DEMOGRAPHIC DIFFERENCES OF BLACK-CAPPED VIREOS (*VIREO ATRICAPILLA*) IN TWO HABITAT TYPES IN CENTRAL TEXAS

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Leslie Noa

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Abstract

Understanding the effects of habitat selection for a declining species is integral to developing effective management strategies; this is particularly important in the case of the endangered black-capped vireo (*Vireo atricapilla*). I analyzed differences in abundance, age structure, and nesting success of black-capped vireos in 2 early successional habitat types found on Fort Hood, an 87,890-ha army base in central Texas. These habitats were: 1) large areas of continuous shrubby vegetation, referred to as shrubland habitat, and 2) small patches of shrubby vegetation centered on one or several large trees, known locally as donut habitat. Black-capped vireos prefer shrubland habitat, and we know that this represents high quality habitat. The objectives of my study were to determine whether there were differences in abundance, age structure, and nesting success in these 2 habitat types and to determine whether donut habitat is high- or low-quality habitat. I used a Wilcoxon Rank Sum test to examine differences in abundance, and I used Fisher's Exact test to examine differences in age structure. The data indicated that there were differences in abundance and age structure of black-capped vireos between shrubland and donut habitat. Donut habitat had a lower abundance of vireos (2 times less than shrubland per point count) and a higher percentage of second-year males. Second–year males are first-time breeders and are presumed to be subordinate to older, experienced breeding males. The younger age structure of male vireos in donut habitat indicates that it is lower quality habitat. Analyses of nesting success using an information- theoretic approach indicated that habitat, nest height, and year were all important variables. In both shrubland and donut habitat daily nest survival increased as nest height increased. Differences in daily survival rates for the 2 years of the study may be explained by environmental fluctuations, which are known to affect food availability, or may be explained by predator/prey cycles. Wildlife biologists on Fort Hood should continue to monitor areas of donut habitat to determine if they represent potential population sinks and continue to manage of vireo habitat through the use of prescribed burning and mechanical disturbance. This study provided clear evidence that habitat is a limiting factor for black-capped vireos at Fort Hood and throughout the range of this federally endangered species.

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Chapter 1. Comprehensive Literature Review

Black-capped Vireo

The black-capped vireo (*Vireo atricapilla*) is a small migratory passerine that was listed as a federally endangered species in 1987 (Ratzlaff 1987) due to population decline throughout its breeding range in North America. The vireo's original breeding range encompassed southern Kansas, Oklahoma, central and southern Texas, and northeastern Mexico (Graber 1961). Brood parasitism by the brown-headed cowbird (*Molothrus ater*), fire suppression, expansion of ranching, and subsequent overgrazing all have contributed to vireo decline(Ratzlaff 1987). In her life history account of the vireo, Graber (1961) noted that it was already a declining species in the 1950's due to the same factors that led to its listing as a federally endangered species.

The black-capped vireo is a habitat specialist that currently breeds in shrubland areas in central Texas, a few isolated locations in Oklahoma, and in areas of northeastern Mexico; they have been extirpated from Kansas (Grzybowski 1995). Their breeding habitat is characterized by low, shrubby vegetation, often oaks (*Quercus spp*.) (Grzybowski 1995). Vireo habitat is constantly changing due to succession, and it is most often created through disturbance by either man-made or natural processes, such as fire. Marshall et al (1985) indicated that high quality vireo habitat was present 10-15 years after a fire. The key component to this type of habitat is that it is characterized by clumps of shrubs that have an "apron" of vegetation completely to the ground. It is in this "apron" of vegetation that vireos most often nest (Grzybowski 1995). Across their breeding range there is much variation in shrub species, but the general vegetation characteristics are consistent (Grzybowski et al. 1994).

Vireos typically arrive at their breeding grounds in late March or early April and remain until fall migration in August and September (Grzybowski 1995). Most vireo research has investigated the breeding biology and ecology of vireos. However, it is known that vireos winter in Mexico along the Pacific slope but little is known about their wintering ecology or habitat. It is believed that little loss of habitat has occurred on their wintering grounds thus making this a low research priority for managers (Grzybowski 1995).

Land-use factors have had a large impact on vireo populations by limiting their habitat. Fire suppression and the expansion of ranching has limited the early successional habitat that vireos use to breed. Although vireo habitat is early successional and therefore short lived across the landscape, it is thought that areas of suitable habitat were more extensive and closer together historically than they are today (USFWS 1991).

In addition to fire suppression and grazing, which limited black-capped vireo habitat, brown-headed cowbird parasitism has also contributed to the decline of this species throughout its historical range. The cowbird has undergone rapid population growth due to clearing of forests for agriculture, increasing cattle ranching, and increasing residential development (Lowther 1993, Robinson et al. 1995). High levels of cowbird parasitism led to low productivity of vireos in Texas and Oklahoma (USFWS 1991). Vireos are a known acceptor of brown-headed cowbird eggs; few parasitized vireo nests are successful (fledging at least 1 vireo young). Cowbird eggs hatch in advance of vireo eggs, and cowbird young then dwarf the vireo nestlings and reduce their chances for survival (Grzybowski 1995). Rates of cowbird parasitism in vireos can be very high where no cowbird control program is in place, and cowbirds are residents in all parts of the vireo's breeding range (USFWS 1996). Some areas of Texas and Oklahoma have seen rates of parasitism as high as 90% (Hayden et al. 2000). Thus cowbird control programs are considered essential to the recovery of this species, in addition to habitat management (USFWS 1991).

Black-capped vireos are sexually dimorphic with males exhibiting a black cap and females being duller overall and with a dark gray cap. In addition, second-year males (first breeding season) often exhibit delayed plumage maturation with similar coloring overall to older males except that the black cap fades to gray on their nape (Grzybowski 1995). However, aging is best done by using other plumage characteristics, such as the coverts and retrices.

Black-capped vireos build small open cup nests 0.5-2.0 meters high in low shrubby vegetation. Clutch sizes are typically 4 eggs for first nesting attempts and 3-4 eggs for later clutches. Vireos make multiple attempts at successful broods and, in the event of success, may attempt a second brood (Grzybowski 1995). Examples of known predators are the Texas rat snake (*Elaphe obsolete lindheimeri*), fire ant (*Solenopsis spp.)*, western-scrub jay (*Aphelocoma californica*), cowbird, and gray fox (*Urocyon cinereoargenteus*). The most common nest predators are snakes (Stake and Cimprich 2003). Predation on passerine nests by snakes is known to be an import factor in nesting success (Martin 1988, Weatherhead and Blouin-Demers 2004).

At this time no good estimate of the population of black-capped vireos exists. The population at the Fort Hood Military Reservation in central Texas has been conservatively estimated at 1,847 males (Cimprich 2003). Earlier studies have placed the population of vireos in Mexico at 3,139 to 9,463 pairs (Benson and Benson 1990; 1991, Scott and Garton 1991, Hayden et al. 2001). It is clear from the lack of recent literature on the subject that new population estimates of the black-capped vireo are needed. These estimates would be difficult to obtain in Texas where areas of breeding habitat may be on private lands and where ranchers are hesitant to allow wildlife biologists to survey their land.

Fort Hood, Texas

Fort Hood Military Reservation is in Coryell and Bell Counties in central Texas and it is an important natural area for the Edwards Plateau region of Texas. Fort Hood is an 87,890 ha army base where troops regularly train; it is a post for nearly 40,000 personnel. Not only is Fort Hood home to the largest artillery range in the United States, it is also home to several endangered species. These endangered species are the black-capped vireo, the golden-cheeked warbler (*Dendroica chrysoparia*), several plants, and an endemic cave salamander. Under the guidelines of the Endangered Species Act of 1973, federal agencies (including military installations) are required to manage for endangered species. Military training is the primary land use at Fort Hood, but in surrounding communities there is pressure from commercial and residential development. Grazing is also permitted on Fort Hood under strict environmental guidelines (Hayden et al. 2001).

Fort Hood contains one of the largest areas of breeding habitat available for the vireo (Cimprich 2002). Since the vireo was listed as an endangered species in 1987, it has been monitored extensively at Fort Hood and much research has been conducted at this site (Weinburg et al. 1998). The black-capped vireo recovery plan outlines several components for managing vireos. These include monitoring vireo abundance and nesting success, color-banding vireos, cowbird control, habitat management and creation, and community outreach. Fort Hood is actively involved in each of these management activities. Fort Hood has an active monitoring program through The Nature Conservancy (TNC). Both the Natural Resources Branch of Fort Hood and TNC are involved in habitat manipulation and creation, and managers actively work with local ranchers to expand their cowbird control program in areas surrounding Fort Hood.

An extensive brown-headed cowbird control program was implemented at Fort Hood in response to high rates of brood parasitism following recommendations in the Black-capped Vireo Recovery Plan of 1991 (Eckrich et al. 1999, Hayden et al. 2000). This program includes trapping, shooting, and removal of cowbird eggs and young from vireo nests. The implementation of this control program has contributed to a steady decrease in parasitism from about 90% in the early 1990's to 6.5% in 2002 and an increase in vireo nesting success from 5% in the early 1990's to 64% in 2002 (USFWS 1996, Weinburg et al. 1998, Hayden et al. 2000, Cimprich 2002). It is programs such as this that will help this species recover in areas where there is suitable habitat.

At Fort Hood black-capped vireos have traditionally been found breeding in shrubland habitat where most of the vegetation is 1-2 meters high and is created by accidental fires or mechanical disturbance (Hayden et al. 2001). Shrubland habitat fits the general description of vireo habitat given earlier. However, recent surveys at Fort Hood have shown that vireos have expanded into several additional types of habitat for breeding. These areas have been called donut, brush pile, and linear habitat by installation and TNC biologists working at Fort Hood. A donut is best described as an area of scrubby vegetation, such as shin oak (*Quercus sinuata*), that grows up around a larger tree or group of trees, whereas donut habitat consists of multiple donuts (Cimprich 2003). This vegetation is created when the vegetation around a tree or group of trees is crushed, often during military training exercises and then allowed to grow back. No description of the general character of the vegetation community exists for donut habitat in the literature.

Brush piles are piles of brush, often ashe juniper (*Juniperus ashei*), created by bulldozers where scrubby vegetation grows back through the brush, thus providing suitable nesting habitat (Gil Eckrich, personal communication). Brush piles do not comprise a substantial amount of vireo habitat at the present time at Fort Hood (Cimprich 2003).

Linear habitat is composed of scrubby vegetation, usually oaks (*Quercus* spp.), growing along trails, roads, and rows, often through areas of golden-cheeked warbler habitat. These trails, rows, and roads are also usually created and maintained by military training activities. Linear habitat is very difficult to detect from the air using Geographical Information Systems; scrubby vegetation along roads, rows or trails is not differentiated from other vegetation on land-cover maps of Fort Hood. There is no way to differentiate a road with scrubby vegetation from a road with no scrubby vegetation growing alongside. Thus it is difficult to quantify the amount of linear habitat that is available at Fort Hood. However promising new means of detecting vertical vegetation are currently being researched through the use of Light Detection and Ranging (LIDAR) by TNC at Fort Hood. It is thought that LIDAR may be a good tool to detect potential areas of all types of vireo habitat (Leyva et al. 2003).

In response to the inability to detect black-capped vireo habitat, TNC Fort Hood Project inventoried vireo habitat to quantify better the amount of suitable habitat available and the abundance of vireos in these areas. In 2002 and 2003 TNC surveyed all of Fort Hood to determine areas of vireo habitat and abundance.   During this survey 6,971 ha of vireo habitat were identified on Fort Hood, with 70% classified as shrubland habitat. The remaining 30% of this habitat was classified as donut, linear, or other (a combination of donut and shrubland). Cimprich (2003) stated that in order to monitor the status of vireos on Fort Hood better, all habitat types should be monitored rather than the current monitoring system that include only shrubland habitat. Donut and linear habitats represent a substantial portion of available breeding habitat at Fort Hood, and it is clearly important to understand the value of these habitats to this endangered species.

Habitat Selection

Habitat selection in birds has been well studied (Cody 1985), and it is known that the way an individual selects habitat affects its reproductive success due to the availability of food, mates, and other environmental conditions (Weins 1985). Thus we can say that differences in habitat types (high quality vs. low quality) can affect a bird's fitness and reproductive success (Bowers 1994). It is known that lower quality habitat may have a higher presence of younger subordinate males, which may have lower reproductive success than older dominant males, found in higher quality habitat (Ralph and Pearson 1971, Holmes et al. 1996).

Understanding habitat quality for a given species is thus an important factor in understanding the population dynamics of that system (source/sink dynamics). Lesser quality habitat for a given species may be a sink, and higher quality habitat may be a source. The manner in which a source and sink interact can be important in determining the dynamics of the system; a source is an area where reproduction is greater than mortality and a sink is an area where mortality is greater than reproduction and where a population is maintained through immigration rather than reproduction (Pulliam 1988). The amount of area that a population occupies that is considered a sink may also be an important factor in how the overall population performs, particularly when more individuals in the population are using sinks (Donovan and Thompson 2001). In addition, the strength of source populations is important in maintaining local and regional populations (Donovan et al. 1995).

Understanding how individual populations are affected by habitat quality differences is an important area of study. In the case of the black-capped vireo, we do not know if donut habitat on Fort Hood is lesser quality habitat than "traditional" shrubland habitat. However there is some evidence that habitat may be a limiting factor in parts of the vireo's range (Grzybowski et al. 1994). In some local populations, such as Kerr County, Texas second-year males have been found using habitat that had less favorable characteristics (Grzybowski et al. 1994). Younger males, particularly those in their first breeding season, are known to have lower reproductive success than older males (Ralph and Pearson 1971).

Literature Review Conclusions

It is clear from the TNC inventory that donut habitat and habitat classified as "other" represents a significant portion of habitat available on the West Range of Fort Hood and that it is used by black-capped vireos for breeding. However little is known about the quality of donut habitat for breeding, because the presence of individuals is not always indicative of population health or habitat quality (van Horne 1983). Fitness indicators are needed to assess quality, and direct measures of fitness, such as survival and reproductive success, are ideal. However, these parameters are extremely difficult to obtain. As a result, biologists are often forced to rely on indirect measures of fitness, which are easier to obtain in the field. Indirect measures of fitness include age ratios, pairing success, and nesting success, where higher quality habitats have age ratios skewed towards older birds, higher pairing success, and higher nesting success (Holmes et al. 1996). In addition, biologists often use measures of relative abundance to look at and determine associations between birds and their habitat (Ralph et al. 1995).

In order to better understand the value of donut habitat to vireos on Fort Hood, measures of fitness and abundance are needed. The objectives of my study were to: (1) describe donut habitat (Appendices 1 and 2), (2) determine relative abundance of black-capped vireos in donut habitat, (3) determine the age structure of vireos in donut habitat, and (4) determine nesting success of vireos in donut habitat. I asked following questions regarding these objectives: What is the relative abundance, age structure, and nesting success of black-capped vireos in donut habitat, and how do these parameters compare to those seen in shrubland habitat found on Fort Hood? Is donut habitat high or low quality habitat? Answers to these questions will provide a better understanding vireo habitat on

Fort Hood, and will also serve as a tool for management of habitat on Fort Hood and the region.

Chapter 2. Demographic differences of black-capped vireos (*Vireo atricapilla*) in two habitat types in central Texas.

Habitat selection occurs when an organism chooses among alternative habitats, which influence survival and reproduction differently (Cody 1985). For species with declining populations, management strategies are driven by our knowledge of how individuals within a population select habitats and how these choices affect individual fitness and population level growth rates. We would expect individuals to choose habitats that maximize fitness, however, there are cases where individuals choose habitats that negatively effect both their survival and productivity (Pulliam and Danielson 1991, Martin 1992, Robinson 1992, Donovan and Thompson 2001).

Habitat selection in birds has been well studied (Cody 1985). The separation of ultimate and proximate factors in habitat selection is an important distinction (Hilden 1965). Ultimate factors in avian habitat selection are food and shelter that influence reproduction and survival (Hilden 1965). Proximate factors are stimuli of the habitat that elicit a settling response such as landscape, terrain, nest and foraging sites, and other animals (Hilden 1965). In birds, more recent studies also indicate that proximate habitat selection may be influenced by factors such as vegetation structure (James 1971, James and Wamer 1982, Weins 1985) that affect food availability, nest sites, predation, and brood parasitism (Weins 1985, Burhans 1997, Burhans et al. 2002, Thompson and Burhans 2003).

Many studies correlate abundance of individuals with habitat features. However the mere presence of individuals is not always indicative of either population health or habitat quality (van Horne 1983). Thus, in addition to abundance, measures of fitness are needed to assess habitat quality (Martin 1992). Fitness indicators include sex ratios (Gibbs and Faaborg 2005), age ratios (Holmes et al. 1996), and nesting success. The assumption is that high quality habitat will be dominated by older individuals, will have equal sex ratios and age ratios dominated by experienced individuals, and high nesting success. In addition, as human activities put more pressure on landscapes and habitats, predation on nests may increase (Robinson et al. 1995) and food availability may decrease (Burke and Nol 1998, Zanette 2001).

Understanding the fitness consequences of habitat selection for declining species will help direct conservation strategies; this is particularly important in the case of the black-capped vireo (*Vireo atricapilla*). The black-capped vireo is a federally endangered species the breeds only in central and south eastern Texas, parts of Oklahoma, and north eastern Mexico (Grzybowski 1995). Preferred black-capped vireo breeding habitat is characterized by low, scrubby vegetation, often oaks (*Quercus spp*.) (Graber 1961, Grzybowski 1995). Historically, this early successional habitat was created by fire, but with the expansion of the livestock industry, dryland farming, and suppression of prairie fire, black-capped vireos have lost most of their former nesting habitat (Grzybowski 1995). At the same time, brown-headed cowbird (*Molothrus ater*) populations have increased dramatically and negatively impacted the breeding success of black-capped vireos (Ratzlaff 1987, USFWS 1991). The combination of habitat loss and increased rates of parasitism are the principle reasons for this species' endangered status (Ratzlaff 1987). Thus, conservation efforts therefore target creating high quality habitat within the species breeding range.

Fort Hood Military Reservation in central Texas supports one of the largest remaining breeding populations of black-capped vireos. Vireo populations at Fort Hood have been monitored by The Nature Conservancy (TNC) since 1993. TNC efforts at Fort Hood have focused on large expanses of shrubland habitat, which have traditionally been seen as the principle breeding habitat for vireos (Cimprich 2003). However, in recent years on Fort Hood a second type of habitat has been recognized as supporting nesting vireos. This habitat is known locally as “donut” habitat (Cimprich 2003). A donut is best described as an area of scrubby vegetation, predominately oaks (*Quercus spp*), that grows up around a larger tree or group of trees and is usually surrounded by grass or barren ground; donut habitat consists of multiple donuts (Figure 1) (Cimprich 2003). This vegetation is created when the vegetation around a tree or group of trees is crushed, often during military training exercises, and then allowed to grow back; the area between 2 donuts is typically at least large enough for a large track vehicle to pass through. Donuts and donut habitat are by definition patchy in distribution. Shrubland represents about 70% of vireo habitat at Fort Hood, but donut habitat constitutes the majority of the remaining area occupied by vireos (Cimprich 2003).

Abundance, age structure, and productivity of black-capped vireos have not been studied in donut habitat. Because these areas represent a significant area at Forth Hood and because scrub oak habitat in other parts of the vireo’s range might occur in small patches, it is important to determine their value to nesting vireos and to compare their productivity to larger areas of shrubland habitat. Donuts might be suboptimal habitat and represent a sink for the local vireo population, but they may be as productive as shrublands, which are traditionally viewed as optimum habitat. Fitness indicators are needed to assess quality, and direct measures such as survival and reproductive success are ideal. However, these parameters are extremely difficult to obtain. Indirect measures of fitness are easier to obtain and include age ratios, pairing success, and nesting success, where higher quality habitats have age ratios skewed towards older birds, higher pairing success, and higher nesting success (Holmes et al. 1996, Petit and Petit 1996).

The objectives of this study were to answer the following questions: What are the relative abundance, age structure, and nesting success of black-capped vireos in donut habitat, and how do they compare to the same variables measured in shrubland habitat on Fort Hood? Given these measures, is donut habitat high or low quality habitat? Answers to these questions will provide a better understanding of vireo habitat on Fort Hood, and will also serve as a management tool on Fort Hood and the region.

Methods

Study Site

Fort Hood is an 87,890 ha military reservation located in central Texas. Under the guidelines of the Endangered Species Act of 1973, federal agencies (including military installations) are required to manage for endangered species. Military training is the primary land use at Fort Hood, but in surrounding communities there is growing pressure from commercial and residential development. Grazing is also permitted on Fort Hood but under strict environmental guidelines (Hayden et al. 2001). An extensive brown-headed cowbird control program was implemented at Fort Hood in response to high rates of brood parasitism following recommendations in the Recovery Plan of 1991 (Eckrich et al. 1999, Hayden et al. 2000). This program includes trapping, shooting, and removal of cowbird eggs and young from vireo nests. The implementation of this control program has contributed to a steady decrease in parasitism from about 90% in the early 1990's to 6.5% in 2002, and an increase in nesting success from 5% in the early 1990's to 64% in 2002 (USFWS 1996, Weinburg et al. 1998, Hayden et al. 2000, Cimprich 2002). Cowbird control efforts are relatively consistent across Fort Hood.

The objectives of my study were met by limiting my study sites to donut habitat only and by using data collected by TNC in shrubland habitat in concurrent years. This study was conducted during the 2003 and 2004 breeding seasons. All donut-habitat data were collected in 15 study sites. Donut sites were randomly selected from the mapped habitat on Fort Hood and chosen only if they were >3 ha and reasonably accessible (either by vehicle or foot). All shrubland data were collected by TNC in 3 long-term monitoring sites and in 5 Environmental Watch Areas (EWAs). My data collection in donut habitat followed the standardized protocols used by TNC to reduce observer inconsistency and to allow comparison of donut habitat data with those of TNC's Fort Hood Project (Ralph et al. 1993, Cimprich 2002).

Field Methods

Relative Abundance

To assess relative abundance of vireos in donut and shrubland habitat, I conducted 42 single observer 6-min point counts in donut habitat. TNC conducted point counts in all their monitoring areas and in the EWAs, and I used 152 of their 6-min point counts from shrubland habitat. All counts were at minimum 250 m apart. Each count was replicated once a month from April to July in both 2003 and 2004. Counts were broken into 3 time intervals (3, 2, and 1 minutes) for removal method analyses (see below) and distances of vireos detected from the point location were recorded.

Age Structure

To determine the age structure of the population, I caught vireos through target mist-netting; plumage characteristics were used to age and sex vireos (D.A. Cimprich, personal communication, Pyle 1997). Care was taken to minimize stress of birds. Once birds were caught they were aged, sexed, banded with unique color combinations, and released.

Nesting Success

Estimates of nesting success for vireos in donut habitat were made through nest searching and nest monitoring. I used behavioral cues during searches of suitable nesting sites. Each observer was responsible for a study site or part of a study site in order to ensure familiarity with the sites (Martin and Geupel 1993). Nests were monitored every 2-3 days, with nest contents and stage recorded at each visit until the nest fledged young or failed. Every effort was made to monitor the nest on the day young fledged, which gives the best measure of how many young have fledged. A successful nest was one from which at least 1 young fledged (Ralph et al. 1993, Cimprich 2002).

Analysis Methods

Relative Abundance

Detection probabilities are the probability a bird will sing and/or the probability the bird is heard if it sings. Detection of birds may vary as a function of habitat type, time of year, or observer (Farnsworth et al. 2002). Therefore, before conducting statistical tests to compare shrubland and donut habitat, I examined differences in detection probabilities of the 2 habitat types and time during breeding season (early/late season). I used the removal method for point count surveys (Nichols et al. 2000, Farnsworth et al. 2002, Moore et al. 2004) in Program SURVIV to test for differences in detection probabilities for the best model. I evaluated 3 models in program SURVIV (Farnsworth et al. 2002): (1) seasonal (early vs. late season), (2) habitat differences (shrubland vs. donut), and (3) seasonal and habitat differences. I used AIC scores to select the best model and used the detection probabilities from the best model to adjust the raw count data. With the corrected data, I tested for differences in relative abundance of vireos between shrubland and donut habitat with a Wilcoxon Rank Sum test in program SAS (Proc Npar1way SAS version 8.2). I used this non-parametric statistical test because both the count data and their residuals were non-normal.

Age Structure

I compared age structure (the ratio of second-year males to after-second year males) between donut and shrubland habitat for both years with a Fisher's Exact test in Program SAS (Proc Freq, SAS version 8.2). Only males known to be breeding in either donut or shrubland habitat were used in the analysis. Females were not used in the analysis because they were harder to mist net and the sample size was too small.

Nesting Success

To compare nesting success between habitats, I located and monitored 163 black-capped vireo nests in donut habitat, and I used 177 nests located and monitored by TNC in shrubland habitat. A nest was considered successful if at least one young fledged. I evaluated 13 models (described below) to describe nest success and evaluated a global model for testing goodness of fit (Table 1). Daily nest survival was the response variable and was calculated following a generalized linear modeling approach outlined by Rotella (2004) and Shaffer (2004) in Program SAS.

Habitat can be an important factor in nesting success (Holmes et al. 1996), and one of my main objectives was to determine how habitat is a factor in nesting success. Therefore, the first 2 models included some combination of habitat, and habitat and year (Table 1). Year (2003 and 2004) was used in the models because it is known that there are often year differences in nesting success rates (Holmes et al. 1986); TNC has also noted an alternating nesting success cycle in vireos (D. A. Cimprich, personal communication).

Donut habitat is structurally different from shrubland habitat therefore there may be differences in the height at which nests are placed. Nest height could be a factor in the probability of nest predation (Martin 1992, Burhans et al. 2002), and there may be interactions between habitat and nest site characteristics (Burhans 1997). Models 3 and 5 focused on habitat and nest height, as well as interactions between the two. Model 4 looked at nest height alone. Model 6 focused on the 3 variables (habitat, year, and nest height) with no interaction between variables. Model 7 focused on the habitat/nest height interaction and year (no interaction with year).

Brown-headed cowbird parasitism is known to have an effect on the reproductive success of song birds, and of vireos in particular (Ratzlaff 1987), and levels of parasitism may differ with habitat type (Robinson et al. 1995). Models 8, 9 and 10 looked at habitat, parasitism, and their interaction. Model 11 focused on the interactions between habitat and nest height, the interaction between habitat and parasitism, and year. Model 12 focused on all 3 variables with no interactions, and model 13 evaluated year alone.

Model 14 was the full model to assess goodness of fit of all the models and was not used in model selection.

Results

Relative Abundance

Of the 3 models evaluated in SURVIV the model that included both habitat and season was the best model. The model with season only had a ΔAICc = 0.81, and the model with habitat only had a ΔAICc = 1.31, indicating that there was also some support for these models. The best model which included habitat and season had an AICc of 46.9 and χ^2 value of 0.69 indicating that the model was a reasonably good fit. Therefore the model that included both habitat and season was used to determine differences in detection probabilities. The detection probabilities from this model were then used to adjust raw point-count data (Table 2). I analyzed abundance in shrubland versus donut habitat with a Wilcoxon Rank Sum test. The results of this test indicated that shrubland habitat had 2 times the number vireos than donut habitat ($p \leq 0.0001$; CI = 0.7644273-0.9689073 in shrubland and CI = 0.3661490- 0.5826697 in donut habitat) (Fig. 2).

Age Structure

I used 2 age classes for male vireos in each habitat: second-year (first breeding season) and after second-year. In donut habitat 63 males were caught and aged: 31 were second-year and 32 were after-second year. In shrubland habitat 115 males were caught and aged: 37 were second-year and 78 were after second-year. I used a Fisher's Exact test to test for differences in vireo age structure between donut and shrubland. This test indicated that there were differences between shrubland and donut habitat ($p<0.0193$;

effective sample size 178). Donut habitat had a higher percentage of second-year males (49%) than shrubland habitat (32%) (Fig. 3).

Nesting Success

Of the 12 models tested, one model in particular was strongly supported by the data with an information-theoretic approach. Model 6 included the following variables with no interaction terms: habitat (donut and shrubland), nest height, and year (2003 and 2004). This was the best model according to the nesting success analysis described by Rotella (2004); it had an AICc value of 1319.74 and weight of 0.692 (Table 3 and Appendix 3), which indicated that this model had the most support of the candidate set of models and had a 69.2% chance of being the best Kulback Leibler model in the model set. The next best model (Model 7) evaluated habitat/height interactions and year, and had an AIC weight of 0.1644. The next best model included parasitism as a term and had an AIC weight of .1156. None of the other models were supported by the data. Thus, clearly habitat, nest height, and year the nest occurred were all important factors in determining nesting success. A goodness of fit test of the global model indicated that the model was a good fit (Pearson χ^2: 2275.4, χ^2/df =1.06) and that there was support for the candidate set of models.

Habitat had an effect on nesting success particularly in 2003 (Fig. 4a), when daily survival probability was lower in donut habitat than in shrubland habitat. One difference between habitat types was brown-headed cowbird parasitism; donut habitat had a higher rate of parasitism (12.3% in donut and 2% in shrubland). Although this does not appear in the best model, it is in the third best model and thus may still play a role in overall nesting success of vireos. Nest height also affected daily survival probabilities. Daily survival probabilities of a given nest increased as nest height increased in both habitats; however in both 2003 and 2004 daily survival probability was lower in donut habitat than in shrubland habitat (Fig. 4b). These results indicated that nest height had a positive effect on survival (Table 4 and Fig. 4b), and this was consistent across both habitat types. The nesting success analysis indicated yearly differences in daily survival probabilities (Figure 4c). In 2003 daily survival probability was much lower than in 2004.

Discussion

Black-capped vireos differed in abundance and age structure between donut and shrubland habitats. Donut habitat had lower abundance and younger adult males than shrubland habitat. Differences in abundance were likely a result of the fact that donut habitat was more open than shrubland habitat and provided fewer nesting sites and foraging areas. Although abundance is not always an indicator of habitat quality (van Horne 1983), it can be important in that fewer birds were able to use donut habitat in comparison to the same amount of shrubland habitat. As the Fort Hood vireo population continues to grow, it is important to continue monitoring the abundance of vireos in both shrubland and donut habitat. We know that as populations grow, they eventually "spill over" into suboptimal habitat (Rosenzweig 1991), which may represent a sink for a population (Pulliam 1988).

Analysis of age structure showed that donut habitat had a higher proportion of second-year males than did shrubland habitat (49% vs. 32%). Second-year males are less experienced and tend to be less successful than their older counterparts (Ralph and Pearson 1971, Holmes et al. 1996), and younger males often occupy habitat that is less than optimal (Holmes et al. 1996, Petit and Petit 1996). Other researchers have also reported areas of suboptimal black-capped vireo habitat that had higher ratios of second-year males than areas of optimal habitat (Grzybowski et al. 1994). Thus, the higher proportion of second-year males in donut habitat is an indication that donuts represent lower quality habitat than shrubland.

Differences in nesting success of black-capped vireos between donut and shrubland habitat were more difficult to assess, though habitat was consistently identified as an important factor. Models with a ΔAICc < 3.0 included habitat, nest height, year, or the interaction between habitat and height (Table 3); these variables were important variables affecting nesting success. However the model with the most weight ($w_i = .69$) did not include a habitat and nest height interaction.

The nesting success analysis indicated that habitat affected daily survival probabilities, however the effect size of habitat was small (0.04). One difference in donut and shrubland habitat was brown-headed cowbird parasitism; donut habitat had a higher rate of parasitism than shrubland habitat (12.3% in donut and 2% in shrubland). Although donut habitat had a higher rate of parasitism, there were no differences in the number of offspring fledged per successful nest between donut and shrubland habitat (L. Noa, unpublished data). Parasitism was not a variable in the best nesting success model however, any vireo nest that is parasitized will fail without intervention. At Fort Hood cowbird eggs are removed after the vireo lays a complete clutch, therefore these vireo nests, if successful, will fledge young. This explains why there were no differences in the number of offspring fledged between donut and shrubland habitat and why this variable was not included in the best model. Cowbird parasitism occurred despite a wellestablished cowbird-control program on Fort Hood in which efforts were made to remove cowbirds in all habitats. Donut habitat generally occurred in smaller areas (or patches) than shrubland and near the edges of fields, which may have made birds nesting there more susceptible to cowbird parasitism. Studies of Neotropical migrants in the Midwest indicate that nests in fragmented forests were more likely to be parasitized than nests in intact forests (Robinson et al. 1995), indicating that landscape factors contribute to parasitism. Perhaps it was proximity to areas off of Fort Hood where there was no cowbird control program, or perhaps donut sites were closer to feeding sites than shrubland that led to increased levels of parasitism in donut habitat. In general, donuts were closer to the perimeter of Fort Hood than were shrubland sites. This is an area of study that deserves further attention.

There was a slight positive trend in daily nest survival as nest height increased in both shrubland and donut habitat. However, daily survival probability was lower in both years of the study in donut habitat. These results indicated that more information is needed to determine how nest site characteristics such as nest height affect nesting success. Studies have indicated that nest height and other nest site characteristics are important factors in nesting success (Martin 1993, Burhans 1997, Burhans et al. 2002).

In addition to habitat and nest height, year was also an important variable. Although my study was only over a 2-year period and could be an unusual occurrence, there is evidence that nesting success varies on a year to year basis for black-capped vireos on Fort Hood (D. A. Cimprich, personal communication). It is documented that in forest ecosystems, food, weather, and predation may regularly affect reproductive success in birds and vary by year (Holmes et al. 1986). Fort Hood climate data for the months of

March through July indicate that the 2003 breeding season was much drier than the 2004 season (2003: 22.91 cm of rain, 2004: 46.89 cm of rain). Environmental fluctuations, such as rainfall, contribute to the availability of food, and food availability affects nesting success of birds (Holmes et al. 1986).

Not only may environmental conditions contribute to yearly differences in daily nest survival, predation may also fluctuate on a yearly basis. In 2003 nest loss to predation was 54%, and in 2004 nest loss to predation was 38% in both habitats. Clearly predation rates were dramatically different from 2003 to 2004. Known vireo nest predators include Texas rat snake (*Elaphe obsolete lindheimeri*), fire ant (*Solenopsis spp.)*, western-scrub jay (*Aphelocoma californica*), cowbird, and gray fox (*Urocyon cinereoargenteus*). The most common nest predators are snakes (Stake and Cimprich 2003). During the course of this study I observed a broad-banded copperhead (*Agkistrodon contortrix laticinctus*) at a depredated nest. In addition, I regularly observed Texas rat snakes on all 15 donut study sites, and vireos were often seen mobbing rat snakes. Predation on passerine nests by snakes is an import factor in nesting success (Nolan 1963, Martin 1988, Weatherhead and Blouin-Demers 2004).

Difference in predation levels, which effected daily nest survival, for the 2 years of my study can be explained by fluctuating populations of predators and of their alternate prey. Predator populations may vary from year to year, but the impact of predators on songbirds may vary with changing rodent populations because predators, such as snakes, may focus more on bird nests in years when rodents are scarce (Schmidt and Ostfeld 2003). Anders et al (1997) indicated that during high predation years, a population may become a sink and during low predation years may be able to sustain itself.

Based on data from abundance, age structure, and nesting success, I conclude that there is evidence that donuts represent lower quality habitat for black-capped vireos than shrubland. Vireos were nearly 2 times more abundant in shrubland than in donut habitat and donut habitat had a higher percentage of younger males than shrubland habitat. Differences in nesting success were also definitive, but year and nest height effects were also important factors. From a population perspective, the lower density and a higher percentage of inexperienced males in donut habitat indicate that fewer young are being produced per unit area in donut habitat versus shrubland habitat. Donut habitat may not constitute suitable habitat, its absolute growth is lower than shrubland habitat strictly due to its reduced density. Two other areas of study would increase our knowledge of black-capped vireos and how to best manage their habitat: 1) a study of nest site characteristics for vireos in all habitat types, and 2) a study of black-capped vireo nest predators, such as snakes.

Management Implications

My study provides clear evidence that donut habitat is lower quality than shrubland habitat for black-capped vireos. There are two important implications that can be drawn from this information. First, biologists should continue to manage for shrubland habitat on and around Fort Hood through the use of prescribed burning and mechanical disturbance, such as bulldozing. Second, wildlife managers at Fort Hood need more information about the productivity of vireos nesting in donut habitat over a longer period of time than the 2 years of my study. It is important that monitoring of productivity in donut habitat be continued to get a better estimate of average productivity, extreme values in productivity, and whether donuts serve as sources or sinks for the local black-capped vireo population. My study was the first to examine vireos nesting in donut habitat, and it is important that it not be the last.

This study also has important implications for vireos throughout their range. It provides clear evidence that habitat is a limiting factor for vireos. Grzybowski (1995) noted that second-year male vireos in the Edward's Plateau region of their range tended to occupy areas that were more open. Donut habitat may be similar to these areas in that they are also more open than shrubland habitat and have a higher percentage of second-year males. It is important for managers throughout the black-capped vireo's range to monitor vireo populations for potential sinks particularly in areas where second-year males are predominant.

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Table 1. Nest success models for black-capped vireos at Fort Hood, Texas.

Model Number	Model	Description
1	$B_0 + B_1{}^*$Hab	Habitat Main Effects
2	$B_0 + B_1{}^*$Hab + $B_2{}^*$Year	Habitat and Year
3	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig	Habitat and Nest Height
4	$B_0 + B_1{}^*$Heig	Nest Height Main Effects
5	$B_0 + B_1$(Hab*Heig)	Habitat/Nest Height Interaction
6	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig + $B_3{}^*$Year	Habitat, Year, and Nest Height (no interactions)
7	$B_0 + B_1$(Hab*Heig) + $B_2{}^*$Year	Habitat/Nest Height Interaction and Year
8	$B_0 + B_1{}^*$Hab + $B_2{}^*$Para	Habitat and Parasitism
9	$B_0 + B_1$(Hab*Para)	Habitat/Parasitism Interaction
10	$B_0 + B_1{}^*$Para	Parasitism
11	$B_0 + B_1$(Hab*Heig) + B_2(Hab*Para) + $B_3{}^*$Year	Habitat/Height interaction and Habitat/Parasitism interaction and Year
12	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig + $B_3{}^*$Para+ $B_4{}^*$Year	Habitat, Height, Parasitism, and Year
13	$B_0 + B_1{}^*$Year	Year
14	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig + $B_3{}^*$Year + $B_4{}^*$Para + B_5(Hab*Heig) + B_6(Hab*Para)	Full Model (all variables and interaction terms)

Table 2 Probability of detection for black-capped vireo point-count data from program SURVIV, Fort Hood, Texas, 2003 and 2004 nesting seasons.

Parameter	p	Standard error	95% Confidence Interval Lower	95% Confidence Interval Upper
Donut Early Season	0.949272	0.026903	0.896544	1.002000
Donut Late Season	0.687260	0.182880	0.328799	1.045720
Shrubland Early Season	0.853632	0.314594	0.791971	0.915292
Shrubland Late Season	0.841355	0.355803	0.771618	0.911093

Early season = April and May
Late season = June and July

Table 3. AIC results for black-capped vireo nesting success, Fort Hood, Texas, 2003 and 2004 nesting seasons.

Model Number	Model	Rank	K	Log Likelihood	AICc	Δ_i	w_i
6	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig + $B_3{}^*$Year	1	4	-651.86	1319.74	0.00	0.692388
7	$B_0 + B_1{}^*$Hab + $B_2{}^*$ Heig + $B_3{}^*$Year + B_4 (Hab*Heig)	2	5	-651.30	1322.62	2.88	0.1644044
12	$B_0 + B_1{}^*$Hab + $B_2{}^*$Heig + $B_3{}^*$Para+ $B_4{}^*$Year	3	5	-651.65	1323.32	3.58	0.1156219

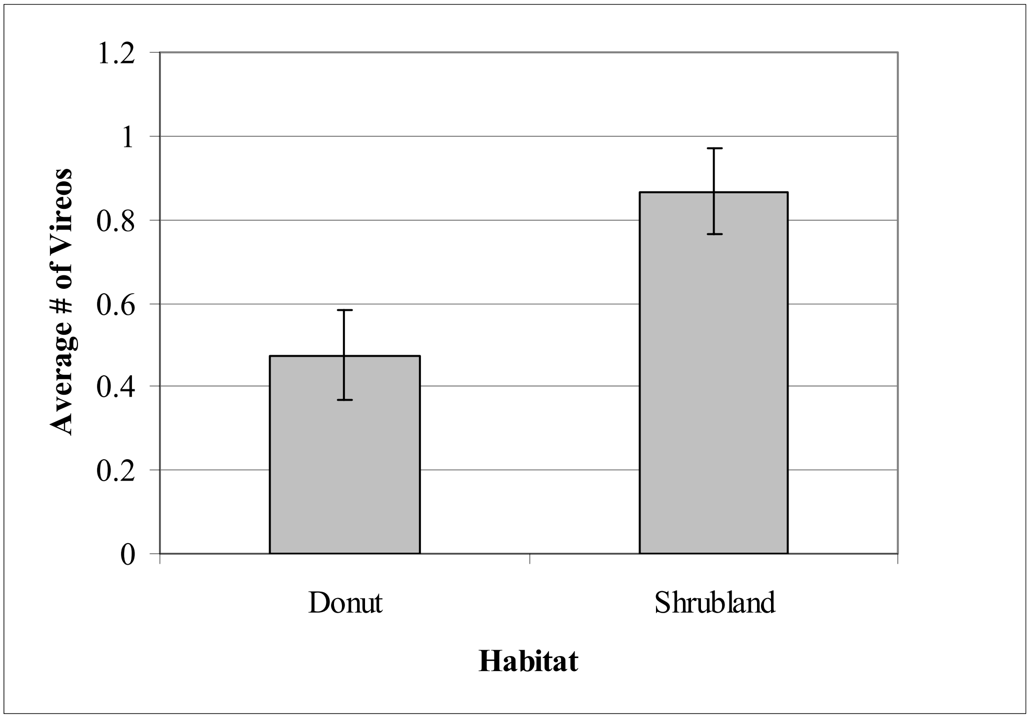
Table 4. Parameter estimates for model 6.

Description	Parameter	Estimate	Standard Error	Lower CL	Upper CL	Prob Chisq
$B_0 + B_1{}^{*}$Hab +	Intercept	3.5960478	0.2140504	3.17652	4.01558	2.44E-63
$B_2{}^{*}$Heig +	Hab1	-0.103118	0.1559737	-0.4088	0.20259	0.508533
$B_3{}^{*}$Year	Hab2	0	0	0	0	
	Year1	-0.831760	0.142844	-1.111729	-0.551791	5.785E-09
	Year2	0	0	0	0	
	Nheig	0.0776379	0.2376155	-0.38808	0.5433557	0.7438663

Estimates of zero were used as the reference point for categorical variables; hab 1 = donut habitat; hab2 = shrubland habitat; para0 = not parasitized; para1 = parasitized; nheig = nest height.

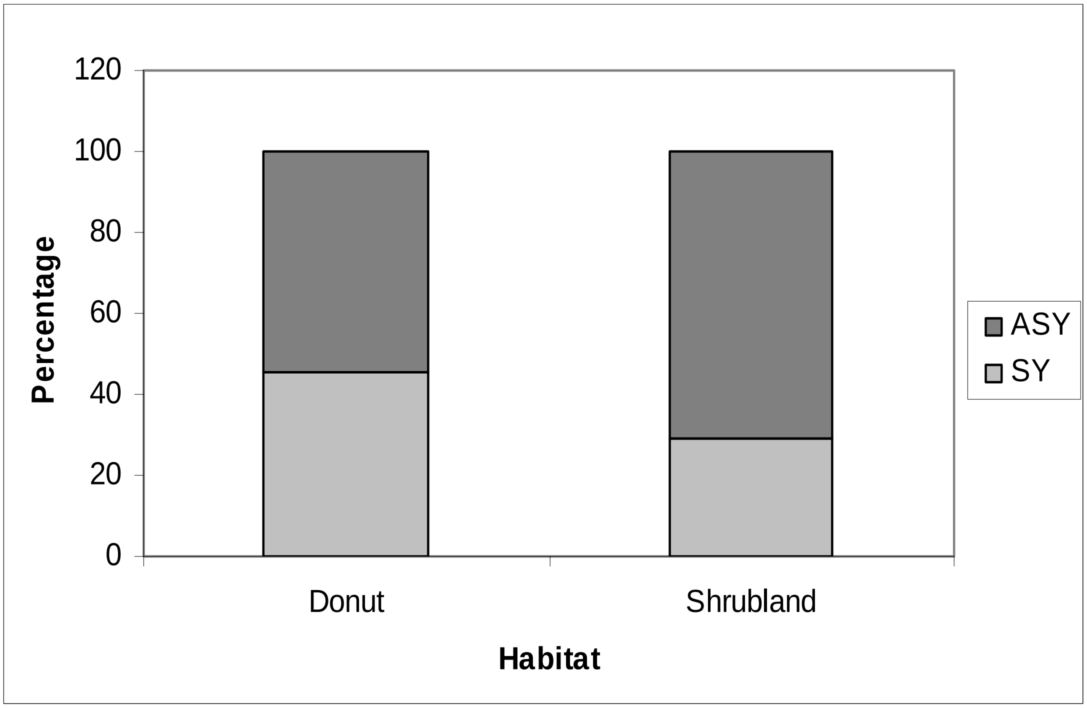
Figure 1. Donut habitat, Fort Hood, Texas.

Figure 2. Average number of vireos detected at each point count in shrubland and donut habitat, Fort Hood, Texas, 2003 and 2004 nesting seasons.



CI = 0.3661490- 0.5826697 in donut habitat
CI = 0.7644273- 0.9689073 in shrubland habitat

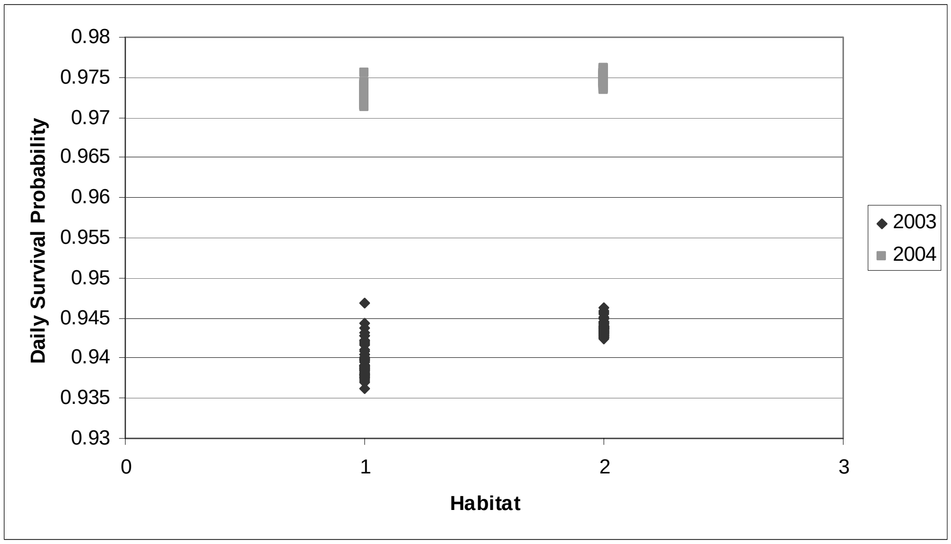
Figure 3. Percent of age class in donut and shrubland habitat at Fort Hood, Texas, 2003 and 2004 nesting seasons.



ASY = After-second-year male
SY = Second-year male

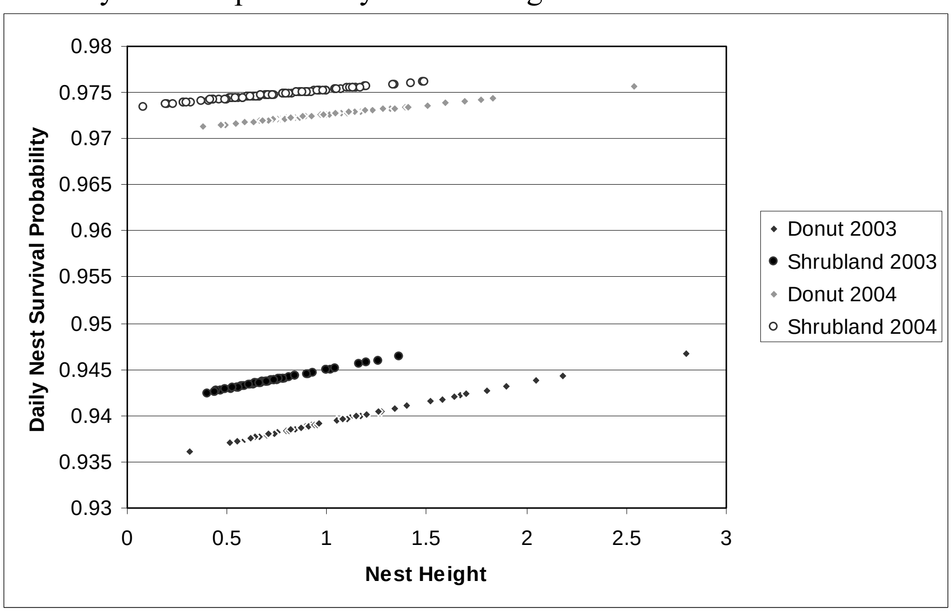
Figure 4. Nesting success plots for black-capped vireos at Fort Hood, Texas, 2003 and 2004 nesting seasons.

4a. Daily survival probability by habitat and year.

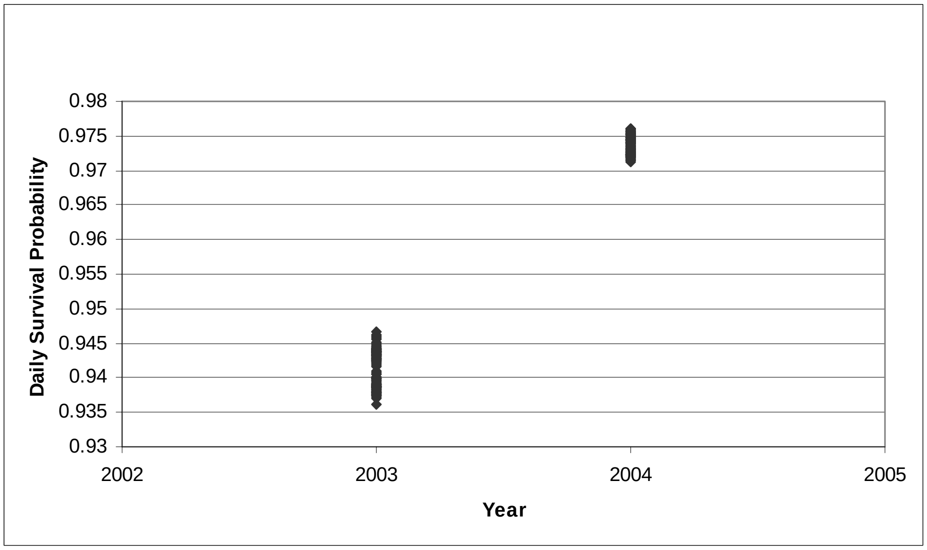


Habitat 1 = donut habitat
Habitat 2 = shrubland habitat

4b. Daily survival probability vs. nest height in donut and shrubland habitat.



4c. Year differences in daily survival probabilities in donut and shrubland habitat.



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Appendix 1

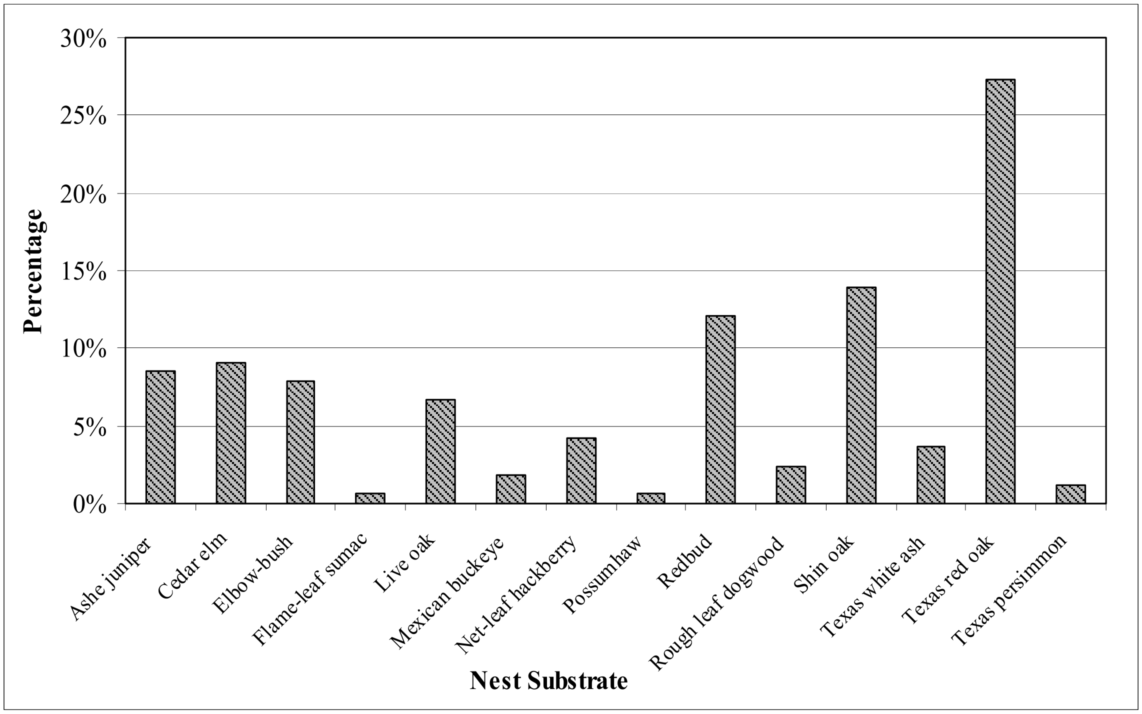
Woody Plant Species in Donut Habitat

Common Name	Scientific name
Ashe juniper	*Juniperus ashei*
Carolina buckthorn	*Frangula caroliniana*
Catclaw	*Mimosa aculeaticarpa*
Cedar elm	*Ulmus crassifolia*
Cow-itch	*Cissus incisa*
Elbow-bush	*Forestiera pubescens*
Eves necklace	*Sophora affinis*
Flame-leaf sumac	*Rhus lanceolata*
Grape spp.	*Vitis Spp.*
Live oak	*Quercus fusiformis*
Mexican buckeye	*Ungnadia speciosa*
Mulberry	*Morus spp.*
Net-leaf hackberry	*Celtis laevigata* var. *reticulata*
Poison ivy	*Toxicodendron radicans*
Post oak	*Quercus stellata*
Prickly-ash	*Ziziphus zizyphus*
Prickly-pear spp.	*Opuntia spp.*
Texas redbud	*Cercis canadensis* var. *texensis*
Saw greenbriar	*Smilax bona-nox*
Shin oak	*Quercus sinuata* var. *breviloba*
Skunkbush	*Rhus trilobata*
Texas white ash	*Fraxinus texensis*
Texas buckeye	*Aesculus arguta*
Texas red oak	*Quercus buckleyi*
Texas persimmon	*Diospyros texana*
Virginia creeper	*Parthenocissus quinquefolia*
Wildgoose plum	*Prunus munsoniana*
Yucca spp.	*Yucca spp.*

Data were collected in 2003 using 100 meter line transepts in donut habitat at each of the 42 randomly places point counts. The bearing for each line transept was chosen at random.

Appendix 2

Percentage of nests found in a given species of plant in donut habitat.



Donut habitat: 163 nests
Shrubland habitat: 177 nests

Appendix 3

Nesting success analysis results

Rank	Description	K	Log Likelihood	AICc	Δ_i	w_i
1	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Heig + $B_3{}^{*}$Year	4	-651.86	1319.74	0.00	0.692388
2	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$ Heig + $B_3{}^{*}$Year + B_4 (Hab*Heig)	5	-651.30	1322.62	2.88	0.1644044
3	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Heig + $B_3{}^{*}$Para+ $B_4{}^{*}$Year	5	-651.65	1323.32	3.58	0.1156219
4	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$ Heig + $B_3{}^{*}$Para+ $B_4{}^{*}$Year + B_5 (Hab*Heig)	6	-651.08	1326.19	6.45	0.0275838
5	$B_0 + B_1{}^{*}$Heig	2	-668.91	1345.82	26.07	1.507E-06
6	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Heig	3	-668.65	1349.31	29.56	2.636E-07
7	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Heig + B_3 (Hab*Heig)	4	-667.78	1351.58	31.83	8.475E-08
8	*B0* + *B1**Year	2	-697.77	1427.613	115.30	7.282E-26
9	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Year	3	-697.71	1407.44	87.69	6.282E-20
10	$B_0 + B_1{}^{*}$Para	2	-719.29	1446.58	126.83	1.991E-28
11	$B_0 + B_1{}^{*}$Hab	2	-719.39	1446.79	127.05	1.788E-28
12	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Para + B_3 (Hab*Para)	4	-716.52	1449.07	129.32	5.731E-29
13	$B_0 + B_1{}^{*}$Hab + $B_2{}^{*}$Para	3	-719.23	1450.48	130.74	2.828E-29