Rotbinson et al. 1992). Univariate analysis of this Solitary Vireo population in 1992-1993 by Chace et al. (*in press*) showed significantly higher frequencies of parasitism near towns, roads, and residences. This nest-site analysis of the same population revealed similiar edge effects, and edge effects created by canopy openings which were not analyzed by Chace et al. (*in press*). Further, this study demonstrates that the relevance of the relationship between distance of the nest to human-induced edge is the opening that it creates in the canopy.

Solitary Vireos do not choose nest sites at random, as nest success depends on features of the landscape around the nests. Nests placed near roads, residences, and openings in the forest have a greater chance of being parasitized by cowbirds, or preyed upon. Thus, forest edges act as ecological traps to this population, vireos nest in what appears to be appropriate habitat but where they are not reproductively successful (Chapter 1). Additionally, the effects of roads and residential areas persist for distances greater into ponderosa pine forests (> 800 m) than Wilcove et al. (1986) found in the Appalachian forest (200-500 m). The effect of canopy openings on nest parasitism in pondeosa pine forests persist for distances similar to those previously described (Paton 1994). Thus, the edges act differently in ponderosa pine forests than in other habitats where they have been previously studied. Nest placement by Solitary Vireos clearly makes a difference in nest success. Future studies in this area should focus on the sizes of forest fragment, movements of cowbirds, and abundances of nest predators and cowbirds in relation to edges in ponderosa pine forests.

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Appendix A. Correlation matrix of vegetation variables measured at Solitary Vireo nests sites (81), 1993-1994, and randomly chosen sites (15), 1994.

Variables	NTDBH	NTHT	NTLB	NHT	NTRK	NTIP	NDIR
NTDBH	1.00						
NTHT	0.81	1.00					
NTLB	0.33	0.56	1.00				
NHT	0.28	0.38	0.33	1.00			
NTRK	0.69	0.61	0.25	-0.11	1.00		
NTIP	0.01	0.12	-0.06	-0.07	0.04	1.00	
NDIR	0.06	0.14	0.17	0.15	0.02	0.13	1.00
SLOPE	-0.26	-0.20	-0.18	0.00	-0.08	0.02	0.07
SDIR	-0.02	-0.03	-0.15	-0.11	0.05	0.01	-0.07
ELEV	-0.15	0.01	0.07	0.02	-0.04	0.04	0.00
TREES	-0.38	-0.20	0.24	-0.03	-0.08	0.05	0.14
SAPL	-0.30	-0.26	-0.14	-0.06	-0.20	-0.03	0.02
MBASAL	0.53	0.34	-0.07	0.09	0.32	-0.06	0.01
BASAL	-0.06	0.13	0.38	0.16	0.10	0.01	0.18
MTRHT	0.09	0.24	0.28	0.06	-0.08	-0.03	-0.05
MLBHT	-0.03	0.20	0.57	0.17	-0.02	-0.07	0.12
SHRUBS	-0.04	-0.18	-0.32	-0.01	-0.10	-0.06	-0.08
STEMS	-0.18	-0.30	-0.22	-0.08	-0.12	-0.02	-0.09
NRTRDIST	0.47	0.28	-0.09	-0.02	0.31	-0.03	-0.09
NRTRDBH	-0.04	-0.07	-0.22	-0.11	-0.01	0.03	-0.03
NRTRHT	-0.05	0.04	-0.02	0.02	0.01	0.04	-0.02
GROUND	0.45	-0067	-0.24	0.06	-0.02	-0.07	-0.09
CANOPY	-0.08	0.09	0.29	0.10	0.13	0.02	0.11
ROAD	0.19	0.22	0.27	0.21	0.08	-0.05	-0.10
TRAIL	-0.02	-0.07	-0.11	-0.10	0.10	-0.04	-0.06
OPEN	-0.08	0.01	0.22	-0.11	0.02	-0.05	0.09
RIPAR	0.10	0.19	0.06	0.07	0.05	0.11	0.01
RESID	0.10	0.11	0.12	0.06	0.12	-0.07	-0.08
TOWN	-0.11	-0.06	-0.17-	-0.20	0.08	0.10	-0.10
NRHUMAN	-0.03	-0.14	0.14	-0.17	-0.01	-0.05	-0.12

Appendix A. Continued

Variables	SLOPE	SDIR	ELEV	TREES	SAPL	MBASAL	BASAL	MTRHT
NTDBH								
NTHT								
NTLB								
NHT								
NTRK								
NTIP								
NDIR								
SLOPE	1.00							
SDIR	0.09	1.00						
ELEV	0.37	0.11	1.00					
TREES	0.20	-0.00	0.17	1.00				
SAPL	0.20	-0.11	0.13	0.22	1.00			
MBASAL	-0.28	-0.09	-0.23	-0.53	-0.10	1.00		
BASAL	0.00	-0.02	0.16	0.68	0.15	-0.03	1.00	
MTRHT	-0.13	-0.04	0.04	-0.04	-0.06	0.16	0.17	1.00
MLBHT	-0.14	-0.09	0.15	0.40	0.06	-0.08	0.66	0.44
SHRUBS	0.23	-0.02	-0.04	-0.16	0.17	0.20	-0.01	0.20
STEMS	0.01	-0.03	-0.15	-0.06	0.05	0.12	-0.01	-0.02
NRTRDIST	-0.13	-0.01	-0.24	-0.54	-0.12	0.49	-0.43	-0.04
NRTRDBH	-0.12	0.03	-0.24	-0.32	0.04	0.42	-0.10	0.03
NRTRHT	-0.11	0.14	0.11	-0.18	0.09	0.28	0.11	0.23
GROUND	-0.18	-0.15	-0.22	-0.56	-0.24	0.34	-0.46	0.10
CANOPY	0.13	-0.05	0.22	0.66	0.23	-0.18	0.74	0.16
ROAD	-0.35	-0.11	0.09	-0.05	-0.06	-0.05	-0.00	-0.01
TRAIL	0.16	0.01	0.15	-0.01	-0.00	0.05	-0.08	-0.10
OPEN	-0.07	-0.03	0.10	0.16	0.03	-0.24	0.04	-0.01
RIPAR	-0.21	-0.07	0.10	-0.13	-0.17	-0.13	-0.15	0.03
RESID	-0.14	0.03	0.43	-0.06	0.01	0.04	0.06	-0.00
TOWN	0.30	0.06	0.41	-0.03	0.15	-0.12	-0.18	-0.13
NRHUMAN	0.16	-0.05	0.08	-0.03	-0.07	-0.03	-0.16	-0.12

Appendix A. Continued

Variables	MLBHT	SHRUBS	STEMS	NRTRDIS	NRTRDBH	NRTRHT	GROUND	CANOPY
NTDBH								
NTHT								
NTLB								
NHT								
NTRK								
NTIP								
NDIR								
SLOPE								
SDIR								
ELEV								
TREES								
SAPL								
MBASAL								
BASAL								
MTRHT								
MLBHT	1.00							
SHRUBS	-0.06	1.00						
STEMS	-0.10	0.18	1.00					
NRTRDIST	-0.36	0.09	-0.11	1.00				
NRTRDBH	-0.14	0.12	0.04	0.23	1.00			
NRTRHT	0.21	0.16	-0.02	0.09	0.57	1.00		
GROUND	-0.31	0.15	0.03	0.28	0.16	0.06	1.00	
CANOPY	0.51	0.01	0.04	-0.51	-0.19	0.06	-0.39	1.00
ROAD	0.15	-0.18	-0.22	-0.10	-0.05	0.01	0.00	0.01
TRAIL	-0.25	0.19	-0.04	0.16	0.12	-0.15	-0.16	-0.13
OPEN	0.21	-0.20	-0.07	-0.07	-0.16	-0.06	-0.26	0.12
RIPAR	-0.01	-0.25	-0.08	-0.19	-0.13	-0.10	-0.00	-0.10
RESID	0.13	0.00	-0.16	-0.06	0.01	-0.04	-0.09	0.04
TOWN	-0.25	-0.01	-0.17	0.08	0.02	-0.05	-0.16	-0.09
NRHUMAN	-0.27	0.06	0.01	0.11	0.03	-0.15	0.05	-0.12

Appendix A. Continued

Variables	ROAD	TRAIL	OPEN	RIPAR	RESID	TOWN	NRHUMAN
NTDBH							
NTHT							
NTLB							
NHT							
NTRK							
NTIP							
NDIR							
SLOPE							
SDIR							
ELEV							
TREES							
SAPL							
MBASAL							
BASAL							
MTRHT							
MLBHT							
SHRUBS							
STEMS							
NRTRDIST							
NRTRDBH							
NRTRHT							
GROUND							
CANOPY							
ROAD	1.00						
TRAIL	-0.00	1.00					
OPEN	0.20	-0.07	1.00				
RIPAR	0.40	-0.16	0.13	1.00			
RESID	0.60	0.43	0.07	0.17	1.00		
TOWN	0.09	0.54	-0.01	-0.07	0.40	1.00	
NRHUMAN	0.24	0.51	-0.06	-0.06	0.34	0.37	1.00

Appendix B. Correlation matrix of Solitary Vireo nest-site variables, 1993-1994.

Variables	NTDBH	NTHT	NTLB	NHT	NTRK	NTIP	NDIR
NTDBH	1.00						
NTHT	0.83	1.00					
NTLB	0.33	0.50	1.00				
NHT	0.41	0.50	0.37	1.00			
NTRK	0.82	0.72	0.33	0.22	1.00		
NTIP	0.01	0.13	-0.08	-0.10	0.02	1.00	
NDIR	0.08	0.17	0.21	0.29	-0.00	0.13	1.00
NCC	-0.42	-0.38	-0.21	-0.15	-0.34	0.10	0.02
NGC	0.31	0.23	-0.18	-0.08	0.34	0.19	-0.13
SLOPE	-0.28	-0.24	-0.21	-0.26	-0.14	0.01	0.07
SDIR	-0.05	-0.07	-0.20	-0.11	-0.05	-0.00	-0.07
ELEV	-0.16	-0.04	0.01	-0.10	-0.12	0.04	-0.02
TREES	-0.42	-0.29	0.19	-0.08	-0.22	0.04	0.13
SAPL	-0.28	-0.25	-0.13	-0.14	-0.28	-0.03	-0.02
MBASAL	0.58	0.39	-0.06	0.24	0.39	-0.06	-0.00
BASAL	-0.06	0.06	0.33	0.20	0.03	0.00	0.17
MTRHT	0.27	0.32	0.12	0.33	0.11	-0.12	0.09
MLBHT	-0.06	0.09	0.50	0.24	-0.09	-0.08	0.14
SHRUBS	-0.05	-0.20	-0.43	-0.07	-0.04	-0.06	-0.08
STEMS	-0.18	-0.31	-0.23	-0.09	-0.18	-0.03	-0.09
NRTRDIST	0.50	0.36	-0.04	0.00	0.39	-0.04	-0.07
NRTRDBH	0.01	-0.02	-0.20	-0.07	-0.01	0.04	-0.04
NRTRHT	-0.01	0.02	-0.10	-0.02	-0.01	0.04	-0.00
GROUND	0.34	0.16	-0.26	0.03	0.26	-0.06	-0.09
CANOPY	-0.12	-0.05	0.20	0.03	0.02	0.03	0.11
ROAD	0.21	0.24	0.26	0.20	0.13	-0.05	-0.10
TRAIL	-0.01	-0.04	-0.06	-0.17	0.12	-0.05	-0.06
OPEN	-0.09	-0.03	0.21	-0.09	-0.07	-0.06	0.09
RIPAR	0.11	0.21	0.08	0.17	0.05	0.11	0.01
RESID	0.10	0.10	0.09	0.05	0.08	-0.08	-0.08
TOWN	-0.13	-0.06	-0.16	-0.29	0.02	0.10	-0.08
NRHUMAN	0.01	-0.08	-0.02	-0.23	0.11	-0.06	-0.10

Appendix B. Continued

Variables	NCC	NGC	SLOPE	SDIR	ELEV	TREES	SAPL	MBASAL
NTDBH								
NTHT								
NTLB								
NHT								
NTRK								
NTIP								
NDIR								
NCC	1.00							
NGC	-0.01	1.00						
SLOPE	0.17	-0.12	1.00					
SDIR	-0.14	-0.04	0.07	1.00				
ELEV	0.18	-0.09	0.29	0.09	1.00			
TREES	0.27	-0.28	0.21	-0.03	0.11	1.00		
SAPL	0.16	-0.18	0.23	-0.11	0.12	0.21	1.00	
MBASAL	-0.16	0.25	-0.26	-0.10	-0.23	-0.58	-0.17	1.00
BASAL	0.17	-0.19	0.01	-0.04	0.09	0.66	0.07	-0.08
MTRHT	-0.02	0.12	-0.15	-0.07	0.07	-0.30	-0.09	0.58
MLBHT	0.12	-0.13	-0.13	-0.12	0.09	0.36	0.04	-0.10
SHRUBS	-0.03	0.06	0.33	-0.00	0.02	-0.14	0.16	0.21
STEMS	-0.09	0.10	-0.01	-0.04	-0.17	-0.07	0.04	0.12
NRTRDIST	-0.07	-0.36	-0.08	-0.03	-0.16	-0.56	-0.14	0.51
NRTRDBH	-0.04	0.04	-0.10	0.05	-0.25	-0.33	0.00	0.39
NRTRHT	-0.00	0.06	-0.13	0.19	0.07	-0.25	0.02	0.25
GROUND	-0.09	-0.08	-0.17	-0.06	-0.15	-0.54	-0.26	0.41
CANOPY	0.11	0.31	0.15	-0.10	0.15	0.65	0.22	-0.26
ROAD	-0.10	-0.20	-0.50	-0.12	0.00	-0.09	-0.08	-0.04
TRAIL	-0.06	-0.17	0.19	0.02	0.24	0.02	0.03	0.06
OPEN	0.09	-0.07	-0.06	-0.06	0.09	0.12	0.04	-0.27
RIPAR	0.01	-0.02	-0.33	-0.10	0.04	-0.14	-0.16	-0.10
RESID	-0.08	-0.14	-0.22	0.01	0.40	-0.12	-0.00	0.06
TOWN	-0.08	0.03	0.29	0.02	0.46	-0.05	0.19	-0.12
NRHUMAN	-0.10	-0.22	0.14	-0.03	0.16	0.08	-0.01	-0.03

Appendix B. Continued

Variables	BASAL	MTRHT	MLBHT	SHRUBS	STEMS	NRTRDIS	NRTRDBH	NRTRHT
NTDBH								
NTHT								
NTLB								
NHT								
NTRK								
NTIP								
NDIR								
NCC								
NGC								
SLOPE								
SDIR								
ELEV								
TREES								
SAPL								
MBASAL								
BASAL	1.00							
MTRHT	0.27	1.00						
MLBHT	0.63	0.52	1.00					
SHRUBS	0.01	0.22	-0.11	1.00				
STEMS	-0.02	0.00	-0.11	0.19	1.00			
NRTRDIST	-0.45	0.16	-0.36	0.06	-0.12	1.00		
NRTRDBH	-0.13	0.18	-0.15	0.12	0.03	0.25	1.00	
NRTRHT	-0.01	0.45	0.13	0.17	-0.02	0.16	0.57	1.00
GROUND	-0.44	0.09	-0.31	0.09	0.06	0.31	0.15	0.06
CANOPY	0.70	0.06	0.45	0.07	0.04	-0.52	-0.20	-0.02
ROAD	-0.07	-0.00	0.11	-0.23	-0.26	-0.07	-0.04	-0.04
TRAIL	-0.03	-0.15	-0.26	0.22	-0.05	0.15	0.11	-0.17
OPEN	-0.01	-0.10	0.19	-0.19	-0.08	-0.06	-0.17	-0.08
RIPAR	-0.14	0.02	0.02	-0.23	-0.08	-0.18	-0.12	-0.07
RESID	-0.01	0.13	0.08	0.06	-0.19	-0.03	0.03	-0.08
TOWN	-0.20	-0.20	-0.29	0.01	-0.21	0.07	0.02	-0.04
NRHUMAN	-0.09	-0.23	-0.27	0.11	-0.07	0.20	-0.02	-0.23

Appendix B. Continued

Variables	GROUND	CANOPY	ROAD	TRAIL	OPEN	RIPAR	RESID	TOWN	NRHUMAN
NTDBH									
NTHT									
NTLB									
NHT									
NTRK									
NTIP									
NDIR									
NCC									
NGC									
SLOPE									
SDIR									
ELEV									
TREES									
SAPL									
MBASAL									
BASAL									
MTRHT									
MLBHT									
SHRUBS									
STEMS									
NRTRDIST									
NRTRDBH									
NRTRHT									
GROUND	1.00								
CANOPY	-0.32	1.00							
ROAD	-0.00	-0.03	1.00						
TRAIL	-0.23	-0.06	0.01	1.00					
OPEN	-0.22	0.06	0.23	-0.06	1.00				
RIPAR	0.03	-0.11	0.50	-0.14	0.14	1.00			
RESID	-0.04	-0.02	0.54	0.50	0.05	0.21	1.00		
TOWN	-0.12	-0.09	0.04	0.55	-0.02	-0.06	0.38	1.00	
NRHUMAN	-0.22	-0.07	0.16	0.84	-0.01	-0.09	0.45	0.40	1.00