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Occasional Publication No. 7
Published by
Texas Ornithological Society
2007

**Dedicated to Warren Pulich
for his pioneering studies of Golden-cheeked Warblers**

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Occasional Publication No. 7
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RESPONSE OF GOLDEN-CHEEKED WARBLERS (*DENDROICA CHRYSOPARIA*) TO WILDFIRES AT FORT HOOD, TEXAS

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Abstract.—Wildfires at Fort Hood, Texas in 1996 destroyed 15% of Golden-cheeked Warbler (*Dendroica chrysoparia*) breeding habitat. In the burn area following the fire, 13 habitat units of varying size were inhabited by Golden-cheeked Warblers. Fire influenced number of territories, number of birds occupying habitat units through time, age structure, return rate, movement, and reproductive success of Golden-cheeked Warblers. Size of habitat units best predicted occupancy and reproductive success of Golden-cheeked Warblers inhabiting the burned area. Although the population experienced instability for a short time, the species was resilient in post-burn habitat, especially larger-size fragments with more intact interior forest. Two years post-burn, the Golden-cheeked Warbler population stabilized in the burned area, however, the abundance of Golden-cheeked Warblers 10 years following the fire remained substantially lower than abundance in unburned areas of Fort Hood. Fire exclusion as a management tool to protect large tracts of old growth Ashe juniper-oak woodlands may prove important in maintaining Golden-cheeked Warbler populations.

INTRODUCTION

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is a rare species with one of the most restricted breeding ranges in North America. It is a medium-sized wood-warbler about 12–13 cm in length with a mass of about 10 g. Adult males in breeding plumage have a black forehead, crown, nape, and back (Fig. 1). The remainder of the head (except chin and throat) is bright golden yellow, split by a black eye-stripe extending from the bill through the eye to the rear auricular region, where it joins with the black nape. The chin, throat, and breast are



Figure 1. A male Golden-cheeked Warbler showing distinctive features of the species.

black with continuing black streaking along the sides and flanks. Underparts are white. Wings are blackish, with two distinct white wing-bars. The tail is blackish, with white tail-spots. Adult females in breeding plumage are similar to breeding males, but generally duller overall, with upperparts olive green, with black streaks or spots (Fig. 2). The chin and upper throat are yellowish having the throat-feathers black, mixed with yellow. The median-coverts have white tips with a black shaft-streak (Dunn and Garrett 1997, Ladd and Gass 1999).

The Golden-cheeked Warbler is a trans-boundary species with breeding and wintering habitats separated by a substantial distance (Fig. 3). The species breeds only in the Ashe juniper-oak woodlands of central Texas and winters in pine-oak forests from the highlands of northern Chiapas, Mexico south to Nicaragua (Pulich 1976, Ladd 1985, Sexton 1987, Wahl et al. 1990, U. S. Fish and Wildlife Service 1992, Vidal et al. 1994, Ladd and Gass 1999, Rappole et al. 1999). Both breeding and wintering habitats have decreased at alarming rates. The synergistic effect of over a century of urbanization and land-clearing for agriculture, especially along the Balcones Escarpment between Austin and San Antonio, has reduced an estimated population of 15,000 to 17,000 individuals in 1975 (Pulich 1975) to an estimated breeding population of 4,800–16,000 pairs in a 30-county area (Fig. 4) encompassing about 20,000 km² of the Edwards Plateau, Lampasas Cut Plains and Central Mineral Region of Texas (Ladd and Gass 1999). It was listed as a federally endangered species in May 1990 in an emergency ruling because of population decline, reduction of distribution, and ongoing and imminent loss of nesting habitat in the core breeding area. Although conservation actions have presumably ameliorated some of this decline, the species continues to be listed by the state of Texas, federal government and the IUCN Red List as endangered.

Golden-cheeked Warblers are the only endemic breeding bird inhabiting mature Ashe juniper-oak woodlands associated with limestone hills and canyons (Pulich 1976, Ladd 1985, Sexton 1987, Wahl et al. 1990, U. S. Fish and Wildlife Service 1992, Ladd and Gass 1999). The species is obligate to the stripping bark of mature Ashe juniper (*Juniperus ashei*) used in nest construction. The Golden-cheeked Warbler is equally dependent on Ashe juniper for foraging substrate along with several broad-leaved hardwood trees and shrubs (Pulich 1976, Beardmore 1994). Optimal breeding habitat consists of intact forests ≥ 100 ha (Wahl et al. 1990, U. S. Fish and Wildlife Service 1996). A tendency to characterize Golden-cheeked Warblers as limited to hardwood-dominated canyon slopes probably results from an artifact of greater detection of singing males in such environs (Bolsinger and Hayden 1992). However, most pristine forests no longer exist on large expanses of less undulating terrain because of removal of trees related to extensive agricultural use; thus, accentuating Golden-cheeked Warbler habitat in canyons (Diamond 1997). Golden-cheeked Warblers also colonizes regrowth Ashe juniper stands on moderately hilly terrain (Ladd and Gass 1999). Proximate factors important in habitat selection include percent composition of hardwood and Ashe juniper trees, woody species diversity, abundance of mature Ashe juniper trees, presence or absence of deciduous oaks, heterogeneity and size of fragments, canopy continuity, landscape slope, foraging habitat, and access to water (Pulich 1975, Kroll 1980, Ladd 1985, Wahl et al. 1990, Beardmore 1994, Ladd and Gass 1999, Dearborn and Sanchez 2001, DeBoer and Diamond 2006, Baccus et al. 2007).

The importance of some of these parameters in habitat selection by Golden-cheeked Warblers has been questioned. Fragment size and extent of landscape fragmentation have been recognized as major limiting factors of habitat (Wahl et al. 1990). However, Benson (1990) did not find a clear relationship between presence of Golden-cheeked Warblers and fragment size and extent of fragmentation. Territorial boundaries at the Kerr Wildlife Management Area and Meridian State Park include grassland/woodland ecotones, trails, and roadways (Kroll 1980, Ladd 1985). Golden-cheeked Warblers have been described as a relic denizen of woodland margins (Morse 1989), and characterization as an edge species using the interface between grasslands and mature juniper-oak woodlands (Kroll 1980, Magness et al. 2006) conflicts with assertions that the species selects for and has greater productivity in large blocks of unfragmented habitat (Wahl et al. 1990, Pease and Gingerich 1989). No quantitative evidence suggests Golden-cheeked Warblers inhabiting woodland edges are more reproductively successful than those in woodland interiors. Conversely, other warbler species exhibit greater reproductive success in unfragmented woodland interiors (Faarborg and Arendt 1992, James et al. 1992, Sauer and Droege 1992). Pulich (1975) documented Golden-cheeked Warbler vulnerability to Brown-headed Cowbird (*Molothrus ater*) parasitism along habitat edges. Engles and Sexton (1994) found Golden-cheeked Warbler avoidance of edge complexes in suburban areas inhabited by Blue Jays (*Cyanocitta cristata*). Research at areas for intensive study of Golden-cheeked Warbler ecology and biology on Fort Hood Military Reservation (hereafter, Fort Hood) suggests Golden-cheeked Warbler productivity is greater in expansive, unfragmented forests (Bolsinger and Hayden 1992).

Wildfires destroyed a substantial amount of Golden-cheeked Warbler habitat on Fort Hood in 1996. The aftermath of wildfires on Fort Hood offered the first opportunity to study demographic and habitat use by Golden-cheeked Warblers in a fire-altered habitat, and whether this fire (or fire in general) had immediate and/or long-term effects on suitability of habitat as measured by abundance and density of singing males. The existing management paradigm for species of concern depends on knowledge of habitat requirements and application of habitat protection for conservation (Martin 1992, Derrickson et al. 1998). Presence or absence of a species after a fire provides an understanding of basic habitat characteristics, but documentation of relative productivity focuses on how species cope with altered habitat types that maximize survival and reproduction (DeSante and Rosenberg 1998). Disturbances (natural or anthropogenic) that destroy habitat and interfere with survival and reproduction can jeopardize species survival. Resilience of species after buffeting by disturbance is critical to its survival. In this paper, we present the first information on responses of Golden-cheeked Warblers to habitat disturbance by wildfire on contiguous forested areas at Fort Hood, Texas. We address effects of fragment size on densities of male Golden-cheeked Warblers and demographic and reproductive responses to community perturbation in the following topics: (1) the role of fragment size on abundance of territorial males and whether small fragments induced by fire cause differences in male abundance compared to regional estimates, (2) whether fragment-specific ecological factors other than size influence abundance and density of territorial males, (3) if movement distances and return rates of males displaced from burned areas differ through time, (4) whether a fire-altered environment influences productivity and subsequent recruitment, (5) if fire disturbance causes instability and change in the population structure, (6) whether Golden-cheeked Warblers show resilience to disturbance, and (7) whether the fire caused a short-term depression of Golden-cheeked Warbler abundance in the fire area. Parameters used for monitoring Golden-cheeked Warblers in fragments included occupancy, type of habitat, size of habitat unit, density of males, age structure, mating status of males, age class, productivity, and floral characteristics of individual fragments.

STUDY AREA

Fort Hood, located at the eastern edge of the Edwards Plateau Ecological Region and the Lampasas Cutplains Physiographic Region, comprises 87,890 ha in Bell and Coryell counties in central Texas (Raisz 1952, U. S. Department of the Army 1989, The Nature Conservancy 1997, Fig. 4). Fort Hood is divided into over 90 training areas of variable size used primarily for military training. A full range of military activities are conducted at Fort Hood, including large-scale troop and ground vehicle maneuvers, live-fire weapons training, and aviation training, by over 40,000 active military personnel (Anders and Dearborn 2004). It is also managed for multiple uses including cattle grazing, hunting, fishing, and recreation. Fort Hood contains approximately 21,496 ha of Golden-cheeked Warbler breeding habitat (Fig. 5) supporting the largest population under one management authority (Hayden et al. 2001). Elevation ranges from 180 m to 375 m above mean sea level. Topography exhibits a stair-step profile with limestone benches 40 to 80 m wide on steep-sloped hills and ridgelines underlain by limestone bedrock (Nakata 1987). Local climate is characterized by long, hot summers with short, mild winters. Mean temperatures range from 8° C in January to 29° C in July. Mean annual precipitation is 81 cm (Nakata 1987).

Although classified as Cross Timbers and Prairies (Gould 1975), the woody vegetation of Fort Hood has an affinity and derivation predominately from the Edwards Plateau flora. The installation includes relatively flat grasslands as well as heavily forested mesas and slopes. Plant associations include perennial grasslands, open savannah, dense hardwood thickets, and oak-juniper woodlands (Tazik et al. 1993, Jetté et al. 1998). Dominant species of Ashe juniper-oak woodlands include Ashe juniper, plateau live oak (*Quercus fusiformis*) and Texas red oak (*Q. buckleyi*) with broadleaf oak woodlands and coniferous, mixed woodlands comprising about 39% and 61% of woodland sites, respectively (Nakata 1987, Tazik et al. 1992, Tazik et al. 1993). The hardwood component of the plant community also includes: shin oak (*Q. sinuata*), chinkapin oak (*Q. muehlenbergii*), Texas white ash (*Fraxinus texensis*), Carolina buckthorn (*Frangula caroliniana*), skunkbush sumac (*Rhus aromatica*), evergreen sumac (*R. virens*), deciduous holly (*Ilex decidua*), redbud (*Cercis canadensis*), Texas persimmon (*Diospyros texana*), Mexican buckeye (*Ungnadia speciosa*), cedar elm (*Ulmus crassifolia*), rough-leaf dogwood (*Cornus drummondii*), netleaf hackberry (*Celtis reticulata*), sugarberry (*C. laevigata*), pecan (*Carya illinoensis*), elbow-bush (*Forestiera pubescens*), woolybucket bumelia (*Bumelia lanuginosa*), and rusty black-haw (*Viburnum rufidulum*).



Figure 2. A female Golden-cheeked Warbler feeding nestlings. Distinctive characteristics of the female are shown.



Figure 3. Principle breeding range of the Golden-cheeked Warbler in North America and winter range in Mexico and Central America.

FIRE CHARACTERIZATION

Military training activities instigated three separate fires on 21 February 1996 in the Live Fire Area of Fort Hood, Texas (Fire Protection Division 1996). These fires, designated as hot because of low humidity and gusting winds, spread rapidly through grasslands and burned into wooded areas. Despite concerted efforts to extinguish them, the intensity of the fires ignited crown fires in mature Ashe juniper and hardwood trees. Crown fires generally ignite under specific climate and physical conditions (high temperatures, low humidity, extremely dry, fine and coarse fuels, strong winds, and ground litter and debris accumulation) that exacerbate the movement of fire through tree canopies (Rothermel 1991). Crown fires in mature Ashe juniper trees are uncommon and usually

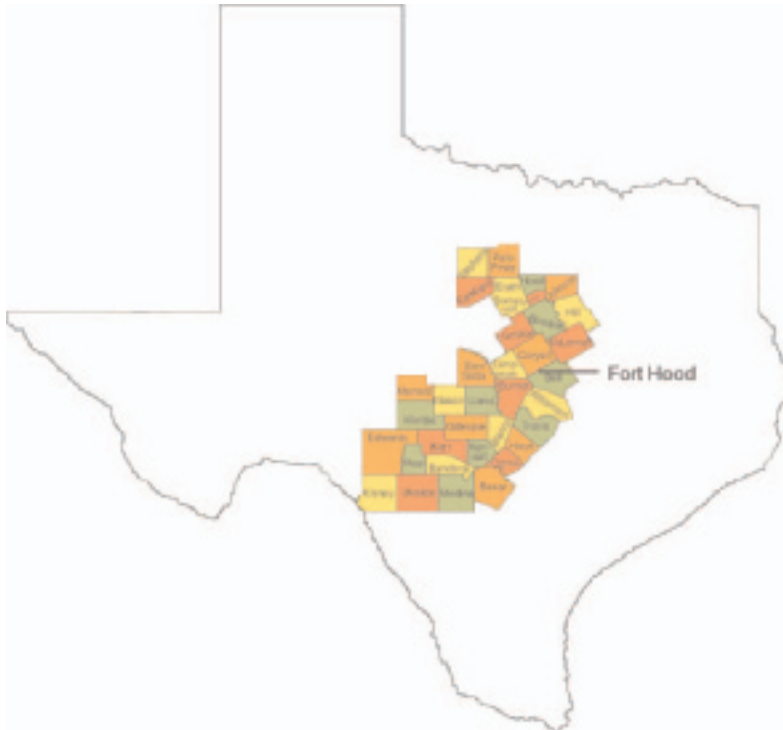


Figure 4. Breeding range of the Golden-cheeked Warbler in a 30-county area of central Texas. The location of the study site at Fort Hood Military Reservation is shown in Bell and Coryell counties.



Figure 5. A view of typical Golden-cheeked Warbler habitat on Fort Hood.

cause severe destruction to a landscape (Fig. 6, Strauss et al. 1989). Fire damage assessment indicated a Composite Burn Index 3, the most severe burn rating designation (U. S. Geological Service 2003). Characteristics of Level 3 intensity fires include complete destruction of litter and duff layers and most above-ground plant parts with only charred major trunks remaining with deposition of a layer of fine white ash (Fig. 6). This type of fire typically results in a heterogeneous landscape with large areas of destruction, isolated unburned fragments, small burned areas within forests from spot fires, and forests with distinct burn lines at points of containment.

The wildfire damaged or totally destroyed 2,108 ha (41.5%) of an estimated 5,075 ha of forest in the north-east quadrant (Fig. 7) of Fort Hood, causing loss of 15% of Golden-cheeked Warbler breeding habitat (Goering 1998). This substantially exceeded the 44 ha of annual incidental take of habitat allowed on Fort Hood (U.S. Fish and Wildlife Service 1993). As a result of the fire, a Fire Study Area (hereafter, FSA) was established in Training Areas (hereafter, TA) 2 and 4A (Fig. 7) to investigate consequences of fire disturbance on habitat selection, use, abundance, and productivity by Golden-cheeked Warblers. Prior to the wildfire, 314 ha of breeding habitat occurred in TA 2 and 755 ha in TA 4. Fire destroyed 150 ha in TA 2 and 154 ha in TA 4A or 28% of habitat in the FSA (Sanchez and Cook 1998).



Figure 6. Landscape view of fire damage to Golden-cheeked Warbler habitat in the Fire Study Area at Fort Hood

METHODS

Fire damage to the plant community was assessed using field surveys and aerial photographs. Thirteen habitat units were identified as a result of the wildfire (Fig. 8) within the FSA. Rectified aerial photographs imported into ArcView 3.02 (ESRI, Inc., Redlands, California) were used to precisely determine locations and shapes of each habitat unit. We measured the size of each habitat unit by digitizing a convex polygon around it. Habitat units were classified as either semifragments or fragments. Semifragments were designated by letters A to C and fragments were assigned letters D to M. Burned woodlands encompassed semifragments on three sides (Fig. 8). Eastern boundaries of semifragments abutted a firebreak adjoining unburned forests with extensive Golden-cheeked Warbler breeding habitat. Fragments existed as isolated forest stands surrounded by burned terrain.

A search area (hereafter, SA) was established in adjacent training areas to track dispersal movements and population trends for Golden-cheeked Warblers outside the FSA. The SA included TAs 1, 3, 4A (southern part of TA 4 beyond the FSA), 5, 13A, 75, and 76 (Fig. 7). Data from point count routes established prior to the fire in the FSA and SA provided information on short-term changes in the Golden-cheeked Warbler population.

Demography

From 1991 through 1995 some Golden-cheeked Warblers were captured and leg-banded in the eventual FSA. Golden-cheeked Warblers were attracted to and captured in 6 m, 24 mm mesh mist nets, using playback recordings of songs recorded for males inhabiting Fort Hood, and banded in April and May 1996–1998 to document movements from the FSA to the SA and vice-versa. An observer sat near the mist net and captured individuals (usually one) were removed from nets within 1 min of capture. No more than three attempts were made to capture individual males during a week to minimize disturbance to their breeding behavior. Each individual was identified by a unique combination of one, size 0A aluminum, numbered leg band (U. S. Geological Service, Biological Resources Division) and one to three colored XF celluloid plastic bands (about 0.023 g each) (Avinet, Dryden, New York) (Fig. 9). We attempted to band all adult males with established territories in the FSA. Females were opportunistically banded. We banded 6-day-old, hatching-year (HY) nestlings in May and June. We recorded age, sex, plumage characteristics for each individual captured (White and Garrot 1990) and a Universal Transverse Mercator (UTM) grid location for the capture site. Data on Golden-cheeked Warblers banded during the study were deposited at the Bird Banding Laboratory.

Band data (excluding HYs) from 1991 to 1998 were used to determine age structure, movements, and population trends in the FSA. Assigned ages were based on plumage characteristics of known-age individuals banded as HYs with multiple captures and classified as second-year (SY) or ASY based on plumage characteristics (Pyle 1997). Second-year males were distinguished by olive mixed into the black of the crown and back and yellowish or white tips on the black throat feathers. Second-year females were recognized by a whitish chin, less extensive black on the throat, fainter black streaking on the sides and flank, and upperparts mainly olive green (Dunn and Garrett 1997, Pyle 1997). We derived the percentage of returning second-year (SY) birds by dividing the number of SY birds by the number of all known-age individuals (Craft 1998). Return rates were based on the percentage of males banded the previous year in the FSA compared to those observed the next year. All banded individuals that returned allowed us to compose a data set for calculating movement distances. Maximum movement distances were calculated by digitizing in a straight line from the first banding site in 1995, 1996, 1997, or 1998 to the most distant recapture or sighting location in the following year. Golden-cheeked Warblers banded or observed in 1996 and 1997 in the FSA and observed in 1998 in the SA were included in the return rate for the FSA. A compilation of all band returns from the SA and elsewhere on Fort Hood allowed a comparison of annual movement distances in the FSA to distances moved on non-burn areas of Fort Hood.

Productivity

Mating status for males in the FSA was based on observations of interactions with females or feeding of young. Male-female interactions included mutual foraging, male following female, female following male, copulation, male guarding female, and feeding at a nest. Reproductive success was calculated based on the percentage of successful pairs compared to all mated pairs. Pairs were designated as successful if they were observed feeding at least 1 HY individual. We estimated an annual productivity rate by dividing the total number of young fledged by the total number of territories determined (Craft 1998). Productivity data collected resulted from observations of territorial males feeding or defending fledglings. The criteria used to incorporate female observations into produc-

tivity data included banded females paired with a known territorial male feeding young; otherwise, we did not include observations of females feeding or defending fledglings in data analyses because breeding females exhibit secretive behavior and the high proportion of unbanded females made it difficult to identify unique individuals or place them with a banded male. We estimated annual productivity for the FSA by summing the number of HY individuals fed or defended by territorial males divided by the total number of territorial males observed in each habitat unit. Only observations of HY birds fed by territorial males were counted; thus, total number of estimated HY individuals in the FSA was likely conservative. Productivity was not monitored in the SA.

Occupancy

A modified consecutive flush method (Bibby et al. 1993) was used to locate and identify males in habitat units. Males were not intentionally flushed or chased but followed and passively observed in flights between no more than five perch points per day to minimize potential effects on individual behavior resulting from our presence. We monitored each fragment at least 30 min weekly and semifragments at least 1 h twice per week; however, monitoring of habitat units lasted several hours on some days. Overall, we attempted to balance observational time for fragments and semifragments as groups; however, monitoring times varied because of presence or absence of Golden-cheeked Warblers and habitat unit size. Monitoring consisted of walking through units and listening for vocalizations or identifying visual cues. Golden-cheeked Warblers were located primarily by audio cues. Audio cues consisted of singing, chipping, bill-snapping, and begging by nestlings or fledglings. After locating a warbler, we determined whether it was banded and attempted to identify banded individuals by their color band combination. Individuals often moved before an exact identification could be made; thus, they were followed to a maximum of five perches on any day in trying to establish identity. UTM coordinates (WGS-84 datum) were recorded for all locations of an individual using global positioning system (GPS) units (Trimble Geo-Explorer, Trimble Navigation Limited, Sunnyvale, California) with real-time correction in 1996 and 1997 and Garmin GPS II Plus units (Garmin International, Olathe, Kansas) in 1998 (± 15 m) and plotted on a 1:4,000 scale orthophoto map. Temporal, site location, behavioral, and banding status data for each individual were noted using standardized codes.

Initially, presence and identity of each adult male were documented by its color band combination in each habitat unit. Thereafter, priority shifted to verification of territory location or relocation. Each habitat unit was monitored at least once per week. Territories were mapped for males with visual confirmation on five different dates and >10 locations. All territorial males were monitored as close to equal amounts of time given the autecology of the species. We calculated an estimated density per ha of territorial males for each habitat unit in 1996, 1997, and 1998 and territory size in 1997 using >10 different point records for the same male in an area. Estimates of territory size were derived by digitizing on-screen polygons around GPS points using the ArcView GIS Program Home Range.

In 1992, protocol was instituted for conducting point counts on Fort Hood after establishing 123 permanent survey points and conducting preliminary surveys in 1991 (Hayden and Tazik 1991). Additional survey points were added after 1991 for increasing the power of detecting changes in population size (Niven 1994, Anders 2000). The numbers of points surveyed each year were: 1992, 206 points along 19 routes; 1993 and 1994, 228 points along 21 routes; 1995, 217 points along 21 routes; 1996, 342 points along 27 routes; 1997, 365 points along 27 routes; and 1998–2005, 428 points along 31 routes. Each point count route consists of 10–18 points spaced 300 m apart along trails. Point count routes on tertiary roads and trails were used to analyze population trends for the FSA and SA (Hayden and Tazik 1991, Bolsinger and Hayden 1992, 1994, Weinberg et al. 1995, 1996, Craft 1998, Holimon and Craft 2000). Points were located by GPS and delineated on orthophoto maps. Surveys on each route followed standard protocol (Ralph et al. 1993, Niven 1994). Counts on all routes began 20 min following sunrise and ended ≤ 4 h post-start. Monitoring for Golden-cheeked Warbler activity at each point lasted 6 min. Date, weather conditions, start time, species identified (aural or visual), sex (aural or visual), time of detection, cardinal direction from point, and estimated distance between bird and observer were recorded at each point. Counts were not conducted during periods of rain or wind strong enough to interfere with detection of birds (Ralph et al. 1995). Observers were trained in field identification techniques prior to fieldwork, including learning songs and calls of Golden-cheeked Warblers and other common birds of Fort Hood. Each observer had their identification skills validated using Thayer's Birds of North America birding software (Version 2.0 CD-ROM, Thayer Birding Software, Cincinnati, Ohio) before conducting point counts.



Figure 7. Fire Study Area and Search Area for Golden-cheeked Warblers on Fort Hood, Texas.

Annual population trends of Golden-cheeked Warblers in the FSA and SA were developed using 1995 abundance data from point count routes 2 (10 points: beginning coordinates 631099 E 3456072 N, ending coordinates 631351 E 3456015 N) and 3 (11 points: beginning coordinates 630751 E 3453691 N, ending coordinates 631566 E 3453823 N) in TAs 2 and 4A (FSA) and routes 11 (11 points: beginning coordinates 635389 E 3456060 N, ending coordinates 635331 E 3455325 N) in TA 3A, 14 (14 points: beginning coordinates 637393 E 3455626 N, ending coordinates 640311 E 3455162 N) in TAs 3A and 3B, and 20 (14 points: beginning coordinates 635964 E 3453811 N, ending coordinates 637213 E 3452325 N) in TA 5B (SA) as a baseline. From 1996 to 2005, we used additional point count routes, 23 (13 points: beginning coordinates 630679 E 3460736 N, ending coordinates 630020 E 3460550 N) in TAs 1A and C, 25 (15 points: beginning coordinates 632561 E 3453751 N, ending coordinates 634522 E 3451737 N) in TAs 4A (south) and 4B, and 26 (15 points: beginning coordinates 631714 E 3460403 N, ending coordinates 633567 E 3458528 N) in TA 1B to monitor population trends in the SA.

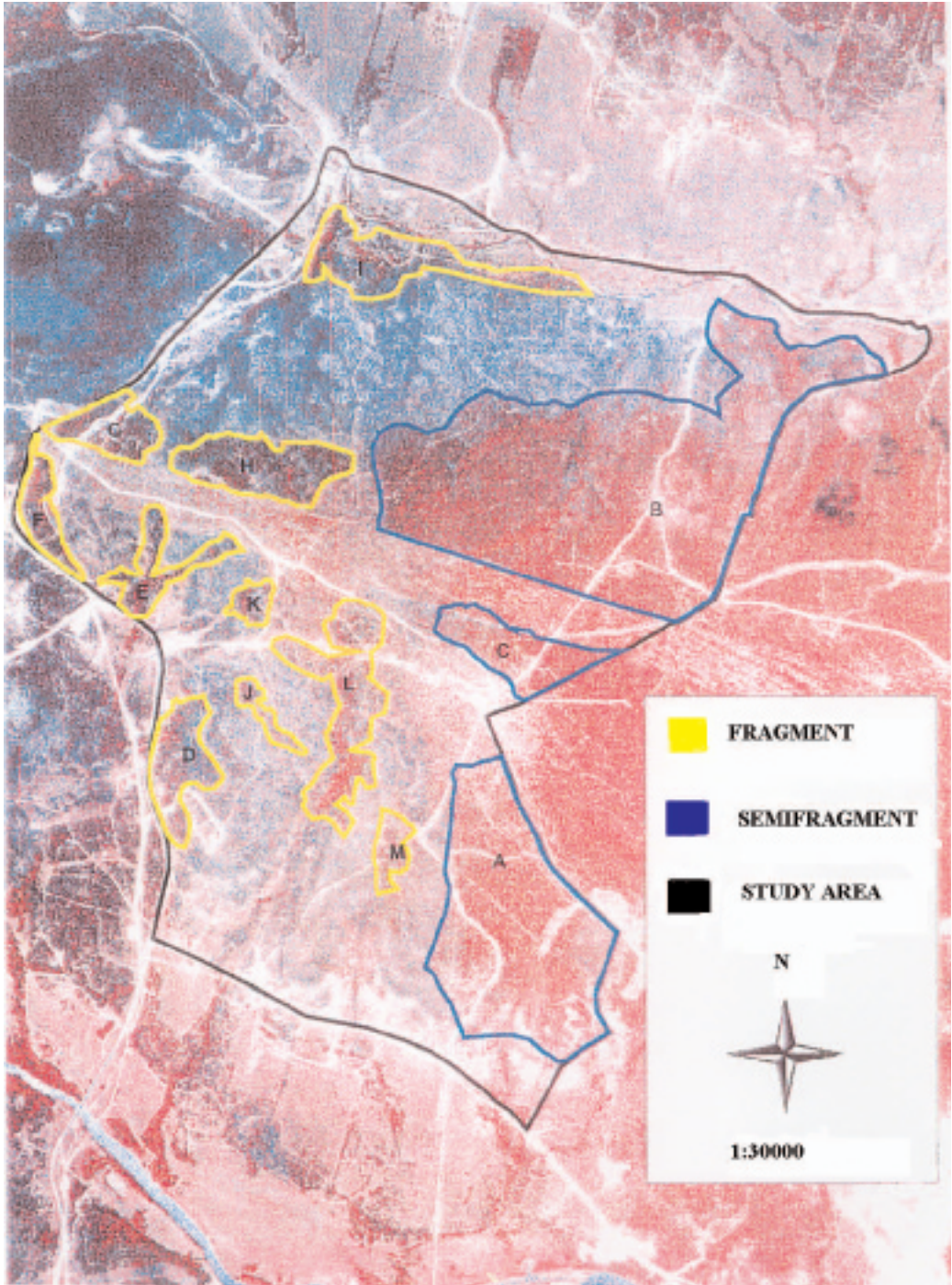


Figure 8. Semifragment (A-C) and fragment (D-M) habitat units resulting from a wildfire on Fort Hood, Texas in 1996.

Vegetative Analysis

Floral composition in habitat units were assessed in 1998 using one or more randomly placed 0.04 ha circular plots (James and Shugart 1970). Size of each habitat unit determined the number of sampling plots (average one plot per 6 ha). Starting at the center point of a plot, four transect lines, 11.3 m in length, extended in four cardinal directions. Range poles were placed at 2-m intervals along each transect (20 points per plot). At each point, presence or absence of woody vegetation was recorded. If woody vegetation contacted one face of the range pole presence was determined. The topmost plant counted when branches of two species occurred within the same interval. We then measured foliage cover, canopy closure, height of vegetation every 0.1 m up to 3 m, and thereafter, every 0.5 m up to 7.5 m, number of Ashe juniper and hardwood trees, and foliage cover of all trees. A growth form category was then assigned and number of individuals by category for plot tallied. Canopy cover was estimated by averaging densiometer (Model C, Forestry Suppliers, Jackson, Mississippi) readings taken in each cardinal direction at the center of each transect.

Landscape data on the composition of the plant community in 13 habitat units was calculated using the point-quarter method (Cox 1990) on 65 transects. Larger habitat units had multiple transects. Transects extended from the center point of plots. Frequency, importance value, percent canopy cover, percent composition of Ashe juniper in understory and canopy vegetation, percent composition of hardwoods in understory and canopy vegetation, percent composition of species other than Ashe juniper in understory and canopy vegetation, and dbh values for all trees were recorded (Cox 1990). Percent slope of each transect line was measured with a clinometer (Model PM5/360PC, Suunto USA, Carlsbad, California).

Statistical Analysis

Effect of habitat size on the response variable abundance of territorial males in habitat units was assessed using linear regression analysis. A positive slope and its steepness were indicative of the degree of fire mediated damage directly to the landscape (as indicated by habitat unit size) and any negative influence to Golden-cheeked Warbler abundance. A negative slope was indicative of the opposite effect, and or no (or negligible slope) was indicative of no effect. When a slope was noted, Chi-square analysis was used to determine whether small fragment size (induced by fire) produced patterns of male abundance that differed from regional estimates of Golden-cheeked Warbler abundance. Density of Golden-cheeked Warblers in semifragments and fragments in comparison to density and abundance of males at unburned sites at Fort Hood was analyzed using a test for proportionality.

A multiple regression analysis using habitat type (semifragment or fragment), percent understory hardwoods, percent canopy hardwoods, and percent canopy cover tested the function each of these ecological variables contributed to abundance and density of territorial males. Prior to analysis, we arcsine square root transformed values for percent understory hardwoods, percent canopy hardwoods, and percent canopy cover because the assumption of normality was violated. In addition, a graphical and correlation approach of the transformed data verified regression assumptions of no heteroscedasticity and no correlation among independent variables, respectively.

Comparisons of abundance of Golden-cheeked Warblers on point count routes from 1996 to 2005 in the FSA and SA were analyzed using a single factor Kruskal-Wallis nonparametric analysis of variance. Since specific point count routes were chosen for the analysis, a fixed effects model was used in the analysis. Means of point count routes were tested for differences by Tukey's (HSD) method and normality was assessed by the Shapiro-Wilk statistic.

Data were collected on territory size in 1997 based on the intuitive *a priori* assumption that the fire caused a high population flux in 1996. Additionally, this allowed us to maximize our resources in 1998 to assessing the distribution of males in habitat units, data we deemed higher priority.

We used a proportions test to ascertain differences in the ratio of SY and ASY males in the population of the FSA. Our interests centered on demographic trends of younger and older-age males in the assemblage. Because there was no significant difference between percent canopy cover of fragments and semifragments, data were pooled and summary statistics calculated.

RESULTS

Occupancy

Shortly after the wildfire, damage to Golden-cheeked Warbler habitat was assessed and 13 unburned habitat units in the FSA were identified, consisting of three semifragments (A, B, and C) and 10 fragments (D-M).

Surveys in the FSA verified the presence or absence of Golden-cheeked Warblers in habitat units. Monitoring abundance of Golden-cheeked Warblers in habitat units required a total of 1,234 h from 2 April through 1 August 1996. Monitoring time in three semifragments (268.5 ha combined) necessitated 468 h and 10 fragments (121.5 ha combined) 766 h.

In 1996, we made 213 observations of both sexes and ages ranging from L (local or nestling) to 6 year-old (6Y) birds in the FSA and 49 observations in the SA. Fifty-four territories were also verified in the FSA with 30 males in three semifragments and one or more males in nine fragments (Table 1). Males briefly occupied fragment J but later established territories elsewhere. Twelve habitat units had a mean density of 28.1 males per 100 ha (SE = 11.6, range 6.9–151.5, Table 1). Nine fragments had higher densities ($F_{8,2} = 46.77$, $P = 0.0211$) of males per 100 ha ($\bar{x} = 33.2$, SE = 15.314, range 9.1–151.5) than the three semifragments ($\bar{x} = 13.0$, SE = 3.8786, range 6.9–20.2) because of higher densities of males in fragments D, K, and M.

In 1997, Golden-cheeked Warblers of both sexes and ages ranging from L to 7 year-old (7Y) birds were verified at 662 locations in the FSA and 88 locations in the SA. Monitoring abundance in the FSA required 851 h from 11 March through 15 July. Total survey time was 505 h in three semifragments and 346 h in 10 fragments. Fifty male territories were verified in the FSA. Forty males occupied semifragments with 10 males in five fragments (Table 1). Of five fragments without territorial males, four had a single observation of a male or observations at one location but no establishment of a territory. Eight habitat units had a mean density of 14.6 males per 100 ha (SE = 2.55, range 7.6–30, Table 1). The mean density of males per 100 ha in three semifragments was higher ($\bar{x} = 18.8$, SE = 5.6956, range 11.4–30) than in five fragments ($\bar{x} = 12.06$, SE = 2.0607, range 7.6–19) ($F_{8,2} = 4.58$, $P = 0.0923$). Comparison of mean density of males in 1996 to 1997 for all habitat units and fragments showed an almost 2-fold higher density in habitat units and an almost 3-fold higher density in fragments for 1996.

In 1997, 15 males met the criteria for territory size calculation. Eleven males inhabited semifragments, two fragments had one territorial male each, and one fragment (D) supported two males. Mean territory size for all males was 2.79 ha (SE = 0.2787, range 1.28–5.03). Males in semifragments had similar size territories as males in fragments ($t = 0.326$, $P > 0.05$). Males in semifragments had a mean territory size of 2.73 ha (SE = 0.351, range 1.28 to 5.03); whereas, males in fragments had a larger mean territory size of 3.01 ha (SE = 0.426, range 2.07 to 4.11).

Golden-cheeked Warblers of both sexes and ages ranging from L (local or nestling) to 8Y were verified at 893 sites in the FSA and 262 in the SA. Monitoring abundance of Golden-cheeked Warblers in the FSA

Table 1. Density of Golden-cheeked Warblers in habitat units in the Fire Study Area on Fort Hood, Texas based on number of male territories by year. Density values were calculated as a ratio of the size of a habitat unit to 100 ha.

Habitat Unit	Size (ha)	1996	Density	1997	Density	1998	Density
Semifragment							
A	79.0	16	20.2	9	11.4	11	13.9
B	172.8	12	6.9	26	15.0	33	19.1
C	16.7	2	11.9	5	30.0	5	30.0
Fragment							
D	14.0	5	35.7	2	14.3	3	21.4
E	10.2	1	9.8	0	0	0	0
F	7.7	1	12.9	0	0	1	13.0
G	10.5	1	9.5	2	19.0	2	19.0
H	19.4	2	10.3	2	10.3	3	15.5
I	22.0	2	9.1	2	9.1	1	4.5
J	3.3	0	0	0	0	0	0
K	3.3	5	151.5	0	0	0	0
L	26.2	5	19.1	2	7.6	2	7.6
M	4.9	2	40.8	0	0	0	0

required 1534 h from 19 March through 14 July in 1998, with 991 h in three semifragments and 543 h in 10 fragments. Sixty-one territories were confirmed in the FSA, an increase of 11 (22.0%) compared to 1997. Forty-nine males occupied semifragments, while one to three males inhabited six fragments (Table 1). Four fragments had a single observation of a male within the fragment but no establishment of a territory. There were twice as many territories in semifragments ($\bar{x} = 39.667$, $SE = 5.4874$, $n = 3$) compared to fragments ($\bar{x} = 15.333$, $SE = 4.3716$, $n = 3$) for the three years following the fire ($t_4 = -3.47$, $P = 0.0256$).

Nine habitat units had a mean density of 16.0 males per 100 ha ($SE = 2.53$, minimum = 4.5, maximum = 30, Table 1). Although three semifragments had a higher mean density ($\bar{x} = 21.0$, $SE = 4.7438$, minimum = 13.9, maximum = 30) of males per 100 ha than six fragments ($\bar{x} = 13.5$, $SE = 2.6628$, minimum = 4.5, maximum = 21.4), the differences in density were not significant ($F_{2,5} = 1.59$, $P = 0.2927$). Although the mean density of males in fragments exceeded that of semifragments in 1996, a comparison of the three years showed no difference ($F_{3,23,28} = 0.70$, $P = 0.6308$).

We used size of semifragments and fragments, number of territorial males in habitat units, and density of males in habitat units to address whether habitat size influenced abundance of territorial males, and if so, the stability of this relationship among years. For each year, habitat size functioned as a significant determinant of male abundance; number of males increased linearly with increasing habitat size (1996: $F_1 = 16.9$, $P = 0.0017$, $r^2 = 0.605$; 1997: $F_1 = 326.4$, $P = 0.0001$, $r^2 = 0.967$; 1998: $F_1 = 331.9$, $P = 0.0001$, $r^2 = 0.964$; Fig. 10). During 1997 and 1998, size of habitat unit explained the majority of variation (97% and 96%, respectively) in male abundance; however, 40% of the variation remained unexplained in 1996 ($r^2 = 0.605$) indicating intrinsic or extrinsic attributes of habitat units beyond size influenced male abundance (Fig. 10).

Another consideration was to determine whether habitat units of small size (induced by fire) produced patterns of male abundance different from regional abundance estimates. We tested whether density of territorial males in the largest habitat unit (172.8 ha), and presumably the least fire-altered, could predict abundance of territorial males in variable sized, fire-altered habitat units. In 1996, abundance in each habitat unit deviated significantly from the expected number of males ($X^2 = 151$, $df = 11$, $P < 0.05$). The pattern of deviation suggested small and intermediate sized habitat units (primarily fragments) were occupied by more males than predicted by density of males in the largest habitat unit (Fig. 10, Table 1, Table 2a). The greatest influence in the test statistic originated in the 79 ha unit (semifragment A). In 1996, this habitat unit had 11 more males than predicted by the model. Similarly, the smallest habitat unit deviated positively but with a lesser magnitude of deviation than the 79 ha habitat unit. In 1997 and 1998, the observed and expected male abundance in habitat units did not differ from one another (1997: $X^2 = 9.47$, $df = 11$, $P > 0.05$; 1998: $X^2 = 10.8$, $df = 11$, $P > 0.05$) indicating that density in the largest habitat unit became indicative of the number of males a habitat unit could sustain across a wide range of available habitat unit sizes.



Figure 9. Male Golden-cheeked Warbler showing band arrangement of its legs.

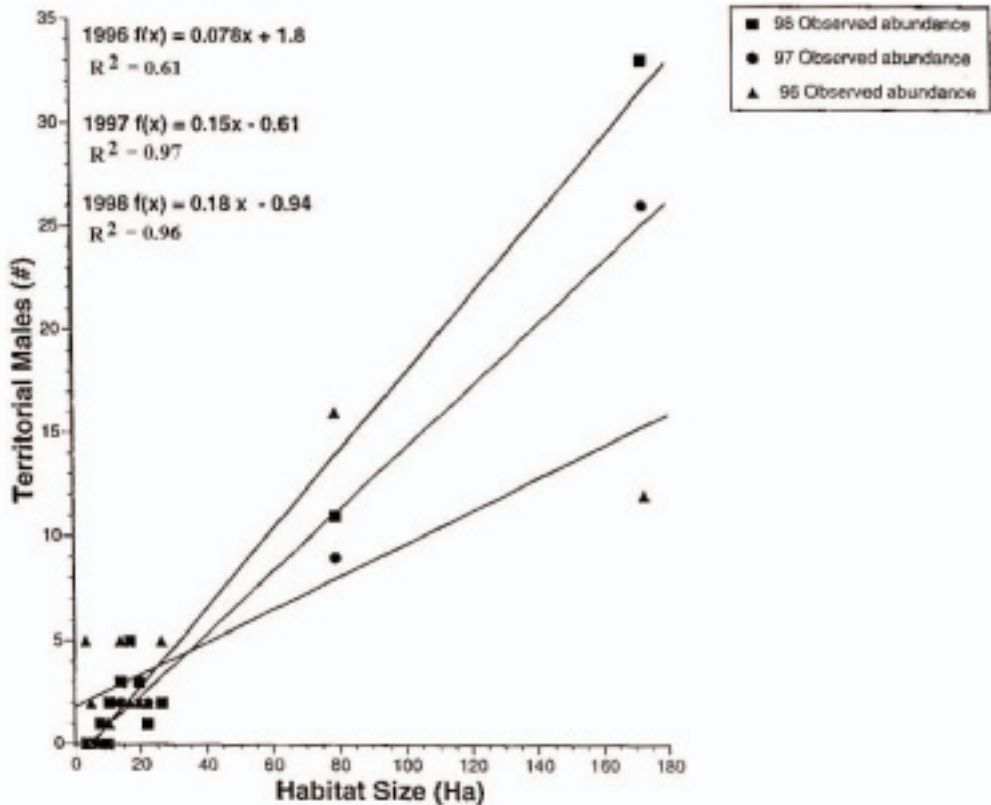


Figure 10. In all study years, habitat size significantly predicted the number of male Golden-cheeked Warblers capable of infiltrating and persisting in a given habitat unit. Considerably more variation in number of males was unexplained in 1996 ($r^2 = 0.61$), than both 1997 ($r^2 = 0.97$) and 1998 ($r^2 = 0.96$), indicating in 1996 other factors may have influenced the suitability of sampling locations harboring territorial males on Fort Hood.



Female Golden-cheeked Warbler feeding young.

Ecological data on composition and structure of plant communities in each habitat unit proved important in addressing ecological factors other than size in determining the abundance and density of territorial males in the FSA. A series of multiple regression models addressed the role of variation in habitat type (semifragment or fragment), percent understory of hardwoods, percent canopy of hardwoods, and percent canopy cover on male abundance. In 1996, the overall model, which incorporated habitat unit variables in addition to habitat unit size, had a marginal insignificance ($F_5 = 3.55$, $P = 0.065$, $r^2 = 0.72$, Table 2a). However, in both 1997 and 1998, the overall model had high significance (1997: $F_5 = 52.4$, $P = 0.0001$, $r^2 = 0.97$; 1998: $F_5 = 47.8$, $P = 0.0001$, $r^2 = 0.97$, Table 2b, c). Most importantly, in the three years, only habitat size contributed toward predicting abundance. This result confirmed the strong influence of spatial scale in determining presence or absence of territorial males and produced doubt as to the value of the other four variables in determining Golden-cheeked Warbler abundance. The marginally insignificant nature of the 1996 model highlighted the ecological reality that other factors at work ultimately prevented detection of clear links between habitat size and male Golden-cheeked Warbler abundance.

The other question associated with these data concerned effects of habitat unit variables on density of territorial males or number of territories expected to occur in a habitat unit. The overall model indicated no statistical significance in the three years (1996: $F_5 = 1.13$, $P = 0.4265$, $r^2 = 0.45$; 1997: $F_5 = 1.20$, $P = 0.3992$, $r^2 = 0.46$; 1998: $F_5 = 0.81$, $P = 0.5794$, $r^2 = 0.37$, Table 3a, b, c). Thus, density of territorial males did not always scale with habitat unit size (as shown in the previous analysis) and can not be predicted on the basis of habitat type (semifragment or fragment), percent understory hardwoods, percent canopy of hardwoods, and percent canopy cover. Regardless of fragment or semifragment size, males established territories of the same size. Our data show no significant difference in the size of territories in fragment and semifragments. Territory density remained the same in the analysis. However, in the regression model, habitat size approached significance ($P = 0.079$, Table 2b). If the fire had produced more semifragments and fragments for study, then habitat size may have been significant as statistical power increased with sample size.

Finally, point count data from 1995 through 2005 were used to compare Golden-cheeked Warblers abundance in the FSA and SA through time as a measure of the stability and resilience of the population buffeted by a perturbation. Although the preburn abundance of Golden-cheeked Warblers recorded for point count routes 2 (34) and 3 (43) in the future FSA equaled or slightly exceeded those for point count routes 11 (33) and 20 (34) in 1995, there was a difference in abundance ($t_4 = 7.65$, $P = 0.0016$) of Golden-cheeked Warblers on point count routes prior to the wildfire because of a lower abundance on route 14 (17) in the SA. The number of Golden-cheeked Warblers recorded on point count routes in the FSA were below those in the SA ($F_{7, 45, 52} = 11.2$, $P < 0.0001$, Fig. 11) in 1996 and continued as such through 2005.

Demography

In 1996, we banded 48 adult males and 10 adult females and captured 13 males banded prior to 1996 in the FSA. However, all did not inhabit the FSA throughout spring. Forty-one males occupied the FSA. Overall return rate to the FSA in 1996 was 21% ($n = 13$). Age classes of banded males with territorial status included five (9%) SY, and 49 (91%) ASY. All SY birds inhabited fragments.

Banding data for 1995 showed adult males moved an average distance of 125.8 m ($n = 4$, SE = 21.2, range 88 to 181 m) from banding sites in the FSA (Table 4). In 1996, adult males moved a mean distance of 408.9 m ($n = 10$, SE = 127.9, range 78 to 1,298 m). Males moved greater distances in 1996 after the fire ($F_{3, 9} = 90.0$, $P = 0.0017$). An A5Y female moved 181 m in 1995, however, in 1996, she moved 1,058 m from a 1995 site destroyed by fire. Because no fragments existed in 1995, no comparisons could be made for returns to habitat units in 1996. In 1996, an A4Y male, whose territory burned in the fire, moved 617 m to the fragment nearest his 1995 territory.

In 1997, thirty-five (71%) adult males, nine (19%) adult females, and five (10%) unknown sex were banded. At least 18 warblers banded in 1996 returned to the FSA during 1997. Of 48 banded males caught in 1996, 15 (31%) returned to the FSA in 1997. Of 10 females banded in the FSA in 1996, three (30%) returned in 1997. Overall return rate for both sexes in 1997 was 31% ($n = 18$). In semifragments in 1997, 8 (20%) of 40 males with territorial status were SY males compared to six (60%) SY males inhabiting 10 fragments. Overall 28% of males with territorial status were SY in age.

One male, banded as an HY in 1991 was not observed until 1997. This individual had moved 2.06 km from the original banding site. In 1997, adult males in the FSA moved a mean distance of 752.7 m ($n = 17$, SE = 242.2, minimum = 7, maximum = 3,314 m, Table 4). Although distances moved by most males were less than the mean,

the extensive distances traveled by five males skewed the movement distribution (Table 4), and thus, male movements were the most variable in 1997. Males moved greater distances in 1997 compared to 1996 ($F_{9,15} = 6.55$, $P = 0.0037$). A female, that moved 1,058 m in 1996, moved only 357 m in 1997. The substantial movements by males in 1997 continued to affect the stability of the population. Males were observed searching in the FSA for suitable territorial habitat by moving from habitat unit to habitat unit, possibly assessing the density of males and habitat suitability. In fragments, only one (A4Y male recaptured 6.9 m from his original banding site) individual banded in a fragment in 1996 returned to a fragment in 1997. This male moved 570 m from one fragment (1996 location) to another fragment in 1997. Twelve birds moved within semifragments. One TY male moved 1.6 km from a semifragment into the SA. Three ATY birds moved an average of 1.6 km from a fragment to a semifragment or from a semifragment into the SA. We concluded these birds moved from unsuitable habitat in 1996 into more suitable habitat in 1997. One ATY male moved 3.3 km into the FSA from an area unaffected by the fire.

In 1998, forty-three adult males and 12 adult females were banded in the FSA. Age classes of adults were 37 (67%) SY and 18 (33%) ASY. Overall return rate for 1998 was 37% ($n = 18$), compared to 31% ($n = 18$) in 1997. Of 35 males banded in 1997, 18 (51%) returned to the FSA in 1998. No females banded in 1997 returned to the FSA in 1998. Of 61 males with territory status, 12 SY males inhabited fragments and 29 SY males inhabited semifragments. Overall 67% of territorial males had an age of SY in 1998. In comparison, five (9%) of 54 males in 1996 and 14 (28%) of 50 territorial males in 1997 were SY birds. A change ($X^2 = 43.07$, $P = 0.00001$) in number of SY males from 1996 to 1998 altered the age structure of the Golden-cheeked Warbler population inhabiting semifragments and fragments.

In 1998, adult males moved a mean distance of 475.0 m ($n = 20$, $SE = 196.5$, range 100 to 3,500 m) in the FSA (Table 4). Males moved smaller distances on average in 1998 compared to 1997 ($F_{15,19} = 1.37$, $P = 0.254$). Fourteen males returned to within 200 m of their 1997 territory or banding site. Thirteen of these males inhabited semifragments. One male, banded in a semifragment in 1996, occupied a site in the SA in 1998 near the site it inhabited in 1997. Four males returned to fragments with three returning to the same fragment occupied in 1997. The fourth, banded in a semifragment in 1997, moved 2.5 km to a fragment. One male banded as a HY in 1991, observed again in 1997 at a site 2 km from the original banding site, occurred as an 8Y at a site <100 m from its 1997 territory. One male banded in 1996 in the FSA with no observation record for 1997 inhabited a site in the SA 3.5 km from the original banding site.

In 1997, forty Golden-cheeked Warblers were observed at 88 sites in the SA. Only two had been banded in the FSA. Age classes for birds banded in the SA included 12 (30%) HY, four (10%) AHY, four (10%) SY, and 20 (50%) ASY.

Activity of transient warblers increased in the SA in 1998. Golden-cheeked Warblers were observed at 262 sites, the most recorded for any year. Of 170 observed, 162 had bands. Age classes for banded birds in the SA included 60 (35%) HY, 47 (28%) AHY, 24 (14%) SY, 39 (23%) ASY. The proportion of young birds observed in the SA was similar to the FSA.

Productivity

In 1996, 41 (75.9%) of 54 territorial males in the FSA had mates. Twenty-eight mated pairs (68.3%) produced 1.07 fledglings per territorial male. In fragments, 10 (41.7%) of 24 males had mates. Six mated pairs (60%) produced nine fledglings. Twenty-seven (90%) of 30 territorial males had mates in semifragments. Twenty-two mated pairs (81.5%) produced 21 fledglings. Successful territorial males in fragments and semifragments had 1.5 and 0.954 fledglings produced per male, respectively.

In 1997, 44 (88%) of 50 territorial males in the FSA had mates. Thirty-two mated pairs (72.7%) produced 1.34 fledglings per territorial male. In fragments, eight (80%) of 10 males had mates. Five mated pairs (62.5%) produced six fledglings. Thirty-six (90%) of 40 territorial males had mates in semifragments. Twenty-seven mated pairs (75%) produced 37 fledglings. Successful territorial male in fragments and semifragments had 1.20 and 1.37 fledglings produced per male, respectively.

In 1998, 55 (90.2%) of 61 territorial males in the FSA had mates. Forty-nine mated pairs (89.1%) produced 1.73 fledglings per territorial male. In fragments, 10 (83.3%) of 12 males had mates. Nine mated pairs (90%) produced 16 fledglings. Forty-four (89.8%) of 49 territorial males had mates in semifragments. Thirty-nine mated pairs (88.6%) produced 69 fledglings. Successful territorial males in fragments and semifragments had 1.78 and 1.77 fledglings produced per male, respectively. There was no difference in fledgling produced per

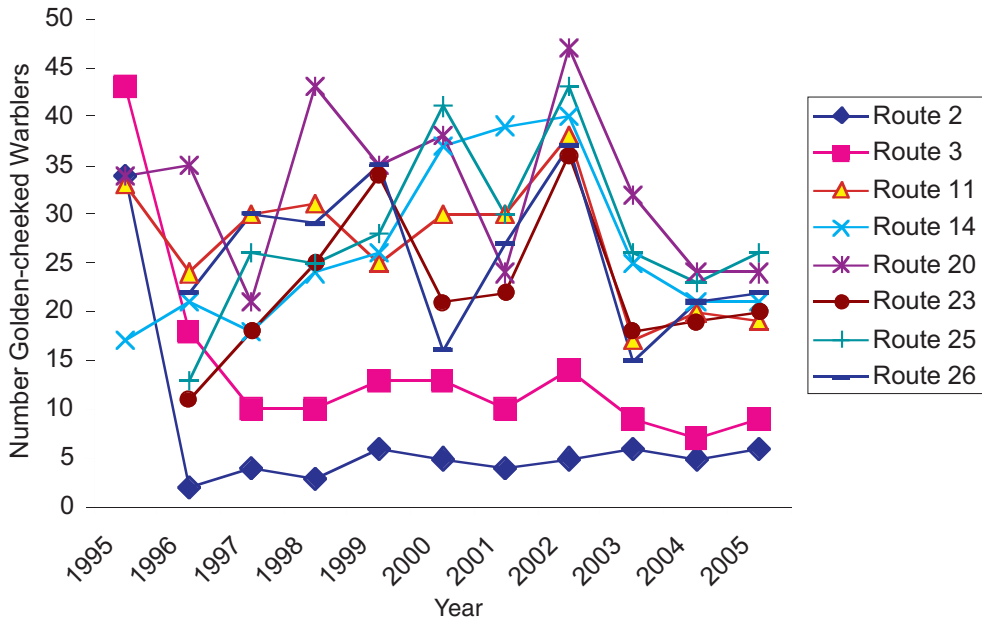


Figure 11. Abundance of Golden-cheeked Warblers on selected point count routes in Fire Study and Search areas from 1995 through 2005 at Fort Hood, Texas. A wildfire occurred between data collection in 1995 and 1996. The decline in abundance specifically shown on point count routes 2 and 3 between 1995 and 1996 is attributed to the loss of habitat from the fire. The decline in number of Golden-cheeked Warblers on point count routes 2 and 3 was maintained until the last sampling information in 2005.

territorial male in semifragments ($\bar{x} = 1.363$, $SE = 0.237$, $n = 3$) and fragments ($\bar{x} = 1.493$, $SE = 0.168$, $n = 3$) for the three years ($t_4 = 0.45$, $P = 0.677$).

Vegetation

Ashe juniper, oak species, and Texas white ash dominated the canopy vegetation in semifragments and fragments in the FSA (Table 5, Fig. 12, Fig. 13). Ashe juniper, shin oak, and several other hardwood species dominated the understory and overstory vegetation (Tables 6, 7). Ashe juniper and hardwoods had a mean percent composition of 76.2% ($SE = 3.01$, range 8% to 100%) and 23.8% ($SE = 3.0$, range 0 to 92%), respectively, on 49 transect lines in semifragments (Table 6). Ashe juniper and hardwoods had a mean percent composition of 62.2% ($SE = 6.52$, range 3% to 96%) and 37.8% ($SE = 6.52$, range 4% to 97%) on 16 transect lines in fragments (Table 5). There was a slight difference in percent canopy cover ($t_2 = -0.79$, $P = 0.514$) for fragments ($\bar{x} = 80.2$, $SE = 4.05$, minimum = 56.7, maximum = 94.5) and semifragments ($\bar{x} = 87.1$, $SE = 0.368$, minimum = 86.4, maximum = 87.6); however, there was a substantial contrast in variance between fragments (163.9) and semifragments (0.405). Since there was no difference between the percent canopy cover of fragments and semifragments, we pooled the two for analysis. The mean canopy cover for the 13 habitat units was 81.8% ($SE = 3.1891$, median = 86.4).

There was no significant difference ($t_2 = 1.13$, $p = 0.3759$) in the mean percent composition of Ashe juniper in understory of fragments ($\bar{x} = 48.5$, $SE = 8.7769$, minimum = 2.0, maximum = 80.0) and semifragments ($\bar{x} = 55.5$, $SE = 2.8087$, minimum = 50.0, maximum = 59.1). The mean percent composition of Ashe juniper in the understory of the 13 habitat units was 52.2% ($SE = 6.412$). There was no significant difference ($t_2 = 1.13$, $P = 0.376$) in the mean percent composition of hardwoods in understory of fragments ($\bar{x} = 48.8$, $SE = 8.381$, minimum = 20.0, maximum = 98.0) and semifragments ($\bar{x} = 44.4$, $SE = 2.809$, minimum = 40.9, maximum = 50.0). Mean percent composition of hardwoods in the understory of 13 habitat units was 47.9% ($SE = 6.412$). We found no difference between fragments and semifragments in the percent composition of Ashe juniper and hardwoods in the understory vegetation ($t_{12} = 0.34$, $P = 0.74$).



Habitat suitability was measured by presence of males.

There was no difference ($t_2 = -1.18$, $P = 0.361$) in mean percent composition of Ashe juniper in the canopy of fragments ($\bar{x} = 58.8$, $SE = 8.591$, minimum = 3.0, maximum = 87.0) and semifragments ($\bar{x} = 74.1$, $SE = 2.248$, minimum = 70.8, maximum = 78.4). Mean percent composition of Ashe juniper in the canopy of the 13 habitat units was 62.3% ($SE = 6.799$). There was no difference ($t_2 = 1.18$, $P = 0.361$) in mean percent composition of hardwoods in the canopy of fragments ($\bar{x} = 41.2$, $SE = 8.591$, minimum = 13.0, maximum = 97.0) and semifragments ($\bar{x} = 25.9$, $SE = 2.248$, minimum = 21.6, maximum = 29.2). Mean percent composition of hardwoods in the canopy of the 13 habitat units was 37.7% ($SE = 6.799$). There was no difference between percent composition of Ashe juniper and hardwoods in the canopy vegetation of fragments and semifragments ($t_{12} = 1.81$, $P = 0.095$).

DISCUSSION

Natural or anthropomorphic stochastic disturbances alter discrete landscapes, create constantly changing mosaics of recently disturbed fragments, and drive temporal dynamics of landscape floristic patterns. A disturbance is any relatively discrete event that disrupts ecosystem, community, or population structure and changes resources, community dynamics, substrate availability, or the physical environment (White and Pickett 1985). Landscape-scale consequences of succession cannot be understood independent of disturbances (Huston 1995) that reset succession and alter distributions of plant and bird populations and individuals and their resources. Disturbances function at a variety of scales and often produce extremely complex effects, causing bird populations and individuals of species dependent on stability in ecosystems to vary in their temporal response and recovery.

Ecological systems subjected to disturbances exhibit a shifting, dynamic mosaic of vegetative fragments in time and space. The presence and relative abundance of bird species and function of various ecological processes may differ considerably between and among fragments (Wiens 1976, den Boer 1981, Pickett and White 1985, Wiens and Rottenberry 1985). Individuals respond to spatial heterogeneity in various ways, including spending long periods within specific fragments, using certain fragments for feeding or reproduction, or moving over a mosaic of fragments in an apparently aimless fashion while distinguishing between fragments and their quality as suitable habitat. Ecosystem structure and biotic succession of fragmented environments change through time and responses of individuals and populations to spatial fragmentation are often dynamic. Subsequently, the structure and dynamics of communities are strongly influenced by spatial variation. Recently, forest fragmentation and the resulting increase in edge have been linked to population declines of neotropical migrant songbirds (Hutto 1988, Terborgh 1989, Robbins et al. 1989, Robinson 1992, Burke and Nol 1998, Hobson and Villard 1998, Meyer et al. 1998, Villard et al. 1999). Habitat fragmentation contributes to an array of problems for species dependent on contiguous habitat, including habitat loss, decreased site

Table 2. Multiple regression ANOVA generated by separately regressing the dependent variable abundance for each study year (1996 = a, 1997 = b, 1998 = c) on the independent variables, habitat (patch) size (HABSIZE), percent understory hardwoods (TUNDER), percent overstory hardwoods (TOVER), habitat type; i.e., edge or island (HABTYPE), and percent canopy cover (TPERCOV). All percent values were arcsine-square root transformed prior to entry into the model. Model equations for each regression ($n = 6$) appear in each subheading.

(a) **Model: 1996 Abundance = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Abundance)**

Source	df	Sum of Squares	Mean Square	<i>F</i>	<i>P</i>
Model	5	193.3788286	38.6757657	3.55	0.0645
Error	7	76.3134791	10.9019256		
Corrected Total	12	269.6923077			

$r^2 = 0.717035$, CV = 79.48793, Root MSE = 3.301806, ABUND Mean = 4.153846

Source	df	Type III SS	Mean Square	<i>F</i>	<i>P</i>
HABSIZE	1	43.16551507	43.16551507	3.96	0.0869
TUNDER	1	10.68296447	10.68296447	0.98	0.3552
TOVER	1	4.68060891	4.68060891	0.43	0.5332
HABTYPE	1	14.56530401	14.56530401	1.34	0.2857
TPERCOV	1	2.78283855	2.78283855	0.26	0.6289

(b) **Model: 1997 Abundance = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Abundance)**

Source	df	Sum of Squares	Mean Square	<i>F</i>	<i>P</i>
Model	5	593.8390811	118.7678162	52.44	0.0001
Error	7	15.8532266	2.2647467		
Corrected Total	12	609.6923077			

$r^2 = 0.973998$, CV = 39.12760, Root MSE = 1.504908, ABUND Mean = 3.846154

Source	df	Type III SS	Mean Square	<i>F</i>	<i>P</i>
HABSIZE	1	239.6949456	239.6949456	105.84	0.0001
TUNDER	1	0.3458907	0.3458907	0.15	0.7076
TOVER	1	0.1503578	0.1503578	0.07	0.8041
HABTYPE	1	3.2050735	3.2050735	1.42	0.2730
TPERCOV	1	0.0536332	0.0536332	0.02	0.8820

(c) **Model: 1998 Abundance = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Abundance)**

Source	df	Sum of Squares	Mean Square	<i>F</i>	<i>P</i>
Model	5	948.9669456	189.7933891	47.79	0.0001
Error	7	27.8022852	3.9717550		
Corrected Total	12	976.7692308			

$r^2 = 0.971536$, CV = 42.47220, Root MSE = 1.992926, ABUND Mean = 4.692308

Source	df	Type III SS	Mean Square	<i>F</i>	<i>P</i>
HABSIZE	1	410.1330541	410.1330541	103.26	0.0001
TUNDER	1	0.0010020	0.0010020	0.00	0.9878
TOVER	1	0.2243403	0.2243403	0.06	0.8189
HABTYPE	1	0.8772473	0.8772473	0.22	0.6527
TPERCOV	1	0.0133468	0.0133468	0.00	0.9554

Table 3. Multiple regression ANOVA generated by separately regressing the dependent variable density for each study year (1996 = a, 1997 = b, 1998 = c) on the independent variables, habitat (patch) size (HABSIZE), percent understory hardwoods (TUNDER), percent overstory hardwoods (TOVER), habitat type; i.e., edge or island (HABTYPE), and percent canopy cover (TPERCOV). All percent values were arcsine-square root transformed prior to entry into the model. Model equations for each regression ($n = 6$) appear in each subheading.

(a) Model: 1996 Density = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Density)

Source	df	Sum of Squares	Mean Square	F	P
Model	5	8302.156265	1660.431253	1.13	0.4265
Error	7	10317.662616	1473.951802		
Corrected Total	12	18619.818880			

$r^2 = 0.445877$, CV = 147.6538, Root MSE = 38.39208, DENSITY Mean = 26.00141

Source	df	Type III SS	Mean Square	F	P
HABSIZE	1	111.939249	111.939249	0.08	0.7908
TUNDER	1	3597.433585	3597.433585	2.44	0.1622
TOVER	1	1626.378020	1626.378020	1.10	0.3284
HABTYPE	1	140.997732	140.997732	0.10	0.7661
TPERCOV	1	3146.623062	3146.623062	2.13	0.1874

(b) Model: 1997 Density = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Density)

Source	df	Sum of Squares	Mean Square	F	P
Model	5	469.1854687	93.8370937	1.20	0.3992
Error	7	549.0624629	78.4374947		
Corrected Total	12	1018.2479316			

$r^2 = 0.460777$, CV = 98.61965, Root MSE = 8.856494, DENSITY Mean = 8.980456

Source	df	Type III SS	Mean Square	F	P
HABSIZE	1	41.4853211	41.4853211	0.53	0.4907
TUNDER	1	32.8499284	32.8499284	0.42	0.5382
TOVER	1	26.5078868	26.5078868	0.34	0.5792
HABTYPE	1	331.0720433	331.0720433	4.22	0.0790
TPERCOV	1	0.7219441	0.7219441	0.01	0.9263

(c) Model: 1998 Density = $\beta_0 + \beta_1$ Habsize + β_2 Understory + β_3 Overstory + β_4 Habtype + β_5 Percov + ϵ (Density)

Source	df	Sum of Squares	Mean Square	F	P
Model	5	426.6485463	85.3297093	0.81	0.5794
Error	7	740.4949456	105.7849922		
Corrected Total	12	1167.1434919			

$r^2 = 0.365549$, CV = 92.80881, Root MSE = 10.28518, DENSITY Mean = 11.08212

Source	df	Type III SS	Mean Square	F	P
HABSIZE	1	22.1730366	22.1730366	0.21	0.6609
TUNDER	1	0.0472431	0.0472431	0.00	0.9837
TOVER	1	2.5995109	2.5995109	0.02	0.8799
HABTYPE	1	214.4923305	214.4923305	2.03	0.1975
TPERCOV	1	0.3880368	0.3880368	0.00	0.9534

Table 4. Distances (m) dispersed by individual male and female Golden-cheeked Warblers by age at time of banding and age at time of last recapture by year in the Fire Study Area at Fort Hood, Texas. The series of letters identify individuals.

Individual	Age ^a	Sex	Last Age ^b	1992	1993	1994	1995	1996	1997	1998
NB/WH:RD/SI	SY	M	7Y	17				78		
NB/OR:RD/SI	HY	M	8Y						2057	<100
RD/GR:BK/SI	ASY	M	A6Y			120	88	109	34	
PI/SI:PI/RD	ASY	M	A4Y				181	335		
YE/SI:OR/BL	HY	M	TY					1299		
GR/MV:OR/SI	SY	M	4Y				97	192		
YE/SI:GR/PI	ASY	F	A5Y				181	1058	357	
PI/OR:MV/SI	AHY	M	A4Y				137	617	570	
PI/SI:YE/WH	SY	M	TY					838		
NB/SI:MV/YE	ASY	M	ATY					129		
WH/SI:OR/YE	ASY	M	ATY					417		
GR/SI:WH/YE	AHY	F	ASY					394		
YE/SI:MG/OR	ASY	M	A5Y					80	129	<200
BK/SI:WH/GR	ASY	M	A4Y						125	<200
BL/BL:YE/SI	ASY	M	A4Y						124	<200
GR/SI:WH/BK	ASY	M	A4Y						126	<200
WH/GR:MV/SI	ASY	M	A4Y						216	<200
YE/BK:WH/SI	ASY	M	ATY						182	
YE/SI:WH/BL	ASY	F	ATY						1326	
PI/SI:RD/BK	ASY	M	A4Y						359	<200
MV/SI:BL/YE	ASY	M	A4Y						3314	<200
OR/WH:OR/SI	ASY	M	A4Y						78	<200
YE/GR:MV/SI	ASY	M	ATY						1831	
MG/SI:GR/YE	ASY	F	ATY						76	
YE/SI:YE/OR	ASY	M	ATY						70	
NB/PI:WH/SI	SY	M	4Y						1681	<200
OR/SI:OR/BL	ASY	M	ATY						1894	
BL/SI:MG/YE	ASY	M	A4Y						7	<200
GY/SI:GR/PI	SY	M	TY							~2500
DB/GR:BK/SI	SY	M	TY							<200
RD/SI:BL/DG	SY	M	TY							<200
WH/SI:GY/RD	SY	M	TY							<200
NB/SI:GR/DB	ASY	M	ATY							<200
DG/MV:GR/SI	ASY	M	ATY							<200
YE/SI:DG/GR	SY	M	TY							<200
PI/DB:BK/SI	ASY	M	ATY							<200
WH/SI:RD/WH	ASY	M	A4Y							~3500

^a Age of bird at banding^b Age of bird at last observation



Figure 12. View of the canopy structure of Golden-cheeked Warbler breeding habitat showing the preponderance of Ashe juniper and hardwood species in the composition.

fidelity, increased isolation, reduced gene flow, increased predation, and higher incidence of nest parasitism (Faaborg et al. 1995). Thus, time becomes a limiting factor in an individual's response to disturbance.

The wildfire at Fort Hood disrupted the Golden-cheeked Warbler population as seen in considerable change in abundance and density of males in habitat units in the FSA. Densities of males per 100 ha ranged from 6.9 to 30.0 in semifragments and 0 to 151.5 males per 100 ha in fragments (Table 1). Nine of 10 fragments in 1996 had one or more territorial males; whereas, in 1997 and 1998, only six fragments had territorial males. No males established territories in fragment J (3.3 ha in size); whereas, fragments K and M of similar area had



Figure 13. Male Golden-cheeked Warbler perched in the canopy dominate Ashe juniper.

five and two territorial males in 1996, respectively, but none in 1997 and 1998. The three fragments differed in percent composition of Ashe juniper and hardwood species in canopy vegetation. Fragment J had a mean percent canopy cover of 83.7%, fragment K 67.2 %, and fragment M 91.2%. The three fragments differed in shape. Fragment J was elongate and narrow (Fig. 8); whereas, fragments K and M were more oval (Fig. 8). Fragment K had a high density of males with five territorial males in 1996. Fragments E, F, and G had similar sizes, but only fragment G had territorial males in all three years. All three fragments occurred near the edge of the study area (Fig. 8), and Golden-cheeked Warblers may have dispersed into these fragments from adjoining, unburned habitat. These fragments also differed in plant composition and shape. Fragment G had an oval shape, whereas, an elongate shape characterized fragments E and F.

The affinity of a species for edge versus interior habitats influences its response to fragmentation. Habitat suitability decreases as size of a habitat fragment diminishes (Levenson 1981, Forman and Gordon 1986). As fragment shape changes from circular to oblong or rectangular without change in area, a circular to oval-shaped fragment would have less edge. Fragments about 10 ha in size did not consistently provide suitable habitat for Golden-cheeked Warblers. Males only inhabited fragments E, F, K, and M in 1996. Fragment F had one male in 1996, no inhabitants in 1997, and one male in 1998. Fragments >15 ha in size and oval in shape with an intact, interior forest consistently provided suitable habitat for territorial males in the FSA. Golden-cheeked Warbler density in fragment G indicated it was as suitable habitat as larger size fragments D and H in 1997 and 1998. Fragment L, the largest fragment, had a density of males similar to semifragments in 1996, but lower densities in 1997 and 1998.

Density of males varied in semifragments between years. Semifragment A decreased in density from 1996 to 1998 (Table 1). Semifragment B showed a steady increase and semifragment C remained stable. By 1998, both semifragments B and C had densities of at least 20 males per 100 ha.

Pulich (1976) based habitat quality on three categories of density estimates: excellent (12.5 pairs/100 ha), average (5 pairs/100 ha), and marginal (3 pairs/100 ha). However, more recently Jetté et al. (1998) recognized excellent habitat as having a density averaging 18.8 males per 100 ha in an intensive study area at Fort Hood. Likewise, a density of 29.1 males per 100 ha in Travis County, Texas was distinguished by Ladd and Gass (1999) as excellent habitat. Based on these studies, excellent habitat for Golden-cheeked Warblers supports a density of about 20 males per 100 ha. Few habitat units consistently had densities of 20 males per 100 ha in

Table 5. Landscape scale characterization of understory and overstory vegetation using the point-quarter method in semifragments and fragments of habitat units occupied by Golden-cheeked Warblers in the Fire Study Area at Fort Hood, Texas. Percent canopy cover and number of transects are indicated for each habitat unit.

Habitat unit	n	Canopy (%)	Percent understory		Percent overstory	
			Ashe juniper	Hardwood	Ashe juniper	Hardwood
Semifragments						
A	11	87.6	59.1	40.9	73.1	26.9
B	33	87.3	57.6	42.5	78.4	21.6
C	5	86.4	50.0	50.0	70.8	29.2
Fragments						
D	3	84.1	68.7	31.3	65.3	34.7
E	1	94.5	2.0	98.0	3.0	97.0
F	1	56.7	32.0	68.0	70.0	30.0
G	2	91.5	60.0	40.0	54.5	45.5
H	3	76.8	52.0	48.0	68.7	31.3
I	1	66.7	15.0	85.0	19.0	81.0
J	1	83.7	55.0	45.0	68.0	32.0
K	1	67.2	80.0	20.0	87.0	13.0
L	2	89.2	73.0	27.0	85.5	14.5
M	1	91.2	74.0	26.0	67.0	33.0

Table 6. Percent composition of understory plants in semifragments (A-C) and fragments (D-M) in habitat units in the Fire Study Area at Fort Hood in 1997. Multiple transects were used to characterize vegetation within most habitat units and means are reported for all transects. Rounding of decimal points caused the summation of percentages of some habitat units to exceed 100%.

Species	Habitat Unit												
	A	B	C	D	E	F	G	H	I	J	K	L	M
Ashe juniper	59	57	50	69	0	32	63	52	5	54	80	87	72
Live oak	3	1	0	0	53	0	2	0	0	11	0	0	0
Texas oak	7	9	3	17	0	22	7	24	5	6	3	0	12
Shin oak	23	25	37	3	0	26	28	19	0	5	10	0	16
Chinkinpin oak	0	0	0	0	0	0	0	0	1	0	0	7	0
Texas white ash	0	5	4	7	7	8	0	0	5	52	24	7	6
Hackberry	0	0	0	0	15	0	0	0	0	0	0	0	0
Pecan	0	0	0	0	0	5	0	0	0	0	0	0	0
Cedar elm	0	3	0	0	0	0	0	0	28	0	0	0	0
Evergreen sumac	2	0	2	0	0	11	0	0	0	0	0	0	0
Skunkbush sumac	0	0	0	0	0	3	0	0	0	0	0	0	0
Redbud	0	0	1	1	0	0	0	0	9	0	0	0	0
Buckthorn	0	0	0	2	0	0	0	0	0	0	0	0	0
Wollybucket bumelia	0	0	0	0	0	0	8	0	0	0	0	0	0
Rough-leaf dogwood	0	0	0	0	0	0	15	0	0	0	0	0	0
Elbowbush	0	0	0	0	0	7	0	0	0	0	0	0	0

the FSA. Less than one-third of density values for the three years would be scored as indicators of excellent habitat (Table 1). Only semifragments B and C and fragments D and G consistently had densities of at least 20 males per 100 ha. Based on this criterion of assessing habitat quality, semifragment A and most fragments in the FSA would be rated as average to marginal Golden-cheeked Warbler habitat for the three years.

Male abundance increased 61.2% from 1996 to 1998 in semifragments A, B, and C; however, abundance of males in fragments (D-M) decreased 50%. The ramifications of fire on the landscape at Fort Hood raises

Table 7. Percent composition of overstory plants in semifragments (A-C) and fragments (D-M) in habitat units in the Fire Study Area at Fort Hood in 1997. Multiple transects were used to characterize vegetation within most habitat units and means are reported for all transects. Rounding of decimal points caused the summation of percentages of some habitat units to exceed 100%.

Species	Habitat Unit												
	A	B	C	D	E	F	G	H	I	J	K	L	M
Ashe juniper	75	81	75	70	5	74	56	71	21	81	87	87	72
Live oak	4	1	0	3	82	3	3	2	0	10	0	0	0
Texas oak	7	5	3	14	0	22	2	14	0	10	0	0	12
Shin oak	7	8	11	0	0	0	38	11	0	0	0	0	16
Chinkinpin oak	0	0	0	0	0	0	0	0	0	0	0	7	0
Texas white ash	7	5	11	13	5	0	2	3	46	0	13	6	0
Hackberry	0	0	0	0	5	0	0	0	4	0	0	0	0
Pecan	0	0	0	0	4	0	0	0	0	0	0	0	0
Cedar elm	0	1	0	0	0	0	0	0	29	0	0	0	0



Figure 14. Progression of plant succession on a steep slope site shortly after the fire (top) and nine years later (bottom) in the Fire Study Area at Fort Hood, Texas. In 2005 the plant community was dominated by hardwoods.



Figure 15. Progression of plant succession on a redland soils site shortly after the fire (top) and nine years later (bottom) in the Fire Study Area at Fort Hood, Texas. In 2005 the plant community was dominated by hardwoods.

questions whether this fire or fire in general has immediate and/or long-term consequences on suitability of habitat for Golden-cheeked Warblers as measured by abundance and density of males. Did habitat size influence abundance of territorial males? We tested the hypothesis whether abundance of territorial males in discrete habitats (semifragments and fragments) was independent of habitat size. We determined that in all three years following the fire, habitat size remained a significant determinant of male abundance as number of males increased linearly (Fig. 10) with increasing habitat size. Virtually all variation (97% and 96%, respectively) in male abundance during 1997 and 1998 could be explained by the size of habitat units; however, in 1996, size did not explain 40% of the variation, indicating intrinsic or extrinsic principle components of individual habitat units other than size may have influenced male abundance. The 40% variation may be explained in part by fidelity to territorial sites, movements of males, population instability, and an overall multiplicity of factors related to fire disturbance to habitat. Male Golden-cheeked Warblers returning to the FSA in 1996 encountered a much different landscape than the one that existed at migration in 1995. The fire destroyed substantial amounts of vegetation and changed the physical structure of the landscape. Some males attempted to establish territories in completely burned sites by singing in the charred remains of trees, presumably in their former territory. These males abandoned burned sites having failed to attract a mate and established territories in nearby woodlands, even small fragments. This may explain the unusually high densities of males in some fragments in 1996.

We addressed whether total abundance of territorial males in variable-size, fire-altered fragments could be predicted on the basis of density of males in the largest (172.8 ha) and presumably least fire-altered habitat unit because of high densities of males in some fragments. Abundance of territorial males in variable-size fragments did not differ from the expected abundance in fragments based on densities of territorial males in the largest habitat unit. Presuming the suite of ecological factors governing male abundance operated most evenly in the largest habitat unit where size homogenized small-scale variation in the environmental grain, then density of territorial males in the largest habitat unit represented the least biased measure of territorial density per ha in the FSA. Upon this rationale, we estimated the expected number of territorial males in each habitat unit using density of males observed in the largest habitat unit. Failure to reject the null hypothesis in this analysis led to our interpretation that smaller fragments operated as simply "smaller versions" of the larger habitat unit. In contrast, rejection of the null hypothesis would have led to the interpretation that smaller fragments operated in a fundamentally different way in accumulating territorial males.

The attractiveness of fragments to Golden-cheeked Warbler males was examined each year. Ultimately, this analysis provided a more detailed assessment of the role of fragment size in determining patterns of male abundance. An important caveat related to our initial assumption that males in the largest habitat unit were as equally detectable as those in the smallest fragments. If this assumption had proved untrue, then our estimate of male density in the largest habitat unit became a biased estimate (underestimate) of regional density. Underestimation of expected male abundance in the largest fragment might make it harder to reject the null hypothesis, since very low abundance values occurred in smaller fragments. Thus, the test was most likely conservative.

Many articles have addressed the role of composition and structure of plant communities in habitat selection by Golden-cheeked Warblers (see Ladd and Gass 1999 for a review). However, a multiple regression model of components of the plant community, using percent canopy cover, percent Ashe juniper composition, percent hardwood species composition, percent understory hardwoods, percent understory Ashe juniper, percent canopy hardwoods, percent canopy Ashe juniper, and habitat type (semifragment or fragment) as variables, did not predict abundance and density of territorial males in habitat units. Although fire changed the Ashe juniper-oak woodland at the landscape level, the fire did not change the basic species composition of plants within intact habitat units from that of surrounding, unburned woodlands. Thus, fragments set apart from the surrounding vegetative matrix by virtue of disturbance differed primarily in size, but plant species composition and physiognomy within and among fragments and semifragments remained the same as the unburned landscape. It should be noted that small sample size ($n = 13$ habitat units) resulted in low statistical power for the test of significance for each variable in every year. Thus, while statistically nonsignificant, any or all variables could have been to some degree ecologically important factors (possibly synergistically) affecting abundance and density of males. Differences in habitat features between fragments may contribute to community patterns, although relationships are not consistent among studies (Whitcomb et al. 1981, Kitchener et al. 1982, Ambuel and Temple 1983, Rafe et al. 1985, Dobkin and Wilcox 1986, Wiens 1994).

Occupancy

Differences in occupancy of semifragments and fragments may be related in part to strong site fidelity in this species (Pulich 1976). Intuitively, some returning males encountered total destruction or substantial damage to the plant community they occupied in 1995 and established territories elsewhere in 1996. Two such males inhabited fragments located near their 1995 territories later in the breeding season (1996). However, other than these two males, we have no information suggesting where males relocated upon leaving fragments in the FSA or existence of empty territory spaces in surrounding TAs for 1996.

The number of territorial males in the FSA declined in 1996 but rebounded by 1998. Males briefly occupied all 13 habitat units in early spring 1996 and 1998 and 12 in 1997. However, most males in fragments did not establish territories. The number of territories in semifragments showed a steady increase from 30 in 1996 to 49 in 1998. Territories in fragments declined from 24 in 1996 to 12 in 1998. Mean territory size (2.79 ha) for males in the FSA was similar to territory size in two Golden-cheeked Warbler intensive study areas, West Fort Hood and TA 13, established to monitor the demography of the species at Fort Hood. Territory size at West Fort Hood (2.81 ha) was larger than TA 13B (2.20 ha), but smaller than the average territory size of 4.15 ha for 135 males at the Belton Lake Outdoor Recreational Area (Weinberg et al. 1996, Craft 1998, Ladd and Gass 1999).

The mean number of Golden-cheeked Warblers detected on each point count route increased steadily each year between 1992 and 1995 (Peak 2004), but the detection rate declined in 1996. At least two factors in 1996 potentially affected Golden-cheeked Warbler population trends. First, a severe drought in winter 1995–1996 continued through the 1996 breeding season making conditions less than optimal for breeding females. Some birds may have foregone breeding, and adult mortalities may have increased during the breeding season. A second factor was the fire. This fire may have caused individuals returning from wintering grounds to establish territories in lesser quality habitat in higher-than-normal densities in remaining habitat on Fort Hood or establishment of territories outside of Fort Hood. Analysis of point count data from breeding habitat outside the FSA allowed us to assess whether this wildfire caused a decline in Golden-cheeked Warbler detection rates on Fort Hood during the 1996 breeding season.

The number of Golden-cheeked Warblers detected on point count routes in the FSA declined in 1996. After the decline, the number of Golden-cheeked Warblers counted was consistent at about five on Route 2 and about 10 on Route 3 from 1997 to 2005 (Fig. 11). The number of Golden-cheeked Warblers counted on all six point count routes in the SA were higher, although more variable than the FSA, from 1996 to 2005. Based on the analysis of point count data for all of Fort Hood at the time of the fire, Holimon and Craft (2000) reported a slight increase in the overall Golden-cheeked Warbler population on Fort Hood. Their estimated annual population size showed a slight decrease in the mean abundance of warblers from 1996 to 1997. Regression analysis of the point count data indicated a significant, positive relationship between mean detections per point and year, suggesting the Golden-cheeked Warbler population size on Fort Hood increased significantly between 1992 and 2000 (Anders 2000). However, comparison of 1996 data with other years indicated that the wildfire did affect the overall detection rate in 1996, but that outside of the localized effects of the wildfire, the Golden-cheeked Warbler population size on Fort Hood continued to increase in 1996 (Anders 2000, Anders and Dearborn 2004).

Disturbance increases the heterogeneity of environments and communities. It is probable that loss of about one-quarter of Golden-cheeked Warbler habitat pressured individuals in the FSA by exposure to both temporal and spatial variations over a spectrum of scales (Wiens 1994). Both alpha and beta diversity changed; thus, providing a mosaic structure with a variety of niche opportunities. The relationship between disturbance and diversity is not always linear. A homogeneous system experiencing disturbance at a moderate rate of intensity may show an increase in diversity. If disturbance is frequent and intense, however, the severity of its effect on some populations may cause population reduction, even local extinction, and a decline in diversity (Denslow 1985, Wiens et al. 1985a, Wiens et al. 1985b). Determining such relationships requires that disturbance be quantified, and because different aspects of disturbance interact and complement one another, deriving biologically meaningful measures of disturbance has proven difficult (Wiens 1994). Although fire disturbance at Fort Hood caused substantial damage to the plant community inhabited by Golden-cheeked Warblers, it seems that loss of suitable habitat in the FSA did not severely alter the species persistence in the FSA, especially in larger habitat units. Although total density of woody sprouts has increased each year since the fire (Sanchez 2002), Golden-cheeked Warbler populations in the FSA have been maintained at levels well below the 1995 preburn population.

Birds may be less sensitive than other organisms to small-scale disturbances. Several studies have described favorable or negative responses of bird species to fires (Marshall 1963, Franzreb 1977, Lowe et al. 1978, Szaro and Balda 1979). Most birds are highly mobile and move to avoid localized disturbance (Cody 1981, Karr and Freemark 1983). Rowley and Brooker (1987) found resident family groups of Splendid Blue Wrens (*Malurus splendens*) flew from their territories into nearby, unburned areas just ahead of advancing flames during a brush fire in open *Eucalyptus* woodland in Western Australia, but some birds returned to territories in smoldering brush within hours, and all groups reoccupied former territories within several days. In shrub steppe habitats, however, birds did not immediately respond to disturbance (Rotenberry and Wiens 1978). Densities of territorial males remained unchanged or changed slowly in response to substantial changes in habitat structure by a range fire and physical removal of shrubs (Wiens and Rotenberry 1985, Wiens et al. 1985b).

Wood-warblers (*Dendroica* sp.) vary considerably in their adaptations to different stages of community succession with some species adapted to early stage of succession, while other species inhabit a climax or near climax community (Morse 1989, Dunn and Garrett 1997). Kirtland's Warbler (*D. kirtlandii*) is a stenotopic species adapted to a fire-influenced environment. Nesting habitat consists of homogeneous stands of jack pine (*Pinus banksiana*). The elimination of periodic fires in jack pine forest early in the last century caused a decline in Kirtland's Warbler populations (Mayfield 1960). In 1962, the Michigan Department of Conservation and the U.S. Forest Service set aside lands for management of Kirtland's warbler and reinstated fire as a disturbance mechanism, resulting in a slow increase in the population of Kirtland's Warbler (Mayfield 1992).

In contrast and unlike its generic cohort *D. kirtlandii*, *D. chrysoparia* requires specific habitat components of mature and old regrowth Ash juniper-oak woodlands with moderate to high densities of mature trees and a well-developed canopy cover in middle and upper layers of the forest (Pulich 1976, Ladd 1985, Sexton 1987, Wahl et al. 1990, U. S. Fish and Wildlife Service 1992, Dunn and Garrett 1997, Ladd and Gass 1999). Thus, damage or destruction of mature plant communities by fire could affect abundance. Possibly, the effect would last for the ~50 years (Diamond et al. 1995) reported necessary for regeneration of mature Ashe juniper-oak woodlands characterized as habitat for Golden-cheeked Warblers. Unlike the response to fire disturbed habitat of the shrub steppe species described above, Golden-cheeked Warblers showed sensitivity to small-scale disturbances and an immediate reaction to loss of habitat.

Some bird species characteristically locate breeding territories on the edge of fragments, whereas, others occupy only the interior forest. Reduction in the size of fragments or a change in fragment shape will likely cause a loss of interior species and an increase in edge species (Butcher et al. 1981, Whitcomb et al. 1981, Lynch and Wigham 1984, Freemark and Merriam 1986, Temple 1986, Freemark et al. 1995). Other species associated primarily with adjacent habitat types may also occur more frequently in smaller habitat fragments. Consequently, overall diversity of avian communities may increase as a response to fragmentation, at least to a point (Noss 1983, Haila et al. 1987). In North America, many long-distance, neotropical migrants breed primarily in extensive stands of mature, floristically diverse forests; whereas, permanent resident species and short-distance migrants associate less closely with forests or may even exhibit opposite distributional patterns (Whitcomb et al. 1981, Lynch and Wigham 1984). Abundances of forest-interior, migrant, canopy bird species closely relate to variations in fragment area, and these species are, therefore, particularly sensitive to forest fragmentation.

A central question associated with our study is the length of time before the habitat burned by the wildfire in the FSA will be suitable for re-occupancy by Golden-cheeked Warblers. Several factors will influence the vegetative succession producing suitable breeding and nesting habitat in the FSA. The intense livestock grazing applied to the land prior to the purchase of lands for Fort Hood in 1942 that contributed to the development of Ashe juniper dominated woodlands does not exist today. Will the current grazing pressure applied to the land produce a vegetative assemblage that will be selected as breeding habitat by Golden-cheeked Warblers? The plant community that developed during the early 1900s was influenced by a series of droughts. What type of climatic variation will be prevalent during the first one-half of the 21st Century? However, the composition of the vegetative community and changes in dominant species will determine the replacement community of the FSA. Currently, the FSA is a mosaic of remnant mature oak-juniper woodland in the 13 habitat units and an early shrub successional community on burned areas (Fig. 14, Fig. 15). Intuitively one would expect species and physiognomic differences in these successional stages.

Reemts et al. (2005) found Ashe juniper stem density in burned areas recovered more slowly than Texas oak,

and Ashe juniper stem density in all vegetative layers was much lower in burned transects than in unburned transects. They recorded no viable Ashe juniper trees and only six saplings on transects in burned areas. Texas oak, a species stimulated to resprout by fire, recovered more rapidly than Ashe juniper (Reemts et al. 2005). Texas oak and Ashe juniper have contrasting responses to crown fires. Texas oak vigorously resprouts but Ashe juniper lacks this capacity (Fonteyn et al. 1988, Russell and Fowler 2002). Reemts et al. (2005) observed increases in Texas oak density, while Ashe juniper density decreased in the FSA between 2001 and 2005.

The absence of Ashe juniper saplings in burned areas is a concern, since the species is a critical component of Golden-cheeked Warbler breeding and nesting habitats (Ladd and Gass 1999). The slow rejuvenation of Ashe juniper in the FSA can be attributed to several features of the species life history such as sensitivity to heat from fire (Wink and Wright 1973, Fonteyn et al. 1984, Fonteyn et al. 1988, Sullivan 1993), inability to resprout (Sullivan 1993), primarily biochore seed dispersal (Chavez-Ramirez and Slack 1993, Chavez-Ramirez and Slack 1994), lack of seed dispersal (Smeins and Fuhlendorf 1997), peak seed germination between November and February (Van Auken et al. 2004), low seedling survival following fire (Van Auken et al. 2004), and seeds lacking fire resistance (Reemts et al. 2005). Based on these factors, re-establishment of breeding and nesting habitat for Golden-cheeked Warblers in burned areas can not be expected in the near future or maybe never. It could well be mid-century or past before a mature oak-Ashe juniper woodland re-emerges on burned areas of the FSA (Huss 1954, Diamond et al. 1995).

Demographics

When Golden-cheeked Warblers returned to FSA in spring 1996, the radical change to the landscape caused greater movements by male and female warblers to find suitable territory and nesting habitat. Males in the FSA in 1996 had an almost 4-fold greater movement distance compared to travel distances in 1995 and an almost 2-fold greater movement distance than males in the Golden-cheeked Warbler intensive study areas on Fort Hood (Holimon and Craft 2000). In 1997 and 1998, average movement distances for males in the FSA continued to be about three times and two times greater than average movement distances for males in an intensive study area on Fort Hood (Holimon and Craft 2000). In 1997, males returned after prior exposure to the fire-modified changes in the FSA in 1996. Substantial movements of individuals into and out of the FSA indicated population instability in 1997. Although mean movement distances for 1996 and 1998 were similar, the higher standard errors for data on movements in both years indicated variability in movement distances within the FSA. In 1998, two males with >2.5 km movement distances skewed the data distribution. The extent of movement within and between habitat units also indicated the instability in the Golden-cheeked Warbler assemblage in the FSA.

Age structure of the Golden-cheeked Warbler assemblage in the FSA changed between 1996 and 1998 with the male segment of the population decreasing in age. In 1996, 9% of known-age males were SY birds, whereas, in 1998, 67% were SY males. Change in percentage of SY males from 1996 to 1998 may be related to site fidelity of older males arriving at the breeding grounds earlier than younger males (Weinberg et al. 1995, Maas 1998). After the fires, older males may have returned to their previous territories and finding them burned moved into the nearest available habitat. Second-year males arriving later at the FSA may have gone elsewhere to establish territories because of saturation of available habitat by older males. Younger males also exhibited a tendency to fly greater distances (Maas 1998).

In 1997, older males returning to the FSA, having been exposed in 1996 to a reduction of habitat in the FSA, possibly moved into suitable habitat outside the FSA. In 1997, we observed older birds (>ASY) moving from poor habitat in the FSA to better habitat in unburned areas. The increase of SY males documented in the FSA in 1997 also occurred in the intensive study area at TA 13B (Jetté et al. 1998). The increase may have resulted from increased recruitment or more available habitat the second year after the fire as older males dispersed elsewhere or did not inhabit fragments. Male return rates for 1996 and 1997 support the second alternative. The male return rate to the FSA in 1996 was 52%, which was higher than the average return rate (48%) in TA 13B from 1993 to 96 (Jetté et al. 1998). In 1997, the male return rate in the FSA decreased to 37%. This decrease probably did not indicate low adult survivorship, but rather, older males dispersing out of the FSA into a more suitable habitat in unburned areas. Return rates for male warblers in TA 13B increased in 1997 from 1996 (Jetté et al. 1998), the opposite of what occurred in the FSA. Male return rate in the FSA, however, increased to 51% in 1998. The 1998 male return rate was about the same as the 1996 male return rate for TA 13B (Jetté et al. 1998). Older adult males arrived at Fort Hood first each year and inhabited the more suitable habitat (Weinberg

et al. 1995). Because of the fire, the age structure of the population shifted to predominantly young males occupying the lesser quality habitat (fragments) in the FSA.

Productivity

No productivity data exists for the FSA prior to the fire. However, an intensive study of productivity at other areas of Fort Hood provided comparative data. Comparable pairing and productivity data were not available for Fort Hood from 1996–1999 because pairing and productivity data were not collected for all territories. However, data from 1993–1995 indicate levels of Golden-cheeked Warbler pairing success and productivity similar to those seen in 2000 (mean pairing success = 91.6%, mean percent of pairs producing fledglings = 93.3%, Bolsinger and Hayden 1994, Weinberg et al. 1995, Weinberg et al. 1996). As in previous years, pairing and productivity rates in 2000 were higher for ASY males than for SY males, with differences in pairing success approaching significance, and differences in productivity per territory being significantly higher for ASY males. Because of similarity of plant community composition and structure in the FSA and other study sites at Fort Hood, we assumed post-burn productivity data collected for Golden-cheeked Warblers to be comparable to sites at Fort Hood where the biology and ecology of the species were intensively studied. West Fort Hood (hereafter, WFH) and TA 13B had a mean fledgling production of 1.0 and 1.06, respectively (Craft 1998, Jetté et al. 1998). Productivity of individuals in habitat units of the FSA did not equal mean productivity at WFH and TA 13B until 1998. Lower productivity in the FSA in 1996 and 1997 was attributed to low numbers of fledglings produced in fragments. Number of fledglings produced in all fragments decreased by over 33% (9 to 6) in 1996 and 1997. However, fledgling production increased over 267% (6 to 16) in 1998. Even though productivity increased in fragments in 1998, productivity in the 10 fragments never reached the overall production in semifragments. Productivity in the FSA was driven by the reproductive success of males in semifragments. The total number of fledglings produced in semifragments increased yearly from 21 (1996) to 37 (1997) to 69 (1998).

Movement data indicated limited dispersal by males from the FSA in 1996. The highest density of territorial males in fragments occurred in 1996. Ecological conflicts (i. e., number of birds per unit area, competition for space, and young inexperienced males) associated with high density may have confounded reproductive effort by Golden-cheeked Warblers in fragments. In 1996, productivity in fragments was substantially below the mean productivity for Fort Hood. Overall productivity for successful males of 1.39 (semifragments 1.41, fragments 1.33) did not approach those for WFH and TA 13B. Mean number of young produced per successful male per year from 1993 to 1996 at WFH and TA 13B was 2.23 (Jetté et al. 1998). The mean for a similar study in Travis County was 2.19 (Ladd and Gass 1999). Mean productivity for semifragments and fragments in the FSA never reached mean values for Travis County (Ladd and Gass 1999) or Fort Hood prior to the fire (Jetté et al. 1998). However, based on increased productivity in the FSA, productivity should have been similar to the intensive study areas at Fort Hood by 2001.

Responses of mobile birds to disturbances may confer on populations and communities a degree of resilience to disturbance (Wiens 1994). Community patterns persisted in small and large islands in the Pearl Archipelago off Panama despite disturbances from fire, windstorms, and drought (Wright et al. 1985). Communities were predictable and highly structured with deterministic processes governing ecological processes and disturbance was deemed of minimal importance (Wright et al. 1985). Their conclusions, however, were based upon limited census data collected by different techniques temporally on different islands in different years by different observers and disturbance effects were not measured directly.

A clear relationship existed between disturbance and species abundance in other studies where effects of disturbances were less inferential. Depending upon variations in the frequency, extent, and magnitude of disturbances, landscapes were fragmented into complex mosaics of patches of different size and habitat types with complex patterns in the composition and age structure of plant communities (White 1979, Sousa 1979, Brokaw 1985, Coldren 1998, Dearborn and Sanchez 2001). Populations and communities of birds as well as individuals face not only habitats with unusually heterogeneous disturbances but continuously changing mosaics. Alteration of spatial configuration of habitats can take a variety of forms. Fragmentation generally involves external disturbances that alter large continuous tracts of forest so as to create isolated or tenuously connected fragments of the original habitat interspersed within an extensive mosaic of other habitat types. At the extremes, however, the effects of habitat disruptions and formation of fragments on birds may be different. Because of their mobility via flight, most birds survive the passage of fire. Following a large fire, how-

ever, nearly all birds undergo immediate adverse effects from the disturbance to some degree. In small fragments, birds may suffer severely from aggressive encounters with other species or individuals extirpated from adjacent, burned territories. Fragmentation of large forest tracts into smaller fragments often results in loss of forest-interior species (especially neotropical migrants) with increases in density or occurrence of edge species (Whitcomb et al. 1981). The isolation of Barro Colorado Island from the mainland by the disturbance induced by the construction of the Panama Canal had major effects on avian guild composition and diversity (Willis 1974, Karr 1982). In prairie habitats, disturbance by grazing alters habitat structure and causes changes in the composition of breeding bird communities (Risser et al. 1981). On smaller scales, the formation of gaps in tropical forest canopies by tree fall creates local fragments occupied by different species than an unbroken forest (Schemske and Brokaw 1981, Wiens et al. 1985b, Wunderle et al. 1987).

Induced fragmentation of a large area of habitat by disturbance causes a complex series of events. Overall area of available habitat is reduced, fragments become isolated, amount of edge habitat relative to interior habitat increases, and spatial relationships change among fragments. Species-specific habitat or space requirements or life history attributes and changes in interspecific interactions determine responses of species and individuals to these changes. One or all of these factors may lead to changes in the distribution and abundance of species. Small size fragments support fewer individuals of a species, and smaller populations may encounter difficulty maintaining a viable level of productivity under the constraints of interspecific and intraspecific competition, predation, or nest parasitism.

Individuals of different species have characteristic spatial requirements and predilections for edge versus interior locations in habitat fragments. These attributes determine the response of species to habitat fragmentation. Differences in individual area requirements are perhaps the most obvious. In Japan, the Japanese Pygmy Woodpecker (*Dendrocopos kizuki*) rarely inhabits forest fragments >100 ha, but the Brown-eared Bulbul (*Hypsipetes amourotis*) occupies fragments as small as 0.1 ha (Higuchi et al. 1982). Common Redstarts (*Phoenicurus phoenicurus*) and Wood Nuthatches (*Sitta europaea*) occur in greater frequencies in large wood lots than most birds; however, Winter Wrens (*Troglodytes troglodytes*) and the Common Blackbird (*Turdus merula*) frequently inhabited the smallest fragments in Britain (Moore and Hooper 1975). Similar differences in minimal-area requirements among species have been documented in the Netherlands (Opdam et al. 1985, Opdam and Schotman 1987), Sweden (Nilsson 1986), North America (Martin 1981, Lynch and Wigham 1984, Lynch 1987), and New Zealand (Diamond 1984, East and Williams 1984).

The Golden-cheeked Warbler assemblage in the FSA at Fort Hood experienced a disturbance in 1996 with a loss of habitat because of wildfire. The fire created a mosaic of different size fragments with variable suitability as nesting and foraging habitat. Upon their return to the FSA in 1996, male warblers showed site fidelity for previously occupied territories damaged or totally destroyed by the fire. As the breeding season progressed, the disruption to the population by the disturbance became apparent by movements of males within habitat units leading to high densities and saturation of small fragments and a reduction of productivity. In 1997, the males apparently adjusted to changes as high densities in small fragments declined. Males apparently searched for suitable habitat as indicated by substantially greater movement distances. This movement explains the reduction of density in small fragments as adult males dispersed to suitable habitat in larger semifragments or unburned areas of Fort Hood. Even though a flux in abundance continued for males in fragments, productivity for the FSA increased slightly in 1997. By 1998, the Golden-cheeked Warbler assemblage in semifragments in the FSA exhibited greater stability with higher productivity, less movement, and more habitat units with or near an optimum (or near optimum) density of males, indicating suitable habitat remained within the FSA.

CONCLUSION

The Golden-cheeked Warbler has been portrayed as dependent on large, unfragmented forest tracts. We documented that abundance of males in fire-disturbed habitat correlated with fragment size. Based on our results, there is merit in the advocacy by ornithologists and conservationists for managing and maintaining large tracts of forest at the landscape level within the breeding range of Golden-cheeked Warblers in Texas. Such conservation measures are underway to ameliorate habitat loss and preserve habitat on a regional scale at the Balcones Canyonlands National Wildlife Refuge in Travis, Burnet and Williamson counties, where a cowbird trapping program and a habitat conservation plan to limit deforestation and purchase land are in place (Ladd and Gass 1999). Various other small reserves are managed for the species in central Texas. However, much of the breeding habitat for Golden-cheeked

warblers in central Texas occurs on privately owned land with little or no habitat management. This is a concern for conservationists. Even if a social and political consensus to manage Golden-cheeked Warbler populations and habitat at the landscape level could be achieved, human land use practices and stochastic events will continue to cause small and large scale disturbances that will affect abundance and habitat integrity of this species.

Our study has shown the need for land managers to be proactive in controlling the destruction of Golden-cheeked Warbler habitat by wildfires. The buildup of hazardous fuels in a landscape is a priority concern because of the risk for catastrophic wildfires. This region is prone to periodic droughts, and the probability of wildfire is exacerbated during droughts. There is a need to protect large tracts of Golden-cheeked Warbler habitat through fire exclusion from the old growth Ashe juniper-oak woodlands. This can be accomplished by developing hard edges along roads and other natural breaks in the forest to suppress fire. Along edges brush management should be implemented to prevent the movement of a fire into the forest by removing all low-growing vegetation that would provide a ladder-effect for the spread of fire. Lower limbs on trees could be trimmed to give a buffer zone of 30–50 m for dampening and controlling the energy of the fire and preventing it from cascading into and through the canopy. The fuel load in these buffer zones should be maintained by periodic prescribed burns. If natural breaks or roads are absent in a landscape, large expanses of forest should be protected by constructing firebreaks with buffer zones. Although some habitat may be lost by cutting firebreaks, this is negligible compare to the potential loss of habitat by a massive crown fire.

Golden-cheeked Warblers responded immediately to a fire disturbance in its habitat after a fire caused fragmentation of a large, intact area of Golden-cheeked Warbler habitat. In the year following the fire, the population was unstable with considerable movement of males within and among patches of habitat. The species proved to be resilient in post-burn habitat of larger-size fragments and semifragments with more intact interior forest. Small fragments with a greater edge ratio did not support a viable assemblage of the species. The population experienced instability for a short time but returned to equilibrium within two years on two point count routes in the FSA. However, the post-burn abundance of Golden-cheeked Warblers in the FSA cannot compare to the abundance that would have occurred in the absence of the wildfire.

ACKNOWLEDGMENTS

Financial support and access to specific training areas were provided by the United States Army. The Nature Conservancy provided administrative support for the project. We thank S. Jester, T. Cook, P. Cavanagh, R. Craft, L. Sanchez, G. Albanese, M. Williams, and M. Buhler at Fort Hood for contributions to research design and field work. J. Ott, R. Reynolds, and M. Small provided assistance in statistical analysis and data interpretation.

This research was in part sponsored by the Department of the Army through cooperative agreements DPW-ENV-97-A-0001 and DPW-ENV02-A-0001. The contents of the information in this report do not necessarily reflect the position or the policy of the United States government, and no official endorsement should be inferred.

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