USACERL Technical Report EN-94/01, Vol III
November 1993

US Army Corps
of Engineers
Construction Engineering
Research Laboratories

(2)

Status of the Black-capped Vireo at Fort Hood, Texas, Volume III: Population and Nesting Ecology

by
David J. Tazik
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The black-capped vireo is an endangered species that resides at Fort Hood, TX during the summer breeding season. A 3-year ecological status survey of the black-capped vireo was conducted on Fort Hood from 1987 through 1989 as part of the effort to fully comply with the Endangered Species Act. Volume I in this series focuses on vireo distribution and abundance, and Volume II on habitat.

This study detailed the population and nesting ecology of the black-capped vireo to document annual survival, site tenacity, reproductive success and production, and evaluate limiting factors, including military activity. Annual survival was estimated at 60 percent for adults and 30 percent for juveniles. Presently, cowbird nest parasitism is the most critical factor limiting vireo reproductive success. Analysis of cowbird control showed that efforts attempted during 1988 and 1989 were ineffective; cowbird removal success would have to increase tenfold to be effective. Vireo production was found to be a linear decreasing function of percent parasitism. A stable population (2.67 young/pair/year) would require that parasitism be reduced to 16 to 38 percent, and an increasing population (3.0 young/pair/year) would require that parasitism be reduced to 3 to 30 percent. Military activities appear to have little impact on vireo survival and reproductive success.

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REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. AGENCY USE ONLY (Leave Blank)

2. REPORT DATE
November 1993

3. REPORT TYPE AND DATES COVERED
Final

4. TITLE AND SUBTITLE
Status of the Black-capped Vireo at Fort Hood, Texas, Volume III: Population and Nesting Ecology

5. FUNDING NUMBERS
IAO 348-87, 66-88, and 268-88;
FAD 89-080046;
MIPR JE26-91

6. AUTHOR(S)
David J. Tazik and John D. Cornelius

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
U.S. Army Construction Engineering Research Laboratories (USACERL)
P.O. Box 9005
Champaign, IL 61826-9005

8. PERFORMING ORGANIZATION REPORT NUMBER
TR EN-94/01, Vol III

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Commander
HQ III Corps and Fort Hood
Fort Hood, TX 76544-5000

ACSIM
ATTN: DAIM-ED-N
600 Army Pentagon
Washington, DC
20310-0600

HQ FORSCOM
ATTN: FCEN-CED
Ft. McPherson, GA
30330-6000

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES
Copies are available from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

12a. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT (Maximum 200 words)

The black-capped vireo is an endangered species that resides at Fort Hood, TX during the summer breeding season. A 3-year ecological status survey of the black-capped vireo was conducted on Fort Hood from 1987 through 1989 as part of the effort to fully comply with the Endangered Species Act. Volume I in this series focuses on vireo distribution and abundance, and Volume II on habitat.

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14. SUBJECT TERMS
black-capped vireo
Fort Hood, TX
endangered species
military training
cowbird parasitism

15. NUMBER OF PAGES
108

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
Unclassified	Unclassified	Unclassified	SAR

FOREWORD

This study was conducted for HQ III Corps and Fort Hood under Project Intra-Army Order (IAO) Nos. 348-87, 66-88, and 268-88; for the U.S. Army Center for Public Works (USACPW), Fort Belvoir, VA, under Funding Authorization Document (FAD) No. 89-080046; and for HQ, Forces Command (HQFORSCOM) under Military Interdepartmental Purchase Request (MIPR) JE 26-91.

The work was performed by the Natural Resources Division (EN) of the Environmental Sustainment Laboratory (EL), U.S. Army Construction Engineering Research Laboratories (USACERL). The Principal Investigator was Dr. David J. Tazik. Dan Salzer and Geralyn Larkin (Hillsboro, OR) conducted much of the field work during 1988 and 1989, including banding, and territory and nest monitoring. They also assisted in data compilation and contributed many suggestions and insight to the benefit of the project. Dennis Herbert and B.R. Jones (Fish and Wildlife Branch, Fort Hood) were most helpful in identifying potential vireo colony sites, coordinating research activities, assisting researchers in gaining access to various areas of the Fort, and assisting in various aspects of the field work. Grant Critchfield (Salado, TX) assisted in cowbird trapping during 1988. Doug Short (Missouri Valley, IA) and Carolyn Bachler (Chicago, IL) trapped cowbirds during 1989. Rus Allen (Scheduling Branch, Fort Hood) and personnel of the Fort Hood Range Control Office coordinated researcher access to colony sites within the live fire training area. David Kowalski (USACERL) created the program to evaluate potential vireo production in parasitized and unparasitized populations based on Nolan's model. Shelia Mochel (USACERL) digitized the vireo territories and assisted with other data entry. Dr. Joseph Grzybowski (University of Oklahoma, Norman) provided many helpful suggestions throughout the course of the study. Robin Musson assisted in compiling the final report. Dr. William D. Goran is Acting Chief, CECER-EL. The USACERL technical editor was William J. Wolfe, Information Management Office.

LTC David J. Rehbein is Commander of USACERL and Dr. L.R. Shaffer is Director.

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1 INTRODUCTION

Background

The U.S. Army is responsible for managing 12.4 million acres of land on 186 major installations worldwide (U.S. Department of the Army [DA] 1989). Many of these lands are used for military training and testing activities, and many are also managed for nonmilitary uses, including fish and wildlife, forest products, recreation, agriculture, and grazing. Proper land management supports the military mission and multiple use activities, but also presents the Army with a unique challenge as a public land steward.

In its effort to promote responsible land stewardship, the Army has initiated the Land Condition-Trend Analysis (LCTA) program, which uses standard methods to collect, analyze, and report natural resources data (Tazik et al. 1992a), and which is the Army's standard for land inventory and monitoring (U.S. Army Engineering and Housing Support Center 1990). LCTA is a major component of the Integrated Training Area Management (ITAM) program, both developed at the U.S. Army Construction Engineering Research Laboratories (USACERL). The three other components of ITAM include: (1) Environmental Awareness, (2) Land Rehabilitation and Maintenance, and (3) Training Requirements Integration. LCTA promotes the principles of sustained yield, land stewardship, and multiple use of military land resources. The major objectives of LCTA are to: (1) characterize installation natural resources, (2) implement standards in collection, analysis, and reporting of the acquired data that enable compilation and evaluation of these data Army-wide, (3) monitor changes in land resource condition and evaluate changes in terms of current land uses, (4) evaluate the capability of land to meet the multiple-use demands of the U.S. Army on a sustained basis, (5) delineate the biophysical and regulatory constraints to uses of the land, and (6) develop and refine land management plans to ensure long-term resource availability.

Such programs help the Army comply with a variety of environmental regulations based on such legislation as the National Environmental Policy Act, the Endangered Species Act, and the Clean Water Act (Donnelly and Van Ness 1986). These regulations require land management personnel at Army installations to take measures to evaluate the impacts of military activities on natural resources including endangered species, on Army land. The black-capped vireo (*Vireo atricapillus*)* was placed on the Federal list of endangered species in October 1987 (Ratzlaff 1987). The Fort Hood population of the black-capped vireo is one of the most significant within its current range (Tazik et al. 1993a). The nearest other major colony sites in Texas are located in Travis County near Austin, and Kerr County. Factors affecting vireo survival and reproduction on Fort Hood will have a significant impact on the regional population and ultimately on recovery of the species.

The large number of black-capped vireos on Army lands, including Fort Sill, OK (Grzybowski and Tazik 1993) and the Camp Bullis Training Site of Fort Sam Houston (Shaw et al. 1989, Rust and Tazik 1990), can be attributed to two factors: (1) that the nature of the military mission serves to protect existing and potential habitat from urban development and excessive rangeland improvement, and (2) that a high fire frequency resulting from artillery and the use of flares helps to create the hardwood scrub

*Common and scientific names of referenced species are listed in Appendix A.

habitat favored by the vireo (Tazik et al. 1993b). In the case of this endangered species, military activities have been beneficial. The Army now has the opportunity to contribute significantly and proactively to the protection of this species on its lands for the national interest while also pursuing its primary mission, national defense preparedness.

One of the most critical factors limiting vireo reproductive success throughout its range is cowbird nest parasitism (Graber 1961, Marshall et al. 1985, Grzybowski et al. 1986). One study suggested that the history of intensive cowbird parasitism on Fort Hood may have been responsible for the absence of vireos during a 1985 survey (Marshal et al. 1985). There is no doubt that available habitat and extensive cattle grazing on Fort Hood attracts numerous cowbirds. The brown-headed cowbird lays its eggs in the nests of other birds, and is known to parasitize over 200 avian species (Friedmann 1929, 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Small passerine species, including a variety of vireos and warblers, are particularly susceptible to cowbird parasitism as the relatively large and rapidly developing cowbird egg and young outcompete host eggs and young, often resulting in a substantial reduction in the host's reproductive success (e.g., Graber 1961, Mayfield 1960, Nolan 1978, Franzreb 1989).

Nest predation has not been identified as a significant threat to the vireo but is a potentially important source of nest failure (Ricklefs 1969). Graber (1961) observed that 9 percent of all eggs laid and 17 percent of all young hatched were lost to predators, probably snakes in most cases. Scrub jays can also be a significant source of nest depredation in some years (Grzybowski 1986). The impact of military activities on population and reproductive ecology of the vireo has never been evaluated.

Based on these considerations, it is important to document the extent of parasitism and its effects on nest success and productivity, to assess the effectiveness of cowbird control techniques in reducing parasitism, to determine the level of parasitism that can be sustained while maintaining a stable and productive population, and to determine the effects of military activity on survival, nest success, and reproduction of this endangered species.

Objectives

The objectives of this report are to document: (1) annual survival and dispersal patterns of Fort Hood vireos, (2) nest success and production, and the factors limiting each (especially cowbird parasitism), (3) the effectiveness of cowbird control in enhancing nest success and production, and (4) the effects of military activity on survival, nest success, and production.

Approach

Researchers monitored representative vireo territories and nests located within colony sites scattered throughout the Fort weekly to biweekly to evaluate vireo population and nesting ecology. Sites were monitored during each of the 3 years of the study. Birds were banded for individual identification to document annual survival and site tenacity, and to delineate territory boundaries.

Scope

This report is the last in a three-part series documenting the ecology of the black-capped vireo on Fort Hood. Evaluation of the population and nesting ecology of the vireo on Fort Hood is critical to an understanding of the present status of the vireo and the impacts of both military and nonmilitary activities on the Fort Hood vireo population. Other reports in the series have dealt with distribution and abundance (Tazik et al. 1993a), and habitat preferences (Tazik et al. 1993b).

Mode of Technology Transfer

This research contributes to a fundamental understanding of the ecology of the endangered black-capped vireo, and serves as an example of a proactive approach to endangered species management on Army lands. Data presented here have already been used to develop a biological assessment required by regulations implementing section 7 of the Endangered Species Act (50 CFR 402; Tazik et al. 1992b). It is anticipated that results of this study will also apply to Fort Sill, OK, and the Camp Bullis Training Site of Fort Sam Houston, TX. As such, the information in this and related studies are being transmitted to military and land and wildlife managers at Fort Hood, Headquarters (HQ) U.S. Army Forces Command, and HQ Department of the Army. It is anticipated that these data will be updated annually and that a computerized data analysis and reporting program will be developed for timely documentation of annual monitoring results, as part of the Army's Land Condition-Trend Analysis Program (LCTA).

2 SITE DESCRIPTION

Fort Hood occupies an 87,890 ha area (U.S. Department of the Army 1987) in central Texas, in Bell and Coryell Counties adjacent to the city of Killeen (Figure 1).* It lies on the eastern fringe of the Edward's Plateau between the cities of Waco, 40 miles to the northeast, and Austin, 60 miles to the south. The climate is characterized by long, hot summers and short, mild winters. Average monthly temperatures for the Fort Hood area range from a low of about 8 °C in January to a high of 29 °C in July. Average annual precipitation is 81 cm.

The Fort lies entirely within the Lampasas Cutplains physiographic region (Raisz 1952). The forces creating the Balcones Fault Zone, just east of the installation, have displaced underlying rock formations as much as 500 ft.** Weathering and erosion over the past 70 million years have produced the present "cutplains" landscape. Soil cover generally is shallow to moderately deep and clayey and underlain by limestone bedrock (Nakata 1987).

Elevation ranges from 180 to 375 m above sea level with 90 percent of the area below 260 meters and about 5 percent in bottomlands (Nakata 1987). The landscape exhibits a stairstep topography consisting of a gently rolling to rolling dissected remnant plateau. Numerous steep sloped hills and ridgelines 40 to 80 m in width rise above the flat to gently rolling plains. This benching is a result of the erosionally resistant limestone cap rocks of the plateau and mesa-hill structures. While the upheld areas exhibit steep slopes, the underlying less resistant shales and marl show more gradual slopes. Higher elevations occur on the western portions of the Fort and the lowest at the Belton Lake shoreline adjoining the Fort on the east. Surface water drains mostly in an easterly direction.

Fort Hood lies in the Cross Timbers and Prairies vegetation area (Gould 1975), which normally is composed of oak woodlands with a grass undergrowth. Woody vegetation on the installation is derived mostly from the Edward's Plateau vegetational area to the southwest and is dominated by ashe juniper, live oak and Texas oak. The grasses are derived from the Blackland Prairie area to the east. Under climax conditions, these would consist of little bluestem and indiangrass.

Data obtained from the U.S. Army's Land Condition-Trend Analysis (LCTA) program at Fort Hood clearly show that the Fort is divided mainly into perennial grassland (65 percent) and woodland (31 percent) community types (Figure 2). Most of the grasslands exhibit a dense or closed vegetative cover (83 percent). As a result of a long history of grazing and military activity, the Fort's grasslands are dominated by Texas winter grass (29 percent) and prairie dropseed (18 percent), with little bluestem grasslands comprising only 9 percent of grassland sites.

Broadleaf woodlands comprise about 39 percent of LCTA woodland sites and typically are dominated by oaks. Coniferous and mixed woodlands comprise 61 percent and are dominated by ashe juniper or a mixture of juniper and various oaks. Additional information can be found in Nakata (1987) and Tazik et al. (1993a).

*All figures are included in Appendix B.
**1 ft = 0.305 m.

3 METHODS

Banding Studies

Birds were caught using 24mm mesh mist-nets and banded with both U.S. Fish and Wildlife Service (USFWS) numbered metal bands and unique combinations of color bands for individual recognition. In this way, returns could be monitored from year to year and the movements of individual birds followed within each season. Estimates of minimum annual survival and between year dispersal distances were obtained on this basis.

The mist-netting procedure was based on Grzybowski (personal communication 1986). Males usually were caught by placing the net between actively used shrub clumps. A carved wooden decoy was placed conspicuously in shrubbery next to the net and a tape of the males song played to attract territory occupants. Males were sometimes accompanied by a female and fledglings. Females most often were caught by placing the net in the vicinity of an active nest, preferably along an observed flight lane leading to and from the nest. The net was placed at some distance from the nest to minimize disturbance. Netting of females was not attempted prior to several days into incubation to minimize nest desertions due to researcher activity. Few attempts were made to band young birds on the nest so as to minimize juvenile mortality.

Age Determination

Individuals caught for banding (see below) were classified as hatching year (HY), second year (SY), after second year (ASY), and after hatching year (AHY). HY birds were those in their first year (the year of hatching). SY birds were yearlings in their second year of life. ASY birds were older than one year, in their second or later year. AHY birds were those of questionable age known to be SY or older.

Ages were determined as described by Grzybowski (1988b, 1989, and personal communication). In contrast to the typically black-headed ASY males, SY males usually are gray from the posterior edge of the eye over the back end of the head and nape. While there is some variation in this regard, variants occur in both directions; i.e., SY birds sometimes appear as ASY, and ASY birds may appear as SY (Grzybowski 1989). Thus, classification errors tend to cancel out.

The tone and wear of the primary coverts is another indicator of age in this species. In SY birds, these feathers tend to be browner and more worn than those of ASY birds (Grzybowski 1988b). This results from the fact that juvenile black-capped vireos retain these feathers into their first breeding season (Graber 1957). This characteristic was used to determine age of both sexes.

Dispersal

The location of each vireo in each year of the study was digitized into the Geographic Resource Analysis Support System (GRASS) geographic information system (GIS) located at USACERL.* When territory data were available for an individual, the approximate center point of the territory was used as that year's location. Otherwise, the approximate sighting point or point at which the bird was netted was

* For more information on GRASS, see: J.D. Westervelt, M. Shapiro, W.D. Goran, and D.P. Gerdes, ADP Report N-87/22rev/ADA255218, *Geographical Resources Analysis Support System (GRASS) Version 4.0 User's Reference Manual* (U.S. Army Construction Engineering Research Laboratory [USACERL], June 1992).

used. Easting and Northing coordinates were obtained from GRASS in the form of Universal Transverse Mercator (UTM) coordinates. These data were used to calculate between year dispersal distances.

Nest Success and Production

Territories were monitored weekly to bi-weekly to document mating success, nest success, and production. During each monitoring event, an observer followed the male vireo for up to 2 hours while attempting to locate its mate, nest site, and fledglings.

Nest success was determined by locating and monitoring vireo nests, which were most easily found by following the male. Males are intimately involved in every aspect of nesting activity and visit the nest frequently throughout the day (Graber 1961, Grzybowski 1985b, personal observation). The pendulous nest is commonly found along the edge of a clump of hardwood vegetation and is located on average about 1 m above the ground. Nests were carefully monitored every 3 to 7 days with every attempt made to avoid disruption of nesting activity especially early in the nesting cycle. Condition and contents of the nest were recorded at each visit until the nest became inactive.

Production was documented by searching territories for fledglings. Fledglings remain on the territory for 40 or more days after leaving the nest, during which time they are tended by one or both parents (Graber 1961). Young have a characteristic "peep" that can be elicited by short playbacks of the male's song (Grzybowski, personal communication), and adult birds typically become agitated when a researcher is near the fledglings.

Cowbird Control

Trapping and shooting were employed in attempts to control cowbird numbers in the vicinity of vireo colony sites. Traps measured 8 x 12 x 6 ft (w x l x h), except for one trap at Area 75 in 1989 that was 16 ft long, and was constructed of 2 x 2-in. lumber and 1-in. poultry mesh* (USDI 1973). Live decoy cowbirds were placed in traps along with abundant seed and water to attract others. At least one female and one to three males were maintained as decoys depending upon availability. Decoy traps were checked at least twice per week from early April through mid-July.

A 410 gauge shotgun was used with 3-in. No. 9 magnum load shells to shoot cowbirds, especially females. A tape recording of the females chatter call was played to attract females to locations were they could be shot most easily (A. Raim, personal communication). Three traps were run at Area 6 during 1988. During 1989, the following treatments were applied:

Colony Site	Treatment
Area 2 Slope:	1 trap April-July
Area 2 Top:	2 traps April-July; shooting June-July
Red Bluff:	1 trap April-July
Area 75:	1 trap April-July
Brown's Creek:	1 trap April-July; shooting June-July
West Fort Hood:	Shooting April-July; 2 traps June-July

*1 in. = 25.4 mm.

Colony site locations are illustrated in Figure 3. During 1988, all cowbirds captured were disposed of in a humane fashion. During 1989, only females were regularly killed, while male and immature cowbirds generally were banded and released.

Military Activities

Impacts of military activities were assessed by recording specific instances of military interference with nesting and territory occupancy, and by comparing banding returns, nest success, and production among different regions of the Fort. The Fort was divided into seven major regions (Figure 3):

1. East Range (EARA)—Areas 2-Slope (AR2S), Area 2-Top (AR2T), Red Bluff (REBL), Area 4, Area 6 (AR6), Area 12 (AR12), Brookhaven Mountain (BHMT).

2. East Live Fire (EALF)—Area 75 (AR75) and Area 81 (AR81).

3. West Range (WERA)—Northwest Fort Hood (NWFH), Williamson Mountain/Shell Point (WMSP), and Manning Mountain (MAMT).

4. West Range Live Fire (WELF)—Brown's Creek (BRCR), Robinette Point (ROPT), Rambo Point (RAPT), and Jack Mountain (JAMT).

5. West Fort Hood (WEFH).

6. North Live Fire (NOLF).

7. South Live Fire (SOLF)—Lone Mountain (LOMT) and Pilot Knob Range (PKRA).

East Range colony sites receive low to moderate levels of use (Figure 4) especially company and platoon level training. West Range is subject to moderate use but much of it involves task force and battalion level operations. In contrast, West Fort Hood receives limited use. The area within the live fire training area is free from maneuver exercises but may receive live fire impacts with the exception of North Live Fire, which is located within a multipurpose maneuver area. Appendix C lists colony site code descriptions for the live and non-live fire training areas.

4 DATA ANALYSIS

Age Structure, Banding Returns, and Dispersal

Population age structure was evaluated with respect to sex, year, and colony type. Colony sites were grouped into main/monitored, peripheral, and unmonitored colony types. Main/monitored sites were those major colony sites with four or more territories that were visited on a weekly basis to monitor reproductive success. Peripheral sites were small colonies that had fewer than four pairs, were disjunct from larger colonies, and were monitored frequently enough to establish return frequency of banded birds. Unmonitored sites were main colony sites visited less frequently than monitored sites, thus reducing the certainty in estimates of return frequency. When possible, three-way analyses of independence were performed using the log-linear model (Fienberg 1980). Where data were insufficient to apply three-way analysis, the two-way contingency table was used to examine various subsets of the data (Conover 1980).

Banding returns were summarized by year and as combined 1-year and 2-year return frequencies. Return data were grouped by colony type, region, sex, and age. Two and 3-way cross-classification analyses were used to evaluate these data.

Dispersal distance (D) between years for each individual was obtained by applying the formula for calculating the hypotenuse of a right triangle where,

$$D^2 = (N_1 - N_2)^2 + (E_1 - E_2)^2 \qquad \text{[Eq 1]}$$

and,

N = Northing UTM coordinate
E = Easting UTM coordinate.

Difference in the distribution of dispersal distance between sexes was evaluated by contingency table analysis. The Wilcoxon 2 sample test (Sokal and Rohlf 1969) was used to test for difference in median dispersal distance between sexes.

Nesting Studies

Nestings were summarized by the nest stage in which nests were found, and by the nest start period. Nestings included any active nest found as well as evidence of nesting due to the presence of fledglings on the territory (Grzybowski 1985b). Five nest stages were recognized—construction (4 days + 1 day inactive), laying prior to incubation (2 days), incubation (12 to 17 days), nestling (11 days), and fledgling (40+ days) (Graber 1961). The 2-day laying period was restricted to the time prior to the beginning of incubation, and assumes that incubation started most often after laying the second egg (Graber 1961). Length of the incubation period depends upon whether the nest was parasitized. Cowbirds hatch in 12 days in black-capped vireo nests (Graber 1961), vireos in 14 to 17 days. A 33-day nest cycle length was used for unparasitized nests, assuming a 15-day incubation period. For parasitized nests, a 30-day incubation period was used.

Mayfield (1960) reported that avian nest success will be overestimated if based directly on the percentage of observed successful nests because many failed nests are never found. Mayfield proposed calculating nest success based on the number of nests lost per nest-day of exposure (see **Mating and Nesting Success** below for more detailed information). However, if active nests are found randomly throughout the nesting cycle, actual nest losses should be about twice those observed (Mayfield 1975).

Thus, it was of interest to determine whether vireo nests were discovered randomly and whether the proposed relationship would hold.

The expected number of nests found in each stage was estimated based on the relative number of nest-days (R_i) available within each stage i, which in turn was dependent upon the daily nest survival rate (DSR). The expected number of nest-days (ND_i) in nest stage i was simply the sum of cumulative daily survival through the length (L_i) of stage i; i.e.,

$$ND_i = \sum_{d=1}^{L} DSR^d \qquad \text{[Eq 2]}$$

and,

$$R_i = \frac{ND_i}{\sum_{i=1}^{4} ND_i} \qquad \text{[Eq 3]}$$

Thus, for five days of the construction phase (i=1) at DSR=0.934,

$$\Sigma\, ND_i = 0.934 + 0.934^2 + 0.934^3 + 0.934^4 + 0.934^5 = 4.093$$

Chi-square goodness of fit analysis was performed to test for differences between observed and expected distributions (Conover 1980).

Differences among years in nest start period and nest fate were evaluated using contingency table analysis. Nest start dates were grouped into 2-week intervals beginning 9 April of each year. Where possible, nests were assigned to an interval by back calculating from a known point in the nesting cycle, e.g., by aging nestlings.

Nest fates were divided into four categories: (1) deserted, (2) destroyed, (3) fledged cowbirds, and (4) fledged vireos. Factors causing desertion and destruction of nests were identified to the extent possible. Desertion was assumed whenever the nest was obviously abandoned with eggs still present. Desertion was attributed to cowbird parasitism when there was no other obvious cause and one or more cowbird eggs recently had been deposited in the nest. Other known causes of desertion were researcher disturbance and weather. Nest destruction was attributed to predators when nest contents had been entirely removed or destroyed. Predation was attributed to birds, snakes, or small mammals when there was no obvious sign of nest disturbance, and where eggs or chicks had been removed. Large mammals were blamed when the nest itself had been damaged, torn, or removed from the nest bush. Predation was attributed to ants on occasions when ants where observed to overrun the nest and dead chicks were present in the nest. Nest damage observed subsequent to a severe storm was attributed to weather. Otherwise nest desertion and destruction were attributed to unknown causes.

Cowbird Parasitism and Cowbird Control

Active nests were characterized as parasitized or unparasitized only after at least one egg was deposited in the nest.

Cowbird control was summarized as the number of individuals caught or removed by trapping or shooting during 2-week time intervals. Removal success by trapping and shooting was estimated as the number of females removed per day. Shooting success also was evaluated as the number of females removed per visit.

The effectiveness of trapping at Area 6 in 1988 and Area 2 in 1989 was assessed by graphically comparing the incidence (in percent) and intensity (number of cowbird eggs/nest) of parasitism between areas by year. These were the only areas fully monitored each of the 3 years.

Three separate analyses were performed to examine the effect of the 1989 cowbird control effort on incidence and intensity of parasitism. In the first, colony sites were classified into three treatment groups based on 1989 control efforts: (1) No Treatment, (2) Trapping, and (3) Shooting. The classification ignored the dual treatments of trapping and shooting after 1 June at Area 2-Top, Brown's Creek, and West Fort Hood. These data were analyzed using logistic analysis (Fienberg 1980) to evaluate the model shown in equation 4.

$$\text{Probability of Parasitism} = \text{Treatment} + \text{Year} + \text{Treatment} \times \text{Year} \qquad \text{[Eq 4]}$$

Probability of Parasitism was treated here as the response variable with the analysis designed to uncover effects of Treatment, Year, and the Treatment x Year interaction. Because the Trapping and Shooting treatments were applied only in 1989 (ignoring Area 6 trapping in 1988), and (given normal annual variability in parasitism) an interaction between treatment and year (Treatment x Year) would indicate a treatment effect. That is, differences between years were expected to differ depending upon the treatment applied, including "No Treatment."

A second logistic analysis evaluated the effectiveness of Single vs. Dual Treatments by examining parasitism before and after 1 June 1989. The model was specified as:

$$\text{Probability of Parasitism} = \text{Treatment} + \text{Period} + \text{Treatment} \times \text{Period} \qquad \text{[Eq 5]}$$

Here, Treatment refers to Single or Dual treatments and Period is the time before or after 1 June during the 1989 breeding season. And again, a significant interaction term was expected to indicate a difference between Single and Dual treatment effects.

Intensity of parasitism (1, 2, or 3 or more eggs/nest) was compared among Trapping, Shooting, and No Treatment treatment groups between No Treatment and Treatment time periods. The No Treatment period corresponded to 1987 and 1988 with the exception that the Area 6 1988 data was placed in the Treatment period (Area 6 was trapped in 1988). The logistic model applied was,

$$\text{Probability of N Eggs} = \text{Treatment} + \text{Period} + \text{Treatment} \times \text{Period} \qquad \text{[Eq 6]}$$

Again a treatment effect would be indicated by a significant interaction term.

Correlation analysis (Sokal and Rohlf 1969) was used to evaluate the relationship between cowbird parasitism and female cowbird trapping success.

Mating and Nest Success

Mating success was estimated based only on territories for which there were at least three monitoring visits totaling at least 3 hours of observation over a 1-month period. Inspection of the data revealed that, for those territories known to be occupied by mated pairs, three visits of at least 3 hours total observation time confirmed mating in 87 percent of the territories. Contingency table analysis was applied to determine if SY males had a lower mating success than ASY males (Grzybowski 1989).

Survival estimates for the construction and the laying periods were based on the observed fates of nests located during construction. However, because nests typically were not found on the first day of construction, construction stage survival was overestimated. Assuming an equal probability of finding a nest on each day that it was active during the construction period, observed survival overestimated expected survival by approximately 15 percent. Observed construction stage survival was adjusted accordingly.

For the construction and the laying periods, results were summarized as daily nest loss rates (DLR) due to desertion and destruction and as overall nest stage survival. Differences in survival between years and between parasitized and unparasitized nests during construction and laying periods were evaluated using contingency table analysis.

Nest success during the incubation and the nestling periods was quantified using the Mayfield method (Mayfield 1960, 1961, 1975, Johnson and Shaffer 1990) rather than directly from fates of observed nests. Because bird nests were found in all stages of the nesting cycle rather than at construction, there was a bias toward finding successful nests. That is, nests that had already been deserted or destroyed could not be found as active nests. To avoid this bias, Mayfield proposed calculating success based on nest-days of exposure. DLR was estimated as nests lost per nest-day of observed exposure. Separate estimates were made for deserted and destroyed nests. Nest survival, S_i, for nest stage i of length L_i was estimated as,

$$s_i = (1 - DLR_i)^{L_i} \qquad \text{[Eq 7]}$$

The variance and the standard error were estimated for DLR following Johnson (1979). The variance (var) was estimated as,

$$var = \frac{(exp - loss) \times (loss)}{exp^3} \qquad \text{[Eq 8]}$$

where,

exp = number of nest-days of exposure
loss = number of nests lost.

The standard error (SE) was obtained as the square root of var. Tests for differences in DLR between years and between parasitized and unparasitized nests during the incubation and the nestling periods were performed using the Z statistic (Hensler and Nichols 1981, Bart and Robson 1982) where,

$$Z = \frac{|DLR_1 - DLR_2|}{(var_1 + var_2)^{1/2}} \quad \text{[Eq 9]}$$

The 95 percent confidence intervals (CI) for DLR estimates were approximated as ± 2SE. Also, a comparison was made between the Mayfield estimates of nest success and nest success inferred from observed nest fates to demonstrate the extent of the bias present in estimates based on the latter.

The effect of cowbird parasitism on nest success also was evaluated by comparing the fates of parasitized and unparasitized nests using contingency table analysis. Further, overall nest success was estimated for two hypothetical vireo populations, one unparasitized and one 100 percent parasitized. For the unparasitized population, the estimate was obtained by multiplying the individual nest stage survival probabilities. For the parasitized population, the calculation was not as straightforward because the probability of parasitism differed among nest stages. Among parasitized nests on Fort Hood, 3 percent were parasitized during construction, 70 percent during laying, and 100 percent during incubation (Table 28).* Only 71.7 percent were parasitized with hatchling cowbirds during the nestling period as some parasitized nests did not hatch cowbirds. Thus, the survival probability for the parasitized population was estimated by weighted average based on the proportion of parasitized and unparasitized nests within each stage.

The effect of the intensity of cowbird parasitism on nest success was examined by a contingency table analysis of the fate of nests in which one, two, and three cowbird eggs had been deposited. A correlation analysis was performed to test for a relationship between intensity of cowbird parasitism and DLR due to desertion using regional estimates of each parameter for each year as variates. The hypothesis was that more frequent contact between vireos and cowbirds at the nest or greater nest disturbance by cowbirds should cause more frequent nest desertions. Potential interrelationships among DLR due to desertion, the incidence of parasitism, and DLR due to destruction were sorted out by partial correlation analysis (Sokal and Rohlf 1969).

The effect of cowbird control on nest success was evaluated graphically by plotting DLR ± 95 percent CI for incubation and nestling stages by year and treatment group—No Treatment, Trapping, and Shooting. Mayfield estimates of nest success for the incubation and the nestling periods combined also were compared graphically among treatment groups.

Pair Success and Production

Pair fledging success and production were estimated based only on fully monitored territories, that is, those that were visited at least three times, and had a total of at least 3 hours observation over the breeding season with at least one, 1-hour visit during mid to late July unless the pair already was observed to have fledged vireos.

Pair success and production of vireo and cowbird young were summarized by year, colony site, and cowbird control treatment group. Pair success and production were compared among years and among treatment groups by contingency table analysis and 1-way analysis of variance (ANOVA) (Sokal and Rohlf 1969) respectively. Production was recorded in the field as a minimum to maximum range as all

*All tables are included in Appendix A.

fledglings might not be seen on the territory at any one time. Analyses generally were performed on the median value assuming that overestimates were made as often as underestimates.

The effect of parasitism on vireo production was examined in two ways. First, regression analysis (Sokal and Rohlf 1969) was applied using observations made in each colony site each year. The simple linear model was specified as:

$$Prod = a + b\,(Para) \quad \text{[Eq 10]}$$

where,

- Prod = production in young/female/year
- a = y intercept
- b = slope
- Para = parasitism in percent.

Second, a procedure was employed similar to that described by Nolan (1978). The expected production in a hypothetical unparasitized population and in a 100 percent parasitized population was estimated by charting the expected nesting activity of 100 mated females in each. Calculations were based on nest success estimated from exposure, length of the nesting cycle, average lifespan of unsuccessful nests, time between renesting attempts subsequent to nest failure, prenesting period prior to second brood attempts, mean start date for first nests, percentage of parasitized nests that produce vireos, average number of vireo or cowbird fledglings in successful nests, and probability of nest replacement. The procedure was programmed in Turbo-Pascal* and allows calculation of production at various levels of parasitism. Below, it is referred to as Nolan's Model.

Critical levels of production ($Prod_c$) and parasitism ($Para_c$) required to maintain a stable population were estimated following May and Robinson (1985). The relevant equations are:

$$Prod_c = \frac{2u_a}{s_j} \quad \text{[Eq 11]}$$

$$Para_c = \frac{Prod_{max} - Prod_c}{Prod_{max} - Prod_{min}} \quad \text{[Eq 12]}$$

where,

- u_a = adult annual mortality
- s_j = juvenile annual survival
- Prod = critical level of production to sustain population
- $Para_c$ = critical level of parasitism necessary to meet $Prod_c$
- $Prod_{max}$ = vireo production in a 0 percent parasitized population
- $Prod_{min}$ = vireo production in a 100 percent parasitized population.

*Turbo Pascal is a product of Borland International, 1800-T Green Hills Rd., Scotts Valley, CA 95066, tel. 408/438-8400.

For a given $Prod_c$, $Para_c$ was compared to that predicted from the regression analysis ($Para_r$). The latter was obtained by rearranging Eq. 7 to solve for,

$$Para_r = \frac{a - Prod_c}{b} \qquad [Eq\ 13]$$

Regional Analysis

Incidence and intensity of parasitism, DLR due to desertion and destruction, nest success, pair success, and production were compared among the five regions of the installation. Incidence and intensity of cowbird parasitism were analyzed using a three-way cross-classification (Region x Year x Parasitism/Number of Eggs). Pair success was analyzed similarly (Region x Year x Success). A two-way ANOVA (Region x Year) (Sokal and Rohlf 1969) was used to assess production. DLR was compared graphically among regions by year.

5 RESULTS

Population Age Structure

The age structure of male and female portions of the population are shown in Table 1 and analyzed in Table 2. Age structure was sex dependent but independent of year. The insignificant likelihood ratio (Table 2) indicates that the model fits without the three-way interaction of Age x Sex x Year. The percentage of SY birds among males was 10.6 percent overall and was consistent among years. SY birds constituted a greater portion of the female population (23.3 percent overall) compared to that of the males, especialiy during 1988 (30.0 percent).

A breakdown by colony type revealed that the proportion of SY and ASY birds differed between main colony sites (monitored and unmonitored) and peripheral sites (X^2=4.925, df=1, $0.025<p<0.05$). SY birds comprised 25.8 percent of populations at peripheral sites (n=31) in contrast to only 11.7 percent (n=283) at main colony sites.

Banding Returns and Survival

A total of 171 male, 59 female, and 11 fledgling vireos were banded during the 3 years. Adult banding data and results of various analyses are presented in Tables 3 through 10. None of the juveniles banded in 1987 (7) or 1988 (2) were observed in subsequent years.

Percentage return of banded birds by year, sex, and region are shown in Table 3 for colony sites where data were available for both 1988 and 1989 returns. The three-way interaction of Sex x Year x Returns is significant (Table 4). This is related to an increase in returns of females between 1988 and 1989 (33.3 to 58.3 percent) that contrasts with a decline in male returns between years (64.7 to 46.8 percent). Thus, the dependency of returns on sex depends on the year, and the effect of year on returns depends on sex.

In an analysis of the relationships among male returns, region, and year, returns were independent of region but dependent on year (Table 5). Male return frequency was lower in 1989 than in 1988 as noted above. Data for females was insufficient to include region in the analysis. A two-way analysis revealed that female return frequency was not significantly higher during 1989 compared to 1988 (Table 3).

Returns by sex and age are shown in Table 6 and analyzed in Table 7. Male return frequency depended on year with higher returns in 1988 compared to 1989, but independent of age. However, the likelihood ratio is close to significant indicating that the three-way interaction of Age x Year x Return may be important, thereby complicating interpretation of the results. That is, the relationship between year and male return frequency may depend on age class. Returns of both SY and ASY males declined between 1988 and 1989 but nearly twice as much among SY (45.5 percent) compared to ASY (23.8 percent) (Table 6). SY males returned as frequently or more so than ASY males in both years. The difference in returns between SY and ASY females during 1989 was insignificant (Table 6).

The 1988 and the 1989 return frequencies are combined into 1-year returns in Table 8 by sex, colony type, and region. Two-year returns are also given here (i.e., birds banded in 1987 that returned in 1989). One-year return frequency was independent of sex but dependent on colony type (Table 9). The latter was due largely to the low return frequencies of both males (31.3 percent) and females (0.0

percent) in peripheral colony sites. Combining sexes yields returns of 55.3 percent at monitored sites, 52.9 percent at unmonitored sites, and 23.8 percent at peripheral sites.

Sample size was too small among peripheral colony sites to apply the above analysis to 2-year returns. However, Table 8 shows that results are consistent between the 1-year and 2-year returns with regard to both sex and colony type. That is, in each case males and females had similar return frequencies by colony type, and peripheral colony sites had lower returns compared to both monitored and unmonitored sites.

The relationships among region, sex, and 1-year returns are analyzed in Table 10. Peripheral colony sites were excluded from the analysis. The only West Range site available was Manning Mountain but was excluded from the analysis due to the lack of females in the sample. Returns were independent of both sex and region. However, sex and region were not independent. This was due to a difference in the ratio of males to females banded among regions. With regard to the West Range site at Manning Mountain, although excluded from the analysis, the male return frequency is similar to that of males at colony sites included in the analysis (Table 8).

For 2-year returns, data were too sparse for a three-way analysis of Sex x Region x Return. Inspection of Table 8 reveals similar 2-year returns for males and females overall. The difference between sexes for monitored sites at East Range (9.1 vs. 26.7 percent) is insignificant (Table 8). Thus, sexes were combined in an analysis of 2-year returns among regions (same regions analyzed for 1-year returns—EARA, EALF+WELF, and WEFH). No significant association was found between region and 2-year returns for sexes combined or for males alone (Table 8).

Between Year Dispersal of Banded Birds

All but six vireos returned to the same colony site occupied during the previous year. Among males, only 2 of 157 (1.3 percent) changed colony sites. One moved 1.9 km from Jack Mountain in 1987 to Manning Mountain in 1989 (Figure 3). The other moved 22.9 km from West Fort Hood in 1988 to Manning Mountain in 1989. The latter was probably the result of a fire that destroyed the habitat where this male held a territory in 1988. Among females, 4 of 49 (8.2 percent) changed sites as follows: 9.6 km from Area 2-Top in 1987 to Area 6 in 1988; 24.2 km from Area 6 in 1988 to Manning Mountain in 1989; 1.2 km from Area 2-Slope in 1987 to Area 2-Top in 1989; and 1.1 km from Area 2-Top in 1988 to Area 2-Slope in 1989.

Between year dispersal distances are presented by sex in Table 11. The small number of SY birds of each sex showed distributions similar to those for all ages combined and were not treated separately. Distance intervals were combined for analysis as shown in Table 11 to minimize the number of cell frequencies less than five. The distribution of dispersal distance differed significantly between sexes (Table 11) with females dispersing longer distances more frequently than males. Difference in median dispersal distance was significant (Table 11).

Nesting Studies

A total of 340 active nestings were observed, 308 of which were discovered prior to fledging young (Table 12). Thirty-seven nestings were observed at four sites during 1987, 121 at 10 sites in 1988, and 182 at 14 sites in 1989. The increase in the number of nestings discovered each year was the result of a greater intensity of effort during 1988 and 1989 over 1987, and the greater efficiency in finding nestings that came with experience.

Nest Stage

The number of nestings found by nest stage was similar among years. Just over 70 percent were found during construction (31.5 percent) and incubation (38.8 percent) combined. Few were found during the laying period prior to the start of incubation (6.5 percent). Of the remainder, 13.8 percent were found during the nestling period, 9.4 percent after young left the nest.

The observed number of nests discovered by nest stage did not differ significantly from that expected when DSR was taken into consideration (Table 13). That is, nests were discovered at random throughout the nesting cycle.

Nest Start Dates

Start dates were estimated for 280 nestings. Overall, the number of observed starts increased steadily from 30 during 9 to 22 April to a peak of 66 during 21 May to 3 June, decreasing thereafter to 6.1 after 2 July (Figure 5). Differences among years were significant (Figure 5). During 1987, peak numbers occurred from 7 to 20 May. The 1988 peak occurred from 4 to 17 June. Two peaks are apparent for 1989: 23 April to 6 May and 21 May to 3 June. During 1989, the percentage of observed nests started early in the season (9 April to 6 May) was substantially higher than during 1987 and 1988 (31.1 percent vs. 17.6 and 16.6 percent, respectively)

Nest Fates

Nest fate was determined for 255 of 308 active nests found prior to fledging. Overall, 37.6 percent were deserted, 36.1 percent were destroyed, and 26.3 percent fledged young (17.3 percent vireos and 9.0 percent cowbirds) (Table 14).

There was a significant difference among years in nest fate (X^2=35.208, df=6, p<0.001). Most notably, the number deserted decreased from 63.6 percent in 1987 to 45.9 percent in 1988 and to 26.3 percent in 1989. This was accompanied by a substantial increase in nests producing vireos from 3 percent in 1987 and 4.7 percent in 1988 to 28.5 percent in 1989. The percentage of nests destroyed was higher in 1988 (40.0 percent) and 1989 (35.8 percent) compared to 1987 (27.3 percent).

The causes of nest desertion did not differ among years (Table 14). Although the percentage of nests deserted decreased from 1987 to 1989, the percentage of desertions attributed to cowbird parasitism remained consistently high, ranging from 69.2 to 80.9 percent. (As demonstrated below, deserted nests almost always were parasitized [Figure 6], excluding those deserted in the construction phase.) Overall, 72.9 percent were abandoned due to parasitism. Few were abandoned due to researcher activity (3.1 percent), while only 1 percent were deserted after a storm. Another 22.9 percent were deserted for unknown reasons, 17.7 percent during construction.

The causes of nest destruction also did not differ among years (Table 14). Most was attributed to unknown predators (77.2 percent overall), probably snakes, birds, and small mammals that left little trace of their presence. Large mammals accounted for 17.4 percent. Only 2.2 percent were destroyed by storms, while another 3.3 percent were lost to ants.

Among the 70 nests that fledged young, the number of nests fledging vireos and the number fledging cowbirds differed significantly among years (Table 14). While twice as many nests fledged cowbirds than vireos during both 1987 and 1988 (10 vs. 5 overall), three times as many nests fledged vireos (39) than cowbirds (13) during 1989.

Nine 1989 nests were excluded from the above sample of 255 nests. These included nests from which cowbird eggs were removed, removed and replaced with nonviable eggs, purposely addled, or in which cowbird hatchlings were removed. The fate of these nests is shown in Table 15. Three were deserted, two were destroyed, three fledged vireos, and one fledged a cowbird.

Cowbird Control

The results of trapping and shooting cowbirds during 1988 and 1989 are shown in Tables 16 through 18. At Area 6 during 1988, three traps were operated from 14 April through 13 July yielding a total of 270 trap-days. (Although traps were set up between 15 and 17 March, decoy birds were not available until 14 April.) During this period, 106 male, 11 female, and 18 immature cowbirds were captured. Of these, 79 males, 10 females, and 13 immatures were removed from the population (Table 16). Female removal success during 1988 was 0.04 female per trap day.

Eight traps operated at six sites during 1989 yielded 639 trap-days and resulted in the capture of 220 male, 51 female, and 167 immature cowbirds, and the removal of 60 males, 36 females and 90 immatures (Table 17). Female removal success varied among colony sites. Removal success at the east range colony sites of Area 75, Area 2 Top, and Area 2 Slope were similar at 0.06 to 0.07 female per trap day. Success at the other east range site of Red Bluff was lower than the above at 0.02. Removal success was lowest at West Fort Hood (0.00), which was trapped only after 1 June, and highest at Brown's Creek Range (0.10). Overall, 0.06 female per trap day was removed.

Shooting at five sites during 1989 removed 39 males and 119 females (Table 18), 3.3 times more females than by trapping. Shooting success varied among colony sites, ranging from 0.88 female removed per visit at West Fort Hood to 1.85 females per visit at Manning Mountain. A peak in success occurred during 1 to 15 May when 21 females were shot in 10 visits for a success rate of 2.1 females per visit. Females removed by shooting averaged 0.30 per day, five times higher than by trapping. Female removed per day was similar among sites except for a low rate at Williamson/Shell Mountain (0.17).

Effect of Cowbird Control on Parasitism

The incidence of cowbird parasitism and the mean number of cowbird eggs per nest for Areas 2 and 6 for 1987 through 1989 are shown in Figure 7A and 7B. Parasitism at Area 6 was similar during both 1987 and 1988 despite the 1988 trapping effort but declined on Area 2 (2-Top and 2-Slope combined) from 86.6 percent to 73.3 percent without trapping during this same period (Figure 7A). Parasitism declined similarly on both areas between 1988 and 1989 with cowbird trapping in operation only at Area 2 during 1989. The number of cowbird eggs/nest appeared to decline more sharply from 1987 to 1989 at Area 6 compared to Area 2 (Figure 7B).

The incidence of parasitism each year at each colony site and treatment group is presented in Table 19. Parasitism was affected by year but not by treatment or by the interaction of treatment and year (Table 20). The lack of significant interaction between year and treatment group indicates that the 1989 treatments were ineffective in reducing parasitism. These results are borne out by simple inspection of the data in Table 19. Overall, parasitism was very high during both 1987 and 1988, averaging 90.8 percent, but declined markedly in 1989 to 65.1 percent. Among the three treatment groups, the declines in parasitism from 1987 to 1988, and 1988 to 1989 were remarkably similar.

Parasitism before and after 1 June 1989 is shown in Table 21 and analyzed in Table 22. Parasitism was unaffected by treatment period (Before vs. After 1 June) and treatment group (Single vs. Dual treatment). The interaction of treatment period and treatment group also was insignificant indicating that the dual treatments applied after 1 June did not influence parasitism. In the Single Treatment group, parasitism was virtually identical in each period (68.0 percent compared to 66.7 percent). In the Dual Treatment group, the apparent decline in parasitism from 72.0 to 50.0 percent was insignificant.

Data on the intensity of cowbird parasitism is presented as the number of cowbird eggs per nest in Table 23. Data analysis is presented in Table 24. Intensity of parasitism was affected significantly only by treatment period, mostly due to a difference between years. The insignificant interaction indicates that the difference between treatment periods was similar among the three treatment groups, and that the applied treatments did not differ in their effect on parasitism intensity. The mean number of cowbird eggs per nest declined similarly between No Treatment and Treatment Periods in each treatment group.

Cowbird trapping success during 1989 was positively correlated with the incidence of parasitism (Figure 8), but not with the intensity of parasitism ($r=-0.215$, $p=0.728$). However, note the low trapping success at Area 6 in 1987, which was excluded from the analysis. Predators, mostly racoons, created a constant nuisance by digging under traps, and by tearing through the top entrance to the trap. Thus, cowbirds frequently were able to escape from the trap if they were not captured by predators so that capture success there was unrelated to the incidence of parasitism.

Mating and Nest Success

Black-capped Vireo

Overall, 93.8 percent of the males adequately monitored were mated. Mating success was 87.5 percent (21 of 24) in 1987, 94.5 percent (69 of 73) in 1988, and 95.0 percent (76 of 80) in 1989. Mating success among SY males (20 of 20 = 100 percent) was not less than among ASY males (130 of 137 = 94.9 percent).

DLR by year, nest stage, and fate are shown in Table 25. Overall, total loss rates appear to be higher during construction (0.0660) and laying (0.0681) compared to incubation (0.0588) and nestling (0.0598). However, the former pair of values fall within the 95 percent CI of the latter.

During both construction and laying, nest stage survival did not differ significantly among years (Table 25). All nest losses during construction, and most during laying were due to desertion. Note in Table 25 that the fractional values for numbers of nests lost (in parentheses) resulted from an occasional problem of not being able to assign losses with certainty to either the laying or incubation period. In such cases, the nest was divided between the two periods, resulting in partial nests.

Total DLR during incubation was similar in 1987 and 1988 but declined significantly in 1989 (Table 25). Similarly, DLR due to desertion decreased from a high in 1987 to a low in 1989. DLR due to destruction was significantly higher during 1988 compared to 1987 but not so compared to 1989. As a result, nest stage survival during incubation increased two fold from 27.1 percent in 1987 to 55.2 percent in 1989.

Nest losses during the nestling period were due solely to destruction. DLR total was significantly lower during 1989 compared to 1987 and 1988, the same pattern observed for the incubation period (Table 25). As a result, nestling stage survival increased fourfold from 15.3 percent in 1987 to 61.1 percent in 1989. Overall fledging success increased tenfold from a low of 2.4 percent in 1987 to a high of 23.7 percent in 1989.

The proportion of nests deserted and destroyed calculated based on data in Table 25 are presented in Figure 9A and 9B. For all years combined, 58.4 percent of nests were deserted, most during construction (28.9 percent) and incubation (22.3 percent) (Figure 9A). Desertions were particularly high in 1987, nearly half of which occurred during incubation, but declined in 1988 and again in 1989. No nests were deserted during the nestling stage.

In all, 27.4 percent of all nests were destroyed (Figure 9B). Losses were substantially higher during 1988 and 1989 compared to 1987. This was due primarily to a substantial increase in the proportion of nests destroyed during incubation from 2.9 percent in 1987 to 15 percent in 1988 and 11.3 percent in 1989. In contrast, nest destruction during the nestling period was similar among years (11.8 to 15.1 percent). No nests were destroyed during construction.

In Table 26, nest loss and success calculated based on exposure are compared to nest fates (Table 14). Observed nest fate data (Table 14) underestimated nest loss due to desertion by 35.6 percent, overestimated nest loss due to destruction by 31.8 percent, and overestimated nest success by 85.2 percent (and underestimated total nest loss by 14.1 percent).

Brown-headed Cowbird

Cowbird nesting success is usually reported as the percentage of eggs that successfully fledge young. On Fort Hood, 357 cowbird eggs observed in 221 active and inactive vireo nests, produced 28 fledglings, a 7.8 percent fledging success. However, this estimate is high because it is based on observed nests. Another approach is to take the observed number of cowbirds fledged per active nest (0.09; next section) and divide by the average number of cowbird eggs deposited per active nest (1.58; Table 23) yielding 5.7 percent egg success. This is reduced to at least 5.4 percent considering that 5.9 percent (13 of 221) of all observed cowbird eggs were laid in inactive nests.

Effect of Parasitism on Nest Success

DLR and nest stage survival for parasitized and unparasitized nests presented in Table 27 were calculated for construction and laying periods based on nests found in construction and by Mayfield's method for incubation and nestling periods. Nest survival during construction and laying did not differ significantly between parasitized and unparasitized nests. However, for the construction stage, the lack of significance is due to the small sample size for parasitized nests.

During incubation, the greater nest survival for unparasitized compared to parasitized nests was due to a substantially lower DLR due to desertion in unparasitized nests (Table 27). DLR due to destruction during incubation did not differ between the two. During the nestling stage, DLR due to destruction was significantly higher in parasitized compared to unparasitized nests, resulting in a higher nestling stage survival in unparasitized nests.

A summary of survival probabilities for nests in parasitized and unparasitized populations of the vireo is presented in Table 28. The expected nest success in the unparasitized population (0.251) is over twice that of a totally parasitized population (0.118).

Nest success in parasitized and unparasitized nests calculated from exposure and excluding the construction phase were different (Figure 6). Parasitized nests were deserted far more frequently, destroyed less frequently, and fledged young substantially less often than unparasitized nests.

Table 29 lists the effect of the intensity of parasitism on nest success. Nest fates did not differ significantly between nests with one cowbird egg and those with two or more cowbird eggs.

A significant correlation was found between the regional nest desertion rate during incubation and the intensity (r=0.703, p=0.035; Figure 10) but not the incidence (r=0.379, p=0.315) of parasitism. Partialing out the effect of the nest destruction rate improved the correlation with intensity (r=0.834, p=0.010) and with incidence (r=0.704, p=0.052). Partialing the effect of both nest destruction and incidence of parasitism reduced the significance of the correlation between desertion and intensity (r=0.702, p=0.079). Partialing out the effect of destruction and intensity of parasitism greatly reduced the correlation between desertion and incidence (r=0.398, p=0.376). Thus, DLR due to desertion during incubation appears to be more closely related to the intensity rather than the incidence of parasitism although incidence and intensity are themselves related (r=0.601, p=0.051).

Vireo young per *successful* nest averaged 2.74 (SE=0.159, n=31) among unparasitized nests, significantly higher than the average of 2.23 (SE=0.281, n=13) among parasitized nests that fledged vireos (t=7.66, df=42, p<0.001). Vireo production per successful parasitized nests that fledged either vireos or cowbirds was 0.86. Vireo young per active nest also was obviously much larger among unparasitized nests (0.68) than parasitized nests (0.10). Losses to cowbird parasitism amounted to 0.58 vireo young per active nest (85 percent).

Cowbirds fledged at a rate of 1.16 young per successful parasitized nest that fledged cowbirds (SE=0.075, n=25). Number of cowbirds fledged per active parasitized nest was 0.09, similar to the number of vireos fledged per active parasitized nest (0.10).

Effect of Cowbird Control on Nest Success

Because parasitism appears to increase nest loss during incubation due to desertion and during the nestling period due to destruction, cowbird control should reduce these nest losses and thereby increase nest success. DLR are plotted in Figures 11A to 11D by year and cowbird control treatment group—No Treatment, Trapping, and Shooting.

For the incubation stage, the desertion rate was highest in the No Treatment group during 1987 (Figure 11A). Rates were otherwise similar within and across treatment groups. Incubation stage DLR due to destruction was similar across year-by-treatment group combinations with the exception of a high rate in the 1988 No Treatment group (Figure 11B). Total DLR was higher in the No Treatment group during 1987 and 1988 compared to other year-by-treatment combinations (Figure 11C). The high loss rate during 1987 was due to the high desertion rate in that year, while the high 1988 rate was due to a high destruction rate during that year. No consistent effect due to cowbird control is apparent in these results. For example, DLR in the No Treatment group during 1989 was as low or lower than DLR in the Trapping and Shooting groups (Figures 11A to 11C).

Patterns in the nestling stage destruction rates reveal no effect due to cowbird control. DLR was highest in the Trapping group during 1988, a trend opposite that expected if control were effective (Figure 11D). DLR was also relatively high during 1987 in the No Treatment Group, but otherwise similar across treatment groups during 1988 and 1989.

Nest success through incubation and nestling stages is shown by treatment group in Figure 12. A consistent effect due to cowbird control is unapparent. Although success was somewhat higher in the Trapping group during 1988 as compared to the No Treatment group, during 1989 success was much higher in the No Treatment group, as compared to both Trapping and Shooting groups.

Pair Success and Production

Vireo and Cowbird Success and Production

Vireo pair success in fledging vireo young is presented in Table 30 by year and colony site. Differences among years in the proportion of successful nests was significant (Table 30), with success considerably higher in 1989 compared to 1987 and 1988.

Vireo production (young/mated pair) by colony site and year is presented in Tables 31A and 31B in 2 versions. The uncorrected version (Table 31A) is based only on the estimated number of fledglings observed in the field. The corrected version (Table 31B) is adjusted for the observation that production based on nestings first observed in the fledgling stage (1.56, SE=0.151) was 57 percent lower than production based on nests observed and monitored prior to fledging young (2.74, SE=0.159). Individual observations of the former were adjusted accordingly. Subsequent analyses were based on the corrected production values in Table 31B.

Vireo production in 1989 was significantly higher than during 1987 and 1988; 1987 and 1988 production was similar (Table 31B). This pattern is comparable to that observed in pair success (Table 30). Production in 1989 (1.80 vireo young/pair) was over four times that of the combined 1987 and 1988 production (0.44 vireo young/pair).

Pair success in fledging cowbirds did not differ significantly among years, and averaged 14.2 percent over the 3 years (Table 32). Cowbird production in vireo nests also did not differ significantly among years (Table 33), averaging 0.193 cowbird young per pair.

Effect of Parasitism on Pair Success and Production

Several parameters were estimated in the application of Nolan's model for hypothetical parasitized and unparasitized vireo populations.

Nest cycle length for unparasitized nests was 33 days. This included 5 days in active and inactive building, 2 in laying prior to incubation, 15 in incubation, and 11 in brooding. For parasitized nests, only the incubation period differed with 12 days instead of 15, for a total length of 30 days. These parameters were derived from Graber (1961).

The expected lifespan of unsuccessful nests was estimated at 11 days for unparasitized nests and 10 days for parasitized nests, based on DLR for each nest stage. It was assumed that nest building usually began on the day following nest loss (Nolan 1978).

Little data were available to estimate the pre-nesting period before initiating a new nest after a successful one. The median for eight nests that fledged cowbirds was six. For seven that fledged vireos the median was 20. (The latter seems high.) Nolan (1978) reported a 10-day period for the Prairie Warbler, with 26 days the longest. Since territories were checked only once per week, missing a nest 1 week that was then lost before the next week's monitoring would effectively increase the apparent length of the prenesting period. Also, it seems reasonable to expect that females would minimize the length of the prenesting interval to increase the probability of success for the second-brood. On this basis, the prenesting period was set at 12, twice that for nests following a successful cowbird fledging.

The start date was set as 16 April. While only 1 percent of all nests were observed from 9 to 15 April, about 10 percent were newly discovered each week thereafter, i.e., beginning 16 April.

Weekly probability of nesting attempts following a successful or unsuccessful nest decreased with time. Data are presented in Table 34.

Vireo young per successful nest was 2.74 in unparasitized nests and 2.23 in parasitized nests. However, evidence suggested that these may be underestimates. Each is the average of the median number of fledglings observed, where the median was derived as the midpoint of the estimated range of young to have fledged from nests. A range was recorded because of uncertainty as to the number of fledglings on a given territory. Grzybowski (1985b) reported that 18 black-capped vireo young were produced in five unparasitized nests, yielding 3.6 young per nest. He also noted that including nestings discovered during the fledgling stage reduced estimated fledging success to about 2.4 young per successful nest as a result of undercounting fledglings. Although a correction factor was applied in the present study to compensate for this latter phenomenon (Table 31), there was still room to undercount fledglings. Studies of other passerine species also suggest that young per successful unparasitized nest should be higher than the figures reported above: Prairie Warbler, 3.4 (Nolan 1978); Bell's Vireo, 3.2 (Franzreb 1989); Solitary Vireo, >3.0 (Marvil and Cruz 1989); Yellow Warbler, 3.3 (Goossen and Sealy 1982); Kirtland's Warbler, 3.44 (Mayfield 1960); and 3.84 ([at 6.1 percent parasitism from 1972 to 1978] Walkinshaw 1983).

The maximum values of vireo young per successful nest were 3.07 and 2.46 for unparasitized and parasitized populations. However, preliminary analysis suggested that there might be significant differences in nest production, depending on the incidence and intensity of parasitism. During 1987 and 1988, when parasitism was 90.8 percent, mean maximum vireo young per successful unparasitized nest was 2.5 (SE=0.500, n=2), compared to 3.10 (SE=0.157, n=29) during 1989 when parasitism was 65.1 percent. Although based on a small sample size for 1987 and 1988, the difference is highly significant ($t=4.525$, $df=29$, $p<0.001$). The difference was not significant for parasitized nests (1987 and 1988, 2.67, SE=0.882, n=3; 1989, 2.40, SE=0.340, n=2) and averaged 2.46 overall. Based on the above considerations, the values used in Nolan's model were 3.10 and 2.46 vireo young per successful nest for unparasitized and parasitized nests respectively.

Estimates of vireo production in hypothetical parasitized and unparasitized populations are shown in Table 35. In the unparasitized population, 100 mated females constructed 395 nests, of which 99 were successful. Pair success was 81 percent (63 single broods and 18 double broods), and production 3.08 vireo young per female. In the parasitized population, 522 nests were constructed. Pair success in fledging vireos was 19 percent; vireo production 0.53 vireo young per female. Thus, in this hypothetical situation, parasitism reduced vireo fledging success by 76 percent and vireo production by 83 percent.

Results of regressing vireo production on percent cowbird parasitism are presented in Figure 13. Production data are from Table 31B, parasitism data from Table 19. The regression is highly significant. It accounts for 55.6 percent of the variation in vireo production, and shows that vireo production decreases linearly with increasing cowbird parasitism. In contrast, cowbird production was unrelated to the incidence of parasitism ($r=0.06$).

Effect of Cowbird Control on Pair Success and Production

Pair success in fledging vireos did not differ significantly among cowbird control treatment groups during either 1988 or 1989 (Table 36). Vireo production also did not differ among treatment groups during either year (Table 37). Similarly, pair success in fledging cowbirds and cowbird production did not differ among treatment groups during 1989 (Tables 38 and 39). During 1988, no cowbird young were observed to have been produced within the Trapping group.

Critical Values of Production and Parasitism

Critical levels of production and parasitism are presented in Table 40 for different levels of adult and juvenile survivorship. $Prod_c$ is the production necessary to offset mortality and maintain a stable population. $Para_c$ is the critical upper bound of parasitism necessary to meet $Prod_c$ (Eq. 9) based on data in Table 35. $Prod_r$ is the critical upper bound of parasitism necessary to meet $Prod_c$ derived from the regression model (Eq 13 [p 32]; see Figure 13).

The relationship between parasitism and production was linear in the regression analysis presented in Figure 13. Output of Eq. 12 also is linear ("Nolan's Model" in Figure 13) but differs somewhat from the regression analysis. Above about 75 percent parasitism, Nolan's model increasingly overestimates production relative to the regression. Under 75 percent parasitism, Nolan's model increasingly underestimates production relative to the regression. As such, the estimated critical level of parasitism is higher when derived from the regression equation than when derived from Nolan's model (Table 40). For example, at an adult annual survival of 60 percent and juvenile survival of 30 percent, $Prod_c$ = 2.67 young/female, $Para_c$ = 16.1 percent, and $Para_r$ = 37.6 percent.

Regional Analysis

Cowbird control had no clear and consistent effect on vireo nest success or production. Thus, a regional analysis of black-capped vireo nest success, pair success, and production that ignores possible treatment effects due to cowbird control was deemed appropriate. The objective was to assess the effect, if any, of colony site location on these variables.

Cowbird Parasitism

The incidence of parasitism by year and region is presented in Table 41. Analysis of the 1988 and 1989 data revealed significant associations between region and parasitism and between year and parasitism (Table 42). Despite the insignificant likelihood ratio, the data are suspicious enough to consider the possibility of a three-way interaction of Region x Year x Parasitism. Parasitism decreased by 39 to 59 percent between 1988 and 1989 to its lowest levels at East Range (52 percent parasitism) and West Fort Hood (59 percent parasitism), but decreased by only 2 percent at West Live Fire to 86 percent parasitism. The declines were more moderate at East Live Fire (20 percent decrease to 80 percent) and West Range (15 percent decrease to 70.8 percent).

The intensity of parasitism by year and region is presented in Table 43. There was a significant association between year (1988 and 1989 data only) and parasitism, but not between region and parasitism (Table 44). During 1989, frequency of nests with two and three cowbird eggs was consistently lower than during 1988. The significant association between region and year was the result of variability among regions in differences in sample size between years. That is, while sample sizes were similar between years at East Range, East Live Fire, and West Fort Hood, there was a substantial increase in sample size between years at the other two regions (Table 43).

Nest Success

DLR during incubation and nestling periods are shown by region and year in Figure 14A to 14D. For the incubation period, the desertion rate showed no obvious regional pattern that was consistent among years (Figure 14A). During 1988, the desertion rate at West Fort Hood was considerably lower than at other regions. But during 1989, regions were similar except for a somewhat higher desertion rate at West Live Fire. For three of the regions—East Range, East Live Fire, and West Range—desertion rates were lower during 1989 compared to 1988. The destruction rate during incubation (Figure 14B) was highest at West Fort Hood in 1988, which offset the low desertion rate (Figure 14A). Also, destruction rates appeared lower region by region in 1989 compared to 1988.

Total DLR was similar across regions within each year (Figure 14C) but tended to be lower in 1989 compared to 1988, consistent with results above and those presented in Table 25 (overall lower DLR total in 1989 compared to 1987 and 1988).

The nestling stage DLR due to destruction was highest at East Range during both 1987 and 1988, and was also relatively high at West Fort Hood in 1988 (Figure 14D). During 1989, DLR due to destruction was very similar across regions.

Patterns of nest destruction differed between incubation and nestling stages (compare Figures 14B and 14D). For example, while incubation stage destruction was low at East Range during both 1987 and 1988 relative to other sites (Figure 14B), nestling stage destruction was relatively high (Figure 14D). At West Fort Hood during 1988, incubation stage destruction was similar during both nest stages. This suggests that different predator groups may have been important at different sites and affected the various nest stages differently.

Pair Success and Production

Pair success in fledging vireo young (Table 45) depended on both year and region (Table 46). As data in Table 30 shows, pair success was higher in 1989 than in 1988. Success improved considerably between years on all areas (increase of 69, to 100 percent) except West Live Fire (11 percent increase). Although the latter had the second highest success in 1988, it had the least success in 1989. These results suggest that despite the insignificant likelihood ratio (p=0.1049, Table 46) the three-way interaction may be important. This pattern is consistent with that observed for the regional incidence of parasitism (Tables 41 and 42).

Vireo production by year and region of the Fort is shown in Table 47. Results of ANOVA are presented in Table 48. The effect of year was highly significant, that of region and the two-way interaction insignificant. Production was substantially higher at each region in 1989 compared to 1988 except for West Live Fire (Table 47).

There was no relationship between cowbird pair success and either year or region (Tables 49 and 50). For cowbird production (Table 51), while the effect of year clearly was insignificant, that of region was nearly significant (Table 52). East Range and East Live Fire appeared to have consistently lower cowbird production compared to the other regions.

Military Impacts

Specific instances of Army activities directly impacting nesting activity and behavior during 1989 include:

1. Area 2-Slope, 26 April: "Pair #2 not located within their usual territory boundaries where Army activity was set up on 13 April. They appear to have shifted away to the northeast."

2. Area 2-Top, 25 May: "In checking nest #2 in territory #8, we discovered that the nest had been abandoned (2 BCV [Black-capped Vireo]/3BHC [Brown-headed Cowbird] eggs). There was recent Army activity near the nest with broken branches on the nest tree and a bush blind built nearby."

3. Area 2-Top, 22 June: "In monitoring territory #9, we discovered that an Army tank has driven through the dense clump of trees and brush where nest #2 's located. The tank came within 2 m of the nest. All trees and other vegetation in its path were flattened. We took photographs around nest area. It appears the tank came through 2-3 days ago. A BHC chick was ready to fledge from the nest on 18 June." (It is not known whether the cowbird chick fledged.)

4. Red Bluff, 29 June: "In monitoring territory #6, we discovered that the nest bush (nest had fledged vireos) had been plowed over by a tank along with all the nearby vegetation."

5. Shell Point, 6 May: "Check territory #1, nest #1. Army has built a sand bag blind within 1.5 m of the nest. The blind was set in a hole they dug into the side of the hill. The blind has been built sometime since 29 April. All the nearby vegetation up slope from the nest was cut away. Nest is still active." (See next entry.)

6. Shell Point, 13 May: "Army sand bag in territory #1 has been removed. Nest is still active." (This nest was later lost in a storm between 13 and 17 May.)

7. Manning Mountain, 20 May: "Could not locate pair #1 within usual territory boundaries. Located the pair on the slope to the south of their original territory away from the area frequently used by the Army."

8. Manning Mountain, 20 June: "Large Army unit set up on Judith Plateau and Mike's Point [areas south of Clabber Point] and throughout surrounding area. Roads show signs of recent heavy traffic. Could not locate BCV's in territory #2." (The pair was found again at the east end of its territory.)

9. West Fort Hood, 30 May: "Lots of trampled vegetation from previous Army activity in territory #2. Could not locate either the male or female BCV's from territory #2 for remainder of the season.

Of these nine events, three resulted in a shift in territory location (no. 1, 7, and 8), one in abandonment of a territory (no. 9), and one in desertion of a nest (no. 2). Of the remaining four, three were of no apparent consequence (no. 5 and 6) and one was of unknown consequence (no. 3). Thus, no more than 2 of 167 nests observed during 1989 (1.2 percent) were directly affected by military activity. And only 4 of 70 territories monitored during 1989 (5.7 percent) were affected seriously enough to cause a shift in or abandonment of the territory.

No such observations were made during 1987 in the course of monitoring 24 territories at Area 6, Area 2-Slope, and Area 2-Top. During 1988, no instances of military impacts were recorded on territory or nest monitoring data forms that were provided to the field crew. However, personnel were not specifically asked to obtain such data.

These data do not include habitat loss due to fires that burned portions of 1988 vireo territories prior to the 1989 breeding season (Tazik et al. 1993b).

6 DISCUSSION

Population Age Structure

Monitoring the age structure of a population is important for recognizing and understanding population trends. In a stable population, the yearling age class must be at least equal to the number of older individuals lost from the population during the annual cycle. The SY male component of the Fort Hood black-capped vireo population was nearly constant during 3 years at 10.6 percent (Table 1). The female component of the population exhibited a higher proportion of SY birds than males at 23.3 percent overall. Each is substantially less than the adult mortality of about 40 percent (see below). Assuming Fort Hood is representative of the regional population, this indicates a declining population. Alternatively, sampling (i.e., mist netting) may have been biased toward ASY birds.

The rate of decline can be estimated as follows (Pease and Gingerich 1989). For a stable age distribution, the rate of population change can be estimated as:

$$r = \frac{S_{asy}}{1 - p_{sy}} \qquad \text{[Eq 14]}$$

where,

$$N_t = r \times N_{t-1} \qquad \text{[Eq 15]}$$

and,

N_t = population size at time t
r = rate of change
S_{asy} = survival of ASY vireos
p_{sy} = proportion of birds that are SY.

Given p_{sy} in the range of 11 to 23 percent and S_{asy} at 60 percent (see below), r is in the range of 0.67 to 0.78, yielding an annual population decline of 22 to 33 percent.

In other areas of Texas, Grzybowski (1989) reported populations comprised of from 4 to 19 percent SY males at nonperipheral colony sites, and 33 percent at a peripheral colony site. Similarly, at Fort Hood peripheral sites had a higher proportion of SY males (22.2 percent) than main colony sites (10.6 percent). The Davenport Ranch vireo population near Austin, Texas, has had the lowest reported SY component (4 percent) and has continued to decline over the past several years (J.A. Grzybowski, personal communication). Thus, a low ratio of SY birds appears characteristic of Texas populations, and unless SY birds are abundant in areas not studied, indications are that a large portion of the population may be in decline.

The higher proportion of SY females compared to SY males in the Fort Hood population is not due to a higher survival rate of SY females compared to SY males; nor is it due to a lower survival rate of ASY females compared to ASY males (Table 6). It may be the result of: (1) disproportionately higher rates of immigration among SY females than SY males, (2) sampling bias, or (3) imperfect recognition of age among females, which lack the distinctive cap coloration that is useful in aging males.

Annual Survival

Adults

Tables 3 and 4 show the complex relationship between sex, year, and return frequency for the 1988 and 1989 annual returns. The difference in returns between males and females depended on the year, and the differences between years depended on sex. In 1988, 64.7 percent of males and 33.3 percent females returned. In 1989, male returns were 46.8 percent, female returns 58.3 percent. Such annual variation has also been documented elsewhere. Grzybowski (1989) reported a range of 55 to 70 percent for male returns, and 25 to 50 percent for females. Graber (1961) reported annual returns of 64.3 and 75.0 percent for males, and 33.3 and 50.0 percent for females. (See also Nolan [1978] for similar data on the Prairie Warbler.)

Despite the interaction of sex and year in return frequency, yearly data were combined for further analysis. Although it is important to document annual variation in returns to document trends, if present, it also is appropriate to ignore normal annual fluctuations, assuming no trends, to characterize average long-term conditions.

Overall, 1-year returns were 53.5 percent for males and 42.9 percent for females. However, peripheral colony sites were found to have lower returns than monitored and unmonitored main colony sites (Tables 8 and 9) as was also documented by Grzybowski (1989). Ignoring peripheral sites yields a 57.2 percent male return and a 47.7 percent female return. These compare with 63 percent for males and 44 percent for females in major colony sites elsewhere in Texas (Grzybowski 1989).

Although female 1-year returns appeared lower than male returns (Table 8), no relationship was found between sex and return frequency (Tables 8, 9, and 10). Graber (1961) and Grzybowski (1989) reported similar discrepancies between male and female returns, but concluded that females probably had a survival rate similar to that of males (see also Mayfield 1960, and Nolan 1978). Given the greater inconspicuousness and dispersion of females and their lesser site tenacity (Table 11), it is appropriate to consider female black-capped vireo survival to be at least equal to that of the male. Also, Dobson (1987) argues that natural selection should favor approximately equal survival of the sexes in birds with a mating system based on male-held territories. The black-capped vireo has such a mating system. Dobson observed a significantly higher male annual survival in only 2 of 13 passerine species in his study of British birds.

Males and females had similar 2-year returns at about 22 percent. Ignoring peripheral colony sites increases this to 23.5 percent. Annualized, this yields a 48 percent annual return, which is substantially lower than the male 1-year return of 57.2 percent in major colony sites but similar to the 47.7 percent for females. The low 2-year return among males is due largely to a low return at East Range colony sites (9.1 percent). This may be in part the result of normal annual fluctuation, but also is related to a significant population decline at Area 6 (see below).

A good working estimate of annual survival for both sexes of the vireo in main colony sites on Fort Hood is 60 percent. Although 57.2 percent is a reasonable estimate of the return rate, it undoubtedly underestimates survival (e.g., Nichols and Pollock 1983, Loery and Nichols 1985). This estimate agrees with Roberts' (1971) observation of an average annual survival of 60 percent or more among North American wood warblers, a group closely related to the vireos (Welty 1975). As most management will and probably should be directed at major colony sites on the Fort, this estimate is used in the analyses that follow.

Juveniles

None of the nine juveniles banded in 1987 and 1988 were observed in years subsequent to banding. Grzybowski (1989) reported a 16 percent banding return among young banded in Texas. This provides a minimum estimate of survival and is probably low since many young likely disperse from their natal areas. For example, Walkinshaw (1983) reported that over half of the male Kirtland's warbler banded as nestlings that were observed in subsequent years, were observed in regions other than where they were banded. Doubling Grzybowski's observed returns for young black-capped vireos yields a return of 32 percent. Based on this and the following considerations, a 30 percent juvenile survival appears to be a reasonable working estimate.

First year survival in juvenile passerines has not been adequately documented. Most agree, however, that juvenile survivorship is lower than that of adults (e.g., Lack 1946, 1954, Dobson 1987), and it appears often to be in the range of 20 to 40 percent: song sparrow, 21 percent (Nice 1937); prairie warbler, 32 percent (Nolan 1978); great tit, 13 percent, redstart, 23 percent, robin, 26 percent (Lack 1954); Kirtland's warbler, 36 percent, mourning dove, 20 percent, and plain titmouse, 25 percent (Mayfield 1960); Kirtland's warbler, 27 to 32 percent (Bergland 1983) and 20 percent (Probst 1986); mourning dove, 35 percent (Tomlinson et al. 1988); tree pipit, 35 percent (Van Hecke 1981, abstract in BIOSIS,* No. 74016168); Galapagos mockingbird, 35 percent (Curry and Grant 1989); brown-headed cowbird, 20 percent (Scott and Ankney 1980). Figure 1 in Roberts (1971) indicates that, for a species with seasonal production of between 2.5 and 3.0 young per pair, juvenile survivorship should be 25 to 30 percent to maintain a stable population.

Another way to approach this is by examining the population age structure. SY birds constituted approximately 11 percent of the male population and 23 percent of the female population (Table 1). With an observed seasonal production of 0.44 vireo young per female for 1987 and 1988 overall, what return rate would be required to establish an 11 to 23 percent SY component in the population? A population of 100 mated adults produces 22 young (i.e., 0.44 for each of 50 females) in the first year, and 60 of the adults return in the second year. To those 60 adults, add 7 to 18 SY birds for a total population of 67 to 78. This establishes an age structure with 11 to 23 percent SY birds. These 7 to 18 SY birds represent 32 to 82 percent of the 22 young produced in the first year. Since males seem to have been more easily and consistently aged because of cap coloration, the male age structure may more accurately reflect the true population structure, suggesting a juvenile survivorship of 32 percent.

This analysis also indicates a 22 to 33 percent annual population decline (100 to between 67 and 78 vireos) as noted above since it is based on the same data presented earlier. A stable population of 100 birds could be maintained only through immigration from other regional populations.

Impacts of Military Activity

The variability in return frequency among major colony sites and between years appears unrelated to military activity. No relationship was found between region and returns (Tables 5 and 10). However, inspection of Table 8 shows that East Range training areas, portions of which receive only light tracked vehicle activity, had lower male returns (48.9 percent) than main colony sites at West Range (63.6 percent at Manning Mountain), which receive uniformly heavier use and larger scale exercises than East Range. Also, main colony sites in the live fire training area each had reasonably high male returns (55.6 to 60.0 percent at Jack Mountain, Robinette Point, and Area 75). West Fort Hood receives little tracked vehicle use and had a relatively high male and female return rate (64.3 percent and 50.0 percent).

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The decline in male returns between 1988 and 1989 was consistent among colony sites with the exception of Area 2-Slope, and contrasts with an increase in female returns (Table 3). It seems unlikely that military activity would affect the sexes differently. At Area 6, the low 1989 male return was related to a population decline rather than military activity. This area is subject to little military disturbance as it is located adjacent to a limited access area set aside for management of the endangered golden-cheeked warbler. However, the population declined substantially from 14 territories in 1987 to 11 in 1988 and 3 in 1989 (Tazik et al. 1993a).

Dispersal and Its Implications

Data on dispersal distances indicates that most returning vireos return to the same or nearby colony sites. Only two males moved to new colony sites. Only one of these was a long distance movement (22.9 km), and was the result of habitat loss on a previously occupied territory. The other was a short distance dispersal (1.9 km) to a neighboring site (Jack Mountain to Manning Mountain [Figure 3]). Also, two of the four female colony site changes were short distance movements (1.1 to 1.2 km) to neighboring colonies (Area 2-Top and 2-Slope [Figure 3]).

The site tenacity obvious in these data suggest that the vireo is adapted to returning to the same colony sites each year until the habitat becomes unsuitable. Although individuals will move to new locations if their habitat is destroyed, assuming other suitable areas are available, the birds prefer areas with which they have previous experience. Furthermore, individuals may continue to use areas that are not as suitable as other available habitat. That is, there may be a lag time in their response to changing conditions (Wiens and Rotenberry 1985).

Females dispersed longer distances between years than did males (Table 11). While only 8.6 percent of males moved more than 1 km between years, 36.8 percent of females did so. This may have contributed to the lower apparent returns of females compared to males as noted above.

These data have important implications for black-capped vireo management at the regional level. For example, dispersal affects the genetic structure of the population by enhancing genetic diversity and reducing inbreeding, important considerations in small and declining populations (e.g., Frankel and Soule 1981, Lande and Barrowclough 1987). Also, Pease and Gingerich (1989) used these data in estimating appropriate size of land reserves necessary to manage the vireo. In their treatment, Pease and Gingerich (1989) applied the following formula (from Skellam 1951) to estimate the reserve area required to maintain a self-contained and sustainable population:

$$\text{radius}_c = \frac{1.2 \times \text{sd}}{g^{1/2}} \qquad \text{[Eq 16]}$$

where,

radius_c = critical radius of the reserve
sd = standard deviation of individual dispersal distances
g = population growth rate.

Assuming that, with adequate management, a population growth rate of 5 percent per year can be attained, then by applying Fort Hood data to this model, a reserve area of approximately 100,000 ha would be required (300,000 ha considering only females, which have longer dispersal distances). This area is larger than Fort Hood indicating that satellite populations within dispersal distance of the installation must be maintained as well. Note however that a single reserve certainly is inadequate. Chance fluctuations in the environment and the population, combined with the possibility of unpredictable catastrophe, make a single population susceptible to severe population decline, even extinction (Shaffer 1987, 1987, Ewens et al. 1987, Lande 1988).

Nesting Studies

A total of 165 territories were fully monitored over 3 years. This provided extensive data on nest success, pair success and production, and the impacts of cowbird parasitism and cowbird control on each. These data will serve as a basis for developing recommendations for the enhancement of vireo reproductive success and production on Fort Hood, which in turn can benefit the regional population.

The 308 active nests were discovered in the various nest stages at random in proportion to the total expected nest-days in each stage (Table 13). It was anticipated that more than expected would have been found during the construction phase since both sexes are highly conspicuous during this period (e.g., Grzybowski 1985b).

Mayfield (1975) suggested that finding nests at random throughout the nesting cycle underestimates nest loss by a factor of 2 (e.g., Coulson 1956). Fort Hood data suggest otherwise. Based on DLR estimates, 85.8 percent of the vireo nests were lost (Table 25). Direct observation of nests found randomly on the Fort throughout the nesting cycle yielded an estimated 73.7 percent nest loss (Table 14). Thus, actual loss (85.8 percent) exceeded observed loss (73.7 percent) by a factor of only 1.16, substantially less than that predicted by Mayfield (1975). Thus, multiplying observed nest losses by 2 will seriously overestimate actual nest losses and underestimate nest success.

The number of nests discovered by nest start period differed markedly among years (Figure 5). This does not mean that the pattern of actual nest starts differed among years, only that the patterns of discovery differed. However, it is useful to document the frequency of nests started early in the season, since these may have the best opportunity for avoiding cowbird nest parasitism. Overall, 61 percent of nests started during 9 to 22 April were parasitized compared to 78 percent for the rest of the season (X^2=4.363, df=1, $0.10<p<0.05$). The difference was most striking in 1989 when only 40 percent were parasitized from 9 to 22 April, in contrast to 68 percent during the remaining period. For 1987 and 1988 combined, the values were 84.6 percent for 9 to 22 April versus 91.7 percent for the rest of the season.

Cowbird Nest Parasitism

Vireos appear to be especially vulnerable to cowbird parasitism (Friedmann 1963, Grzybowski 1985b). The cowbird has been implicated in the decline of the federally endangered least Bell's vireo (Goldwasser et al. 1980, Franzreb 1989), and may be impacting western populations of the warbling vireo (Rothstein et al. 1980, Verner and Ritter 1983) and the solitary vireo (Marvil and Cruz 1989). High parasitism of Bell's vireo nests has been documented elsewhere by several workers (Ely 1957, Mumford 1952, Barlow 1961, Wiens 1963), and the species has shown a decline throughout its range (Robbins et al. 1986). Bell's is a summer resident on Fort Hood along with the white-eyed, red-eyed and black-capped vireos.

Cowbird parasitism at Fort Hood during 1987 and 1988 (90.8 percent) was among the highest reported for the black-capped vireo. Graber's (1961) populations experienced 61 percent parasitism overall, but her Texas colony site reached 87 percent (in Grzybowski 1985b). In Texas, during 1983 to 1988, 73 percent of black-capped vireo nests were parasitized with a high of 90 percent at the Kerr Wildlife Management Area in 1988 (Grzybowski 1989). In Oklahoma, 76 percent of vireo nests were parasitized during this same period with a high of 92 percent in 1986 (Grzybowski 1989).

Cowbird Control

Cowbird trapping was relatively ineffective during both 1988 and 1989. In 1988, 10 females were removed from three traps in 270 trap-days, yielding 0.04 female per trap-day. In 1989, 36 were removed from eight traps in 639 trap-days for a trapping success of 0.06 female per trap-day. This is within, but at the low end of the range of trap success reported for other locations (Table 53).

Unexpectedly, a positive correlation was found between female trapping success and the incidence of parasitism (Figure 7). There are at least two possible explanations. First, while trap success and parasitism may have been independent of one another, each may have been positively correlated with cowbird abundance. In other words, trapping success was positively related to cowbird abundance, but the effort was ineffective in reducing cowbird abundance sufficiently to reduce the level of parasitism. Second, trapping may have helped to attract cowbirds to the colony sites trapped. A detailed analysis of parasitism at Area 2-Top revealed that parasitism was more frequent among territories closer to the traps (67 percent) than among those further distant (43 percent), although the sample size was too small to reveal statistical significance (X^2=1.471, df=1, $0.10 < p < 0.25$).

In Table 53, female cowbird trapping success per trap-day is shown to vary considerably—0.0 to 0.26 in Oklahoma, and 0.04 to 0.71 in Texas. The greatest success was achieved during 1988 at the Kerr Wildlife Management Area (Grzybowski 1989). Parasitism was reduced from 90 percent in areas without cowbird removal to 9 percent in areas with removal at a female capture rate of 0.71 per trap-day. This success was achieved by constant trap maintenance and rotation of cattle grazing in such a way so as to concentrate cowbirds at the trap sites. Cowbird trapping success on Fort Hood will have to increase tenfold to achieve similar results.

Also noteworthy is the 0.99 female per day trap success obtained at sites in the northern lower peninsula of Michigan where cowbird control is aimed at enhancing reproductive success of the endangered Kirtland's warbler. Cowbird trapping reduced parasitism from 69 percent during 1966 through 1971 to 6 percent during 1972 through 1977 (Walkinshaw 1983). In California, cowbird trapping reduced parasitism in the endangered least Bell's vireo from 47 percent to under 10 percent (Franzreb 1989).

Routine shooting of female cowbirds at colony sites was expected to be an efficient means of removal. Although neighboring females were expected to establish ranges in areas vacated by females shot, the time it took for the new female to become familiar with the new range was expected to reduce nest-finding efficiency (Rothstein et al. 1987, Dufty 1982, Raim, personal communication). Shooting did remove 5 times more females per day than trapping (Table 18). Yet, shooting did not affect cowbird parasitism (Tables 20 and 24). Perhaps the number of days between shooting events was too long to be effective given the abundance of cowbirds on Fort Hood. Neighboring or floating females may have moved into vacated territories too rapidly to make shooting effective. Also, the effectiveness of this method depends on the ability of females to exclude other females from their territory, and it is not clear just how territorial Fort Hood female cowbirds are.

The cowbird mating system and degree of territoriality appear to vary geographically in response to cowbird population density (Dufty 1982, Rothstein et al. 1984). At moderate densities in the northeast, monogamy and territoriality have been observed (Dufty 1982). At high population densities in Kansas, Elliott (1978) documented a promiscuous mating system with little evidence of territoriality. In the latter situation, territoriality may be too costly in time and energy when balanced against the need for females to locate nests for egg laying (Dufty 1982). At low populations in the eastern Sierra Nevada of California, Rothstein and co-workers (1984) also found no evidence of territoriality and Yokel (1986) documented monogamy. Here, the benefits of territoriality may be too few. A high host nest-to-cowbird ratio would ensure adequate access by females to nests thereby eliminating the need to defend host nests as a critical resource.

In Illinois, Raim (1979) reported female territoriality among cowbirds. Darley (1983) also provided evidence of territoriality, but ranges overlapped considerably. At Fort Hood, preliminary radio tracking data collected at Area 6 during 1989 indicate significant overlap of breeding ranges. Given an apparent high density on Fort Hood, female cowbirds may not be highly territorial, thereby reducing the effectiveness of periodic shooting. Further investigation of cowbird territoriality and mating system on Fort Hood may help in designing a more efficient control program.

Combining trapping and shooting was expected to enhance cowbird control efforts. However, dual treatments implemented after 1 June during 1989 did not yield to expectation (Tables 21 and 22). While parasitism did appear to decline at Area 2-Top after initiation of shooting, parasitism remained high at Brown's Creek Range (Table 21). At West Fort Hood, an apparent decline in parasitism after 1 June upon initiation of trapping was independent of the trapping effort as no females were caught by the two traps located there. Nevertheless, given low overall trapping success and a higher shooting success early in the season (Table 18), shooting (if applied early in the season) in combination with trapping may prove beneficial.

The difference in parasitism between years (Table 19) was unrelated to cowbird control and probably was the result of normal annual variability. For example, at the Kerr Wildlife Management Area in Texas, parasitism varied from 65 to 90 percent over 4 years on areas not trapped for cowbirds, and in Oklahoma from 58 to 92 percent on such areas over a 3-year period (Grzybowski 1986, 1988a, 1989). Some of the variability may be related to variation in cowbird abundance. Observations by several individuals indicated that cowbird numbers may have been low during 1989 throughout the region (Espey Houston & Assoc., Inc 1989, personal observation [JDC]). On Fort Hood, cowbird abundance may have been down in 1989 due to a reduction in cattle numbers that year (D. Jones, personal communication), and this may have resulted in the low level of parasitism observed. This appears to be the case during 1990 as well with 63 percent parasitism and continued low cattle numbers (Hunt 1990).

Mating and Nest Success

Black-capped Vireo

Mating success was quite high at 93.8 percent overall. This compares with 77.7 percent at other Texas localities (Grzybowski 1989). Also, Grzybowski (1989) reported that SY males had a lower mating success (44.7 percent) than ASY males (84.3 percent). At Fort Hood, mating success did not differ between age classes.

The nest fates reported in Table 14 differ substantially from those based on Mayfield's method as presented in Table 25 (see Table 26). Thus, analysis of the former data is suspect. Data in Table 26 and Figure 9 indicate that nest desertion decreased from a high of 82 percent in 1987 to a low of 48 percent in 1989. This undoubtedly was related to a decrease in the incidence and intensity of parasitism over this period (Tables 19 to 24) as most nest abandonment, excluding the construction period, was associated with parasitism (Table 14 and Figure 6). However, nest destruction increased twofold between 1987 and 1988 from 16 to 31 percent (Table 26) so that despite the decrease in desertions, nest success remained low in 1988. Nest success was markedly higher in 1989 coincident with a decrease in desertions, and leveling off of nest destruction (Figure 9).

Brown-headed Cowbird

Cowbird nest success usually has been reported as the percentage of eggs that fledge. While several studies report an average egg success of about 25 percent (e.g., Young 1963), actual success is probably lower. Many of the studies were based on nests discovered at various times throughout the nesting cycle, thereby missing many unsuccessful nests and biasing estimates upward. Also, cowbirds sometimes lay eggs in abandoned nests (Scott and Ankey 1980, personal observation). Scott and Ankey (1980) considered 15 percent a more reasonable overall average.

On Fort Hood, cowbird eggs had a 5.4 percent success rate in vireo nests. This is in agreement with Nolan's (1978) estimate of 5 percent cowbird success in prairie warbler nests. Mayfield (1965) reported a 6 percent success rate in black-capped vireo nests based on Graber's data, and a 6 percent success rate in the Bell's vireo based on several studies.

Effect of Parasitism on Vireo Nest Success

Cowbird nest parasitism clearly had a negative impact on vireo nest success. During the construction phase, although only two nests were observed to have been parasitized, a higher desertion rate for the parasitized than the unparasitized nests was expected (Table 27) as host nests are frequently deserted when cowbird eggs are deposited prior to or early in laying (see below). Losses during the laying stage were not much different between parasitized and unparasitized nests. This is important in cowbird reproductive success as about 70 percent of cowbird eggs were deposited during the laying period.

Laying is the most appropriate time for the cowbird to deposit its eggs in host nests. Cowbird eggs deposited prior to host laying run the risk of being buried in the nest lining or deserted (Nolan 1978, Clark and Robertson 1981, Wiley 1985, Wolf 1987). Those deposited later may disrupt incubation sufficiently to cause desertion (Nolan 1978, Wiley 1988), or the cowbird eggs may lose advantage by hatching later than host eggs.

During incubation, desertion and total DLR were markedly higher in parasitized than in unparasitized nests (Table 27). Parasitized nests also had a higher destruction and total DLR during the nestling period. Similarly, Finch (1983) observed that parasitized nests of Abert's towhee had higher DLR during both incubation and nestling stages than unparasitized nests. In Kirtland's warbler, Mayfield found that DLR during incubation did not differ between parasitized and unparasitized nests either due to desertion or destruction. During the warbler nestling stage, however, DLR due to destruction was significantly higher among parasitized nests.

Although Mayfield (1960) did not consider the difference in nestling stage DLR to be real because of a small sample size, he suggested that nests containing cowbirds may be more easily found by predators because they are larger and noisier than warblers. The most common predators of the warbler were thought to be birds. In black-capped vireo colonies at Fort Hood, snakes probably were the primary agents of predation (see also Graber 1961). While blue jays and scrub jays were seen occasionally, several snake species were frequently encountered that might prey on vireo eggs or young: Texas rat snake, western coach whip, rough green snake, and broad-banded copperhead. Others agree that snakes are important predators in oldfield habitats (Best 1978, Nolan 1978, Zimmerman 1984).

If snakes do not respond primarily to visual clues and rely on chance encounters aided by olfaction (Zimmerman 1984), then the higher destruction rate during the nestling period in parasitized vireo nests is unexpected. On the other hand, coach whips often were observed prowling with head held high as they appeared to visually scan shrub vegetation at heights that might contain vireo or other passerine nests. A larger, active, and vocal cowbird might attract the attention of a snake hunting in this manner.

Vireos fledged from parasitized nests with surprising frequency (35 percent), but only when cowbird eggs did not hatch (n=12), or when cowbirds hatched after the vireo chicks were ready to fledge (n=1). Vireos might also fledge from parasitized nests if cowbird nestlings were preferentially removed from nests by predators (Nolan 1978).

The intensity of cowbird parasitism may have some affect on nest success. During incubation, DLR due to desertion was shown to be more closely related to the intensity than the incidence of cowbird parasitism. However, the frequency of nests producing vireos was unrelated to the number of cowbird eggs in the nest (Table 29).

For the Fort Hood black-capped vireo, overall nest success was over two times higher among unparasitized nests (25.1 percent) than among parasitized nests (11.8 percent) (Table 28). This agrees with results for several other species (Table 54). The numbers of vireo young per successful nest and per active nest were larger in unparasitized than parasitized nests (2.74 vs. 0.86/successful nest, and 0.68 vs. 0.10/active nest). The ratio of unparasitized to parasitized successful nests was about 3:1 compared to 2:1 for the average among several other species (Table 54). For active nests, the ratio was about 7:1, compared to about 3:1 for other species. Other species with similarly high ratios include Kirtland's warbler, prairie warbler, and grasshopper sparrow. In the black-capped vireo, successful parasitized nests produced few host young, thus resulting in a low number of host young per successful parasitized nest. The relatively low number of vireo young per active parasitized nests is attributable to frequent desertion of these nests, and the fact that vireo young generally are outcompeted by cowbird nest mates.

Nest desertion appears to be a common response to cowbird parasitism among small passerines (Table 54; Graham 1988). Among black-capped vireo nests in which eggs were laid, only 8 percent of unparasitized nests were deserted compared to 49 percent of parasitized nests (Figure 6). In contrast, nest destruction was somewhat less among parasitized vireo nests (34 percent) than unparasitized vireo nests (57 percent) as appears to be true in other species as well (Table 54). This result does not contradict the finding that DLR due to destruction in the nestling stage was significantly higher in parasitized than unparasitized nests (Table 27). The higher desertion rate during incubation simply makes many fewer nests available for destruction in the nestling stage. It does indicate, however, that as the incidence of parasitism is reduced, predation may become more important as a factor limiting reproductive success and production. Thus, future black-capped vireo studies should examine predation more closely.

The number of cowbird eggs per active nest was 1.93 in 1987, 1.67 in 1988, 1.40 in 1989, and 1.58 overall. This compares with a range of 1.13 to 3.1 among the studies listed in Table 55. The 0.09 cowbird young fledged per active parasitized nest for the Fort Hood black-capped vireo is lower than that reported for many other species (Table 55). However, it is close to that reported by Mayfield (1965) for both the Bell's and the black-capped vireo. Thus, while the black-capped vireo is a favorite host of the cowbird, the success rate of the cowbird in nests of this vireo is quite low.

Effect of Cowbird Control on Vireo Nest Success

Cowbird control efforts had no discernable effect on nest success (Figures 11 and 12), not surprising given that trapping and shooting had no effect on parasitism. Although the greatest control effort was applied during 1989, the higher nest success at that time is attributable to a decrease in parasitism arising from normal annual variation that was independent of control efforts. The 1989 decline in parasitism was associated with a decrease in DLR due to desertion during incubation and DLR due to destruction during the nestling period (Table 25). This agrees with the finding that unparasitized nests had lower desertion rates during incubation and lower destruction rates during the nestling stage than parasitized nests (Table 27).

Pair Success and Production

Black-capped Vireo

Pair success and vireo production were highest in 1989 (Tables 30 and 31), the year of lowest cowbird nest parasitism (Table 19). In 1989, 61.4 percent of the mated pairs produced 1.80 vireo young per mated pair. This compares with a low of 9.5 percent success and 0.29 young per pair in 1987, and 18.8 percent success and 0.49 young per pair in 1988. Vireo young per successful pair (production ÷ pair success) was similar in 1987 and 1989 at 3.07 and 2.94 respectively, but lower in 1988 at 2.60. Graber (1961) reported pair success of 59.7 percent at 61 percent parasitism (parasitism reported in Grzybowski 1985b), similar to the 1989 results at Fort Hood. However, she observed production of only 0.56 vireo young per pair, and production per successful pair of only 0.94, both considerably lower than at Fort Hood during 1989.

Recent estimates of production in Texas and Oklahoma range from 0.0 to 2.58 (Grzybowski 1986, 1988b, 1989). The highest production was observed in a population at the Kerr Wildlife Management Area in which cowbird control through trapping reduced parasitism to only 9 percent (Grzybowski 1989). The lowest production occurred in a population at Kerr without cowbird trapping and with 90 percent parasitism.

Brown-headed Cowbird

Despite a sharp decline in the incidence and intensity of cowbird parasitism during 1989, both pair success in producing cowbirds and cowbird production did not vary markedly among years. Pair success averaged 14.2 percent, while cowbird production averaged 0.19 young per pair overall, yielding 1.24 cowbird young per vireo pair successfully fledging cowbirds.

Although not statistically significant, cowbird production tended to be higher during 1989 (Table 33). Thus, if anything, the sharp decline in parasitism during 1989 benefited cowbirds as well. This suggests that cowbird success may depend on cowbird pressure with this host species as McGeen (1972) observed in two other hosts—the yellow warbler and the song sparrow. Cowbird production may increase with increasing parasitism up to a maximum point at which increasing parasitism itself interferes with both cowbird and host production. Also, cowbird production was not correlated with the incidence of parasitism perhaps because the relationship is not linear.

Low cowbird success in vireo nests indicates that while the vireo may be a preferred host, it is not a beneficial one. However, the large number of nests that the vireo seems to be capable of building combined with the large number of eggs a cowbird can lay may make the vireo a better host than expected.

Effect of Parasitism on Production

The effect of parasitism on seasonal production was assessed using an approach similar to that applied by Nolan (1978). Two hypothetical populations were constructed, one with no cowbird parasitism, the other 100 percent parasitized. Results indicated that 3.08 young per female per year would be produced in the unparasitized population, while only 0.53 would be produced in the parasitized population, an 83 percent reduction in potential vireo production (Table 35). During 1987 and 1988 combined, cowbird parasitism thus reduced vireo production by 86 percent, from a potential of 3.08 to an observed 0.44 young per female. For 1989, the reduction was 42 percent from 3.08 to 1.80.

The 3.08 young per female in the unparasitized population is higher than the 2.58 young per mated pair observed by Grzybowski (1989) in a population with 9 percent parasitism. Assuming a linear relationship between parasitism and production (e.g., Figure 13), and production of about 0.5 vireo young per female at 100 percent parasitism, Grzybowski's data point can be extrapolated to 2.79 at 0 percent parasitism, still lower by about 9 percent but probably within the range of expected variability.

Both the regression analysis and Nolan's model indicate a linear relationship between vireo production and parasitism (Figure 13). The two models differ increasingly above and below about 75 percent parasitism, with the regression giving higher production below 75 percent parasitism, and lower parasitism above. Yet, the two models are reasonably similar above about 50 percent parasitism. For the regression analysis, all but one data point were above 50 percent parasitism. Thus, the regression model for parasitism of 0 to 50 percent may not be valid. For example, production of 4.1 young per female at 0 percent seems unreasonably high (Table 54). Nolan's model may be more appropriate in this region. Further sampling of colony sites with parasitism in the 0 to 50 percent range may yield a closer correspondence between the two models. Also, it may be that the relationship between parasitism and production is curvilinear. Above 50 percent parasitism, parasitism may be the major factor limiting production. Under 50 percent, factors other than parasitism such as predation and food availability may become more limiting. Thus, while the relationship may be linear between 50 and 100 percent parasitism, under 50 percent, the curve may flatten out in the manner illustrated by segment (A) in Figure 13.

Effect of Cowbird Control on Production

Cowbird control had no effect on pair success in fledging either vireos or cowbirds, and no effect on seasonal production of vireos and cowbirds. This result is not surprising as cowbird control also had no effect on parasitism or nest success. As with nest success, pair success in fledging vireos and production of vireos was markedly higher during 1989 than during the earlier years due to a decrease in parasitism that was independent of cowbird control efforts.

As noted above, Grzybowski (1989) was able to reduce cowbird parasitism from 90 to 9 percent at the Kerr Wildlife Management Area with a successful cowbird trapping program. This resulted in a dramatic increase in seasonal vireo production from 0.0 to 2.58 vireo young per female. Also, production in Oklahoma was increased from 0.36 to 1.31 by reducing parasitism from 81 to 24 percent. These results were achieved through nearly daily attention to the traps to keep them operational.

Cowbird trapping also has been successful in enhancing seasonal production in two other endangered passerines. It has had its most noteworthy success in halting a decline in and stabilizing the Kirtland's warbler population by reducing parasitism from 69 to under 10 percent and increasing seasonal production from less than one to over three young per pair (Kelly and DeCapita 1982, Walkinshaw 1983, Probst 1986). In the least Bell's vireo, a reduction in parasitism from 47 to 10 percent increased seasonal production from 2.08 to 2.86 vireo young per nesting pair (Franzreb 1989).

Critical Values of Production and Parasitism

The level of parasitism that can be sustained by the vireo population while maintaining a stable population was evaluated based on knowledge of potential seasonal production, and adult and juvenile mortality (Table 40). At 60 percent adult annual survival, and juvenile survival of 30 percent, estimated critical production is 2.67 vireo young per female per year. Applying Eq. 12 from May and Robinson (1985) gives a critical level of parasitism of 16 percent, while the regression equation (Eq. 13) yields 38 percent. The curvilinear relationship between production and parasitism indicated by (A) in Figure 13 yields critical parasitism of about 35 percent. An adult survival more similar to that in other major colony sites in Texas, of about 65 percent (Grzybowski 1989), yields values in the range of 29 and 46 percent parasitism by Eq. 12 and 13 respectively. Clearly, estimates of juvenile and adult survival have a significant effect on estimates of the critical level of parasitism (Table 40).

An analysis presented by Pease and Gingerich (1989) suggested that parasitism would have to be reduced to near zero to maintain a stable vireo population even at 100 percent juvenile survival. However, data presented there indicate production of only about 1.6 vireo young per pair at 0 percent parasitism, which seems far too low, and about one-half the value derived for Fort Hood (3.08).

Regional Analysis

A regional analysis was performed to detect the effects, if any, of the impact of differing intensities and uses of the land on parasitism, nest success, and production. This was feasible as cowbird control activities had no discernable effect on these variables. That is, differences among regions were not due to varying levels of cowbird control.

Cowbird Parasitism

The incidence of parasitism was associated with both year and region (Table 42). As noted elsewhere, parasitism was much reduced in 1989 compared to the previous years. However, the decrease between 1988 and 1989 did appear to vary among regions (Table 41). Thus, both parasitism and the annual variability in parasitism may vary among regions, perhaps in relationship to annual and spatial variability in the distribution and abundance of cowbirds. For example, field technicians noted that cowbirds were particularly abundant at the Brown's Creek colony site within the West Live Fire region. This observation is supported by the higher than average daily capture rate of females at Brown's Creek (Table 17). Also, high percentage parasitism was observed there during both 1988 (100 percent) and 1989 (94 percent) despite cowbird control efforts in 1989. It is not clear, however, whether spatial variability in parasitism and cowbird abundance might be due to differences in military activity, habitat, the distribution and density of cattle, or some combination of these.

Parasitism intensity was associated with year but not with region, and the decrease in frequency of multiple parasitism between 1988 and 1989 was similar among regions.

Nest Success

There was no consistent relationship between nest success and region (Figure 14A-D). Overall, DLR during the incubation and nestling stages decreased during 1989. For the incubation period, the decrease between 1988 and 1989 was similar across regions although somewhat less at West Fort Hood than other regions (Figure 14C). However, for the nestling stage, the decline occurred only at East Range and West Fort Hood (Figure 14D), the same two regions where the incidence of parasitism declined the most between years (Table 41). This latter result is related to the fact that parasitized nests were more frequently destroyed than unparasitized nests during the nestling stage (Table 27).

Pair Success and Production

Results of the analysis of the relationship between pair success, year, and region (Table 46), were remarkably similar to that between parasitism, year, and region (Table 42). Pair success was related to both year and region, and there was some indication of a possible three-way interaction. That is, while pair success increased between 1988 and 1989 at each region, there appeared to have been some variation among regions in the extent of that increase (Table 45). For example, pair success at West Live Fire increased only 11 percent compared to increases of 69 to 100 percent at the other regions. This is the same region that showed the least decline in the incidence of parasitism between years (2 percent).

While regional production was markedly higher in 1989 compared to 1988, no difference was detected among regions, nor in the extent of the between year increase (Table 48). However, in keeping with the pattern of pair success, West Live Fire increased only 19 percent compared to increases of 61 to 100 percent elsewhere (Table 47).

It appears that a relatively high incidence of parasitism at the West Live Fire region during 1989 was responsible for suppressing nest success, pair success, and possibly production there. Within this region, percentage parasitism during 1989 was 94 percent at Brown's Creek, 83 percent at Robinette Point, and 60 percent at Jack Mountain compared to 60 percent on all other areas combined (Table 19). As these three sites are inhabited by 34 percent of Fort Hood vireos (Tazik et al. 1993a), actions need to be taken to reduce the level of parasitism there.

Pair success and production of cowbird young were similar among regions and years (Tables 49 to 52). Although pair success in producing cowbirds appeared to be higher at West Live Fire during 1989 (Table 49), in keeping with results above, production was not (Table 51).

Military Impacts

Based on 1989 data, only about 1 percent of all nests can be expected to be lost to direct interference by military activities. Nolan's model predicts 470 nests constructed by 100 females at the 1989 parasitism rate of 65 percent. Less than five of these nests would be affected by the military. This is insignificant relative to the total of losses due to desertion (48 percent) and destruction (29 percent) during 1989.

Vireos shifted territory location on three occasions as a result of military activity. In each case, the resident pair was still able to fledge young; pair #2 at Manning Mountain was double brooded. A territory was abandoned in only one case out of 70 (1.4 percent) closely monitored territories during 1989.

These impacts are inconsequential and more than balanced by the extensive habitat created by the Army at Fort Hood. Also, these losses can be mitigated by a management program that reduces the impacts of cowbird parasitism and enhances vireo nest success and production. Nonetheless, given the nature of the training mission, the potential does exist for substantial negative impacts on individual colony sites.

7 CONCLUSIONS

The age structure of the black-capped vireo population on Fort Hood, TX combined with adult mortality data suggest a vireo population decline as high as 22 to 33 percent. However, inventory data indicate that vireo numbers on Fort Hood are stable. It is possible that the apparently stable population is supported by immigration from areas off post. Adult annual survivorship at major colony sites on Fort Hood was about 60 percent, somewhat lower than that reported elsewhere. Juvenile survivorship was probably in the range of 20 to 40 percent with 30 percent considered a reasonable working estimate.

Both sexes exhibit a high degree of site fidelity, but females disperse greater distances than males. Although both sexes are capable of relocating to new colony sites after the loss of previously occupied territory, the species is adapted to recolonizing the same areas each year. The goal of a stable population will benefit from a policy that protects existing habitat.

Fort Hood appears to be smaller than necessary to sustain a self-contained population, and is not alone an adequate area to ensure continued existence of the species. At a minimum, several additional reserve sites should be maintained, and numerous satellite populations should be identified or established within dispersal distance of each (<20 km).

As with many other vireo species, the black-capped vireo is highly susceptible to cowbird nest parasitism. Unfortunately, the cowbird control efforts used in this study—trapping, shooting, and combined trapping and shooting—had no effect on the incidence or intensity of parasitism, vireo nest success, or vireo production. In fact, trapping may have attracted cowbirds to some colony sites and increased parasitism within nearby territories. The decline in parasitism between 1988 and 1989, and the attendant increase in reproductive success was apparently unrelated to cowbird control. It could have been caused by normal annual fluctuation, but may also have been related to a decline in cowbird abundance in 1989. The latter was associated with a decrease in cattle numbers on the Fort during that year.

Cowbird parasitism was a major factor limiting reproductive success of the vireo on Fort Hood by increasing both the nest desertion rate during incubation and the nest destruction rate during the nestling stage. This resulted in nest success among unparasitized nests (25 percent) twice as high as that among parasitized nests (12 percent). Desertion appears to be an adaptive response to parasitism that is shared with several other passerine species. Cowbird trapping success will have to increase tenfold to attain a reduction in parasitism adequate to increase reproductive success to a level above that required to maintain a stable population through reproduction alone (excluding immigration).

Despite the higher nest destruction rate among parasitized compared to unparasitized nests, the percentage of all nests destroyed was actually lower overall among parasitized nests than among unparasitized nests. This was due to a substantial loss of parasitized nests to desertion early in the incubation stage, which reduced the number of parasitized nests available for destruction. Thus, with a reduction in parasitism due to cowbird control or normal annual variability, predation likely will increase in importance as a factor limiting vireo reproductive success on Fort Hood. Nonetheless, production should benefit from a decrease in parasitism.

Both Nolan's model and the regression model indicate a linear relationship between vireo production and percent parasitism—more parasitism causes less vireo reproductive success. Although Nolan's model may be the more reasonable of the two, it appears to be somewhat conservative at low parasitism. The relationship may in fact be curvilinear. Sampling of colony sites with parasitism in the range of 0 to 30 percent will help to better define the relationship.

Assuming an average annual adult survival rate of 60 percent, and an annual average juvenile survival rate of 30 percent, annual production required to maintain a stable population is 2.67 fledglings per female, nearly 50 percent above the highest production recorded at Fort Hood (1.80 during 1989). This level of production requires parasitism to be reduced to 16 percent according to Nolan's model, 35 percent by the curvilinear model, and 38 percent by the regression model.

Percent parasitism, nest success, and pair success were related to region, whereas intensity of parasitism and production were not. Most notable was the fact that the West Live Fire region decreased least in parasitism and increased least in pair success compared to all other regions between 1988 and 1989. A substantial portion of the Fort Hood vireo population (34 percent) is located in this region and warrants a significant cowbird control effort.

This study concludes that military activity did not impact the return frequency of banded vireos on Fort Hood. The military has had little direct impact on nesting and territorial behavior especially relative to the losses attributable to parasitism and predation. Successful management to reduce parasitism and enhance vireo reproductive success will adequately compensate for incidental losses due to military activity under current conditions.

However, given the nature of the military mission on Fort Hood, the potential does exist for substantial negative impact on individual territories and colony sites. Such impacts could result in violations of the Endangered Species Act. Potential for military impacts on vireo colony sites varies across the installation. Colony sites located in intensively used areas require the most vigilant protection, while those in low use intensity areas may be the best candidates for intensive management and expansion provided mission conflicts are not increased.

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APPENDIX A: Common and Scientific Names of Referenced Animal Species

Common Name	Scientific Name
Birds	
Abert's Towhee	*Pipilo aberti*
Bald Eagle	*Haliaeetus leucocephalus*
Bell's Vireo	*Vireo bellii*
Black-capped Vireo	*Vireo atricapillus*
Blue Jay	*Cyanocitta cristata*
Brown-headed Cowbird	*Molothrus ater*
Common Yellowthroat	*Geothlypis trichas*
Dark-eyed Junco	*Junco hyemalis*
Dickcissel	*Spiza americana*
Eastern Meadowlark	*Sturnella magna*
Field Sparrow	*Spizella pusilla*
Galapagos Mockingbird	*Nesomimus parvulus*
Golden-cheeked warbler	*Dendroica chrysoparia*
Grasshopper Sparrow	*Ammodramus savannarum*
Great Tit	*Parus major*
Kirtland's Warbler	*Dendroica kirtlandii*
Least Bell's Vireo	*Vireo bellii pusillus*
Lark Sparrow	*Chondestes grammacus*
Mourning Dove	*Zenaida macroura*
Ovenbird	*Seiurus aurocapillus*
Peregrine Falcon	*Falco peregrinus*
Plain Titmouse	*Parus inornatus*
Prairie Warbler	*Dendroica discolor*
Redstart	*Phoenicurus phoenicurus*
Red-eyed Vireo	*Vireo olivaceous*
Robin	*Erithacus rubecula*
Scrub Jay	*Aphleocoma coerulescens*
Solitary Vireo	*Vireo solitarius*
Song Sparrow	*Melospiza melodia*
Tree Pipit	*Anthus trivialis*
Warbling Vireo	*Vireo gilvus*
White-eyed Vireo	*Vireo griseus*
Willow Flycatcher	*Empidonax traillii*
Yellow Warbler	*Dendroica petechia*

Common Name	Scientific Name
Mammals	
Raccoon	*Procyon lotor*
Snakes	
Broad-banded Copperhead	*Agkistrodon contortrix*
Rough Green Snake	*Opheodrys aestivus*
Texas Rat Snake	*Elaphe obsoleta lindheimeri*
Western Coach Whip	*Masticphis flagellum testaceous*

APPENDIX B:

Tables and Figures

Table 1

Black-capped Vireo Population Age Structure by Year and Sex

Age[a]	1987	1988	1989	Overall
Male				
AHY		2		
ASY	45 (88.2)[b]	92 (89.3)	90 (90.0)	227 (89.4)
SY	6 (11.8)	11 (10.7)	10 (10.0)	27 (10.6)
Female				
AHY	18	2	1	
ASY		21 (70.0)	25 (83.3)	46 (76.7)
SY		9 (30.0)	5 (16.7)	14 (23.3)

[a] AHY-after hatching year; ASY-after second year; SY-second year.
[b] SY and ASY only.

Table 2

Results of 3-Way Analysis of Independence of Age, Sex, and Year in Black-capped Vireo Population Age Structure

Source[a]	df	X^2	p
Age	1	76.36	0.0000
Year	1	0.39	0.5298
Age*Year	1	0.74	0.3896
Sex	1	21.53	0.0000
Age*Sex	1	6.48	0.0109
Year*Sex	1	0.06	0.8118
Likelihood Ratio	2	0.79	0.3754

[a] Data from Table 1; Analysis includes only years 1988 and 1989, and ages SY and ASY.

Table 3

Black-capped Vireo Banding Returns in Percent for 1988 and 1989 by Year, Sex, Region, and Colony Site.

	1988		1989	
Region/Colony Site[a]	**Male**	**Female**	**Male**	**Female**
East Range				
Area 2-Top	66.7 (6)[b]	40.0 (5)	37.5 (8)	50.0 (2)
Area 2-Slope	0.0 (4)	100.0 (3)	75.0 (4)	75.0 (4)
Area 6	66.7 (12)	14.3 (7)	27.3 (11)	75.0 (4)
Total	54.5 (22)	40.0 (15)	39.1 (23)	70.0 (10)
Live Fire Training Area				
Area 75	71.4 (7)		53.8 (13)	50.0 (2)
Jack Mountain	100.0 (3)		46.7 (15)	50.0 (2)
Total	80.0 (10)		50.0 (28)	50.0 (4)
West Fort Hood	72.7 (11)	0.0 (2)	58.8 (17)	62.5 (8)
West Range				
Manning Mountain	75.0 (4)		57.1 (7)	
Area 52	100.0 (1)	0.0 (1)	0.0 (1)	
Williamson Mountain	33.3 (3)		0.0 (3)	0.0 (2)
Total	87.5 (8)	0.0 (1)	40.0 (10)	0.0 (2)
Overall	64.7 (51)	33.3 (18)[b]	46.8 (79)	58.3 (24)[b]

[a] Includes only sites with 2 years of banding data.
[b] Numbers previously banded in parentheses.
[c] X^2(Return*Year-Female)=2.577, df=1, $0.10<p<0.25$.

Table 4

Results of 3-Way Analysis of Independence of Sex, Year, and Return Frequency of Banded Adult Black-capped Vireos

Source[a]	df	X^2	p
Sex	1	38.13	0.0000
Year	1	4.13	0.0422
Sex*Year	1	0.22	0.6404
Returns	1	0.09	0.7580
Sex*Returns	1	0.54	0.4639
Year*Returns	1	0.86	0.3550
Likelihood Ratio	1	5.78	0.0162

[a] Data from Table 3.

Table 5

Results of 3-Way Analysis of Independence of Region, Year, and Return Frequency of Banded Male Adult Black-capped Vireos

Source[a]	df	X^2	p
Region	3	11.54	0.0092
Year	1	6.63	0.0100
Region*Year	3	5.42	0.1434
Returns	1	1.84	0.1746
Regions*Returns	3	3.79	0.2848
Year*Returns	1	4.98	0.0257
Likelihood Ratio	3	0.66	0.8820

[a] Data from Table 3.

Table 6

Black-capped Vireo Banding Returns in Percent for 1988 and 1989 by Age and Sex

	1988		1989	
Age[a]	Male	Female	Male	Female
AHY		33.3 (18)[b]	100.0 (2)	0.0 (2)
ASY	60.0 (45)		45.7 (92)	57.9 (19)[c]
SY	100.0 (6)		54.5 (11)	33.3 (9)[c]

[a] AHY-after hatchling year; ASY-after second year; SY-second year.
[b] Numbers previously banded in parentheses.
[c] X^2(Female Returns-1989)=1.474, df=1, $0.10<p<0.25$; male returns analyzed in Table 7.

Table 7

Results of 3-way Analysis of Independence of Age, Year, and Return Frequency of Banded Male Adult Black-capped Vireos

Source[a]	df	X^2	p
Age	1	54.42	0.0000
Year	1	7.42	0.0064
Age*Year	1	0.00	0.9468
Returns	1	3.93	0.0474
Age*Returns	1	2.35	0.1256
Year*Returns	1	4.38	0.0364
Likelihood Ratio	1	3.44	0.0637

[a] Data from Table 6; Analysis includes only ages SY and ASY.

Table 8

Black-capped Vireo 1-Year and 2-Year Banding Returns in Percent by Sex, Colony Type, Region, and Colony Site

Colony Type/Region/Site[a]	Total 1-Year Returns Male	Total 1-Year Returns Female	Total 2-Year Returns[b] Male[c]	Total 2-Year Returns[b] Female
Main/Monitored				
EARA Area 2-Top	50.0 (14)[d]	42.9 (7)	0.0 (6)	20.0 (5)
EARA Area 2-Slope	37.5 (8)	85.7 (7)[e]	0.0 (4)	66.7 (3)
EARA Red Bluff	0.0 (1)			
EARA Area 6	47.8 (23)	36.4 (11)	16.7 (12)	14.3 (7)
Subtotal	48.9 (46)	52.0 (25)	9.1 (22)	26.7 (15)[f]
EALF Area 75	60.0 (20)	50.0 (2)	28.6 (7)	
WERA Manning Mt	63.6 (11)		25.0 (4)	
WELF Brown's Creek	66.6 (6)	33.3 (3)		
WEFH West Fort Hood	64.3 (28)	50.0 (10)	45.5 (11)	0.0 (2)
Subtotal	63.1 (65)	46.6 (15)	36.4 (22)	0.0 (2)
Total	57.3 (111)	50.0 (40)	22.7 (44)	23.5 (17)
Peripheral				
EARA Brookhaven Mt	0.0 (1)			
WERA Shell Point	50.0 (2)	0.0 (1)		
WERA Williamson Mt	16.7 (6)	0.0 (2)	0.0 (3)	
WERA NW Fort Hood	50.0 (2)	0.0 (1)	0.0 (1)	0.0 (1)
EARA Ruth Cemetery	0.0 (1)	0.0 (1)		
NOLF North Live Fire	50.0 (2)			
SOLF Black Mt	50.0 (2)			
Subtotal	31.3 (16)	0.0 (5)	0.0 (4)	0.0 (1)
Unmonitored				
WELF Jack Mt	55.6 (18)	50.0 (2)	33.3 (3)	
WELF Robinette Pt	58.3 (12)	0.0 (2)		
Subtotal	56.7 (30)	25.0 (4)	33.3 (3)	
Overall	53.5 (157)	42.9 (49)	21.6 (51)	22.2 (18)

[a] Colony site is the original banding site; Regions: EARA-East Range, WERA-West Range, EALF-East Range Live Fire, WELF-West Range Live Fire, NOLF-North Live Fire, SOLF-South Live Fire, WEFH-West Fort Hood.

[b] X^2 (Region*2-Year Return)=2.959, df=2, $0.10<p<0.25$ (sexes combined)

[c] X^2 (Region*2-Year Return-Males only)=5.765, df=2, $0.10<p<0.25$ (EARA, WEFH, EALF + WELF).

[d] Numbers previously banded in parenthesis.

[e] Includes one female banded in 1987 at Area 2-Slope that was present in 1989 at Area 2-Top but not observed in 1988.

[f] X^2 (Sex*2-Year Return)=2.025, df=1, $0.10<p<0.25$, (EARA only).

Table 9

Results of 3-Way Analysis of Independence of Colony Type, Sex, and 1-Year Return Frequency of Banded Adult Black-capped Vireos

Source[a]	df	X^2	p
Colony Type	2	82.91	0.0000
Sex	1	31.22	0.0000
Colony Type*Sex	2	3.40	0.1826
Returns	1	3.25	0.0716
Colony Type*Returns	2	6.76	0.0340
Sex*Returns	1	2.22	0.1366
Likelihood Ratio	2	3.03	0.2199

[a] Data from Table 8

Table 10

Results of 3-Way Analysis of Independence of Region, Sex, and 1-Year Return Frequency of Banded Adult Black-capped Vireos

Source[a]	df	X^2	p
Region	2	10.79	0.0045
Sex	1	35.45	0.0000
Region*Sex	2	7.86	0.0196
Returns	1	0.54	0.4625
Region*Returns	2	0.94	0.6249
Sex*Returns	1	0.83	0.3612
Likelihood Ratio	1	1.91	0.3851

[a] Data from Table 8; Analysis includes regions EARA, EALF + WELF, AND WEFH. Peripheral sites excluded.

Table 11

Between Year Dispersal Distance of Male and Female Black-capped Vireos

Distance (m)	Males (%)	Females (%)[a]
0 to 49	11 (13.6)	2 (11.1)
50 to 99	21 (25.9)	1 (5.6)
100 to 249	26 (32.1)	4 (22.2)
Subtotal	58 (71.6)	7 (36.8)
250 to 499	14 (17.3)	4 (22.2)
500 to 999	2 (2.5)	1 (5.6)
Subtotal	16 (19.8)	5 (26.3)
1000 to 2499	5 (6.2)	5 (22.2)
2500 to 4999	1 (1.2)	0 (0.0)
5000 to 9999	0 (0.0)	1 (5.6)
10000 +	1 (1.2)	1 (5.6)
Subtotal	7 (8.6)	7 (36.8)
Median[b]	119	327

[a] X^2 (Distance*Sex)=11.919, df=2, $0.001<p<0.005$.
[b] t_s (Medians)=2.030, $0.02<p<0.05$ (Wilcoxon test)

Table 12

Number of Active Black-capped Vireo Nestings Discovered by Year and Colony Site

Colony Site	1987	1988	1989	Total
Area 2 (Slope & Top)	16 (16)[a]	23 (20)	37 (37)	76 (73)
Red Bluff		1 (0)	10 (10)	11 (10)
Area 75		19 (18)	22 (17)	41 (35)
Area 6	18 (17)	22 (20)	6 (6)	46 (43)
Area 12			4 (4)	4 (4)
Ruth Cemetery			1 (0)	1 (0)
Blackwell Mountain			2 (0)	2 (0)
Manning Mountain		7 (6)	20 (19)	27 (25)
Williamson Mt/Shell Pt		6 (6)	7 (7)	13 (13)
Northwest Fort Hood			1 (1)	1 (1)
Brown's Creek Range		6 (4)	19 (19)	25 (23)
Robinette Point		4 (3)	13 (8)	17 (11)
Jack Mountain	1 (1)	12 (8)	7 (6)	20 (15)
West Fort Hood	2 (1)	21 (21)	33 (33)	56 (55)
Total	37 (35)	121 (106)	182 (167)	340 (308)

[a] Number of nests in parentheses.

Table 13

Observed vs. Expected Number of Nests Discovered by Nest Stage

Nest Stage[a]	L	DSR[b]	ND	R	Exp	Obs[c]
Construction	5	0.9340	4.093	0.3165	97.5	108
Laying	2	0.9319	1.280	0.0989	30.5	22
Incubation	13	0.9412	5.386	0.4165	128.3	131
Nestling	11	0.9402	2.174	0.1681	51.8	47
Total	31		12.933	1.0000	308.1	308

[a] L-length of the nest stage; DSR-daily nest survival rate; ND-expected nest-days per nest stage; R-relative number of expected nest- days (ND ÷ 12.941); Exp-expected number of nests found (308 x R); Obs-actual number of nests found during each stage.

[b] See daily nest loss rates in Table 25 (DSR=1-DLR).

[c] X^2 (Exp vs Obs)=4.024, df=3, $0.25<p<0.50$.

Table 14

Observed Nest Fates by Year and Suspected Cause

Fate[a]	1987 (%)	1988 (%)	1989 (%)	Total (%)
Deserted[b]				
Parasitism	17 (80.9)	27 (69.2)	6 (72.9)	70 (72.9)
Researcher	1 (4.8)	1 (2.6)	1 (2.8)	3 (3.1)
Weather	0 (0.0)	1 (2.6)	0 (0.0)	1 (1.0)
Unknown	3 (14.3)	10 (25.6)	9 (25.0)	22 (22.9)
Total	21 (63.6)	39 (45.9)	36 (26.3)	96 (37.6)
Destroyed[c]				
Unk Predators	7 (77.8)	24 (70.6)	40 (81.6)	71 (77.2)
Large Mammal	1 (11.1)	8 (23.5)	7 (14.3)	16 (17.4)
Ants	1 (11.1)	1 (2.9)	1 (2.0)	3 (3.3)
Weather	0 (0.0)	1 (2.9)	1 (2.0)	2 (2.2)
Total	9 (27.3)	34 (40.0)	49 (35.8)	92 (36.1)
Fledged[d]				
Vireos	1 (3.0)	4 (4.7)	39 (28.5)	44 (17.2)
Cowbirds	2 (6.1)	8 (9.4)	13 (9.5)	23 (9.0)
Total	3 (9.1)	12 (14.7)	52 (38.0)	67 (26.3)

[a] X^2 (Fate*Year)=35.208, df=6, $p<0.001$ (Deserted, Destroyed, Fledged Vireos, Fledged Cowbirds).

[b] X^2 (Desertion Cause*Year=0.964, df=2, $0.50<p<0.90$ (Researcher, Weather, and Unknown combined).

[c] X^2 (Destruction Cause*Year)=1.392, df=2, $0.50<p<0.90$ (Ants, Large Mammals and Weather combined).

[d] X^2 (Fledged*Year)=8.965, df=2, $0.01<p<0.025$.

Table 15

Observed Fates of Nine Nests in Which Cowbird Eggs or Hatchlings Were Manipulated

Fate	Egg Addled	Egg Removed	Egg Replaced	Hatchling Removed
Deserted		1	2	
Destroyed			1	1
Fledged Vireos		1	1	1
Fledged Cowbirds	1			
Total	1	2	4	2

Table 16

Results of Cowbird Trapping at Area 6 During 14 April Through 13 July 1988 (270 Trap Days)

	Male		Female		Immature	
Dates[a]	Cap	Rem	Cap	Rem	Cap	Rem
April 1-15	7	1	1	1		
April 16-30	11	6				
May 1-15	17	12	1			
May 16-31	24	13	1			
June 1-15	25	28	7	3	5	3
June 16-30	16	9		4	9	3
July 1-15	6	1	1		4	1
July 16-31		9		2		6
Total	106	79	11	10	18	13
Female/TD				0.04		

[a] Cap=captured; R=removed; TD=trap-days.

Table 17

Results of Cowbird Trapping During 1989 by Colony Site and Date

	Male		Female		Immature	
Dates[a]	**Cap**	**Rem**	**Cap**	**Rem**	**Cap**	**Rem**
Area 75 (1 Trap; 86 TD)						
April 1-15						
April 16-30	5					
May 1-15	17	10	5	4		
May 16-31	5	3				
June 1-15	4				6	
June 16-30	4	1			29	10
July 1-15	9		3	1	23	22
July 16-31				1	12	1
Total	44	14	8	6	70	33
Female/TD				0.07		
West Fort Hood (2 Traps; 98 TD)						
April 1-15						
April 16-30						
May 1-15						
May 16-31						
June 1-15	25	6	1		2	
June 16-30	7					
July 1-15					1	
July 16-31						
Total	32	6	1	0	3	0
Female/TD				0.00		
Area 2-Top (2 Traps; 188 TD)						
April 1-15						
April 16-30	11	1	8	3		
May 1-15	20	4	3	4		
May 16-31	7	6	2	2		
June 1-15	11				2	
June 16-30	4	2	2	1	18	9
July 1-15		3	2	1	10	9
July 16-31				1	11	
Total	53	16	17	12	41	18
Female/TD				0.06		

[a] Cap=captured; R=removed; TD=trap-days

Table 17 (cont'd)

Dates[a]	Male Cap	Male Rem	Female Cap	Female Rem	Immature Cap	Immature Rem
Area 2-Slope (1 Trap; 94 TD)						
April 1-15						
April 16-30	15	9	5	2		
May 1-15	4	3	2	1		
May 16-31	1		1			
June 1-15		1				
June 16-30	2		2	1		
July 1-15				2		
July 16-31				1	1	
Total	22	13	10	7	1	0
Female/TD				0.07		
Red Bluff (1 Trap; 87 TD)						
April 1-15						
April 16-30	1					
May 1-15	15		2	1		
May 16-31	8					
June 1-15	3	3				
June 16-30	2	1			6	2
July 1-15	2		1		14	10
July 16-31		1		1	1	
Total	31	5	3	2	21	12
Female/TD				0.02		
Brown's Creek (1 Trap; 86 TD)						
April 1-15						
April 16-30	6		2			
May 1-15	12	1	3	2		
May 16-31	7		2	1		
June 1-15	5	4		2	1	
June 16-30	3		1		16	13
July 1-15	3		4	2	13	13
July 16-31	2	1		2	1	1
Total	38	6	12	9	31	27
Female/TD				0.10		
Total (8 Traps; 639 TD)						
April 1-15						
April 16-30	38	10	15	5		
May 1-15	68	18	15	12		
May 16-31	28	9	5	3		
June 1-15	48	14	1	2	11	
June 16-30	22	4	5	2	69	34
July 1-15	14	3	10	6	61	54
July 16-31	2	2		6	26	2
Grand Total	220	60	51	36	167	90
Female/TD				0.06		

[a] Cap=captured; R=removed; TD=trap-days

Table 18

Results of Cowbird Shooting During 1989 by Colony Site and Dates

	West Fort Hood			Manning Mountain			William/Shell		
Dates[a]	V	M	F	V	M	F	V	M	F
April 1-15	4	5	4	4	3	8	2		3
April 16-30	4	2	5	4	6	11	4	1	3
May 1-15	6	2	8	3	4	9	1		4
May 16-31	3		2	3	2	6	0		
June 1-15	2	1	1	3		2	1		2
June 16-30	2	1	2	1			1		2
July 1-15	2		2	1			0		
July 16-31	1			1		1	0		
Other		3	9						
Total	24	14	33	20	15	37	9	1	14
Female/Visit			0.88			1.85			1.56
Days			106			106			82
Female/Day			0.31			0.35			0.17

	Area 2-Top			Brown's Creek			Total			
	V	M	F	V	M	F	V	M	F	F/V
April 1-15							10	8	15	1.50
April 16-30							12	9	19	1.58
May 1-15							10	6	21	2.10
May 16-31	1	1	4	2		4	9	3	16	1.78
June 1-15	2	1	5	2		3	10	2	13	1.30
June 16-30	4	2	3	3	2	5	11	5	12	1.09
July 1-15	3	1	3	3	1	7	9	2	12	1.33
July 16-31	2	1	1	1			5	1	2	0.04
Other								3	9	
Total	12	6	16	11	3	19	76	39	119	
Female/Visit			1.33			1.73			1.45	
Days[b]			53			56			403	
Female/Day			0.30			0.34			0.30	

[a] V=number of visits; M=males; F=females.

[b] Days are total number of days from first to last day of shooting.

Table 19

Incidence of Cowbird Nest Parasitism in Percent by Year, 1989 Treatment Group, and Colony Site

Treatment/Site[a]	1987	1988	1987 & 1988	1989
1989 Trapping				
EARA Area 2-Top	71.4 (7)[b]	66.7 (9)	68.8 (16)	53.9 (26)
EARA Area 2-Slope	100.0 (8)	83.3 (6)	92.2 (14)	60.0 (10)
EARA Red Bluff				30.0 (10)
EALF Area 75		100.0 (16)	100.0 (16)	80.0 (15)
WELF Brown's Creek		100.0 (2)	100.0 (2)	94.1 (17)
Total			87.5 (48)	65.4 (78)
1989 Shooting				
WERA Manning Mountain		83.3 (6)	83.3 (6)	64.7 (17)
WERA Williamson/Shell		83.3 (6)	83.3 (6)	85.7 (7)
WEFH West Fort Hood	100.0 (1)	100.0 (19)	100.0 (20)	58.6 (29)
Total			93.8 (32)	64.2 (53)
1989 No Treatment				
EARA Area 6	93.8 (16)	94.1 (17)	93.9 (33)	66.7 (6)
EARA Area 12				50.0 (4)
WELF Robinette Point		100.0 (2)	100.0 (2)	83.3 (6)
WELF Jack Mountain	100.0 (1)	75.0 (4)	80.0 (5)	60.0 (5)
Total			92.5 (40)	66.6 (21)
Grand Total	90.9 (33)	90.8 (87)	90.8 (120)	65.1 (152)

[a] Area 2-Top: trapping only before 1 June and trapping and shooting after 1 June. Brown's Creek and West Fort Hood: shooting only before 1 June; shooting and trapping after 1 June. Area 6: trapped during 1988 with little effect (see text for explanation).

[b] Number of nests in parentheses.

Table 20

Results of Logistical Analysis of the Effects of Year and Treatment Group on the Incidence of Cowbird Parasitism

Source[a]	df	X^2	p
Intercept	1	57.34	0.0000
Year	1	19.22	0.0000
Treatment	2	0.82	0.6646
Year*Treatment	2	0.87	0.6646

[a] Data from Table 19.

Table 21

Incidence of Cowbird Parasitism at Colony Sites Before and After 1 June 1989 by Treatment Group and Colony Site

Treatment/Site	Treatment Period			
	Before 1 June		After 1 June	
Single Treatments[a]				
Trapping				
Area 2-Slope	71.4	(7)	33.3	(3)
Red Bluff	12.5	(5)	100.0	(2)
Area 75	85.7	(7)	75.0	(8)
Subtotal	63.2	(19)	69.2	(13)
Shooting				
Manning Mountain	63.6	(11)	66.7	(6)
Williamson Mt/Shell Pt	75.0	(4)	100.0	(3)
Subtotal	66.7	(15)	77.8	(9)
No Treatment				
Area 6	80.0	(5)	0.0	(1)
Area 12	100.0	(2)	0.0	(2)
Robinette Point	75.0	(4)	100.0	(2)
Jack Mountain	60.0	(5)		
Subtotal	75.0	(16)	40.0	(5)
Overall	68.0	(50)	66.7	(27)
Dual Treatments				
Trapping/Shooting[b]				
Area 2-Top	61.1	(18)	37.5	(8)
Brown's Creek	92.9	(14)	100.0	(3)
Subtotal	75.0	(32)	54.5	(11)
Shooting/Trapping[c]				
West Fort Hood	66.7	(18)	45.5	(11)
Overall	72.0	(50)	50.0	(22)

[a] Same treatment both periods
[b] Trapping before 1 June; trapping and shooting after 1 June.
[c] Shooting before 1 June; shooting and trapping after 1 June.

Table 22

Results of Logistic Analysis of the Effect of Treatment Group and Treatment Period on the Incidence of Cowbird Nest Parasitism

Source[a]	df	X^2	p
Intercept	1	10.60	0.0011
Treatment Period	1	1.87	0.1712
Treatment Group	1	0.47	0.4940
Period*Group	1	1.45	0.2289

[a] Data from Table 21

Table 23

Number of Cowbird Eggs Per Nest by Treatment Period, Treatment Group, and Colony Site

	Treatment Period					
	No Treatment[a]			Treatment[b]		
Treatment/Site	1	2	3 (eggs)	1	2	3 (eggs)
Trapping 1988						
Area 6				10	5	1[c]
Trapping 1989						
Area 2-Top	9	2		10	3	1
Brown's Creek			1	9	5	2
Area 2-Slope	2	4	7	3	2	1
Red Bluff				1	2	
Area 75	9	3	4	6	5	1
Total	20	9	12	39	22	6
Mean		(1.80)			(1.51)	
Shooting 1989						
Manning Mountain	2	3		8	2	1
William Mt/Shell Pt	1	1	2	5	1	
West Fort Hood	9	9	2	15	2	
Total	12	13	4	28	5	1
Mean		(1.72)			(1.21)	
No Treatment 1989						
Area 6	4	8	3[d]	3	1[d]	
Area 12				1	1	
Robinette Point			1	3	1	1
Jack Mountain	2	2		2	1	
Total	6	10	4	9	4	1
Mean		(1.90)			(1.43)	

[a]1987 plus 1988 data unless otherwise noted.
[b]1989 treatments unless otherwise noted.
[c](1988); [d](1987); [e](1989)

Table 24

Results of Logistic Analysis of the Effects of Treatment Group and Treatment Period on the Intensity of Cowbird Nest Parasitism

Source[a]	df	X^2	p
Intercept	2	30.67	0.0000
Treatment Group	2	4.33	0.3637
Treatment Period	4	12.75	0.0017
Period*Group	4	7.43	0.1147

[a] Data from Table 23.

Table 25

Daily Nest Loss Rates by Year, Nest Stage, and Overall Nest Stage Survival

Nest Stage[a]	1987		1988		1989		Overall	
Construction[b]	n=15		n=31		n=47		n=93	
Deserted/Total	0.0700	(3)	0.0839	(8)	0.0538	(6)	0.0660	(17)
Survival[c]	0.6957	(12)	0.6452	(23)	0.7586	(41)	0.7106	(76)
Laying[b]	n=17		n=31		n=47		n=95	
Deserted	0.0925	(3)	0.0765	(4.5)	0.0217	(2)	0.0518	(9.5)
Destroyed			0.0255	(1.5)	0.0163	(1.5)	0.0165	(3)
Total Loss	0.0925	(3)	0.1020	(6)	0.0380	(3.5)	0.0681	(12.5)
Survival[c]	0.8235	(14)	0.8065	(25)	0.9255	(43.5)	0.8684	(82.5)
Incubation e	n=22/nd=145.5		n=49/nd=380.5		n=105/nd=939.5		n=176/1465.5	
Deserted (SE)	0.0962a	(0.02445)	0.0421ab	(0.01029)	0.0287b	(0.00545)	0.0390	(0.00505)
Destroyed (SE)	0.0069a	(0.00685)	0.0342b	(0.00931)	0.0160ab	(0.00409)	0.0198	(0.00364)
Total Loss (SE)	0.1031a	(0.02521)	0.0763a	(0.01360)	0.0447b	(0.00674)	0.0588	(0.00614)
Survival	0.2710		0.3858		0.5518		0.4548	
Nestling e	n=11/nd=51		n=25/nd=174		n=82/nd=66		n=118/nd=887	
Destroyed/Total	0.1569a		0.0920a		0.0438b		0.0598	
(SE)	(0.05092)		(0.02191)		(0.00795)		(0.00796)	
Survival	0.1530		0.3459		0.6110		0.5075	
Overall Success	0.0238		0.0694		0.2367		0.1424	

[a] n=number of nests; nd=number on nest days.
[b] Observed number of nests lost in parentheses (construction stage loss adjusted as described in text).
[c] X^2 (Survival*Year-Construction)=2.162, df=2, $0.25<p<0.5$.
[d] X^2 (Survival*Year-Laying)=2.683, df=2, $0.25<p<0.5$.
[e] Numbers in each row with same letter not significantly different.

Table 26

Comparison of Nest Loss Estimates

Fate[a]	1987	1988	1989	Total
Deserted				
Observed	63.6	45.9	26.3	37.6
Exposure	81.7	62.5	47.6	58.4
Difference	-18.1	-16.6	-21.3	-20.8
% Difference	-22.2	-26.6	-44.7	-35.6
Destroyed				
Observed	27.3	40.0	35.8	36.1
Exposure	16.0	30.6	28.8	27.4
Difference	11.3	9.4	7.0	8.7
% Difference	70.6	30.7	24.3	31.8
Fledged young				
Observed	9.1	14.1	38.0	26.3
Exposure	2.4	6.9	23.7	14.2
Difference	6.7	7.2	14.3	12.1
% Difference	279.2	104.3	60.3	85.2

[a] Based on the Fates of Observed Nests (Table 14) with estimates based on exposure (Table 25).

Table 27

Daily Nest Loss Rates of Unparasitized and Parasitized Nests by Nest Stage, and Overall Nest Stage Survival

Nest Stage[a]	Unparasitized	Parasitized
Construction	n=91	n=2
Deserted/Total	0.0645 (16)[c]	0.1534 (1)
Total Loss	0.0645 (16)	0.1534 (1)
Survival[b]	0.7166 (75)	0.4349 (1)
Laying	n=40	n=55
Deserted	0.0257 (2.0)	0.0710 (7.5)
Destroyed	0.0321 (2.5)	0.0047 (0.5)
Total Loss	0.0578 (4.5)	0.0757 (8.0)
Survival[d]	0.8877 (35.5)	0.8543 (47.0)
Incubation	n=41/nd=422	n=135/nd=1043.5
Deserted	0.0024 ***	0.0537
(SE)	(0.00237)	(0.00698)
Destroyed	0.0261	0.0173
(SE)	(0.00776)	(0.00403)
Total Loss	0.0285 ***	0.0710
(SE)	(0.00809)	(0.00795)
Survival	0.6481	0.4132
Nestling	n=63/nd=476.5	n=55/nd=410.5
Destroyed/Total	0.0441 *	0.0780
(SE)	(0.00940)	(0.01323)
Survival	0.6089	0.4093

[a] n=number of nests; nd=number of nest-days. Symbols: * $0.10<p\leq0.05$, ** $0.001<p\leq0.10$, *** $p\leq0.001$.

[b] X^2 (Survival*Parasitism-Construction)=1.377, df=1, $0.10<p<0.25$.

[c] Observed number of nests lost in parentheses.

[d] X^2 (Survival*Parasitism)=3.848, df=2, $0.10<p<0.25$.

Table 28

Success of Black-capped Vireo Nests in Unparasitized and Parasitized Populations

Nest Stage	Unparasitized Population	Parasitized Population		
		Unweighted	Proportion Parasitized	Weighted[a]
Construction	0.7167	0.4349	0.030	0.7082
Laying	0.8877	0.8543	0.700	0.8643
Incubation	0.6481	0.4132	1.000	0.4132
Nestling	0.6089	0.4093	0.717	0.4658
Overall Success	0.2511			0.1178

[a] Weighted average of the survival of parasitized and unparasitized nests in the parasitized population. See text for further explanation.

Table 29

Effect of the Number of Cowbird Eggs Per Nest on Black-capped Vireo Nesting Success

Fate	Number of Cowbird Eggs[a]	
	1 (%)	$\geq$ 2 (%)
Fledged Vireos	11 (10.9)	2 (2.6)
Fledged Cowbirds	14 (13.9)	10 (12.8)
Deserted	42 (41.6)	35 (44.9)
Destroyed	34 (33.7)	31 (39.7)

[a] X^2=4.796, df=3, 0.1<p<0.25.

Table 38

Pair Success in Fledging Black-capped Vireo Young by Year and Colony Site

Area	1987	1988	1989
Area 2-Top	0.0000 (6)[a]	0.3333 (6)	0.7000 (10)
Area 2-Slope	0.2500 (4)	0.3333 (3)	1.0000 (4)
Red Bluff			0.8333 (6)
Area 75		0.1000 (10)	0.5556 (9)
Area 6	0.0909 (11)	0.2000 (10)	1.0000 (3)
Area 12			1.0000 (2)
Manning Mountain		0.3333 (6)	0.7500 (8)
Williamson Mt/Shell Pt		0.0000 (4)	0.5000 (2)
Brown's Creek		0.0000 (4)	0.2857 (7)
Robinette Point			0.6667 (3)
Jack Mountain		0.5000 (8)	0.3333 (6)
West Fort Hood		0.0000 (13)	0.4000 (10)
Overall[b]	0.0952 (21)	0.1875 (64)	0.6143 (70)

[a] Number of pairs monitored in parentheses.
[b] X^2 (Overall*Year)=33.949, df=2, $p<0.001$.

Table 31

Uncorrected and Corrected Median Estimates of Black-capped Vireo Production (Young/Mated Pair) by Year and Colony Site

Area	1987	1988	1989
A. Uncorrected			
Area 2-Top	0.000 (6)[a]	0.917 (6)	2.050 (10)
Area 2-Slope	0.875 (4)	0.333 (3)	3.250 (4)
Red Bluff			2.833 (6)
Area 75		0.100 (10)	1.278 (9)
Area 6	0.136 (11)	0.200 (10)	2.167 (3)
Area 12			2.500 (2)
Manning Mountain		0.750 (6)	1.625 (8)
Williamson/Shell Pt		0.000 (4)	1.250 (2)
Brown's Creek		0.000 (4)	1.071 (7)
Robinette Point			1.000 (3)
Jack Mountain		0.875 (8)	0.583 (6)
West Fort Hood		0.000 (13)	1.500 (10)
Overall	0.238 (21)	0.328 (64)	1.686 (70)
(SE)	(0.17802)	(0.09398)	(0.19039)
Range[a]	0.190-0.286	0.297-0.359	1.500-1.871
B. Corrected			
Area 2-Top	0.000 (6)	1.294 (6)	2.050 (10)
Area 2-Slope	0.875 (4)	0.585 (3)	3.250 (4)
Red Bluff			2.833 (6)
Area 75		0.100 (10)	1.697 (9)
Area 6	0.239 (11)	0.351 (10)	2.167 (3)
Area 12			2.500 (2)
Manning Mountain		1.065 (6)	1.719 (8)
Williamson/Shell Pt		0.000 (4)	1.250 (2)
Brown's Creek		0.000 (4)	1.071 (7)
Robinette Point			1.755 (3)
Jack Mountain		1.347 (8)	0.835 (6)
West Fort Hood		0.000 (13)	1.500 (10)
Overall[c]	0.292 (21)[b]	0.487 (64)[b]	1.804 (70)[c]
(SE)	(0.20347)	(0.14430)	(0.19841)
Range[b]	0.226-0.358	0.450-0.524	1.597-2.011

[a] Number of pairs monitored in parentheses.
[b] Based on low and high estimates of individual mated pair production.
[c] F(among years-Overall)=18.81, ms=36.07630, df=2/152, p=0.0001; values with same letter are not significantly different.

Table 32

Pair Success in Fledging Cowbird Young by Year and Colony Site

Area	1987	1988	1989
Area 2-Top	0.1667 (6)	0.0000 (6)	0.0000 (10)
Area 2-Slope	0.2500 (4)	0.3333 (3)	0.2500 (4)
Red Bluff			0.1667 (6)
Area 75		0.0000 (10)	0.0000 (9)
Area 6	0.0000 (11)	0.0000 (10)	0.0000 (3)
Area 12			0.0000 (2)
Manning Mountain		0.3333 (6)	0.1250 (8)
Williamson/Shell Pt		0.5000 (4)	0.5000 (2)
Brown's Creek		0.5000 (4)	0.4286 (7)
Robinette Point			0.0000 (3)
Jack Mountain		0.1250 (8)	0.1667 (6)
West Fort Hood		0.1539 (13)	0.2000 (10)
Overall[a]	0.0952 (21)	0.1563 (64)	0.1429 (70)

[a] Number of pairs monitored in parentheses.
[b] X^2 (Overall*Year)=0.484, df=2, $0.5<p<0.9$.

Table 33

Cowbird Production (Young/Mated Pair) by Year and Colony Site

Area	1987	1988	1989
Area 2-Top	0.167 (6)[a]	0.000 (6)	0.000 (10)
Area 2-Slope	0.250 (4)	0.333 (3)	0.250 (4)
Red Bluff			0.333 (6)
Area 75		0.000 (10)	0.000 (9)
Area 6	0.000 (11)	0.000 (10)	0.000 (3)
Area 12			0.000 (2)
Manning Mountain		0.333 (6)	0.500 (8)
Williamson Mt/Shell Pt		0.500 (4)	0.500 (2)
Brown's Creek		0.500 (4)	0.571 (7)
Robinette Point			0.000 (3)
Jack Mountain		0.125 (8)	0.167 (6)
West Fort Hood		0.154 (13)	0.500 (10)
Overall[a]	0.095 (21)	0.156 (64)	0.257 (70)
(SE)	(0.0656)	(0.0457)	(0.0880)

[a] Number of pairs monitored in parentheses.
[b] F(among years-Overall)=0.92, ms=0.28755, df=2/152, p=0.402.

Table 34

Weekly Probability of a Renesting Following Successful and Unsuccessful Nesting Attempts

Week	Successful Nests	Unsuccessful Nests
1[a]	100.0 (15)[b]	100.0 (104)
2	100.0 (15)	100.0 (104)
3	100.0 (15)	100.0 (101)
4	100.0 (15)	99.0 (101)
5	100.0 (15)	98.9 (93)
6	93.8 (16)	96.5 (86)
7	85.7 (14)	94.4 (72)
8	78.6 (14)	85.2 (54)
9	71.4 (14)	79.2 (48)
10	45.5 (11)	62.5 (48)
11	30.0 (10)	50.0 (44)
12	6.7 (15)	37.8 (37)
13	0.0 (20)	18.2 (33)
14	0.0 (22)	0.0 (33)

[a] Week 1 begins April 16.
[b] Sample size in parentheses.

Table 35

Estimated Black-capped Vireo and Cowbird Production Per Year for Hypothetical Unparasitized and 100 Percent Parasitized Populations

	Unparasitized	Parasitized	
Females	100	100	
Nests built	395	522	
Nest success	25.1%	11.8%	
Successful nests	99	62	
Fledging vireos	99 (100%)	22 (35%)	
Fledging cowbirds	0 (0%)	40 (65%)	
Female Success		Vireos	Cowbirds
0 Broods	19	45	45
1 Brood	63	17	31
2 Broods	18	2	5
Vireo Production			
Per successful nest	3.10	2.46	
Per active nest	0.77	0.10	
Per female	3.08	0.53	
Cowbird Production			
Per successful nest		1.16	
Per active nest		0.09	
Per vireo female		0.46	

Table 36

Pair Success in Fledging Black-capped Vireo Young by Year and Treatment Group

Treatment[a]	1987	1988[b]	1989[c]
No Treatment	0.0952 (21)	0.1852 (6)	0.6429 (14)
Trapping		0.2000 (10)	0.6389 (36)
Shooting			0.5500 (20)

[a] Number of pairs monitored in parentheses.
[b] X^2 (among treatments-1988)=0.012, df=1, p>0.9.
[c] X^2 (among treatments-1989)=0.489, df=2, 0.5<p<0.9.

Table 37

Black-capped Vireo Production (Young/Mat-d Pair) by Year and Treatment Group

Treatment	1987	1988	1989[a]
No Treatment	0.292 (21)[b]	0.513 (6)	1.555 (14)
(SE)	(0.20347)	(0.16595)	(0.35402)
Trapping		0.351 (10)	2.035 (36)
(SE)		(0.23397)	(0.37866)
Shooting			1.563 (20)
(SE)			(0.29398)

[a] F(among treatments-1989)=0.71, ms=1.97881, p=0.494
[b] Number of pairs monitored and standard errors in parentheses.

Table 38

Pair Success in Fledging Cowbird Young by Year and Treatment Group

Treatment	1987	1988	1989[a]
No Treatment	0.0952 (21)[b]	0.1852 (54)	0.0714 (14)
Trapping		0.0000 (10)	0.5000 (36)
Shooting			0.1944 (20)

[a] X^2 (among treatments-1989)=2.755, df=2, 0.1<p<0.25.
[b] Number of pairs monitored in parentheses.

Table 39

Cowbird Production (Young/Mated Pair) by Year and Treatment Group

Treatment	1987	1988	1989[a]
No Treatment	0.095 (21)	0.185 (6)	0.071 (14)
(SE)	(0.06564)	(0.05336)	(0.07143)
Trapping		0.000 (10)	0.194 (36)
(SE)		(0.00000)	(0.08746)
Shooting			0.500 (20)
(SE)			(0.25649)

[a] F(among treatments-1989)=1.70, ms=1.80397, df=2/67, p=0.-191.

[b] Number of territories monitored and standard errors in parentheses.

Table 40

Critical Levels of Black-capped Vireo Production and Cowbird Nest Parasitism Required To Maintain Stable Black-capped Vireo Population on Fort Hood

s_a	u_a	s_j	u_j	$Prod_c$	$Para_c$	$Para_r$
0.60	0.40	0.40	0.60	2.00	42.4	55.2
		0.30	0.70	2.67	16.1	37.6
		0.20	0.80	4.00	<0.0	2.6
0.65	0.35	0.40	0.60	1.75	52.2	61.8
		0.30	0.70	2.33	29.4	46.4
		0.20	0.80	3.50	<0.0	15.7

s_a=adult annual survival
u_a=adult annual mortality
s_j=juvenile first year survival
u_j=juvenile first year mortality
$Prod_c$=critical level of production to sustain population
$Para_c$=critical level of parasitism necessary to meet $Prod_c$ (See text for further explanation).

Table 41

Incidence of Cowbird Nest Parasitism in Percent by Year and Region

Region	1987	1988	1989
East Range	90.3 (31)[a]	84.4 (32)	51.8 (56)
East Live Fire		100.0 (16)	80.0 (15)
West Range		83.3 (12)	70.8 (24)
West Live Fire	100.0 (1)	87.5 (8)	85.7 (28)
West Fort Hood	100.0 (1)	100.0 (19)	58.6 (29)

[a] Number of nests in parentheses

Table 42

Results of Three-Way Analysis of Independence of Region, Year, and Cowbird Nest Parasitism

Source	df	X^2	p
Region	4	49.09	0.0000
Year	1	26.77	0.0000
Region*Year	4	6.95	0.1383
Parasitism	1	54.20	0.0000
Region*Parasitism	4	12.17	0.0161
Year*Parasitism	1	17.53	0.0000
Likelihood Ratio	4	7.67	0.1045

[a] Data from Table 41; analysis includes only years 1988 and 1989.

Table 43

Number of Cowbird Eggs per Black-capped Vireo Nest by Year and Region

	1987			1988			1989		
Region	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
East Range	9	12	7	16	7	4	18	9	2
East Live Fire				9	3	4	6	5	1
West Range				3	4	2	13	3	1
West Live Fire	0	1	0	2	1	2	14	7	3
West Fort Hood	0	1	0	9	8	2	15	2	0
Total	9	14	7	39	23	14	66	26	7
Mean No./Nest		1.93			1.67			1.40	

Table 44

Results of Three-Way Analysis of Independence of Region, Year, and Number of Cowbird Eggs per Black-capped Vireo Nest

Source	*df*	X^2	*p*
Region	4	10.94	0.0273
Year	1	0.05	0.8211
Region*Year	4	12.85	0.0120
Parasitism	2	42.94	0.0000
Region*Parasitism	4	5.05	0.7519
Year*Parasitism	2	7.83	0.0199
Likelihood Ratio	8	9.47	0.3038

[a] Data from Table 43; analysis includes only years 1988 and 1989

Table 45

Pair Success in Fledging Black-capped Vireo Young by Year and Region

Region	1987[a]	1988	1989
East Range	0.0952 (21)	0.2631 (19)	0.8400 (25)
East Live Fire		0.1000 (10)	0.5560 (9)
West Range		0.2000 (10)	0.7000 (10)
West Live Fire		0.3333 (12)	0.3750 (16)
West Fort Hood		0.0000 (13)	0.4000 (10)

[a] Number of mated pairs monitored in parentheses.)

Table 46

Results of Three-Way Analysis of Independence of Region, Year, and Pair Success in Fledging Vireos

Source	df	X^2	p
Region	4	16.99	0.0019
Year	1	2.39	0.1219
Region*Year	4	1.19	0.8791
Success	1	9.49	0.0021
Region*Success	4	11.13	0.0251
Year*Success	1	22.08	0.0000
Likelihood Ratio	4	7.66	0.1049

[a] Data from Table 45; analysis includes only years 1988 and 1989.

Table 47

Black-capped Vireo Production (Young/Mated Pair) by Year and Region

Region	1987	1988	1989
East Range	0.292 (21)[a]	0.686 (19)	2.480 (25)
(SE)	(0.20347)	(0.31654)	(0.28355)
East Live Fire		0.100 (10)	1.697 (9)
(SE)		(0.10000)	(0.64669)
West Range		0.639 (10)	1.625 (10)
(SE)		(0.46148)	(0.36374)
West Live Fire		0.898 (12)	1.111 (16)
(SE)		(0.40863)	(0.39227)
West Fort Hood		0.000 (13)	1.500 (10)
(SE)		(0.0000)	(0.68718)

[a] Number of territories monitored and standard errors in parentheses.

Table 48

Results of Two-Way Analysis of Variance on Black-capped Vireo Production for Year and Region

Source	df	Type III SS	Mean Square	F	p
Year	1	44.89151	44.89151	22.22	0.0001
Region	4	13.49244	3.37311	1.70	0.1542
Year*Region	4	11.83400	2.95850	1.49	0.2090
Error	124	246.06245	1.98437		

[a] Data from Table 47; analysis includes only years 1988 and 1989.

Table 49

Pair Success in Fledging Cowbird Young by Year and Region

Region	1987	1988	1989
East Range	0.0952 (21)[a]	0.0526 (19)	0.0800 (25)
East Live Fire		0.0000 (10)	0.0000 (9)
West Range		0.4000 (10)	0.2000 (10)
West Live Fire		0.2500 (12)	0.2500 (16)
West Fort Hood		0.1539 (13)	0.2000 (10)

[a] Number of mated pairs monitored in parentheses.

Table 50

Results of Three-Way Analysis of Independence of Region, Year, and Pair Success in Fledging Cowbirds

Source	df	X^2	p
Region	3	1.88	0.7569
Year	1	0.03	0.8724
Region*Year	3	1.31	0.7267
Success	1	34.32	0.0000
Region*Success	3	5.95	0.1139
Year*Success	1	0.05	0.8208
Likelihood Ratio	3	1.13	0.7702

[a] Data from Table 49; analysis includes only years 1988 and 1989.

Table 51

Cowbird Production (Young/Mated Pair) by Year and Region

Region	1987	1988	1989
East Region (SE)	0.095 (21)[a] (0.06564)	0.053 (19) (0.05263)	0.120 (25) (0.08794)
East Live Fire (SE)		0.000 (10) (0.00000)	0.000 (9) (0.00000)
West Range (SE)		0.400 (10) (0.16330)	0.500 (10) (0.40139)
West Live Fire (SE)		0.250 (12) (0.13056)	0.313 (16) (0.15052)
West Fort Hood (SE)		0.154 (13) (0.10415)	0.500 (10) (0.34157)

[a] Number of territories monitored and standard errors in parentheses.

Table 52

Results of Two-Way Analysis of Variance on Cowbird Production for Years and Regions

Source	df	Type III SS	Mean Square	F	p
Year	1	0.40145	0.40145	1.17	0.2805
Region	4	3.09645	0.77411	2.27	0.0659
Year*Region	4	0.40811	0.10202	0.30	0.8784
Error	124	42.36718	0.34167		

[a] Data from Table 51; analysis includes only years 1988 and 1989.

Table 53

Female Cowbirds Trapped per Trap Day in Oklahoma, Texas, California, and Michigan

Location and Number Trapped	Year	County	Source
Oklahoma			
0.20 (7/35)	1985	Canadian	Grzybowski (1985b)
0.00 (0/55)	1986	Comanche	Grzybowski (1987)
0.09 (8/92)	1986	Canadian	Grzybowski (1987)
0.18 (65/364)	1987	Comanche	Grzybowski (1988a)
0.09 (4/23)	1987	Canadian	Grzybowski (1988a)
0.26 (130/500)	1988	Comanche	Grzybowski (1989)
Overall 0.20 (214/1069)			
Texas			
0.19 (12/62)	1985	Travis	Grzybowski (1985b)
0.06 (3/50)	1985	Kerr	Grzybowski (1985b)
0 18 (10/56)F&Y	1986	Kerr	Grzybowski (1986)
0.16 (27/174)F&Y	1986	Travis	Grzybowski (1986)
0.38 (22/58)F&Y	1987	Kerr	Grzybowski (1988b)
0.10 (18/180)F&Y	1987	Travis	Grzybowski (1988b)
0.71 (203/284)	1988	Kerr	Grzybowski (1989)
0.10 (38/378)	1988	Travis	Grzybowski (1989)
0.09 (145/1543)	1989	Travis	Espey Huston & Assoc, Inc (1989)
0.04 (10/270)	1988	Bell	This Study
0.06 (36/639)	1989	Coryell	This Study
Overall 0.17 (478/2785) (F&Y=females and young)			
California			
0.03 (24/973)	1986	San Diego	(Riparian) Beezley & Rieger (1987)
0.07 (22/321)	1986	San Diego	(Foraging) Beezley & Rieger (1987)
0.06 (140/2366)	1988	San Diego	Sweetwater Env. Biologists (1989)
Overall 0.05 (186/3660)			
Michigan			
0.99 (2881/2920)		Lower Penninsula	Espey Huston & Assoc, Inc. (1989)

Table 54

Comparison of Nesting Success Between Parasitized and Unparasitized Nests of Several Selected Bird Species

	Success (%)				Host Young Fledged[a]				Destroyed		Desertion		
	Nest		Egg		(A)		(B)		(%)		(%)		
Species	**Unp**	**Par**	**Unp**	**Par**	**Unp**	**Par**	**Unp**	**Par**	**Unp**	**Par**	**Unp**	**Par**	**Source[b]**
Yellow Warbler[c]			80	44							3	24	(1)
Yellow Warbler	53	24	41	17	1.8	0.7	3.3	2.8	79	57	8	30	(2)
Yellow Warbler	64	47			2.3	0.9	3.6	1.9					(3)
Kirtland's Warbler	43	46	32	7	1.5	0.3	3.5	0.7					(4)
Common Yellowthroat					1.9	0.4							(5)
Prairie Warbler	19	7			0.7	0.1	3.4	0.9					(6)
Solitary Vireo			69	18	2.4	0.5							(7)
Eastern Meadowlark	33	18	25	12	0.7	0.2	2.2	1.2	30	29	46	46	(8)
Willow Flycatcher	56	18											(9)
Dickcissel	25	22	25	11	0.5	0.3	2.0	1.3	50	61	0	17	(8)
Dickcissel(prairie)			52	18			3.7	1.8					(10)
Dickcissel" (old field)			31	13			3.2	2.0					(10)
Lark Sparrow	59	29	49	20	1.9	0^	3.2	2.1					(11)
Grasshopper Sparrow	33	22	19	6	0.8	0.1	2.5	0.5	56	33	22	22	(8)
Brown-headed Junco			94	85	2.7	1.5							(12)
Eight Species			36	19									(13)
Bell's Vireo			22	7									(13)
Eight Species			44	28									(14)
Bell's Vireo				12									(14)
Five Species											4	35	(15)
Mean	43	26	44	21	1.6	0.5	3.1	1.5	54	45	14	29	
Black-capped Vireo	25	12			0.7	0.1	2.7	0.9	57	34	8	49	This study[d]

[a] (A) Host young per active nest; (B) Host young per successful nest.

[b] (1) Clark and Robertson 1981; (2) Goossen and Sealy 1982; (3) Weatherhead 1989; (4) Mayfield 1960; (5) Stewart 1953; (6) Nolan 1978; (7) Marvil and Cruz 1989; (8) Elliot 1978; (9) Sedgwick and Knoph 1988; (10) Zimmerman 1984; (11) Newman 1970; (12) Wolf 1987; (13) Wiens 1963; (14) Ely 1957 in Wiens 1963; (15) Graham 1988.

[c] Predated nests excluded.

[d] Percent destruction and desertion based only on laying through nestling periods.

Table 55

Brown-headed Cowbird Success in Nests of Selected Passerine Species

Species	Cowbird Eggs per Nest	% of Eggs Fledging Cowbirds	Cowbird Young per Nest	Source
Willow Flycatcher	1.19	15	0.18	Sedgwick and Knoph 1988
Bell's Vireo	1.25	20	0.25	Wiens 1963
Bell's Vireo	1.50	7	0.10	Ely 1957 in Wiens 1963
Bell's Vireo	1.35	6	0.09	Mayfield 1965
Red-eyed Vireo	1.80	23	0.42	Young 1963
Solitary Vireo	1.62	45	0.73	Marvil and Cruz 1989
Black-capped Vireo	1.74	6	0.11	Mayfield 1965
Ovenbird	1.90	23	0.43	Young 1963
Prairie Warbler	1.13	5	0.06	Nolan 1978
Kirtland's Warbler	1.57	23	0.37	Walkinshaw 1983
Kirtland's Warbler	1.67	41	0.68	Mayfield 1960
Yellow Warbler	1.50	8	0.12	Young 1963
Yellow Warbler	1.25	16	0.20	Mayfield 1965
Common Yellowthroat	1.80	28	0.51	Young 1963
Common Yellowthroat	1.80	22	0.40	Stewart 1953
Lark Sparrow	1.27	16	0.21	Newman 1970
Grasshopper Sparrow	2.00	7	0.22	Elliot 1978
Field Sparrow	1.28	13	0.16	Mayfield 1965
Song Sparrow	1.50	31	0.46	Mayfield 1965
Abert's Towhee		4		Finch 1983
Dickcissel	2.40	11	0.33	Elliot 1978
Eastern Meadowlark	3.10	6	0.36	Elliot 1978
7 Species		13		Scott and Ankney 1980
8 Species	1.19	24	0.29	Wiens 1963
8 Species	1.56	22	0.34	Ely 1957 in Wiens 1963
36 Species	1.47	25	0.37	Young 1963
Mean	1.62	18	0.31	
Black-capped Vireo	1.58	6	0.09	This Study

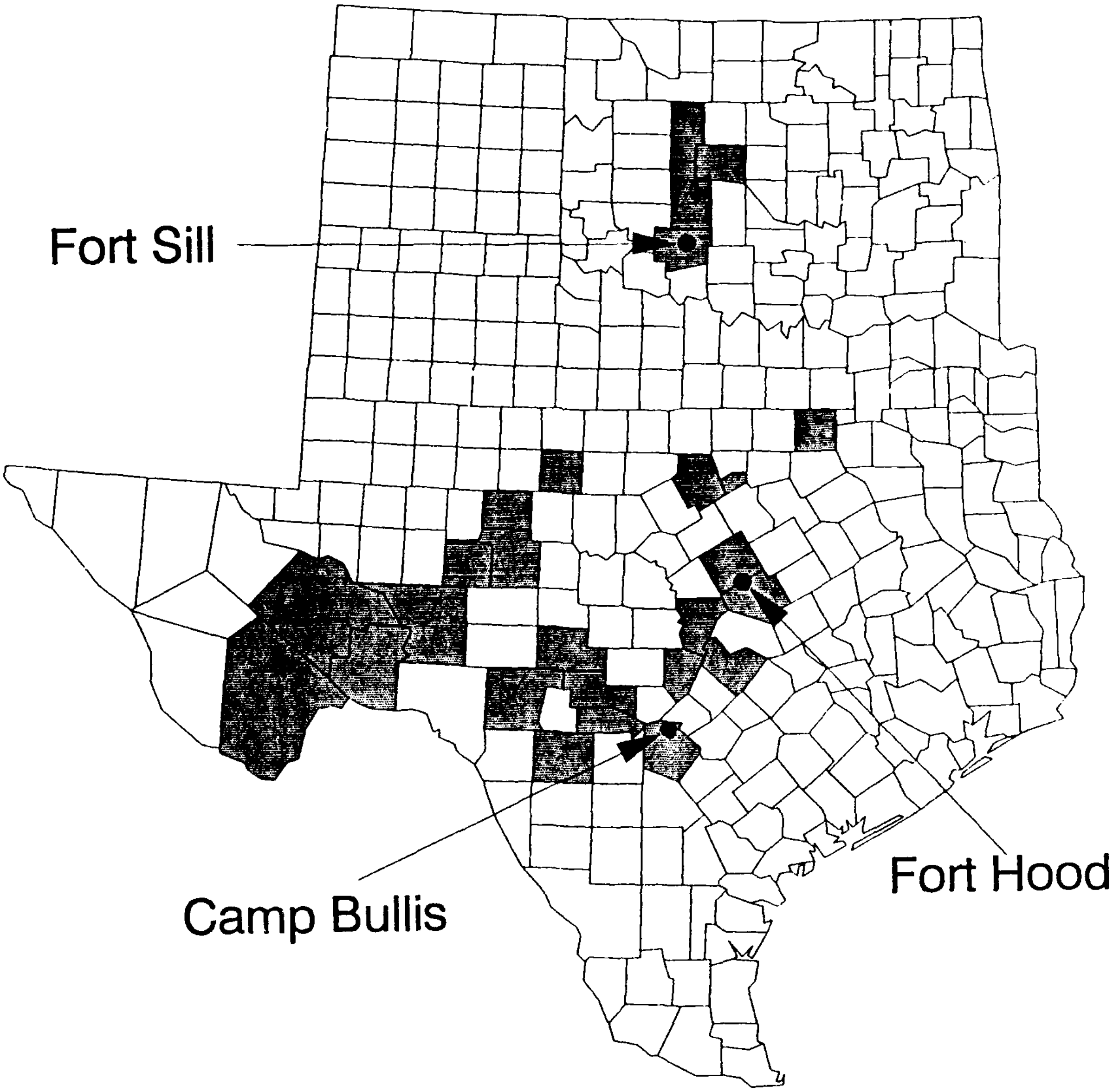

Figure 1. Current Distribution of the Black-capped Vireo in Texas and Oklahoma by County.

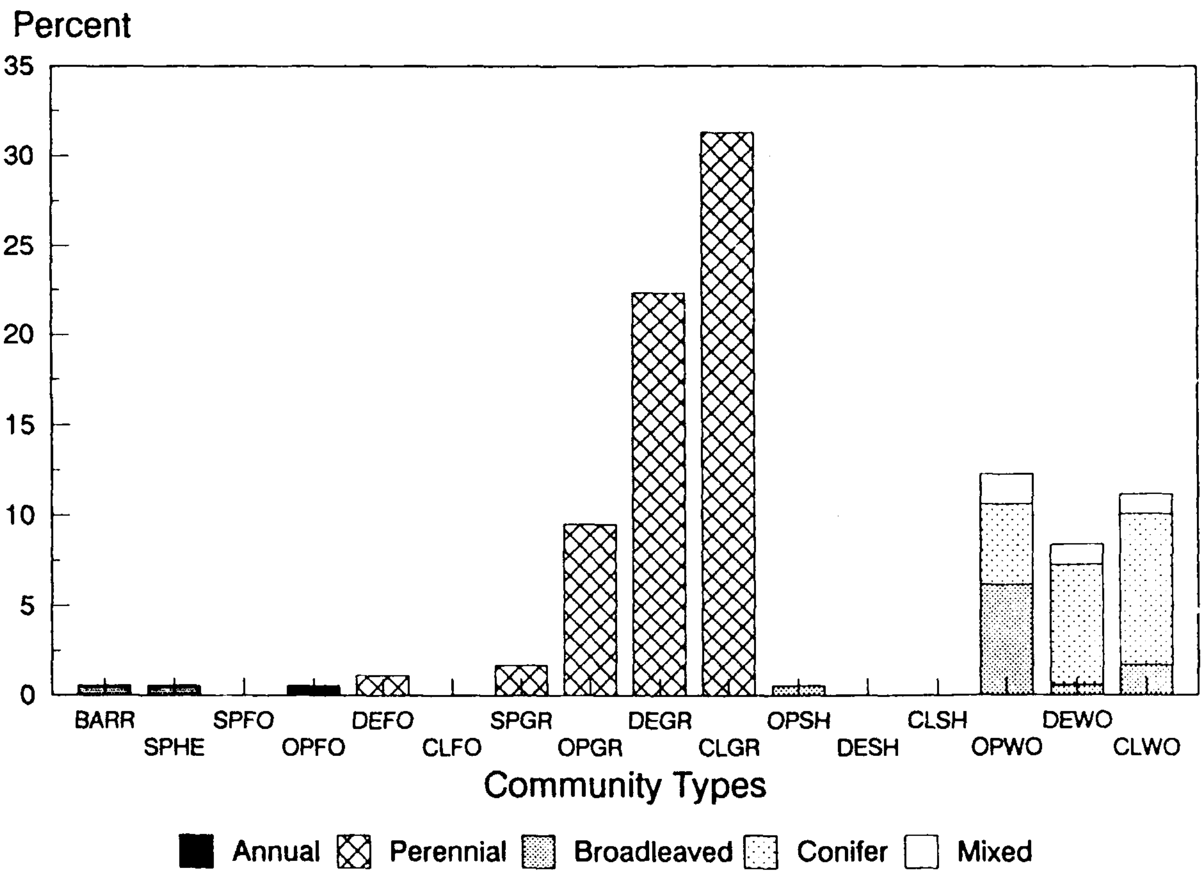

Figure 2. Fort Hood Plant Community Types.

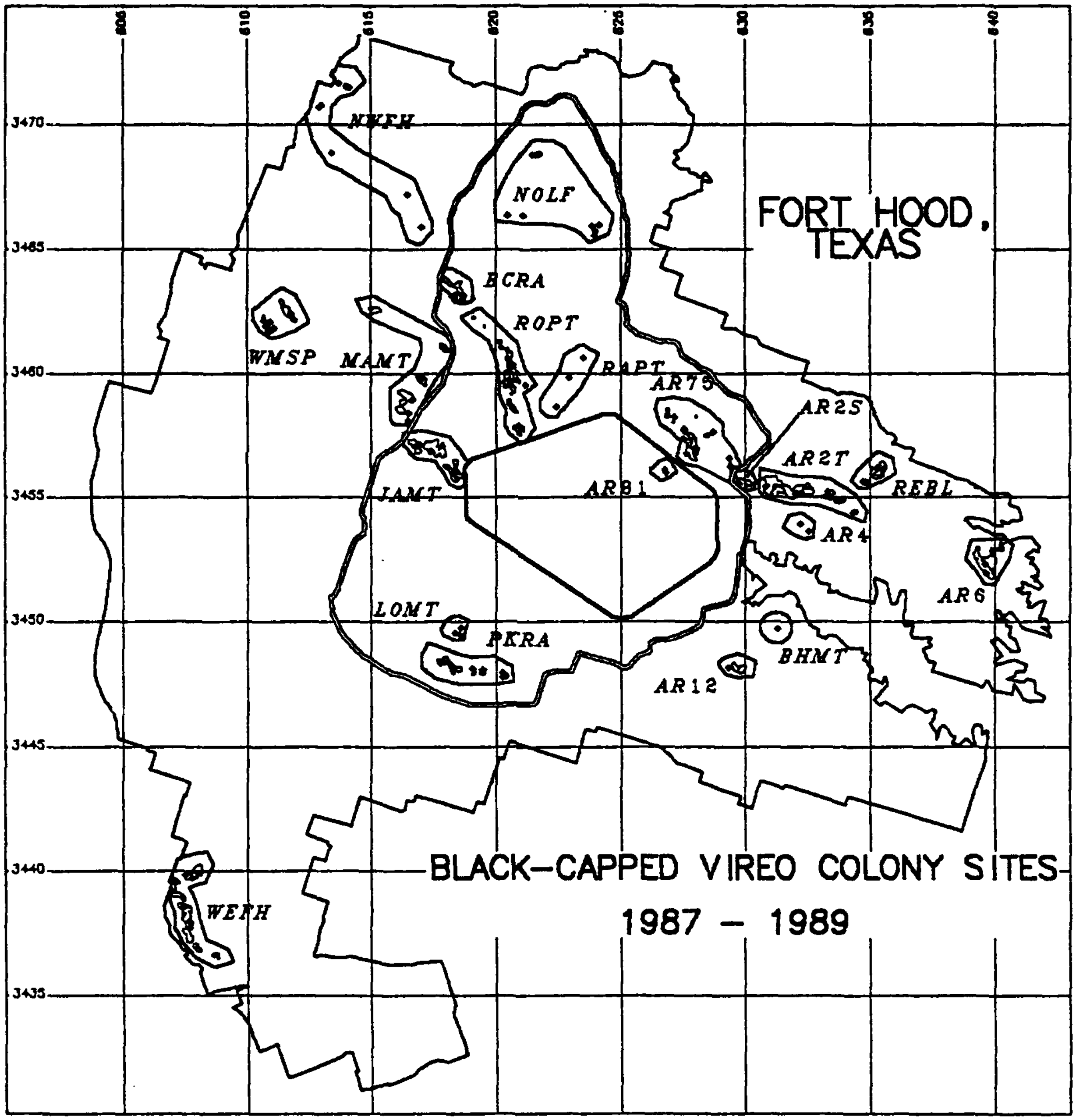

Figure 3. Black-capped Vireo Colony Sites on Fort Hood (grid: 5000 m).

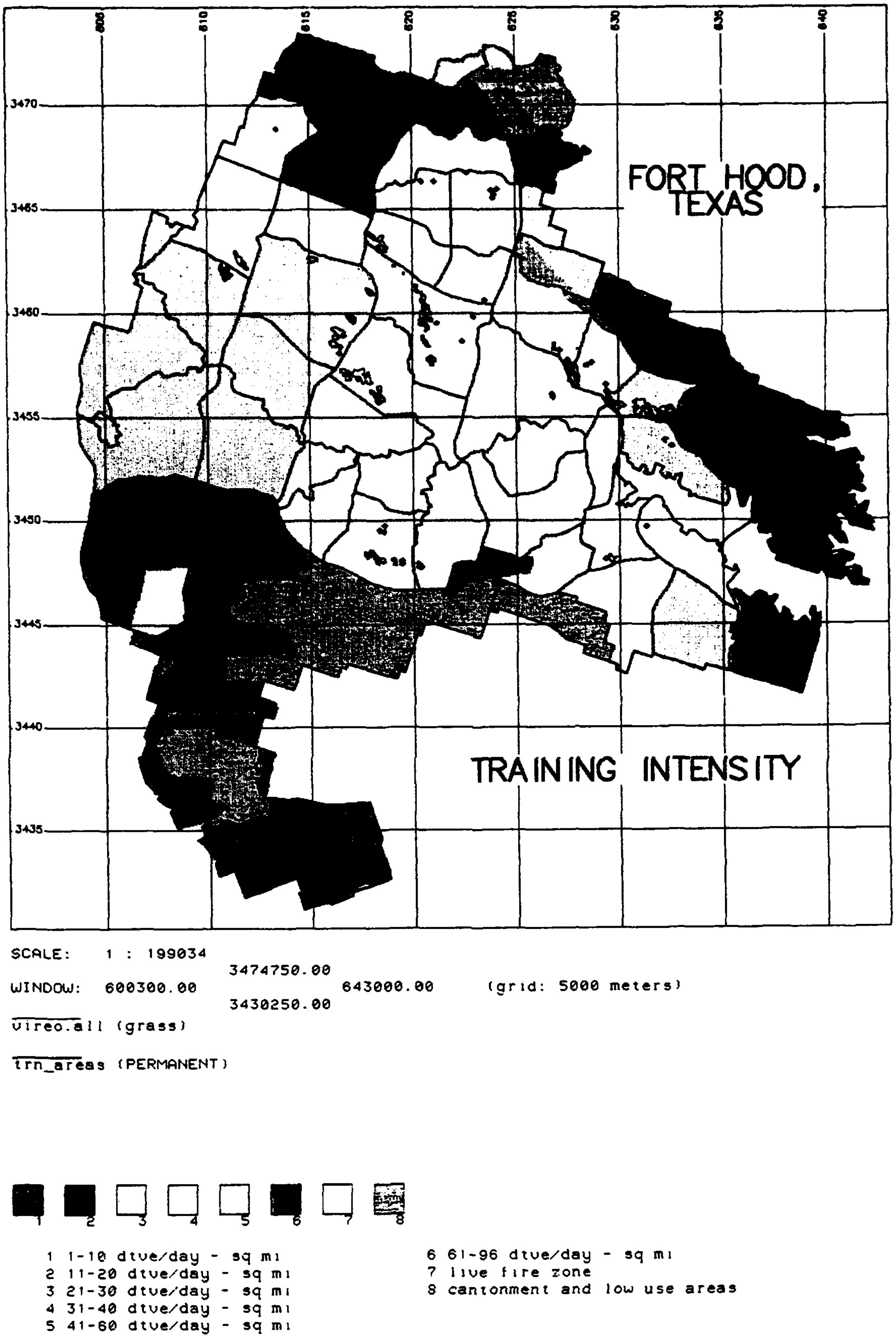

Figure 4. Fort Hood Training Intensity Map (grid: 5000 m).

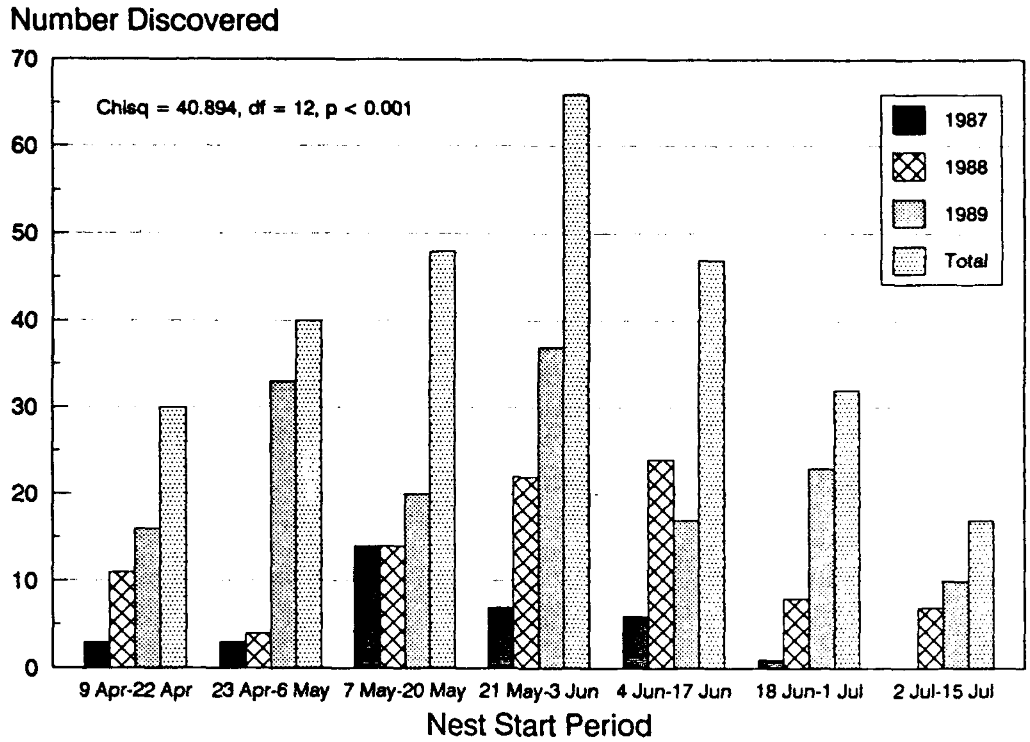

Figure 5. Number of Black-capped Vireo Nestings Discovered by Nest Start Period and Year.

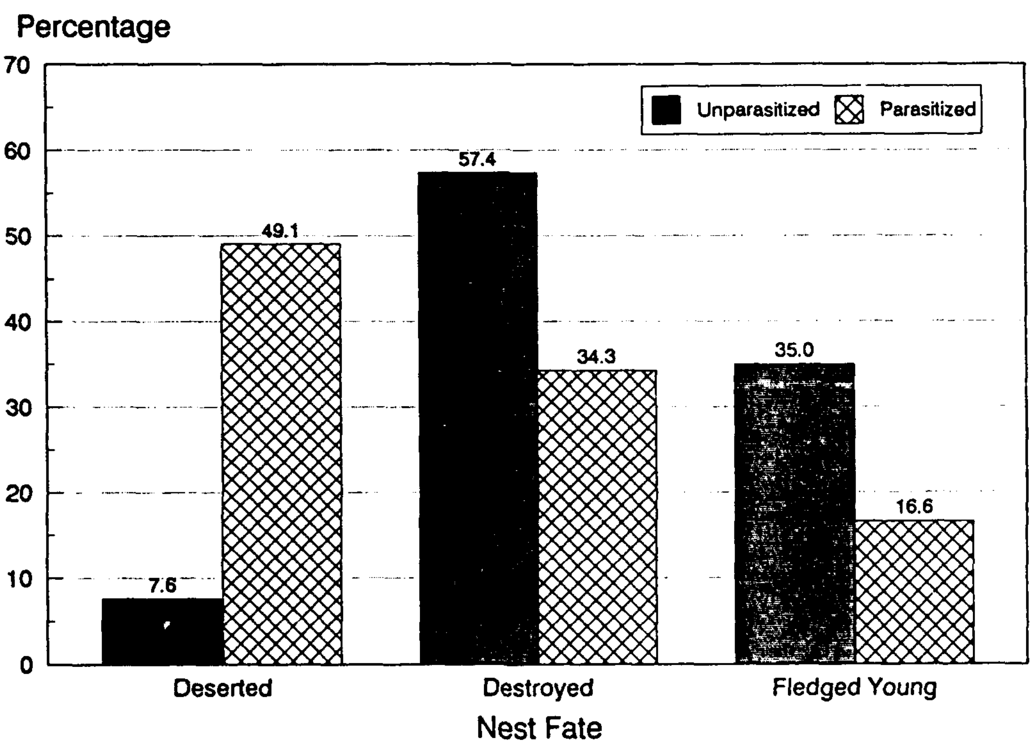

Figure 6. Comparison of the Fates of Unparasitized and Parasitized Nests During the Laying Through the Nestling Stage as Calculated From Exposure.

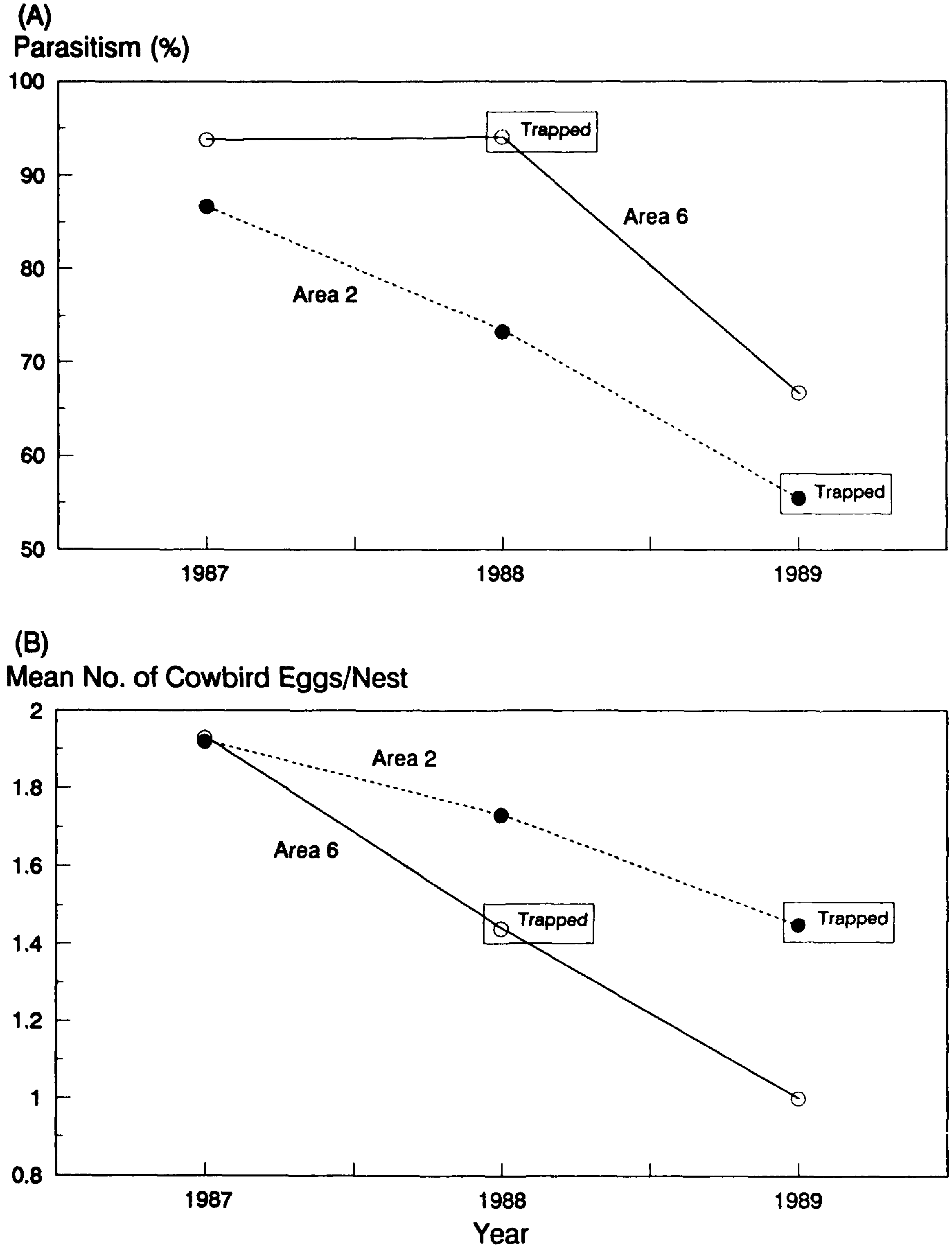

Figure 7. Effect of Cowbird Trapping on (A) Incidence and (B) Intensity of Cowbird Parasitism at Areas 2 and 6.

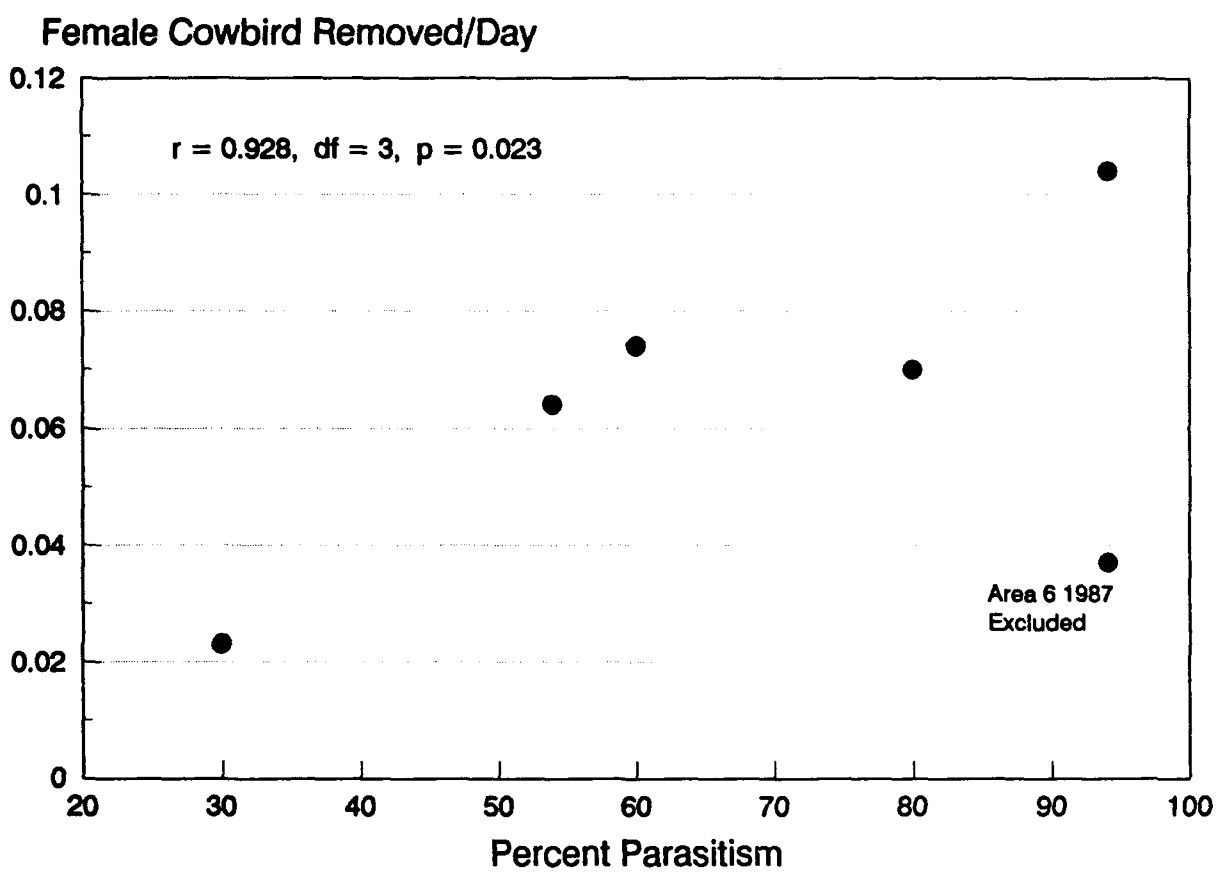

Figure 8. Correlation Between Female Cowbird Trapping Success and Percent Cowbird Parasitism.

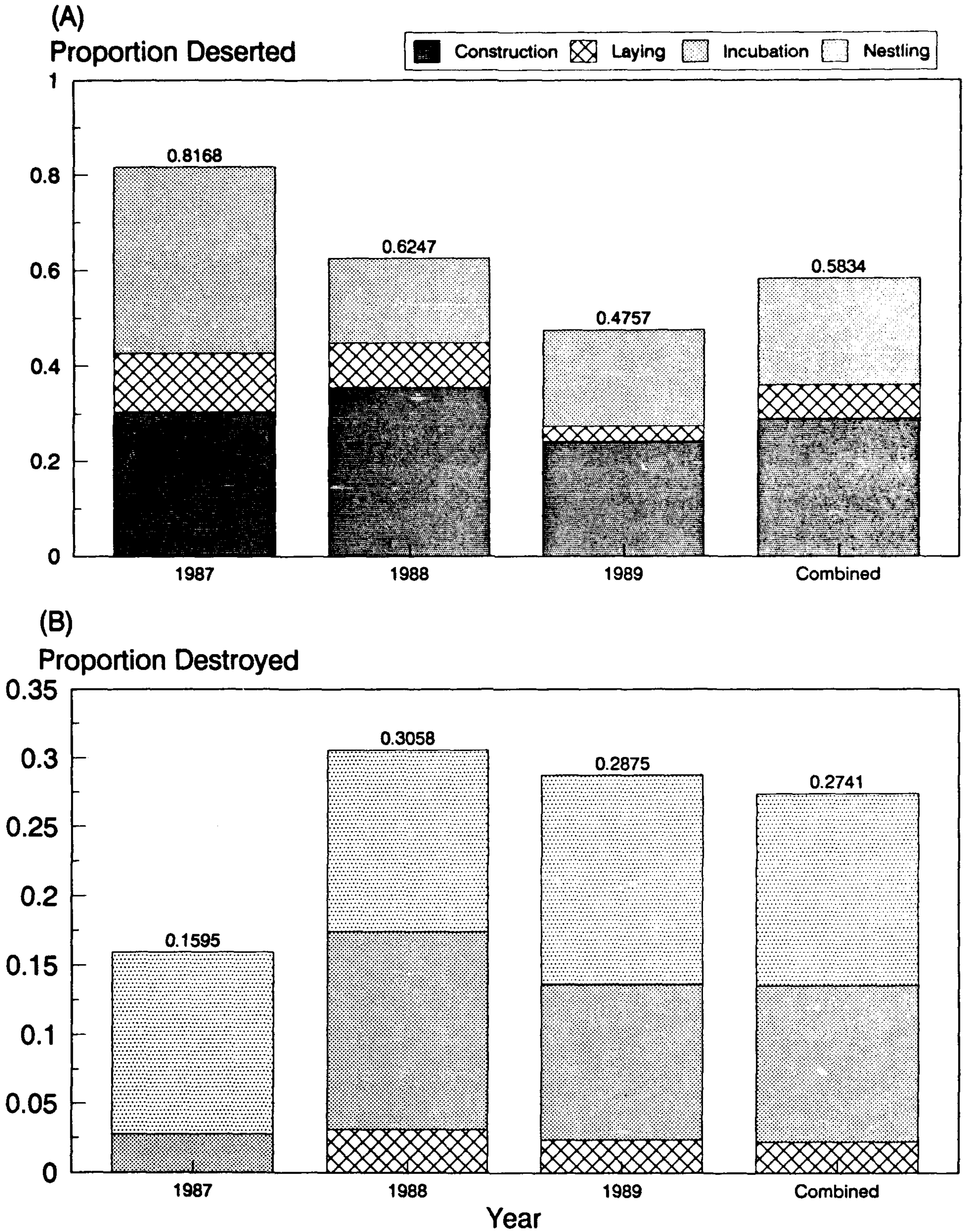

Figure 9. Proportion of Black-capped Vireo Nests (A) Deserted and (B) Destroyed by Year and Nest Stage as Calculated From Exposure.

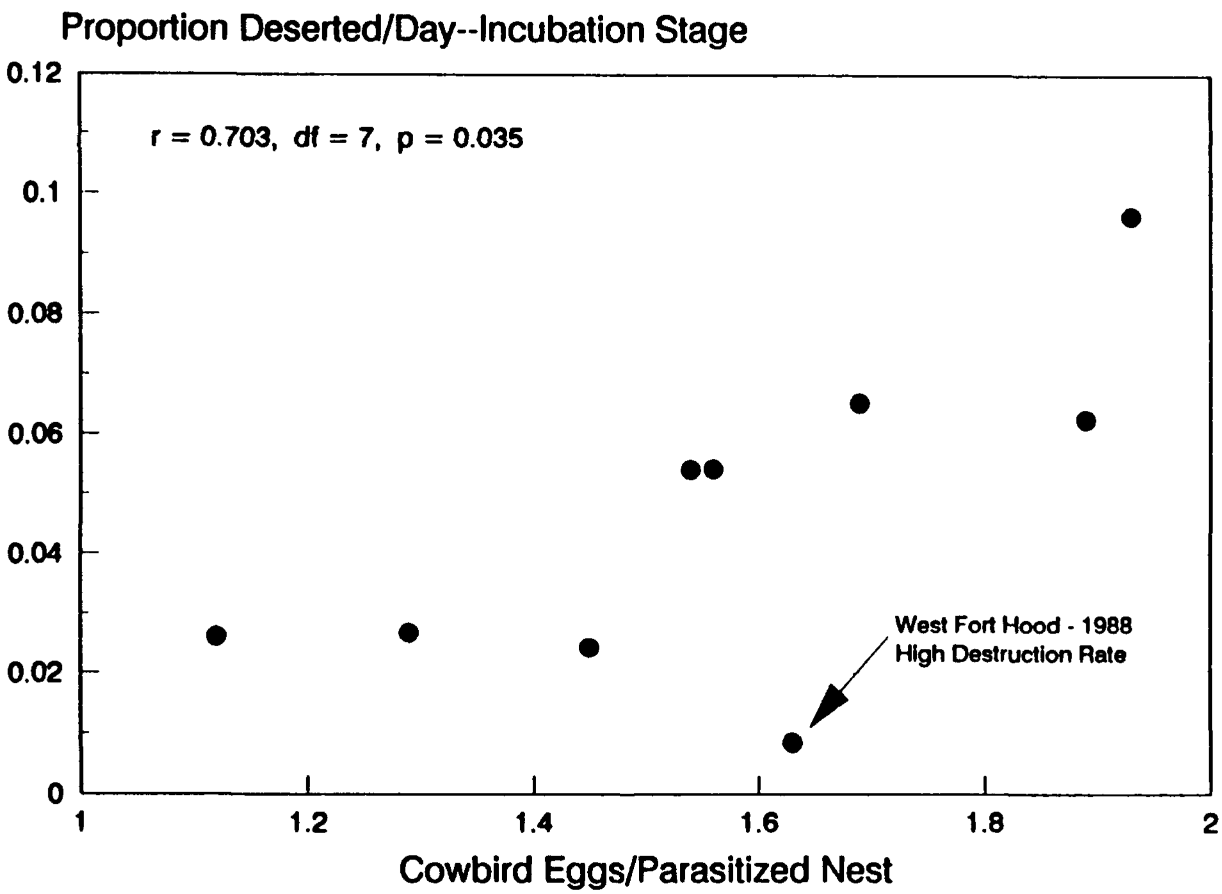

Figure 10. Correlation Between Daily Nest Losses Due to Desertion During the Incubation Stage and the Intensity of Cowbird Parasitism.

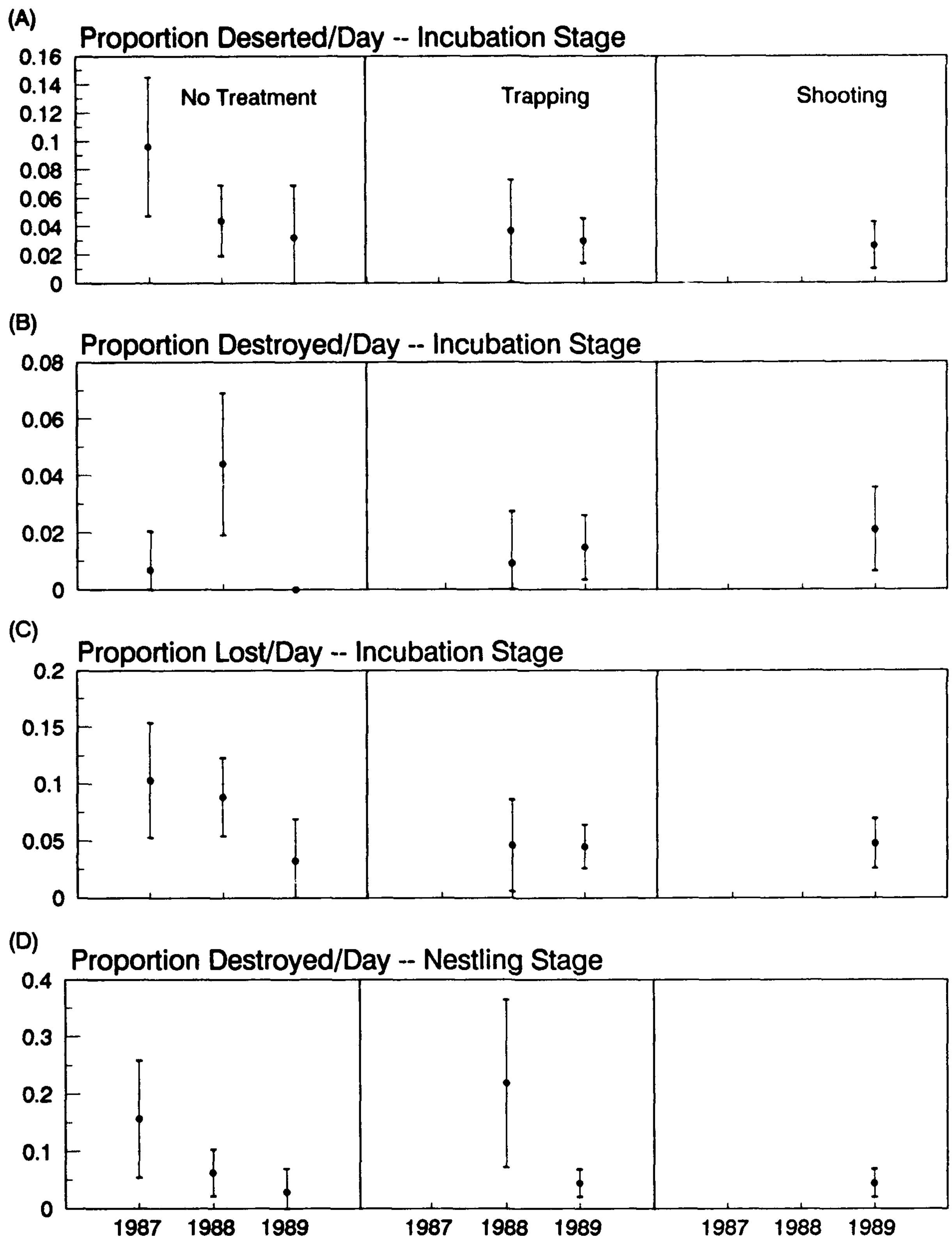

Figure 11. Mean Daily Nest Loss Rate From (A) Desertion, (B) Destruction, and (C) in Total During the Incubation Stage, and From Destruction During (D) Nestling Stage Among Cowbird Control Treatment Groups by Year.

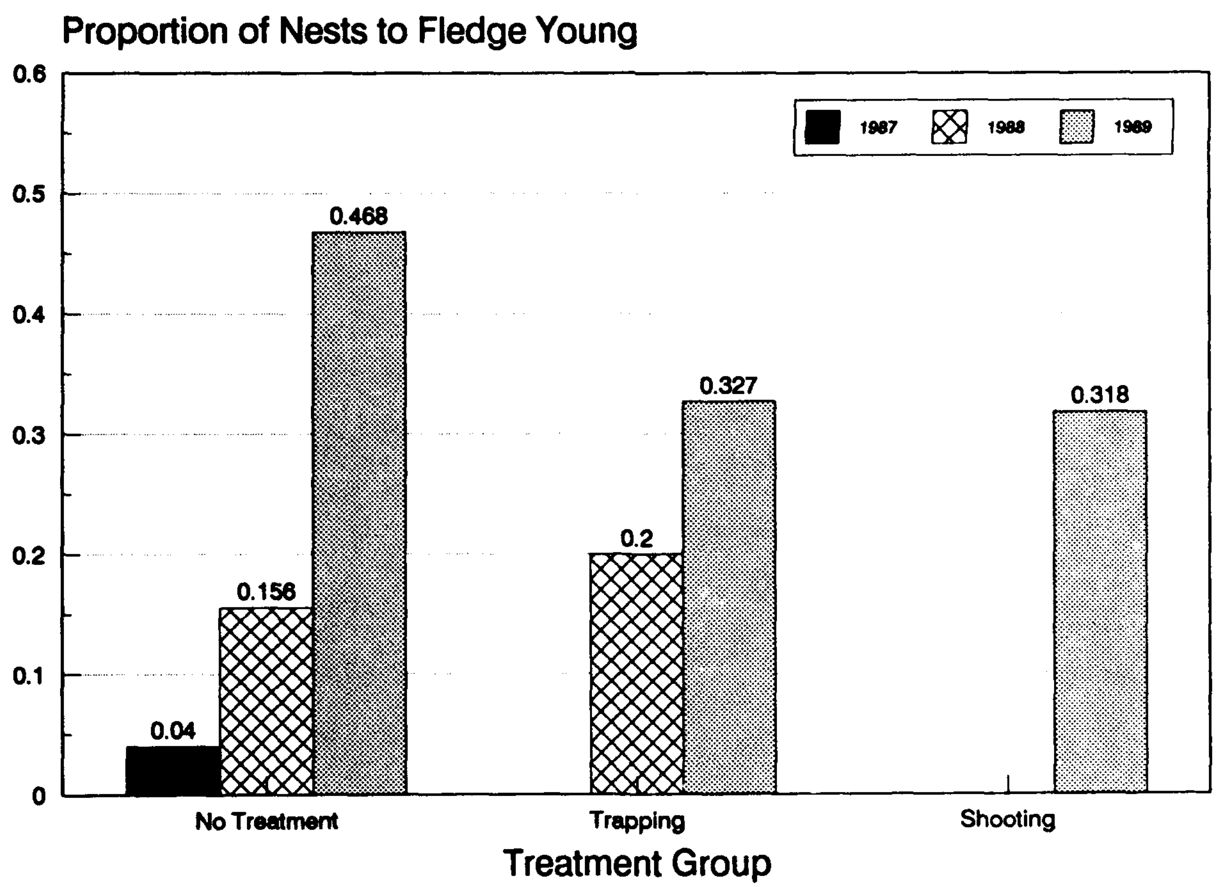

Figure 12. Black-capped Vireo Nesting Success by Year and Cowbird Control Treatment Group Calculated From Exposure for the Incubation and Nestling Periods.

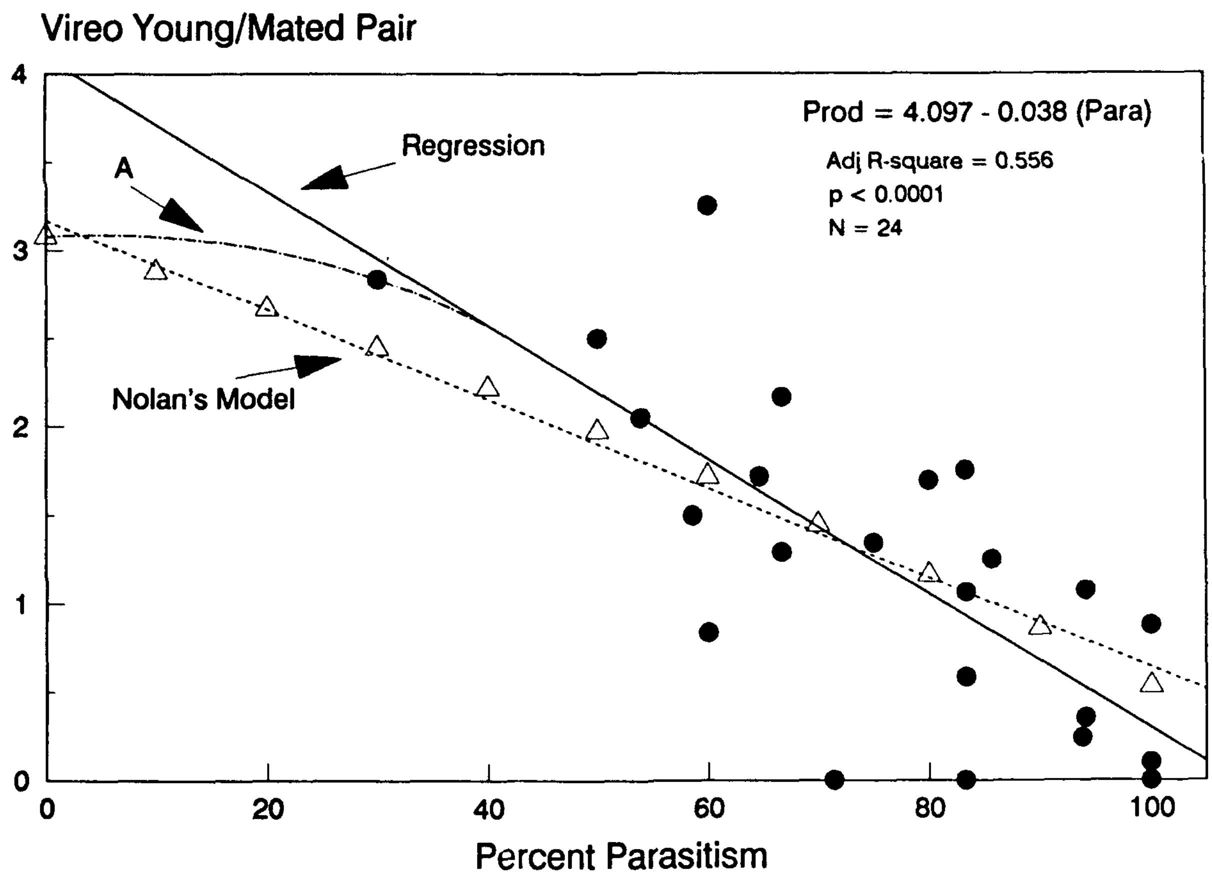

Figure 13. **Results of Regression of Vireo Production on Percent Parasitism, Nolan's Model Relating Production and Parasitism, and a Possible Curvilinear Relationship Between Production and Parasitism (A).**

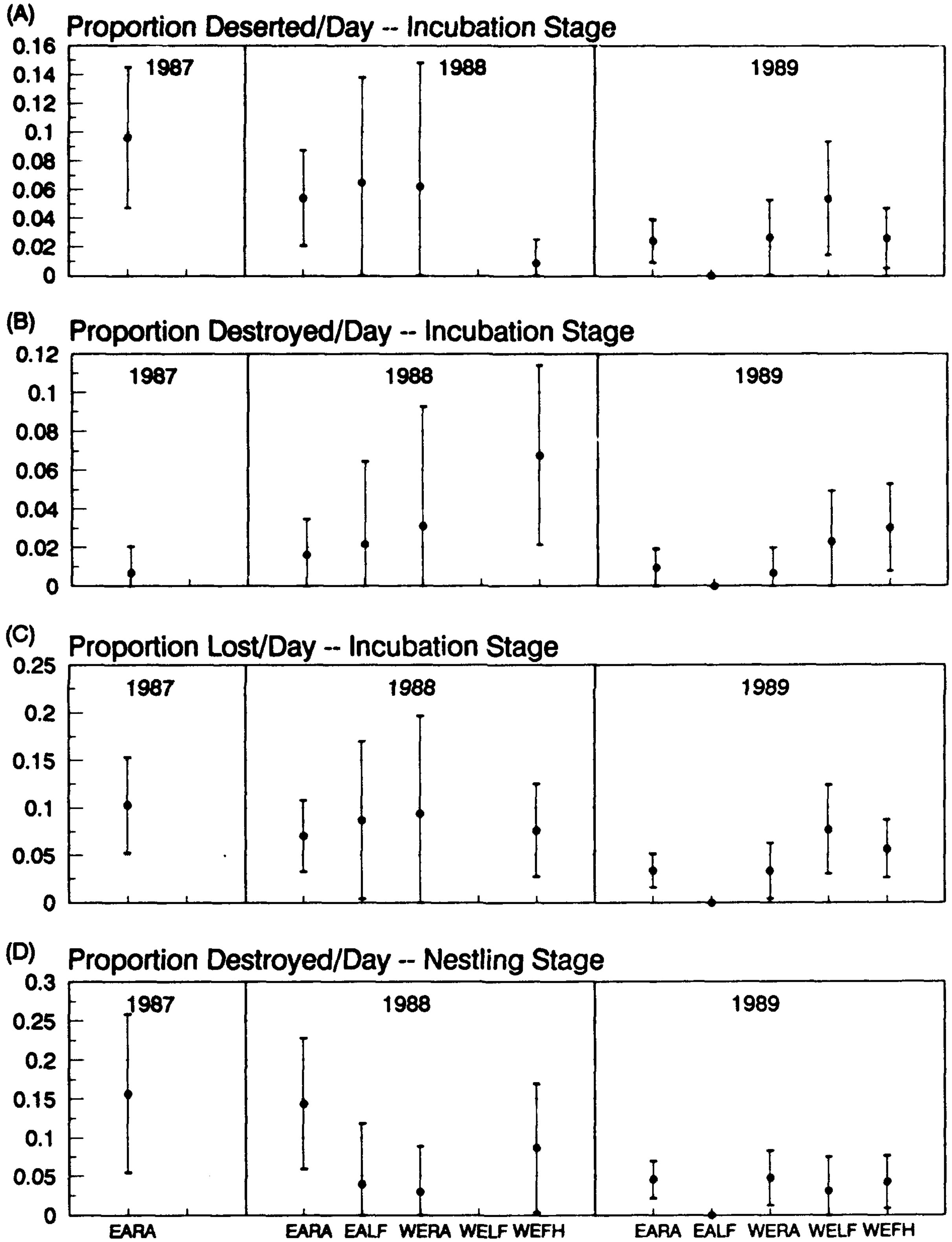

Figure 14. Mean Daily Nest Loss Rate From (A) Desertion and (B) Destruction, and in Total (C) During the Incubation Stage, and From Destruction During the (D) Nestling Stage Among Regions of Fort Hood by Year.

APPENDIX C: Colony Site Code Descriptions

Site	Description
Non-live fire training area	
AR2T	Area 2-Top
AR2S	Area 2-Slope
AR 6	Area 6
AR 12	Area 12
REBL	Red Bluff
BHMT	Brookhaven Mountain
MAMT	Manning Mountain
WMSP	Williamson Mountain
WMSP	Shell Point
NWFH	Northwest Fort Hood
WEFH	West Fort Hood
Live fire training area	
AR 75	Area 75
ROPT	Robinette Point
RAPT	Rambo Point
BRCR	Brown's Creek
JAMT	Jack Mountain
NOLF	Ruth Cemetery
NOLF	Dalton Mountain
NOLF	Henson Mountain
LOMT	Lone Mountain
PKRA	Pilot Knob Range
AR 81	Area 81

APPENDIX D: Plant Community Code Descriptions

BARR	Barren (<10% ground cover)
SPHE	Sparse Herbaceous
SPFO	Sparse Forb
OPFO	Open Forb
DEFO	Dense Forb
CLFO	Closed Forb
SPGR	Sparse Grass
OPGR	Open Grass
DEGR	Dense Grass
CLGR	Closed Grass
OPSH	Open Shrub
DESH	Dense Shrub
CLSH	Closed Woodland
OPWO	Open Woodland
DEWO	Dense Woodland
CLWO	Closed Woodland

Sparse:	<25% cover
Open:	25 to 50% cover
Dense:	51 to 75% cover
Closed:	76 to 100% cover

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