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THE EFFECT OF PREDATION AND BROOD PARASITISM ON SOLITARY VIREOS NESTING IN THE FOOTHILLS OF BOULDER COUNTY

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INTRODUCTION

Neotropical migratory songbirds have received a great deal of attention due to the recent population declines of many species (Wilcove and Whitcomb 1983, Robbins et al. 1989, Terborgh 1989, Finch 1991). Previously, wintering ground tropical deforestation was believed to be the cause of migrant declines (Morse 1980, Terborgh 1980, Rappole and Morton 1985, Terborgh 1989). Recently, habitat loss, habitat fragmentation, and human related disturbance on the breeding grounds are thought to be, at least, equally detrimental to these populations (Morton 1980, Wilcove and Whitcomb 1983, Wilcove and Terborgh 1984, Hutto 1988, Askins et al. 1990).

Forest fragmentation by human related disturbance (e.g. roads, clearcut logging, residential development) decreases the patch size of intact forest and increases the area of edge to interior ratio. These edge effects result in the decline of reproductive success of nesting migrants due to an increase in 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 increased with an increase in distance to edge. Similarly, Wilcove (1985) found higher nest predation on smaller woodlots, than lager woodlots, where there was a greater edge to interior area. Brown-headed Cowbirds (*Molothrus ater*) are brood parasites which have shown a recent range expansion with increasing fragmentation of eastern forests and livestock movement into forested areas (Mayfield 1965, Brittingham and Temple 1983, Rothstein et al. 1980, 1984). High rates of cowbird parasitism is strongly correlated with forest patch size in the midwest (Robinson 1992). Neotropical migrants typically accept cowbird eggs and are highly parasitized by cowbirds which usually results in a reduction of nest success as the parents raise a young cowbird (Payne 1977). Elevated rates of cowbird parasitism and nest predation in fragmented and disturbed landscapes can 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 which breeds in the temperate forests throughout North America (AOU 1983). A localized population breeding in the greenbelt surrounding the highly urbanized city of Boulder, Colorado was studied by Marvil and Cruz (1989). They determined that nearly 50% of the vireo nests in this population were parasitized by Brown-headed Cowbirds, resulting in significantly reduced reproductive success, and speculated that this population may be a "sink" replaced by emmigrants from some "source" population (Marvil and Cruz 1989). However, rates of nest predation have not been reported, and the effects of parasitism and predation have not been modeled, for this population.

The purpose of this paper is to determine the impact of nest predation and brood parasitism on the reproductive success of Solitary Vireos breeding in the foothills of Boulder, Colorado. The effects of parasitism and predation are determined for this population as a test of a "sink" population model proposed by Marvil and Cruz (1989).

METHODS

This study was conducted during the summers of 1993-1994 in the foothills of western Boulder County, Colorado. Study sites were on City of Boulder Mountain Parks and Open Space, Boulder County Open Space, and Roosevelt National Forest and ranged in elevation from 1,800 m to 2,400 m (Fig. 1). The vegetation of the field sites was dominated by a ponderosa pine (*Pinus ponderosa*) overstory interspersed with Douglas fir (*Psuedotsuga menziesii*). The understory was dominated by chokecherry (*Prunus virginiana*), wax current (*Ribes cereum*), skunkbrush (*Rhus aromatica*), small ninebark (*Physocarpus monogynus*), Oregon grape (*Mahonia repens*), and various grasses (*Bromus, Achillia,* and *Artemesia*).

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 attaction of nest predators to the nest site (Major 1990, MacIvor et al. 1990, Ralph et al. 1993). Only nests in which eggs were laid (active nests) were used in the analysis. The outcome 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 was taken on 54 vireo nestlings and 9 cowbird nestlings. Weights (nearest 0.1 g) were taken with 30- and 50-g Pesola spring scales.

Only nests in which the final outcome were known were included in the analysis. Nesting success was calculated using the

Mayfield Method (1975) to reduce the error induced 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 data were not normally distributed.

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. Frequency of parasitism and predation were both independent of year and therefore data for both years are combined (Table 1 and 2). Predation upon vireo nests was independent of parasitism, therefore a nest that was parasitized did not have a greater likelihood of being preyed upon than a nonparasitized nest (Table 3).

The percentage of initiated Solitary Vireo nests parasitized increased as the breeding season progressed (Fig. 2). The majority of cowbird eggs (67.2%, N =61) were laid during vireo egg-laying. Cowbird eggs hatched ca. 11 days of incubation and fledged ca. 11 days later. Solitary Vireo eggs hatched ca. 16 days of incubation and fledged ca. 14 days later. The majority of parasitized nests contained one cowbird egg (70.4%, N= 44), 10 nests (22.7%) contained two cowbird eggs, 2 nests (4.5%) contained 3 cowbird eggs, and 1 nest (2.3%) contained 4 cowbird eggs. Nest desertion was rare. The one deserted nest was parasitized prior to clutch initiation.

Clutch size of parasitized vireo nests were smaller than nonparasitized nests, however the difference was not significant (Table

4). Cowbird host egg ejection may account for the smaller clutch size of parasitized vireo nests. Egg removal was suspect in 5 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 egg hatched than nonparasitized nests (Table 5). Nonparasitized nests fledged significantly more vireos per nest (1.51) than parasitized nests (0.26) (Table 5). Development of vireo chicks in parasitized nests (n= 9) was slower than vireo growth in nonparasitized nests (n= 45) (Fig. 3). Additionally, growth differences between vireos and cowbirds (n= 9) probably accounts for the lower fledging success of vireos in parasitized nests (Fig. 2). Competition probably accounts for the differences in vireo starvation between parasitized nests (16 cases) and nonparasitized nests (0 cases). The presence of a Brown-headed Cowbird chick has a strong negative affect on the growth rate of Solitary Vireos.

The timing of cowbird parasitism had a large effect on the reproductive success of the parasitized vireo nest. Parasitized nests which had cowbirds hatch two or more days ahead of the host young (n= 27) resulted in 2 vireos fledging and 16 cowbirds fledging. In nests where cowbirds were the same age or younger than vireos (n= 6) 0 vireos and 1 cowbird fledged. In this case, success is nearly equal for cowbirds and vireos. Some cowbird eggs did not fledge because the eggs did not hatch (10 eggs), eggs were laid to late (8 eggs), two cowbirds hatched and only one fledged (2 eggs), or due to predation (23 eggs).

Nest predation caused reduced reproductive success in 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. The most common nest predator was probably the Steller's Jays (*Cyanocitta stelleri*) because most nests (95.0%) showed no disturbance to the structure of the nest (i.e. avian predation) and Steller's Jays were common on the study site. Other potential nest predators include the American Crow (*Corvus brachyrhynchos*), Common Raven (*Corvus corax*), Abert's squirrel (*Sciurus aberti*), Colorado chipmunk (*Eutamias quadrivittatus*), and the bull snake (*Pipuophis 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 nest 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 being successful than nonparasitized nests (Table 6).

DISCUSSION

Solitary Vireos nesting in the ponderosa pine foothills along the Colorado Front Range in Boulder County in 1993-1994 had a relatively low probability of successfully fledging young due to nest parasitism and predation. 22.2% of all active nests escaped both predation and parasitism (Table 3). 64 Solitary Vireos fledged from all nests (0.82 per nest) observed during both years of study (Table 5). This resulted in a 27% nest success probability for Solitary Vireo nests (40% nonparasitized, 17% parasitized) (Table 6). This success is similar to other studies of parasitized host species: Abert's Towhee had a 31% nonparasitized and 4.6% parasitized nest success probability (Finch 1983); Eastern Phoebe had a 43% to 61% nest success probability in nonparasitized nests and 0.1% in parasitized nests (Klaas 1993); and cardinals had a 15% overall nest success probability (predation only) (Filliater et al. 1994). Parasitized vireo nests have a higher success than other passerines, however the success of parasitized vireo nests is significantly lower than nonparasitized nests (Table 6). I conclude that nest predation and cowbird parasitism negatively impact the reproductive success of Solitary Vireos in Boulder County.

Cowbird Parasitism

Solitary Vireos accept cowbird eggs. Cowbird parasitism results in reduced reproductive success by: 1. reducing vireo clutch size, 2. cowbirds hatching earlier than vireos, and reduce vireo hatching success, and 3. nestling cowbirds out compete vireo nest-mates for food and space. Cowbirds often remove host eggs when parasitizing a nest (Sealey 1992). In the Solitary Vireo nests studied, parasitized nests had a smaller clutch size (0.27 fewer eggs) than nonparasitized nests and there was direct evidence of egg removal by cowbirds (Table 4). This indicates that female cowbirds remove host eggs from about 25% of nests parasitized.

Several hypotheses have been advanced to explain cowbird host egg removal behavior. Cowbirds may attempt to deceive the host that counts eggs 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). Sealey (1992) showed that cowbirds often remove a host egg from Yellow Warbler (*Dendroica petechia*) nests before laying its own egg, possibly to test the incubation status of the host (Livessey 1936, Sealey 1992). Cowbird host egg removal would possibly 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 one or more host eggs. Sealey (1992) determined that egg removal did not increase the acceptance of cowbird eggs in Yellow Warbler nests, and that warblers did not abandon nests with up to two host eggs removed. It is not clear why Brown-headed Cowbirds remove eggs from Solitary Vireo nests, however any cowbird which ingested a host egg would undoubtedly gain nourishment.

Cowbirds have a shorter incubation period than vireos, and hatch sooner when cowbird eggs are laid during vireo clutch initiation. Nests in which cowbirds lay prior to clutch initiation are likely to be abandoned and the nest not found by an investigator. Cowbirds grow faster and larger than vireo nestlings (Fig. 3) and are able to outcompete their nest-mates for food and space. Only 11 vireos fledged from 44 parasitized nests, of the 49 vireos which hatched the remaining 38 died from nest predation or starvation. By the cowbirds fifth day after hatching it usually took up the space of the entire nest and completely covered vireo nestlings which, then, were not able to receive food from the adults. The cowbird fledges earlier than the vireos and disperses from the nest site by the second day, usually both parents follow the juvenile cowbird and leave any remaining vireo nestlings in the nest to starve. Starvation was the proximate cause of vireo nestling mortality in parasitized nests.

Cowbirds are successful in fledging young from Solitary Vireo nests, nearly half the parasitized nests yield a fledgling whereas vireos are not successful in fledging their own young (Table 5). Solitary Vireos are a good host species for Brown-headed Cowbirds in Boulder County. Even though parasitized vireo nesting success is higher than that for other parasitized species, Abert's Towhee (Finch 1983), Eastern Phoebe (Klaas 1993), Dickcissel (Zimmerman 1983), given the mortality rates of first year passerines parasitized nests probably do not act as net producers of young (CITE). 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 cowbird egg acceptance by cowbird hosts. Rothstein (1975), speculates that hosts long exposed to cowbird parasitism and do not reject cowbird eggs have not evolved the genetic information to preform such a behavior. This is based on the phenomenon of 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 population because of the great reproductive advantage (Rothstein 1975). Solitary Vireos in Boulder County have historically occurred within the range of the Brown-headed Cowbird and most likely parasitism is not a novel phenomenon within this population. Therefore, according to Rothstein hypothesis vireos have not evolved an anti-parasite behavior. Alternatively, Rowher and Spaw (1988) suggest that small hosts are unable to grasp eject cowbird eggs based on bill constraints, and do not puncture eject because the hard shell of the cowbird egg will cause glancing blows to damage the hosts own eggs before the cowbird egg can be removed (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. Consequently, an earlier nest has a lower probability of parasitism than a later nest (Fig. 2), most likely a renest attempt will be parasitized. Additionally, all parasitized nests did not fail completely and it is possible that the fledging one young one year and attempting to nest again in subsequent years out weighs the effort of abandonment and 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.

Cowbird parasitism has a negative effect on vireo nests and caused reduced reproductive success. However, the reduced success is not as low as it is in other host populations and therefore acceptance of the cowbird egg may be better than renesting given the increased probability of parasitism again.

Nest Predation

Nest predators caused the loss of approximately half the active vireo nests on the study sites. Similiarily, Ricklefs (1969) estimated that predation accounts for 55% of egg losses and 66% of nestling losses of 6 passerine species. Predation occurred on 20 (50%) of egg stage and 20 (50%) nestling stage Solitary Vireo nests. Nest predation usually caused a complete nest failure. If predation occurred early in the egg stage the adults would build and a new nest and initiate a new clutch.

However, later nests had a greater chance of parasitism (Fig. 2), the last 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 a predation event.

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 the Solitary Vireo in this area.

Sink Population

Since predation is random with respect to parasitism and equally impacts both parasitized and nonparasitized nests, I determined the maximum rate of parasitism that will allow a host population to replace itself 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 adult mortality of 9 warbler species (in Morse 1989): $\mu = 0.33$, and known juvenile mortalities of Prairie Warbler (*Dendroica discolor*): $\mu_o = 0.67$ (Nolan 1978).

The value of P_c yielded by these calculations is -39.2%. This value is negative because the mortality of females each year is greater than the number of young fledged per nonparasitized nest each year. Which suggests that the present rate brood parasitism strongly decreases the vireo population over time. The strongly negative rate would also suggest that predation has a strong negative effect on the population because of the low number of young fledged per nonparasitized female.

It would appear that 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, and is maintained as a vireo breeding site only because of a "source" population, with lower rates of predation and parasitism overproduces young each year which are forced into the marginal habitat of Boulder County.

I tested the population "sink" hypothesis for this population first proposed by Marvil and Cruz (1989), using the above estimates of mortality and assuming complete recruitment of females back into the population and zero emmigration. The calculated population growth of the Solitary Vireo population (N=35 in 1994) in strongly negative and quickly goes to zero in 16 years (2010) (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 emmigration from other "source" areas which probably have a positive net production of young. While this is a hypothetical curve with weak assumptions it points to the strong negative impact of cowbird parasitism and nest predation on this neotropical migrant population.

Why is cowbird parasitism and nest predation 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 area 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. Frequency of predation and parasitism is similar to that 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 the population. Cowbird parasitism results in almost complete nest failure for the hosts while nearly half fledge cowbird young. Nests which are preyed upon result in total nest loss but often allows the adults to renest. Ultimately, few nests are successful and this population is only able to sustain itself with the emmigration of vireos from other areas. Human caused disturbance and fragmentation of the lower elevation ponderosa pine, where the vireos nest, may possibly increase rates of parasitism and predation beyond which the population is able sustain itself.

LITERATURE CITED

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Ambuel, B. and S. A. Temple. 1983. Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64: 1057-1068.

American Ornithologists' Union. 1983. Check-list of north American birds, 6th ed. Washington, D. C. American Ornithol. Union.

Askins, R. A., J. F. Lynch, and R. Greenburg. 1990. Population declines in migratory birds in eastern north America. Current Ornithology 7: 1-57.

Blankespoor, G. W., J. Oolman, and C. Uthe. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. Auk 99: 363-365.

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33: 31-35.

Davies, N. B. and M. DeL. Brook. 1988. Cuckoos versus Reed Warblers: adaptations and counter-adaptations. Anim. Behav. 36: 262-284.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96: 761-768.

Finch, D. M. 1983. Brood parasitism of the Abert's Towhee: timing, frequency, and effects. Condor 85: 355-359.

Finch, D. M. 1991. Population ecology, habitat requirements and conservation of neotropical migratory birds. Gen. Tech. Rep. RM-205. Fort Collins, CO U.S. Dept. Agric., Forest Service. Rocky Mountain Forest and Range Experiment Station.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59: 871-883.

Hamilton, W. J. III, and G. H. Orians. 1965. Evolution of brood parasitism in altricial birds. Condor 67: 361-382.

Hutto, R. L. 1988. Is tropical deforestation responsible for the reported declines in neotropical migrant populations? American Birds 42: 375-379.

Livesey, T. R. 1936. Cuckoo problems. J. Bombay Nat. Hist. Soc. 38: 734-758.

MacIvor, L. H., S. M. Melvin, and C. R. Griffin. 1990. Effects of research activity on Piping Plover nest predation. J. Widl. Manag. 54:443-447.

Major, R. E. 1990. The effect of human observers on the intensity of nest predation. Ibis 132: 608-612.

Marvil, R. E. and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism in the reproductive success of the Solitary Vireo. Auk 106: 4760-480.

May, R. M. and S. K. Robinson. 1985. Population dynamics of avian brood parasitism. Am. Nat. 126:475-494.

Mayfield, H. 1965. The Brown-headed Cowbird with new and old hosts. Living Bird 4:13-28.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456-466.

Morse, D. H. 1980. Population limitation: breeding or wintering grounds? Pp. 505-516 in, Keast, A. and E. S. Morton eds., Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithson. Inst. Press, Washington, D.C.

Morse, D. H. 1989. American Warblers: an ecological and behavioral perspective. Havard University Press, Cambridge, MA.

Nolan Jr., V. 1978. The ecology and behavior of the Prairie Warbler, Denroica discolor. Ornithol. Monogr. 26.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Albany, CA, U.S. Dept. Agric., Forest Service. Pacific Southwest Research Station.

Rappole, J. H., and E. S. Morton. 1985. Effects of habitat alteration on a tropical avian forest community. Ornithol. Monogr. 36: 1013-1021.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9.

Robbins, C. S., J. R. Sauer, R. S. Greenburg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86: 7658-7662.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pp. 408-418 in, Hagan III, J. M. and D. W. Johnston eds., Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington D.C.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S. I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97: 253-267.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65: 77-88.

Rowher, S. and C. D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evolutionary Ecology 2: 27-36.

Scott, D. M. and C. D. Ankney. 1980. Fecundity of the Brown-headed Cowbird in Southern Ontario. Auk 97: 677-683.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94: 40-54.

Spaw, C. D. and S. Rowher. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89: 307-318.

Temple, S. A. and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2: 340-347.

Terborgh, J. W. 1980. The conservation status of neotropical migrants: present and future. Pp. 21-30 in, Keast, A. and E. S. Morton eds., Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithson. Inst. Press, Washington, D.C.

Terborgh, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, NJ.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pp. 237-256 in Soule, M. E. ed., Conservation biology: science of diversity. Sinauer Associates, Sunderland, MA.

Wilcove, D. S. and J. W. Terborgh. 1984. Patterns of population declines in birds. American Birds 38: 10-13.

Wilcove, D. S. and R. F. Whitcomb. 1983. Gone with the trees. Nat. Hist. 1983 (9): 83-91.

Yahner, R. H. and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. J. Wildl. Manag. 52: 158-161.

Zimmerman, J.L. 1983. Cowbird parasitism of Dickcissels in different habitats and at different nest densities. Wilson Bull. 95: 7-22.

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 Solitatry 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 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 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 fledge per egg hatched between nonparasitized and parasitized nests are significant (G= 21.3819, df = 1, $p < 0.01$).

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

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

	Probability of Survival [a]		
	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

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

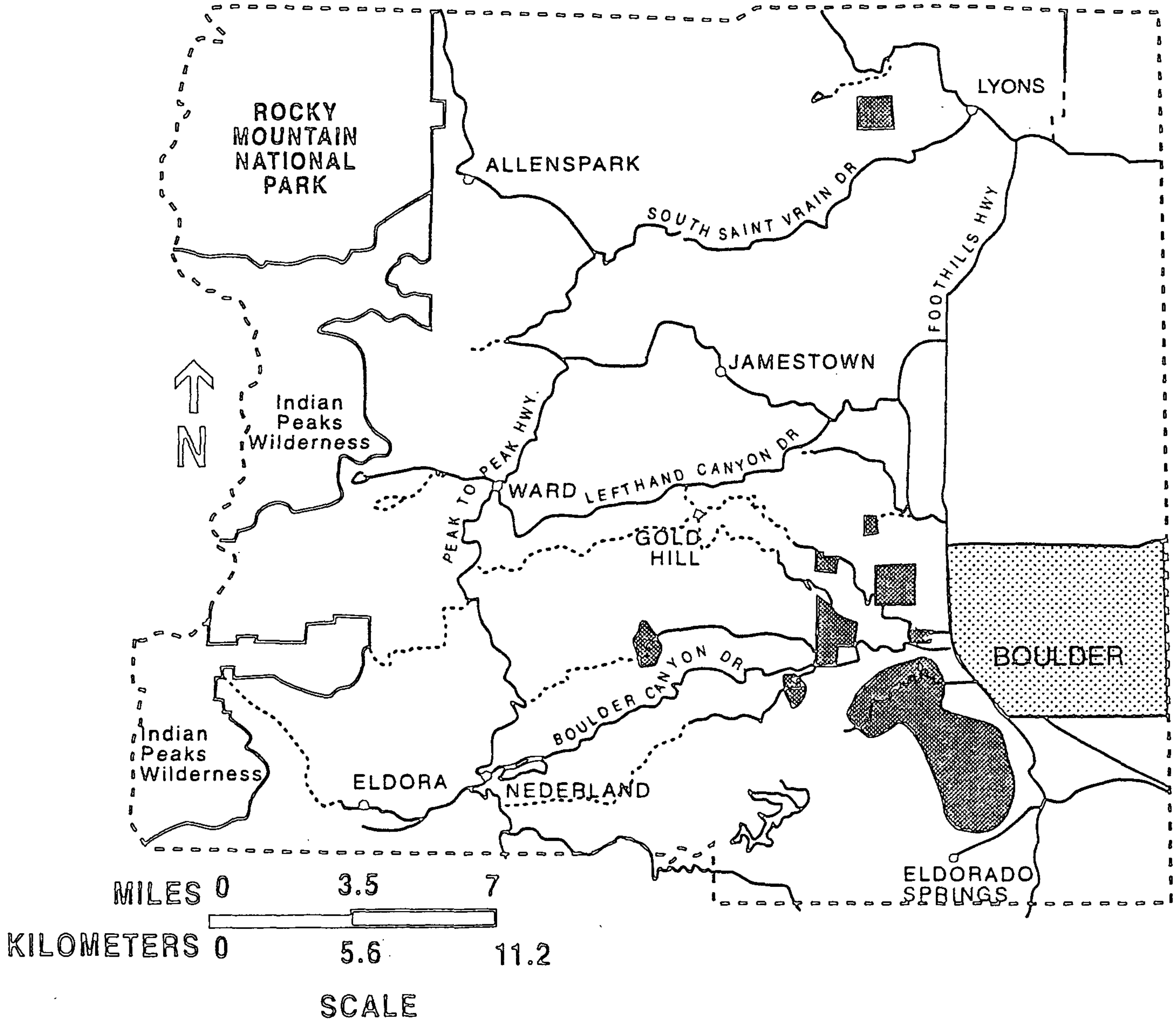
FIGURE CAPTIONS

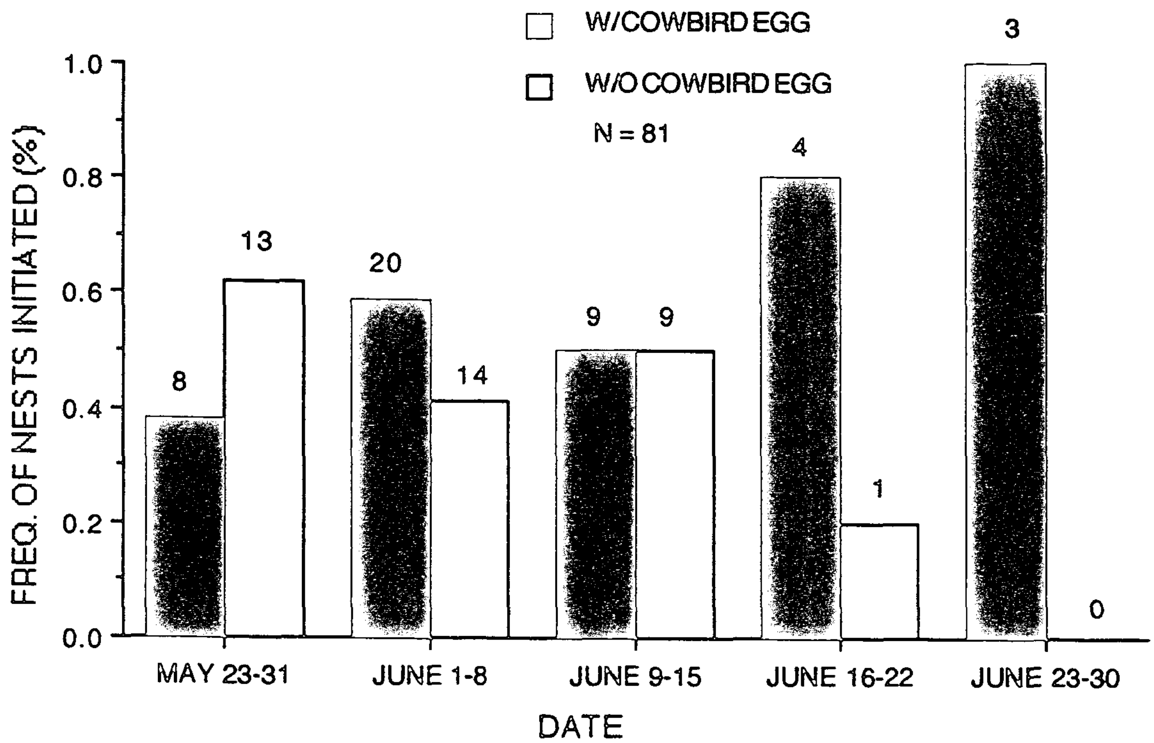
Figure 1. Solitary Vireo study sites hatched on map, Boulder County, Colorado.

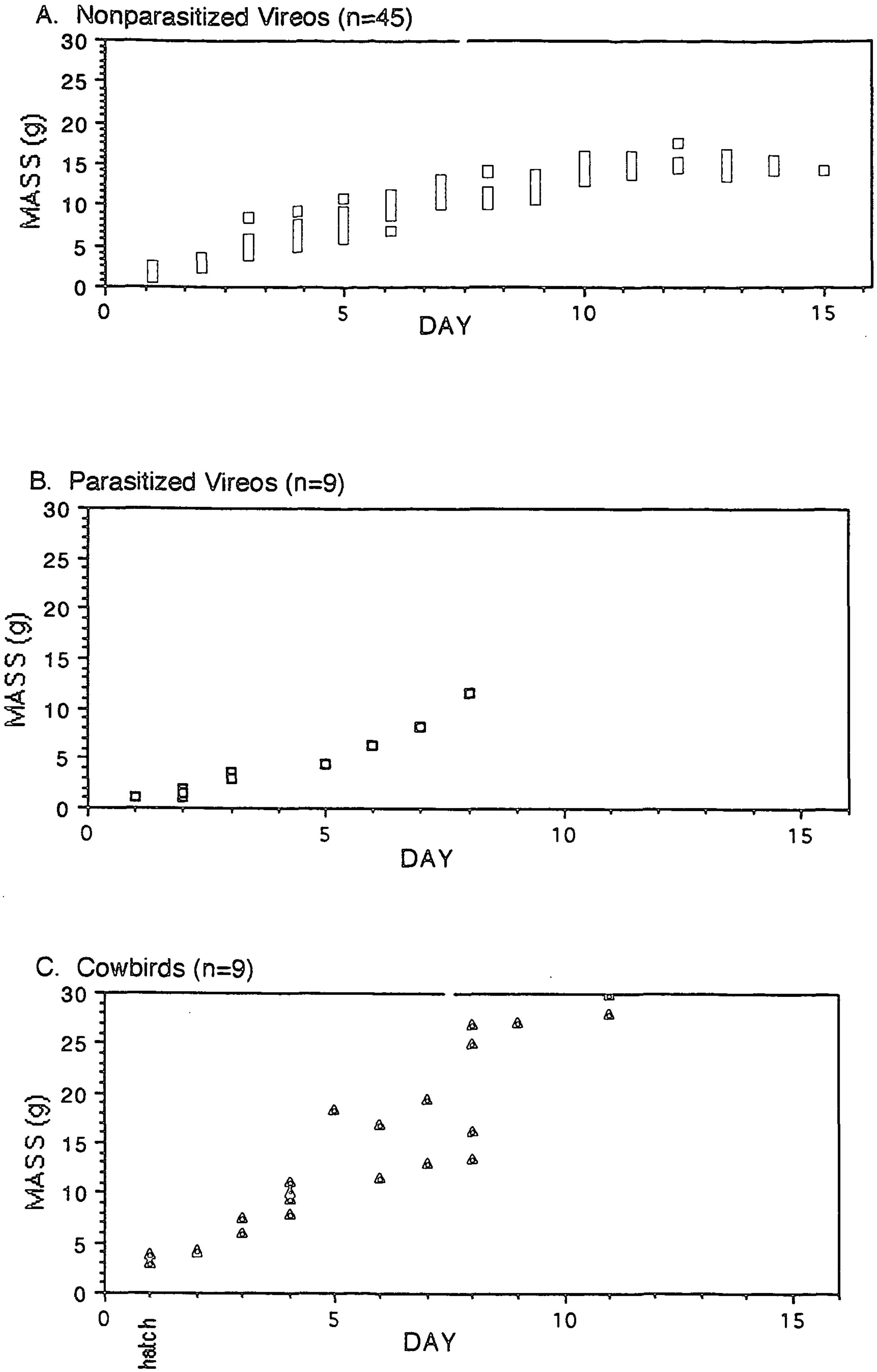
Figure 2. Frequency of cowbird parasitism on Solitary Vireo nests by date of nest initiation.

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: $y = 2.66x - 0.478$, $R^2 = 0.868$, $F = 150.635$, $p = 0.0001$.

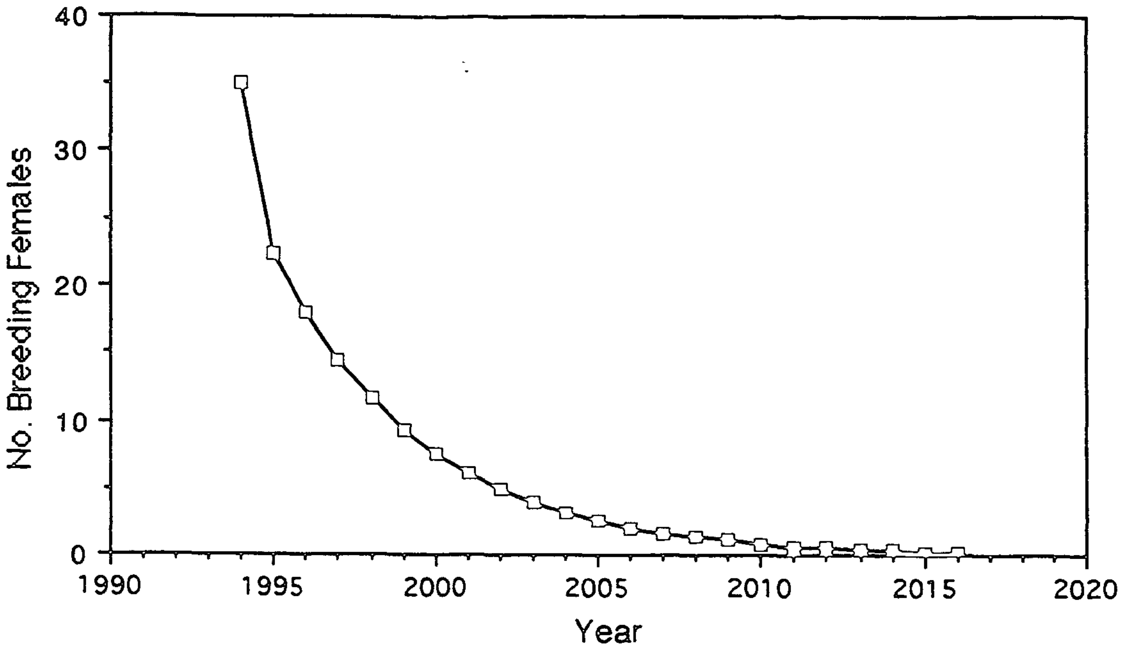
Figure 4. Hypothetical growth curve for the Solitary Vireo population in Boulder County, Colorado. Population size beginning in 1994 is 35 females. Growth curve is a test of the population "sink" hypothesis in which there is no immigration into, or out of, the population, and there is complete recruitment of females back into the breeding population. Curve shows that the population is unable to maintain itself without immigration given set rates of mortality, cowbird parasitism, and nest predation.


ROCKY MOUNTAIN NATIONAL PARK
ALLENSPARK
LYONS
SOUTH SAINT VRAIN DR
FOOTHILLS HWY
JAMESTOWN
N
Indian Peaks Wilderness
PEAK TO PEAK HWY
WARD
LEFTHAND CANYON DR
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


W/COWBIRD EGG
W/O COWBIRD EGG
N = 81
FREQ. OF NESTS INITIATED (%)
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



A. Nonparasitized Vireos (n=45)
MASS (g)
DAY
B. Parasitized Vireos (n=9)
MASS (g)
DAY
C. Cowbirds (n=9)
MASS (g)
DAY
hatch



40
30
20
10
0
No. Breeding Females
1990
1995
2000
2005
2010
2015
2020
Year