THE EFFECTS OF HABITAT FRAGMENTATION ON THE GOLDEN-CHEEKED WARBLER

A Dissertation

by

CADE LAWRENCE COLDREN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 1998

Major Subject: Wilder and Fisheries Sciences

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Approved as to style and content by:

Keith A. Arnold
(Chair of Committee)

Robert C. Maggio
(Member)

R. Douglas Slack
(Member)

Robert D. Brown
(Head of Department)

Kirk O. Winemiller
(Member)

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ABSTRACT

The Effects of Habitat Fragmentation on the Golden-cheeked
Warbler. (August 1998)
Cade Lawrence Coldren, B.S., Texas A&M University;
M.S., Texas A&M University
Chair of Advisory Committee: Dr. Keith A. Arnold

Habitat fragmentation has been implicated in the declines of some species of migratory songbirds. Effects on species within the remaining fragments may result from habitat loss, reduced patch size, increased isolation, increased edge, and the nature of the surrounding landscape matrix. I investigated the effects of habitat fragmentation on the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) at 100 sites in central Texas from 1993 through 1995. I found positive relationships of patch size with both pairing success and reproductive success. The degree of isolation showed no apparent effects on warbler reproductive success. Distribution of warbler territories relative to the edge was bimodal with peaks at 0-50 m and 100-200 m. Reproductive success was greatest in territories farther than 100 m from the edge, leading to the conclusion the Golden-cheeked Warbler is slightly forest-interior. Fourteen land uses were identified adjacent to habitat patches, but agriculture and grasslands more commonly abutted occupied patches while both medium-density and high-density residential development more commonly occurred adjacent to unoccupied patches. Territorial placement within a patch appeared to be influenced by adjacent land uses, with warblers selecting agriculture and grasslands as the nearest land use, and selecting against commercial development, entertainment, forested non-warbler habitat, and high-density transportation. Lowest reproductive success occurred in territories closest to forested non-warbler habitat. Distance to the edge and territory size were greatest for territories closest to land uses with the highest levels of human disturbance. Insect availability may best explain many of the patterns observed while nest predation and brood parasitism appear to exert less influence on warbler distribution and reproductive success. Management recommendations include minimizing further fragmentation, minimizing the types of land uses which occur adjacent to occupied patches, providing a buffer zone of natural grassland around occupied patches, and minimizing the extent of edges.

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INTRODUCTION

Many North American bird species appear to be experiencing population declines (Askins 1993). The group that has generated the most attention in recent years are those species which breed in North America and winter in Latin America (Terborgh 1989), collectively known as nearctic migrants (Hayes 1995), even though few of those species are endangered. The declines may result from factors occurring throughout the species annual cycle, including events on the breeding grounds, the wintering grounds and during migration. Considerable debate has centered on the relative roles of problems on the breeding grounds compared to the wintering grounds (Rappole and McDonald 1994, Latta and Baltz 1997), but evidence exists that closely ties the declines to problems during the breeding season (Wilcove 1988, Askins et a1. 1990, Sherry and Holmes 1992, Robinson and Wilcove 1994). Factors acting on the breeding grounds which may result in declines include habitat loss, habitat fragmentation, increases in nest predation and brood parasitism, and adverse weather on the breeding grounds (Hagan and Johnston 1992).

Fragmentation is a disruption of continuity (Lord and Norton 1990) and constitutes a major threat to the preservation of biodiversity (Wilcox and Murphy 1985). A dynamic process (Wiens 1989), fragmentation produces both habitat loss and isolation of remaining patches, which together lead to a decline in diversity (Wilcox 1980). Understanding how fragmentation produces such declines is an important conservation problem (Wilcox and Murphy 1985). The effect of habitat loss on a species is obvious, but the effects of isolation are more subtle. Populations in the remaining fragments are smaller, leaving them more vulnerable to extinction

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This dissertation follows the style and format of The Auk.

for a variety of reasons (Shaffer 1981, Wiens 1989). These extinctions may result from inadequacies of the remaining patches, but seemingly more important are the impacts that originate in the surrounding landscape matrix outside the patch (Saunders et al. 1991). Unfortunately, few studies have quantitatively evaluated the effects of the surrounding landscape mosaic on birds living within the remaining fragments (Hagan and Johnston 1992). Species-level studies have particular importance since they may yield more insight into what features make a species susceptible to fragmentation than community-level studies (Opdam 1991). Because fragmentation appears to be the prevalent trajectory of landscape changes in human-dominated forest regions of the world (Hansen and Urban 1992), species-level studies have become increasingly necessary in order to plan and coordinate conservation efforts.

One nearctic migrant that appears to have declined in recent decades is the Golden-cheeked Warbler (*Dendroica chrysoparia*) (U.S. Fish and Wildlife Service 1992). Listed as endangered in 1990, it breeds exclusively in central Texas, while wintering in southern Mexico (Vidal et al. 1994) and Central America (Pulich 1976). A habitat specialist during the breeding season, it requires a mostly closed-canopy forest consisting of a mixture of mature Ashe juniper (*Juniperus ashei*) and a variety of hardwood species (U.S. Fish and Wildlife Service 1992). Vidal et al. (1994) found Golden-cheeked Warblers occupying a variety of habitats during the non-breeding season and concluded that declines were probably due to factors occurring on the breeding grounds. Habitat fragmentation and sensitivity to urbanization have been listed as possible factors contributing to warbler declines (U.S. Fish and Wildlife Service 1992), but little quantitative data exist to support those contentions.

In this study I examined the effects of fragmentation on Golden-cheeked Warblers. Specific objectives were 1) to determine the effects of patch size, shape, and degree of isolation on warbler distribution and reproductive success; 2) to determine effects of habitat edge on warbler distribution and reproductive success; and 3) to determine the effects of adjacent land uses on warbler distribution and reproductive success. Specific hypotheses tested were 1) the Golden-cheeked Warbler is an edge species; 2) nearby land uses have no impact on warbler reproductive success; 3) patch size does not affect warbler reproductive success; 4) patch shape has no effect on warbler reproductive success; and 5) no relationship exists between warbler reproductive success and patch isolation.

REVIEW OF THE LITERATURE

Habitat Fragmentation

Fragmentation is a disruption of continuity (Lord and Norton 1990) and occurs when part of a large tract of vegetation is converted to other vegetation types or land uses, leaving scattered remnants of the original vegetation (Faaborg et al. 1995). These remnants are also referred to as fragments, patches, isolates, and habitat islands. They differ from the original tract by several factors, including decreased area, different shape, and different land uses on the periphery.

Fragmentation in its most severe form is called “insularization” and leaves isolated blocks in relatively inhospitable habitats. But fragmentation can be more subtle, as when logging leaves blocks of mature forest in a landscape of secondary growth, or when roads or power lines cross natural grasslands (Robinson 1997). Fragmentation may also result in a matrix of suitable habitats with islands of unsuitable habitat embedded within (Rudolph and Conner 1994). As a result, fragmentation exists as a continuum from a series of isolated patches in a sea of unsuitable habitats to a matrix of suitable habitats with islands of unsuitable habitat (Wiens 1994). The majority of studies on fragmentation have dealt with the former case.

Fragmentation implies a reduction in the total area of the original habitat type (Rolstad 1991) which is the most obvious effect of fragmentation (Faaborg et al. 1995). However, reduction of the habitat area can occur without fragmentation (Rolstad 1991), making the distinction between loss of habitat and fragmentation a crucial one. In some cases, habitat loss that occurs on the edge of a large habitat block may mimic the effects of fragmentation without actually breaking the original patch into multiple smaller ones. The biotic and abiotic processes acting on the patch may be altered in the vicinity of the habitat loss, effectively influencing the organisms in the patch in ways similar to that seen as a result of fragmentation.

Local extinctions in remnants may follow fragmentation for several reasons (Faaborg et al. 1995). An individual's home range may exceed the size of the remnant habitat patches (Wilcove et al. 1986). However, some species disappear from remnant habitat even though those remnants may be orders of magnitude larger than their average territory size (Knick and Rotenberry 1995). Some species’ dispersal capabilities may not be sufficient to allow movement between patches (Robinson and Wilcove 1994). Dispersing young may have more difficulty finding mates in landscapes with extensive patches of non-habitat (Conner and Rudolph 1991). Critical microhabitats may be missing from small fragments (Wilcove et al. 1986). Edge effects may reduce reproduction through increased rates of nest predation and brood parasitism (Robinson and Wilcove 1994). Food availability may differ with patch size (Ambuel and Temple 1983, Burke and Nol 1998). Effects of the landscape matrix surrounding the remnants may also result in local extinction (Wilcove et al. 1986). Taken together, these mechanisms indicate that the important attributes of the remnants for conservation efforts are patch density, isolation, size, edge effects and vulnerability to extrinsic disturbances (Lord and Norton 1990). These attributes are not necessarily independent of one another.

Defining fragmentation as a disruption of continuity permits application at any scale, both spatial and temporal (Lord and Norton 1990, Faaborg et al. 1995). Throughout this dissertation, scale refers to the extent of the region of interest. Thus, local scale corresponds to a small area, typically a portion of a patch, while landscape scale corresponds to a larger area, such as a patch. A regional scale encompasses an area containing multiple patches. Since different processes occur at different scales, it may be insufficient to study fragmentation effects at only one spatial or temporal scale (Addicott et al. 1987). In a review of the effects of fragmentation, Saunders et al. (1991) examined the effects at two spatial scales: within a patch and between patches. The advantage of this approach for most organisms lies in being able to examine the patterns and underlying processes at the scale of the individual and of the population. The scale of the individual appears analogous to the scale within a patch, while the population scale corresponds to the scale between patches. Most studies of fragmentation have adopted these scales. However, an understanding of how landscape-scale processes affect species distributions and metapopulation dynamics requires moving beyond those scales and adopting a regional scale (Robinson et a1. 1995). It appears that landscape-scale studies depend in part on knowledge gained from local-scale studies, but unfortunately, most species lack even local-scale studies.

Effects at a Local Scale

On a local scale, fragmentation affects species both temporally and spatially. Immediately after fragmentation occurs, displaced individuals crowd into remaining patches. Bierregaard and Lovejoy (1989) observed an increase in capture rates in fragments accompanied by an increase in vocalizations, indicating that behavioral changes may have also occurred. Working with Ovenbirds (*Seiurus aurocapillus*), Hagan et al. (1996) found increased densities along edges and subsequent lower pairing success and nest production. They suspected these reflected behavioral dysfunction, possibly from the inability of males to maintain territories at higher densities, or from the avoidance of fragments by females. However, these effects decrease with time as excess individuals emigrate or suffer mortality.

Edge Effects

Fragmentation results in a higher proportion of edge relative to interior habitat than existed in the original large habitat blocks (Temple 1986, Wiens 1989). Edge is defined as the junction between two different landscape elements (Yahner 1988) and may exist as either a well-defined boundary or as a transition zone (Harris 1988). Traditionally, wildlife management advocated increasing amounts of edge (Leopold 1933) because many game species tend to be associated with edges. In recent decades, focus on non-game species has altered that viewpoint of edge as being universally beneficial to encompass its detrimental impacts on some species as well. Spatially, edge affects species by influencing their distributions within a patch and their reproductive success. Changes in diversity, abundance, and spatial distribution of organisms associated with the transition between habitat types have been termed edge effects (Yahner 1988). Edge has width (Matlack 1993) and the width of effects differs for different processes acting along the edge (Bradshaw 1992). Thus, each fragment has an edge width along the boundary and interior habitat that is relatively unaffected by the processes acting along the edge. That interior habitat has been termed the core area (Temple 1986). Edge width has often been estimated by a variety of means, such as diversity indices (Yahner 1987), distribution of nests and territories (Gates and Mosher 1981, Kroodsma 1987), or occurrences of nest predation and brood parasitism (Brittingham and Temple 1983, Wilcove 1985). Unfortunately, the width of edge effects can be difficult to determine in ecologically meaningful terms (Kroodsma 1987). As a result, determination of edge width is usually subjective (Chen et al. 1996), but may best be defined by the functional use of edges by wildlife (Yahner 1988). Although defining edge width in this manner may seem circular, imposing edge width values based on researchers' preconceived notions of edge may obscure understandings of how various species perceive edge. Edge as defined by humans may not correspond to the features species may respond to as an edge (Hawrot and Niemi 1996).

Type of edge may also influence species responses and has been studied in two manners. One is the difference in productivity between two adjacent landscape elements. Angelstam (1986) felt that edge effects should be more pronounced with increasing steepness of the productivity gradient. The second way of viewing edge type has been to investigate the effects of different vegetative structures occurring along the edge. A gradual change in vegetation between two landscape elements has been termed “soft”, “subtle”, or “feathered”, while a sharp change has been called “hard” or “abrupt” (Ratti and Reese 1988, DeGraaf 1992, Hawrot and Niemi 1996). Ratti and Reese (1988) found that predation rates on artificial nests along hard edges were higher than in soft edges. The soft edges have greater vegetative complexity and may reduce predator search efficiencies. Hawrot and Niemi 1996) concluded that each species life history determines its response to different edge types. They also felt that edge type may ultimately become more important than the amount of habitat available and its juxtaposition in the landscape as fragmentation proceeds.

Edge affects species differently, with some benefiting and others being adversely impacted (Wiens 1989). Those species that depend on edge rely on increased amounts of either nesting or foraging habitats or both, generally resulting in population increases after fragmentation (Askins et a1. 1990). Other species occur in lower numbers near edges, possibly due to high rates of nest predation (Temple and Cary 1988), brood parasitism (Brittingham and

Temple 1983) or edge-related changes in vegetation structure (Kroodsma 1984). However, those species may not actively avoid edge (King et al. 1997), but simply occur in lower abundances near edges due to selection for mature habitat which generally occurs away from edges (Kroodsma 1984, Rich et al. 1994). This results in many fragments appearing unsuitable for those species because of insufficient amount of core area for species occupation.

Creation of edge affects species by inducing changes in both abiotic and biotic factors (Saunders et al. 1991). Abiotic factors affected by the presence of edge include solar radiation, wind and water flux. These combine to produce changes in vegetative composition and structure (Ranney et al. 1981). As a result of vegetation changes and the influence of the surrounding landscape, changes occur in the vertebrate and invertebrate fauna along the edge (Saunders et al. 1991). Individuals living within the patch come into contact with a new suite of species. Some of these species are adapted to life along the edge. Others occur there as a result of changes in the surrounding landscape while being supported in part by that landscape. Ultimately, individuals within the patch may experience decreases in pairing success and reproductive success due to increases in such processes as nest predation and brood parasitism (Faaborg et al. 1995, Robinson et al. 1995). However, linking the effects of predation and parasitism to subsequent population changes has often proven elusive (Newton 1993, Robinson and Wilcove 1994).

Nest Predation

The impacts of nest predation and brood parasitism on nearctic migrants have received much attention in recent years and merit closer examination. Increases in the amount of edge due to fragmentation have apparently resulted in increased rates of nest predation along those edges (Wilcove 1985), but the results are equivocal. In a comprehensive review of predation studies on both artificial and real nests, Paton (1994) concluded that edge effects from nest predation were most strongly felt within 50 m of the edge. Most of the studies he reviewed were of open cup nests placed on or near the ground and were in simplified systems consisting of woodlands and fields. However, other studies have failed to find a relationship between nest predation and the edge. For example, Rogers (1994) documented nest predation as the greatest cause of nest failure in Alaska, but found the number of fledglings per nest and the distribution of nest predators to be edge-independent. Thus, distinctive patterns of predation appear to emerge in different regions (Santos and Telleria 1992, Hannon and Cotterill 1998). Nour et al. (1993) found that predation by birds, mostly corvids, occurred more frequently near edges and diminished with increasing distances from the edge. Mammalian depredation increased in the interior, effectively compensating for the drop off in avian predation, resulting in no clear edge effects. Hannon and Cotterill (1998) obtained similar results. Failing to find increased nest predation near edges, Berg et al. (1992) suggested the edge effect of nest predation depends on habitat types and concluded that higher predation is not a general rule for edges between all habitats. Apparently the vegetational characteristics of the edge may also determine whether nest predation is edge related (Ratti and Reese 1988). Hard edges appear more conducive to edge effects from nest predation than soft edges.

The predator assemblage may influence rates of nest predation in fragments in several ways. Densities of predators may be higher in smaller fragments, resulting in increased predation rates (Wilcove 1985). Densities of generalist predators, specifically corvids, may relate to the extent of different land uses in the surrounding landscape matrix (Andren 1992). As certain land uses such as agriculture increase, predator densities increase, resulting in higher predation rates in fragments (Chamberlain et al. 1995). Nest predation may be a function of predator species composition and abundance (Leimgruber et al. 1994, Telleria and Diaz 1995). In some cases, the predator assemblage occurring within fragments may exert a greater influence than predators associated primarily with the surrounding landscape (Hannon and Cotterill 1998). Mammalian and reptilian nest predators may exert a greater influence on predation rates than avian predators (Patnode and White 1992, Morton et al. 1993). However, nest predators may be subject to fragmentation effects resulting in impoverished predator assemblages in small patches (Telleria and Santos 1992). Also, predator species composition may change with patch size (Haskell 1995). This may account for the lower predation rates found on small patches by Berg et al. (1992). Studies of nest predation using quail eggs in artificial nests may overestimate the impacts of fragmentation on nest predation rates (Haskell 1995). Thus, the attributes of the predator assemblage and the experimental design used to test edge effects must be considered when evaluating nest predation rates resulting from fragmentation. As a result, increased rates of nest predation due to fragmentation may not be a universal pattern in all landscapes.

One extension of possible edge effects on nest predation rates is the ecological trap hypothesis (Gates and Gysel 1978) in which birds nest near edges because of increased food abundances and foraging areas, but suffer higher rates of nest predation as a result. In a test of the ecological trap hypothesis, Ratti and Reese (1988) found that nest predation did not increase with higher nest densities along the edge. Santos and Telleria (1992) put forth another way to view the ecological trap hypothesis when they could not document an edge effect in small patches and concluded that the patches themselves were acting as ecological traps.

Brood Parasitism

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite that lays its eggs in the nests of other birds and relies on the host adults to raise the cowbird young to independence (Lowther 1993). Cowbird parasitism lowers host reproductive success by reducing the number of host young that reach independence. Consequently, high rates of parasitism may be one of the factors responsible for the declines seen in nearctic migrant populations (Brittingham and Temple 1983, Robinson et al. 1995). Brown (1994) estimates that parasitism rates of over 30% may lead to unstable populations, making them susceptible to extinction from stochastic events. Declines in some species are directly attributable to high rates of parasitism, including the Least Bell's Vireo (*Vireo bellii pusillus*) (Goldwasser et al. 1980), Black-capped Vireo (*Vireo atricapillus*) (Grzybowski et al. 1986), and Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1977). Rates of parasitism appear to be higher near forest edges, but are also related to the amount of nearby open habitat for cowbird foraging (Brittingham and Temple 1983). As with nest predation, the results of parasitism studies are equivocal. Hahn and Hatfield (1995) found parasitism rates on migrant hosts were no higher than on residents and that parasitism rates were not higher closer to the edge. They also observed low parasitism rates on some host species that appear vulnerable elsewhere. Additionally, some hosts seem more susceptible than others (Donovan et al. 1995b). Thus, while parasitism may impact populations by reducing reproductive success, its effects differ by species, geographic region, and the nature of the surrounding landscape.

Effects at a Landscape Scale

On a larger scale, fragmentation affects species both temporally and spatially, just as it does at a local scale. After fragmentation, species occurring in the remaining fragments may eventually go extinct, a process known as faunal relaxation (Diamond et al. 1987). After a change in a controlling variable, such as patch size in the case of fragmentation, species diversity decreases over time from one equilibrium value to another. Local extinctions and the resulting decline in diversity may arise due to small population sizes and changes occurring within the fragments, including habitat alterations, disturbance, and secondary extinctions. As an example of faunal relaxation, Temple and Cary (1988) reported the gradual loss of American Redstarts (*Setophaga ruticilla*) from patches smaller than 100 ha in the 75 years following severe fragmentation in Wisconsin. They suggest this loss over time may result from a lack of good-quality interior habitat in the remaining small patches.

Fragmentation affects species at a landscape scale by affecting the characteristics of the remaining fragments, including patch size and shape, the degree of isolation, and the nature of the surrounding landscape matrix (Lord and Norton 1990). One might consider all of these characteristics at the scale of the individual (Knick and Rotenberry 1995), but the effects would then be most apparent only for species with territories greater than the area of the remaining patches. Those species will simply not exist in patches smaller than their territorial requirements. The effects of these patch characteristics may also be apparent for species with large home ranges, such as some raptors, but those species may then view the results of fragmentation merely as fine-grained heterogeneity in the landscape (Rolstad 1991).

Patch Size

The patch characteristic that has received the most attention from researchers is patch size, and most of that research has been directed toward its effects on species diversity. Stated simply, larger patches support more species (Galli et al. 1976, Askins et al. 1987), whether the patches are woodlots in suburban areas (Tilghman 1987), different aged forest stands in a clear-cut landscape (Helle 1984), or woodlots in an agricultural landscape (Blake and Karr 1987). Species occurrences in isolated woodlots appear non-random in a pattern of nested subsets (Blake 1991), suggesting that species occurrences are based on biological processes and not chance. Since patch size itself is a problematic ecological variable (Helle 1986), those processes are probably correlated with patch size and may include food limitation (Blake 1983, Burke and Nol 1998) and microhabitat loss (Karr 1982). Although patch-size effects appear widespread, they are not universal. In the western United States, Johns (1993) found forest-interior species to be dependent on patch size, yet Schieck et al. (1995) failed to find an area effect with old-growth species. He concluded that species in western montane landscapes probably evolved with a high degree of habitat heterogeneity and may be less sensitive to fragmentation. In Brazil, Stouffer and Bierregaard (1995) did not detect area effects on a hummingbird assemblage, probably due to the birds' willingness to cross open areas while foraging.

While the species-area relationship determines approximately how many species may occupy a patch, it provides no insight into which species may be lost from fragments (Saunders et al. 1991). In North America, species that tend to disappear from small patches generally are area-sensitive nearctic migrants (Whitcomb et al. 1981). One approach to resolving the dilemma as to when smaller patches lose a species has been to consider the minimum area requirement for each species, although this approach has been relatively unsuccessful (Faaborg et al. 1995). Minimum area estimates vary widely across the range of a species (Hayden et al. 1985, Robbins et al. 1989) and tend to be based on presence/absence data and neglect reproductive success. True estimates should include information on both demography and dispersal (Shaffer 1981). Interestingly, species known to be area-sensitive on the breeding grounds also preferentially use large patches during migration (Cox 1988).

Patch size appears to affect reproductive success. In a review of a variety of studies on edge effect, Paton (1994) also found a positive relationship between patch size and nest success for both artificial and real nests. Working with Ovenbirds in Pennsylvania, Noojibail (1995) documented higher nesting success in larger patches than in small ones. Whether patch size effects on reproduction hold for other species remains to be seen. One mechanism which may produce lower reproductive success in patches is a patch size effect on food (Ambuel and Temple 1983). Burke and Nol (1998) documented an area effect of Ovenbird food supplies, resulting in decreased pairing success in smaller fragments and ultimately in reduced reproductive success.

Patch Shape

Shape determines the amount of edge relative to the amount of core habitat in a patch with core defined as the area >100 m from the patch boundary (Temple 1986). Long narrow patches have higher ratios of edge to core than circular or square patches. For forest-interior species, core area predicts species occurrences better than patch size. As a result, patch shapes that maximize core area appear more suitable for occupation by forest-interior species than narrow patches where edge dominates (Wilcove et al. 1986).

Degree of Isolation

The degree of isolation has usually been estimated in terms of the distance between patches in the landscape. MacArthur and Wilson (1967) stated that isolated patches will support fewer species or at lower densities than less isolated patches. Distance may affect populations by limiting dispersal because of unfavorable habitat separating patches (Faaborg et al. 1995). Some research on nearctic migrants supports this. Lynch and Whigham (1984) found that nearctic migrants appeared more sensitive to isolation than either resident or short-distance migrant species. They showed that even a slight degree of isolation may reduce local abundances. For example, local densities of Red-eyed Vireos (*Vireo olivaceus*) and Wood Thrushes (*Hylocichla mustelina*) declined 2% with each 100 m of isolation. Askins and Philbrick (1987) reported a positive relationship between migrant abundance and the amount of forest within 2 km of a patch. They also found an increase when nearby areas were allowed to regrow into forest. Similar patterns were found by Howe and Jones (1977) and Johns (1993). Askins et al. (1987) concluded that patch size was most important in determining total density and diversity of forest-interior species for small patches, but isolation was most important for large patches. However, Turchi et a1. (1995) failed to find a relationship between isolation and species richness in aspen groves in the western United States. Ultimately, the distance from other patches may be less important for migrants who effectively “colonize” each patch every spring (Harris and Wallace 1984).

Surrounding Landscape

One of the most striking aspects of fragmentation is the change in the landscape surrounding each remaining patch. The original vegetation type is replaced with a land use that can be quite different from the original vegetation. How those new land uses impact the species in the remaining patches remains largely unstudied (Hagan and Johnston 1992). The internal ecosystem processes acting within a patch will continue to operate, but the patch is now subject to external influences arising from the surrounding landscape matrix (Hobbs 1993). As a result, patches of similar size and vegetation may not be ecologically equivalent because of differences in their surroundings (Friesen et al. 1995). Models indicate the surrounding landscape may be more important than distance to the edge or patch size (Donovan et al. 1995a), with the overall landscape quality and pattern governing reproductive success. For example, Wood Thrushes breeding in large blocks (>10,000 ha) in a highly fragmented landscape showed the same reduced reproductive success as in small fragments in the same landscape (Donovan et al. 1995a). As a result, patches probably should be viewed as part of the landscape matrix with interactions between the patches and their matrix, instead of viewing the patches as separate entities (Webb 1989). Additionally, the adjacent land uses may exert a stronger influence in a patch than more distant land uses (Dunning et al. 1992).

Landscape-scale studies of fragmentation effects reveal that landscape variables can be important in determining patch occupancy (Knick and Rotenberry 1995) and reproductive success of individuals within the fragments (Porneluzi et al. 1993, Donovan et al. 1995a, Robinson et al. 1995). These studies all looked at landscape variables such as the amount of forest cover within a certain distance of each patch. No attempts were made to quantify the effects of different land uses. At a local scale, land use effect studies have centered around evaluating the effects of one land use category on species in small patches compared to controls, usually a large patch. Studies that directly evaluated the differences between varying land uses compared them only in general terms, such as “rural” compared to “suburban” (Wilcove 1985).

Impacts of Single Land Use Categories

Several studies have considered the impacts of fragmentation in an agricultural landscape without directly evaluating the effects of agriculture *per se* (i.e. Andren l992). Rates of nest predation typically increase with increasing amounts of agriculture in the surrounding landscape. Reproductive success of Black Grouse (*Tetrao tetrix*) decreased as the amount of agriculture in the landscape increased (Kurki and Linden I995). Robinson (1997) speculated that agriculture may introduce agrochemicals, both pesticides and herbicides, which potentially could affect mortality and reproduction. Pesticides could impact birds directly through lethal poisoning or indirectly by reducing food levels. Herbicides could affect birds by simplifying the vegetative species composition and structure, potentially reducing the amount of cover and food resources (Gard and Hooper 1995).

Roads affect species in adjacent patches by influencing species distribution, abundance, and reproductive success. Ferris (1979) found road effects up to 400 m from a highway with some species abundances correlating positively with increasing distance from the highway. Populations in patches adjacent to a two-lane road did not differ significantly from those adjacent to four-lane roads. Rich et al. (1994) showed that road corridors as narrow as 8 m differentially attract avian nest predators and Brown-headed Cowbirds. Also, egg predation was edge-related along a minor dirt road through a tropical forest (Burkey 1993). Thus, land uses as subtle as a dirt road may affect species breeding in forests on either side of the road. Willow Warbler (*Phylloscopus trochilus*) males showed lower pairing and reproductive success near a road compared to those farther away, implying a lowered habitat quality near the road (Reijnen and Foppen 1994). However, the effects of a road *per se* differ from the effects of human activities on the road (Van der Zande et al. 1980). These two effects appear difficult to separate.

Residential impacts may affect species more seriously than other land uses, such as logging, because residential development results in permanent fragmentation (Askins 1992) while reducing habitat value of adjacent wetlands and forests through incidental impacts such as erosion, sedimentation, pollution, deposition of debris, and proliferation of non-forest species (Dowd 1992). These effects on wetlands and forests from the adjacent residential development may produce a variegated landscape (McIntyre and Barrett 1992) with areas of intermediate disturbance. The level of disturbance associated with residential development might best be measured by the frequency of maintenance of structures, such as roads, buildings, and plantings, within the developed area (Blair 1996). Studies of residential impacts generally fall into two categories: urbanization effects within a patch and development effects on adjacent patches. Urbanization studies typically consider the effects along a gradient from “natural” to “urban”

(Aldrich and Coffin 1980, Sodhi 1992, Jokimaki and Suhonen 1993, Blair 1996, Konstantinov 1996). In general, avian diversity declines while abundances increase along the gradient from natural to urban, but the results are equivocal. In some cases, diversity increased (Aldrich and Coffin 1980) or remained the same (Sodhi 1992). Blair (1996) found that diversity was highest at intermediate levels of human disturbance. In all cases, human-adapted species replaced forest species as the levels of human disturbance increased.

Avian diversity and abundances are lower in areas adjacent to increasing densities of houses and other buildings (Tilghman 1987, Friesen et al. 1995), a result that was independent of patch size. In fact, Friesen et al. (1995) found greater diversity and abundance in 4 ha patches with no adjacent development than in 25 ha patches adjacent to development. Herkert et al. (1993) believed that detrimental influences from urban sprawl may explain why many species appear to be declining in areas where forest regeneration has occurred.

Transmission line corridors through forests cause declines in abundances of some nearctic migrants in the vicinity of the corridor (Anderson 1979, Kroodsma 1984). Chasko and Gates (1982) reported edge type as an important factor affecting forest species, with hard edges functioning more as natural territorial boundaries than soft edges. Nest predation rates along hard edges increased near the edge, resulting in increasing fledgling success with increasing distance to the edge. Along corridors, overall diversity tends to increase due to the addition of shrubland (Chasko and Gates 1982) or grassland (Anderson 1979) species along the corridor. Some forest species may be sensitive to corridor effects because of greater specialization in nest microhabitat requirements than the invading grassland or shrubland species (Chasko and Gates 1982). Interestingly, some migrant species documented as sensitive to fragmentation do not move away from corridors, implying a sensitivity to other factors associated with fragmentation such as patch size and isolation (Kroodsma 1984).

GOLDEN-CHEEKED WARBLER

One nearctic migrant that has apparently declined is the Golden-cheeked Warbler (U.S. Fish and Wildlife Service 1992). The United States Fish and Wildlife Service listed it as endangered on 4 May 1990 by means of an emergency rule with final listing taking place on 27 December 1990. Loss of habitat appears to be the greatest threat facing the Golden-cheeked Warbler (US. Fish and Wildlife Service 1992). On-going and imminent habitat destruction, particularly from urbanization and clearing for agricultural purposes, was used to justify its emergency listing. Secondary threats include cowbird parasitism, loss of oaks to “oak wilt” fungus (*Ceratocystis fagacearum*), habitat fragmentation and proximity to urbanized areas. The importance of each of these factors, particularly the latter two, remains largely unknown.

The impacts of several aspects of fragmentation on Golden-cheeked Warblers, including patch size, predation, parasitism, and the surrounding landscape matrix, have received attention since its listing in 1990. Arnold et al. (1996) found that warblers consistently occupy patches larger than 23 ha. Additionally, they consistently found young warblers in patches larger than 23 ha, but patch size effects on rates of reproduction and pairing success were not determined.

In his detailed study of Golden-cheeked Warblers, Pulich (1976) documented only one case of nest predation. He observed a rat snake (*Elaphe obsolete*) that had eaten a brood of warbler nestlings. Engels and Sexton (1994) reported a negative correlation between warblers and Blue Jays (*Cyanocitta cristata*), but the findings of Arnold et al. (1996) showed positive relationships between warblers and a variety of avian predators. In a study of artificial nests placed in Golden-cheeked Warbler habitat, Fink (1996) found high rates of nest predation (63%)

and documented predation by rat snake, Blue Jay, and Western Scrub-Jay (*Aphelocoma californica*). Also, he found only one case, out of 20 possible cases, of a significant difference in predation between edge and interior nests. Despite these research efforts, rates of predation on actual nests and their impacts on warbler populations remain unknown.

Like nest predation, the impact of parasitism on warbler populations remains uncertain. Pulich (1976) reported a parasitism rate of over 57% (19 out of 33 nests), although he gave no details on the land uses in the vicinity of his study site. In contrast, Beardmore (1994) found a parasitism rate of 8.3% (one out of 12 territories) while Arnold et al. (1996) found only four cowbird chicks accompanied by Golden-cheeked Warbler adults while monitoring more than 700 territories over the three years of their study.

Knowledge of the effects from the surrounding landscape on Golden-cheeked Warblers is rudimentary. Engels (1995) could predict warbler presence/absence with a reasonably high degree of success (83%) based on a model incorporating three variables: number of homes within 500 m of his sample points, percentage of urbanized area within 1 km of his sample points, and the presence/absence of water within 300 m of his sample points. He defined urbanization as including homes, buildings, manicured lawns, paved roads, campgrounds and other recreational areas, golf courses, refuse areas and parking lots. He excluded livestock pastures, farm land, unmanicured grasslands, unpaved roads, and hiking trails from urbanization. Engels did not test the relative effects of each land use lumped into his urbanization category. nor consider effects on reproductive success. Arnold et al. (1996) investigated the effects of agriculture, commercial development, industry and residential development on warbler presence/absence and reported agriculture as the most compatible land use of these four. They found that Golden-cheeked Warblers occur in patches near commercial and residential development given sufficient patch size. Industry had more pronounced effects than agriculture, but less so than commercial or residential development. Regarding reproductive success, they found that commercial development, industry and residential development occurred significantly less often than expected by chance within 100 m of successful territories.

The effects of many aspects of fragmentation on Golden-cheeked Warblers remain poorly studied. Nothing is known about the possible effects of patch shape or degree of isolation on warbler populations. The importance of edge for the warbler requires further study. Kroll (1980) described the Golden-cheeked Warbler as an edge species and recommended cutting warbler habitat into narrow strips. This result differs from the viewpoint of Wahl et al. (1990) who feel warblers reproduce better in large blocks of unfragmented habitat with minimum amounts of edge. Unfortunately, no quantitative studies of the impacts of edge on Golden-cheeked Warbler territorial placement, pairing success or reproductive success exist (US. Fish and Wildlife Service 1992). Additional information on landscape effects is needed. The land use categories used by Engels (1995) and Arnold et al. (1996), collectively being urbanization, agriculture, commercial development, industry, and residential development, are oversimplified and do not adequately cover all land use possibilities, such as roads.

METHODS

STUDY SITES

I conducted this study on the effects of fragmentation on Golden-cheeked Warblers at 100 sites, 99 in western Travis County and one in western Williamson County, central Texas, during the breeding seasons of 1993 through 1995. This region represents a unique setting to study the effects of various land uses. Urbanization is increasing on the east due to the growth of the city of Austin, while ranching dominates in the west. By limiting my study to the western portions of Travis and Williamson counties, I controlled for differences in elevation, topography, rainfall, temperature, vegetation, and avian species compositions.

Woody vegetation at these sites consisted of Ashe juniper and a variety of hardwood species. Listed in decreasing order of abundance (Arnold et al. 1996), these include Texas oak (*Quercus buckleyi*), plateau live oak (*Q. fusiformis*), scaleybark oak (*Q. sinuata* var. *breviloba*), Texas persimmon (*Diospyros texana*), Texas ash (*Fraxinus texana*), hackberry (*Celtis reticulata*), cedar elm (*Ulmus crassifolia*), deciduous holly (*Ilex decidua*), escarpment black cherry (*Prunus serotina*), Arizona walnut (*Juglans major*), coma (*Bumelia lanuginosa*), evergreen sumac (*Rhus virens*), roughleaf dogwood (*Cornus drummondii*) and Texas mountain laurel (*Sophora secundiflora*).

FIELD TECHNIQUES AND MAPPING

I generated random latitude-longitude coordinates using a computer-based random-number generator and limiting the coordinates to the western portion of Travis County. These were then overlaid on maps showing all potential warbler habitat in western Travis County. These maps were generated by the Center for Mapping Sciences, Texas A&M University, and based on a computer classification of satellite imagery. Each potential study site was chosen as the habitat block nearest to each random latitude-longitude coordinate. Many of the habitat blocks were composed of multiple parcels with different owners, so permission was requested from all landowners. Some potential study sites were discarded because the portions with landowner permission were smaller than 5 ha, the minimum deemed necessary to include at least one warbler territory (Pulich 1976). Only the portions of the study sites with landowner permission were surveyed for warblers.

Teams conducted a minimum of three censuses in each study site, all in good weather and between the following dates to meet U.S. Fish and Wildlife Service guidelines for Golden-cheeked Warbler censuses: 16 March to 31 May 1993, 20 March to 12 May 1994, and 20 March to 10 May 1995. Teams conducted additional censuses until 2 July of each year to determine warbler reproductive success. Broadcast tapes of Golden-cheeked Warbler territorial song were used to verify the absence of warblers. Each site was surveyed as completely as possible, with exact routes for each site based on the particular natural and man-made features at each site. All warblers were spot-mapped using standard mapping techniques (International Bird Census Committee 1970). Locations were registered using Trimble Pathfinder Basic Global Positioning System (GPS) units.

Golden-cheeked Warbler reproductive success was determined by following each individual bird as long as possible without knowingly disrupting its behavior, and observing all possible indications of breeding. Signs of breeding included nest building, adults carrying food and the presence of fledglings. Fledgling young are most easily found by listening for the rapid “chipping” given by the young when begging or by the adults while feeding the young (Pulich 1976). The locations of all young were registered via GPS. No attempts were made to locate warbler nests due to concern over the possibility of increased risks of nest abandonment or nest loss due to predation or parasitism. For analyses of reproductive success, I classified each territory as having "high" reproductive success if any indication of breeding was observed. All other territories were classified as having "low" reproductive success. Further, I classified each site based on the overall reproductive success for all territories located within each site. High success sites had at least 50% of all territories classified as having high reproductive success, while low success sites had less than 50% of the territories being successful. Pairing success of a territory was based on either the presence of a female or any of the indications of breeding as used for determining reproductive success.

To determine if differences in Golden-cheeked Warbler reproductive success were correlated with differences in habitat, the teams conducted vegetation analyses at each site. They made all measurements in July of each year after the end of the breeding season. Vegetative measurements were taken at the location of the first visually recorded warbler for each site. Only trees taller than 1 m and with a diameter greater than 3 cm, measured 10 cm above ground, were included (Ladd 1985). Circumference, height, and species were recorded for all trees in a 2 m wide by 50 m long area extending in each of the cardinal directions from the sample point. Canopy cover was estimated at 10 m intervals in each of the cardinal directions using a spherical densiometer (Lemmon 1956) and then averaged to obtain a mean canopy cover for each site. Mean slope was determined by averaging slope as measured with a compass/clinometer at 10 m intervals.

I classified all land uses adjacent to the study sites into one of 14 categories as defined in Table 1. Site boundaries were determined as the extent of apparently suitable warbler habitat. Additionally, I classified all land uses across roads from my study sites into the categories described in Table 1 and one additional category: warbler habitat. All classifications were based both on aerial photographs and, particularly for agriculture and grasslands, ground truthing. I classified all edges into two edge types. Hard edges occur where the change from warbler habitat to the adjacent land use is less than 3 m wide, while soft edges exceed 3 m in width. I based my edge type classifications mostly on ground truthing, but to a lesser extent, on aerial photographs.

I entered all GPS locations of Golden-cheeked Warblers into Arc/Info, a Geographic Information System (GIS) software package at the Center for Computing Sciences, Texas A&M University. I determined warbler territorial locations by approximating the territorial center based on all observations and the occurrence of contemporaneous contacts between multiple singing males (International Bird Census Committee 1970). Site boundaries, land uses, and edge types were mapped on U.S.G.S. 7.5 minute topographic quadrangle maps (scale 1224000), based on field observations and recent aerial photographs. These maps were digitized at the Center for Mapping Sciences, Texas A&M University. I created GIS cover layers for the site boundaries, land uses, edge types, and warbler territorial locations. I calculated patch sizes and perimeters from the GIS site boundary cover and approximated the distance to the edge to the nearest 10 m for each warbler territory using territorial coordinates and the site boundary cover. 1 determined which land use category and edge type occurred closest to each territorial center using the land use and edge type covers overlaid on the territorial cover.

TABLE 1. Land use classification for areas adjacent to Golden-cheeked Warbler habitat patches.

Land use	Definition
Agriculture	Active livestock operations, either cattle or goats, or grasslands showing evidence of grazing
Commercial	Businesses and churches
Entertainment	Golf courses and campgrounds
Forested non-warbler habitat	Stands of young Ashe juniper with few hardwoods
Grassland	Predominantly grass with a few scattered trees and no visible signs of livestock grazing
Industrial	Highway construction, water treatment facilities, electrical substations, and quarries
Open water	Lake Travis and the Colorado River
Low-density residential	Single-family housing units separated by at least 100 m
Medium-density residential	Single-family housing units separated by less than 100 m
High-density residential	Multiple-family housing units
Low-density transportation	Unpaved roads
Medium-density transportation	Two-lane paved roads
High-density transportation	Four-lane paved highways
Utilities	Powerline corridors maintained as predominantly grassland

STATISTICAL ANALYSES

Because each study site was chosen as a separate habitat patch, all sites were considered statistically independent. I included for analyses only Golden-cheeked Warbler territories with more than one observation because one observation is insufficient to determine territorial boundaries or warbler reproductive success. All statistical analyses were performed using the SAS statistical analysis software package (SAS Institute 1988) with all alpha levels set at 0.05.

I tested differences in reproductive success between years using Chi-square test of homogeneity. Since reproductive success did not differ between years (see Results Section), I combined data for all years for further analyses. To determine whether reproductive success was based on the survey effort for each site, I calculated the average survey time per territory at each site and compared sites with high and low reproductive success, using Wilcoxon ranked-sum test.

To look at patch size effects at occupied patches, I first grouped all sites into three patch size classes: small sites (<32 ha), intermediate sized sites (between 32 ha and 100 ha), and large sites (>100 ha). To test whether warblers selected patches based on patch size, I used Chi-square goodness-of-fit test. I based expected values for each size class on the combined area in each size class. For patch size effects on reproductive success, I calculated a reproductive ratio for each site from the number of territories with high success to the total number of territories at a site. I then regressed the reproductive ratio against log-transformed patch size values. I performed a similar analysis to look at patch size effects on pairing success using a pairing ratio for each site, defined as the ratio of the number of paired males to the total number of males at a site.

I considered patch shape effects two ways. First, I calculated the perimeter-to-area ratio for each site. I then regressed the reproductive ratio for each site against its log-transformed perimeter-to-area ratio. Next, I determined the fractal dimension by regressing the log-transformed perimeter against the log-transformed patch size for each site, with the fractal dimension equaling two times the slope of the regression line (O'Neill et al. 1988).

Using vegetative measurements, I determined the following parameters for each site: average slope, average canopy cover, density of understory junipers, density of canopy junipers, density of understory hardwoods, density of canopy hardwoods, basal area of understory junipers, basal area of canopy junipers, basal area of understory hardwoods, basal area of canopy hardwoods, average height of understory junipers, average height of canopy jumpers, average height of understory hardwoods, and average height of canopy hardwoods. I defined understory trees as those shorter than 4.5 m. All variables were log-transformed prior to analyses. I tested the vegetative variables to determine if differences in vegetation account for differences in reproductive success among sites and if any of the vegetation variables vary with patch size. I used principal component analysis to graphically examine the differences between high and low reproductive success sites using all vegetation variables. Using t-tests, I examined the differences between sites with high and low reproductive success for each vegetation variable. I tested each variable between patch size classes, regardless of reproductive success, using analysis of variance (ANOVA). Additionally, I examined whether vegetative species composition affected warbler reproductive success or varied with patch size. Separate diversity values were determined for all woody species together, for shrub layer species only, and for canopy species only. I used Wilcoxon ranked-sum test to compare diversity values between sites of high and low reproductive success and Kruskal-Wallis test to compare diversity values among the three patch size classes.

I grouped all territories, based on their distance from territorial center to the nearest edge, into the following distance classes: 0-50 m, 51-100 m, 101-150 m, 151- 200 m, 201-250 m, and >250 m. Using Chi-square goodness-of-fit test, I evaluated the relationship between warbler territorial placement and edge, both for all sites combined and among patch size classes. Since the areas within each distance class differed, I determined the expected values for each Chi-square cell by allotting the total number of territories uniformly across distance classes, based on the total area contained within each distance class. Similar analyses were used to look at edge effects on warbler reproductive success. Expected values in this case were based on the overall reproductive success rate of 39.58%.

Chi-square tests of homogeneity were used to test whether Golden-cheeked Warblers selected for edge types and whether edge types affected reproductive success. I also grouped all territories based on edge type and the land use category nearest to each territorial center and tested edge type-land use associations with Chi-square test of homogeneity. Distance to the edge was log-transformed and compared between edge types using t-tests.

Because Temple and Cary (1988) originally considered core area as all interior area greater than 100 m from the edge whereas Paton (1994) found edge effects to be felt most strongly up to 50 m from the edge, I felt that analyses on core area should incorporate a variety of distances from the edge. Therefore, I performed separate analyses on core area effects at 50 m intervals up to 250 m from the edge. I chose 250 m as a maximum because few territorial centers occurred at distances greater than 250 m in both small and intermediate sized sites. For each site and each 50m interval, I determined overall site reproductive success based only on the territories within the core. I then compared patch size between high and low reproductive success sites using Wilcoxon ranked-sum test.

To determine the impact of each land use as a source of fragmentation, I summed the length of edge in contact with each land use category and then compared the totals for each land use between warbler occupied and unoccupied patches using Chi-square test of homogeneity. To test whether the importance as a source of fragmentation of one or more land uses varied with patch size, I performed similar analyses using Chi-square test of homogeneity within each patch size class. I also tested each land use category as a source of fragmentation based on the percentage of sites adjacent to each land use category. I used Chi-square test of homogeneity for all sites combined and for each patch size class.

I examined Golden-cheeked Warbler territorial placement within a patch relative to the land uses along the edge to see if Golden-cheeked Warblers selected for or against any of the land use categories. To do this, I computed two ratios for each land use at each site. The first ratio was the length of edge for each land use relative to the total perimeter of each site. The second ratio was the number of territorial centers closest to each land use category relative to the total number of territories at each site. I designated a land use category as “selected against” when the edge ratio at a site exceeded the territory ratio, while a land use category was “selected for” when the territory ratio exceeded the edge ratio. I then tested selection of land uses by comparing the number of sites selected “for” and “against” using Chi-square test of homogeneity as suggested by Thomas and Taylor (1990) to control for experiment-wise error rates, rather than test each land use separately. I used ratios because the use of absolute edge lengths for each land use would produce erroneous results. A site that was completely surrounded by one land use category would theoretically support fewer territories than a larger site with multiple land uses along the edge but with an equal edge length for the same land use surrounding the small site. In those cases, a comparison of the number territories closest to each land use category based on edge length would be disproportionately influenced by those sites surrounded by only one land use. I used the number of sites as the sample units because the two ratios are not independent. When the edge ratio equals 1.0, the territory ratio must also equal 1.0. When the territory ratio equals zero, the edge ratio must be less than 1.0.

I tested land use effects on reproductive success by comparing the number of high success and low success territories closest to each land use category using Chi-square test of homogeneity. Land use effects on pairing success were tested in a similar manner. Additionally, I used Chi-square test of homogeneity to test whether land use effects on reproductive success varied within each patch size class. The use of Fisher's exact test and Chi-square test of homogeneity permitted examination of land use effects on reproductive success between patch size classes.

I used ANOVA on log-transformed distances to the edge to determine whether land uses affected Golden-cheeked Warbler territorial placement by impacting the distance from territorial centers to the edge. This analysis was performed separately for each patch size class because the range of distances differed between size classes. Warblers occupying large sites had a greater range of distances from the edge to choose from for territorial placement than warblers in small sites.

To test if land uses influenced territory size, I calculated the approximate territory size relative to each land use category as follows. For each land use category at each site, I multiplied the edge ratio, as determined previously, by patch size and then divided by the number of territorial centers closest to the land use. I then averaged all territory sizes for each land use category. I used this approach because I lacked absolute territorial boundaries for all territories. As a result, these territory sizes are not absolute because they are not based on the actual area used by each individual warbler and, as such, should be used with caution. Nonetheless, they appear useful in understanding the relative effects of different land uses on territory size.

Several Golden-cheeked Warblers located their territories near a second land use category which also may have exerted an influence on those territories in addition to the land use closest to the territorial center. Although selection of which territories for inclusion in this analysis was somewhat subjective, I included all territories reasonably close to more than one land use category. I tested for differences in the distance from territorial centers to the edge using ANOVA on log-transformed distances. Due to small sample sizes for several land use categories, I lumped all secondary land uses into two categories: rural and urban. Rural land uses included agriculture, forested non-warbler habitat, grassland, and open water. I combined all other land uses into the urban category. I compared the reproductive success of territories near those two secondary land use categories using Chi-square test of homogeneity. I did a similar analysis within patch size classes using Chi-square test of homogeneity for large and intermediate-sized sites and Fisher’s exact test for small sites.

To determine whether land uses across roads influenced Golden-cheeked Warbler territorial placement or reproductive success, I classified all land uses on the other side of roads bordering my study sites using the land use categories described previously. In a manner similar to that used earlier while testing land use selection, I used Fisher’s exact test to determine if warblers selected for or against any of the land uses categories. Separate analyses were performed for each transportation land use category. I tested for differences in reproductive success for territories nearest to roads using Fisher’s exact test, with a separate test for each transportation land use category.

Using aerial photographs, I located the habitat patch nearest each of my study sites and measured the interpatch distance as the distance between each study site and its nearest habitat patch. These patches were also mapped and entered into the GIS. I measured two different interpatch distances: the distance between patches at the nearest point and the distance between patch centers. I determined the interpatch distance at the nearest point using two methods. For patches where it was logistically possible, I measured the interpatch distance using a 100 m tape measure. All other interpatch distances, both at the nearest point and between patch centers, were approximated using the site boundary cover in the GIS. I investigated the effect of isolation on reproductive success within my study sites by testing the interpatch distance between my high and low reproductive success study sites using Wilcoxon ranked sum tests. Separate analyses were performed using the two types of interpatch distance. I could not test any effects on my study sites by levels of warbler reproduction in the nearest patches due to lack of permission from landowners to survey those nearby patches. For each of the nearest patches, I also determined patch size using the GIS. I looked at the effect of patch size of the nearest patch on reproductive success in my study sites by testing between my high and low reproductive success sites using Wilcoxon ranked sum test.

RESULTS

During the three years of Golden-cheeked Warbler surveys, 100 study sites were surveyed; 63 of those sites supported warblers. I monitored 624 warbler males that were encountered on at least two surveys. Of those males, 312 (50.0%) were known to be paired and 247 (39.58%) were known to have produced young. The reproductive success rate of the 312 paired males was 79.20%. Reproductive success did not vary between years (Chi-Square test of homogeneity, X^2=3.80, df=2, P=0.15), so I combined the data from all years for all further analyses.

The average survey time per territory did not differ between sites of high and low reproductive success (Wilcoxon ranked-sum test, P=0.24), indicating that my determination of the reproductive success at a site was not a direct result of the time spent surveying each site. Although the results are not statistically significant, I spent more time per territory in sites with low success than sites with high success (low success: 309 minutes/territory; high success: 231 minutes/territory).

PATCH SIZE

Mean patch sizes were 232.21 ha (n=12, SE=31.49) for large sites, 55.52 ha (n=33, SE=2.94) for intermediate sized sites and 22.94 ha (n=18, SE=1.36) for small sites. Golden-cheeked Warblers selected patches based on patch size (Chi-square goodness-of-fit test, X^2=67.68, df=2, P<0.0001). Expected values for the Chi-square test were based on the total area in each size class. Warblers selected for large patches (361 observed, 260 expected) and against small sites (49 observed, 75 expected) and intermediate sized sites (214 observed, 289 expected).

Patch size influenced both reproductive success and pairing success. Regression of the reproductive ratio at each site against the log-transformed patch size showed a significant trend (F=11.03, P=0.0014) with a positive relationship, indicating that as patch size increases, overall reproductive success at a site increases. Regression of the pairing ratio at each site on log-transformed patch size also revealed a positive relationship (F=4.96, P=0.030) indicating that as patch size increases, pairing success increases. Therefore, the lower reproductive success seen at smaller sites may result from lowered pairing success.

PATCH SHAPE

Regression of the reproductive ratio at a site against the log-transformed perimeter-to-area ratio revealed a significant negative relationship (F=l 1.58, P=0.0011). As the perimeter-to-area ratio decreases, the overall reproductive success at a site increases. Regression of log-transformed site perimeter on log-transformed patch size revealed a fractal dimension of 1.13 (F=353.36, P<0.0001, r^2=0.87). Figure 1 shows the scatterplot along with the regression line. No change in slope is apparent with differing patch sizes. Thus, the processes acting to create the patch boundaries do not appear to differ from small to large sites (Krummel et al. 1987), while the relationship between reproductive success and the perimeter-to-area ratio appears to be based on the relationship between reproductive success and patch size.

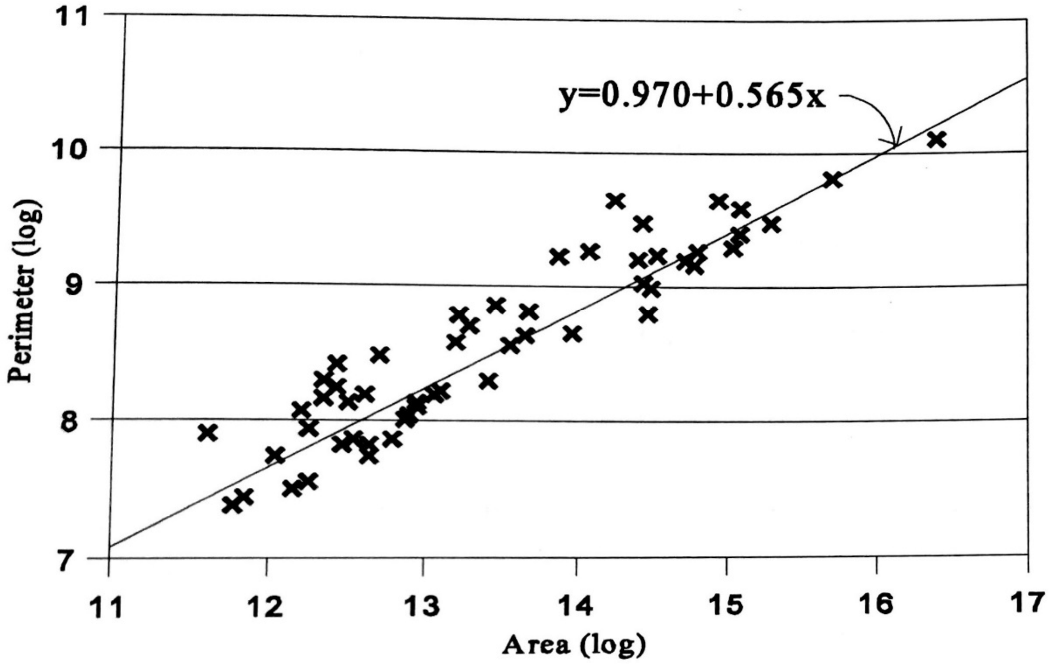

FIG. 1. Fractal dimension of Golden-cheeked Warbler patch boundaries. Actual fractal dimension equals 1.13 (two times the slope of the regression line).

VEGETATIVE CHARACTERISTICS

Table 2 lists the vegetative characteristics at all patches occupied by Golden-cheeked Warblers. Only understory juniper basal area (small sites: two-tailed t-test, t=2.37, P=0.03), average understory juniper height (large sites: t=2.49, P=0.03), and average slope (small sites: t=2.76, P=0.014) differed between high and low reproductive success sites, and then only for one patch size class per variable. Disregarding differences in reproductive success, only average understory juniper height differed between patch size classes (ANOVA, F=3.3, P=0.032). Principal component analysis using all vegetative variables reveals considerable overlap between high and low reproductive success sites (Fig. 2). Together, PRIN1, PRIN2, and PRIN3 explain only 52% of the total variation. PRIN1 represents increasing canopy cover and canopy hardwood basal area. PRIN2 represents decreasing canopy juniper basal area and canopy juniper density, whereas PRIN3 represents decreasing average canopy juniper height and increasing average understory juniper height. Tests of differences in species composition show no difference between high and low reproductive success sites (high: 12.58 species, SE=1.15, n=24; low: 12.72 species, SE=0.92, n=39; Wilcoxon ranked sum test, P=0.98). When categorized by vegetation layer, high success sites have a canopy diversity of 8.25 species (SE=0.78) and a shrub diversity of 4.33 species (SE=0.55) while low success sites have a canopy diversity of 8.34 species (SE=0.55) and a shrub diversity of 4.38 species (SE=0.47). These differences are not significant (canopy: P=0.74; shrub: P=0.84). By patch size classes, regardless of reproductive success, canopy diversity was 7.50 species (SE=0.62, n=12) for large sites, 8.59 species

TABLE 2. Vegetative characteristics for all Golden-cheeked Warbler occupied patches, by patch reproductive success. Values are mean ± standard error. High reproductive success sites are those with 50% or more of the territories being successful, while low reproductive success sites have less than a 50% success rate.

	All Sites		Large Sites		Intermediate Sites		Small Sites	
	High (n=24)	Low (n=39)	High (n=8)	Low (n=4)	High (n=13)	Low (n=20)	High (n=3)	Low (n=15)
Density (stems/ha)								
Understory Juniper	1085±l60	942±80	1073±276	966±334	1080±249	969±127	1145±127	899±100
Canopy Juniper	646± 82	634±55	770±191	859±146	571± 83	548±66	640+259	683± 99
Understory Hardwoods	277± 65	328±46	309±121	202± 71	198± 68	344±73	530+282	343± 70
Canopy Hardwoods	304± 70	297±34	319±136	341± 56	326± 93	296±52	101±0	287± 54
Basal Area (m^2/ha)								
Understory Juniper	8.0±1.9	6.1±0.8	5.3±1.4	6.3±3.9	8.6±3.1	6.9±1.1	13.0±5.5	5.1±1.0 *
Canopy Juniper	23.7±2.3	24.4±2.1	23.1±4.0	28.7±4.6	25.2±3.4	22.4±2.9	19.0±6.1	25.6±3.5
Understory Hardwoods	1.3±0.4	1.6±0.2	0.9±0.3	2.7±1.4	1.0±0.3	1.7±0.4	4.1±2.3	1.2±0.2
Canopy Hardwoods	8.5±1.6	8.7±1.3	6.2±1.5	14.7±6.5	10.6±2.5	9.6±2.0	3.8±2.1	6.0±1.2
Average Height (m)								
Understory Juniper**	2.9±0.1	3.0±0.1	2.6±0.1	3.1±0.1 *	3.1±0.1	3.0±0.1	2.8±0.1	2.9±0.1
Canopy Juniper	6.1±0.2	6.0±0.1	6.4±0.4	6.1±0.4	6.0±0.2	6.1±0.2	6.0±0.8	5.9±0.2
Understory Hardwoods	3.0±0.1	2.9±0.1	2.9±0.2	3.0±0.5	3.0±0.2	2.9±0.1	2.7±0.1	3.0±0.2
Canopy Hardwoods	6.7±0.2	6.5±0.2	6.3±0.4	7.2±0.9	7.0±0.4	6.4±0.3	6.6±0.4	6.5±0.3
Average Cover (%)	83.3±2.2	79.3±2.7	80.8±3.3	86.7±3.2	87.0±2.4	80.8±3.9	74.1±10.2	77.9±4.5
Average Slope (^{o})	8.7±0.8	9.9±0.7	8.6±1.5	8.7±2.6	9.7±1.0	9.9±1.0	4.2±1.9	10.1±1.1 *

* t-test, $P<0.05$ for comparisons between high and low reproductive success sites.

** ANOVA, $P<0.05$ for comparison between patch size classes regardless of reproductive success.

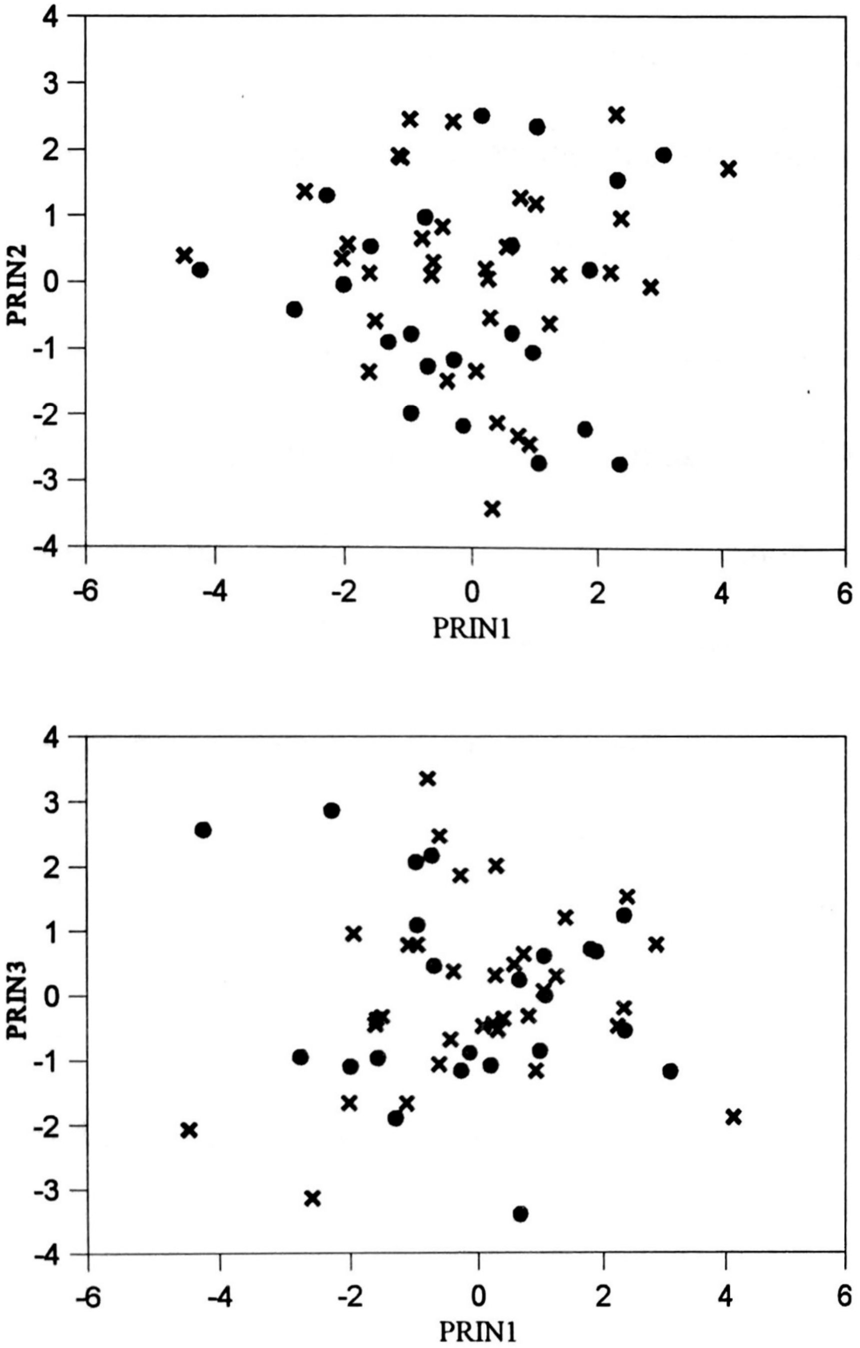

FIG. 2. Principal component analysis plots of vegetative characteristics at Golden-cheeked Warbler occupied patches. Closed circles represent patches with high reproductive success, while 'X' represents patches with low reproductive success.

(SE=0.63, n=33) for intermediate sized sites and 8.32 species (SE=0.98, n=18) for small sites. Shrub diversity was 4.00 species (SE=0.62) for large sites, 4.53 species (SE=0.55) for intermediate sites, and 4.37 species (SE=0.65) for small sites. Large sites supported a total diversity of 11.5 species (SE=1.0), while intermediate sites supported 13.12 species (SE=1.04) and small sites supported 12.69 species (SE=1.50). No difference exists in diversity between patch size classes, regardless of reproductive success (Kruskal-Wallis test, canopy: P=0.70; shrub: P=0.97; total: P=0.87). Thus, with minor exceptions, all of the sites had similar vegetative structure, canopy cover, and average slope. Therefore, differences in vegetation do not appear to explain the differences in reproductive success either within or between patch size classes.

EDGE

None of the approximate territorial centers of Golden-cheeked Warblers fell within 30 m of an edge. Table 3 shows a significant relationship between the distribution of warbler territorial centers and distance to the edge (Chi-square goodness-of-fit test, X^2=18.53, df=5, P=0.003). Most of the significance is driven by higher numbers than expected in the 0-50 m distance class and fewer than expected in the >250 m class. By patch size class, the only significant relationship occurred with intermediate sized sites (X^2=72.51, df=5, P<0.0001). In this case, the significance is driven by higher numbers of warbler territorial centers than expected in the 0-50 m distance class and fewer than expected in the >250 m class. Based on the overall reproductive success rate of 39.6%, Table 4 shows that no significant relationship exists between the reproductive success of each territory and distance from the territorial center to the edge (Chi-square goodness-of-fit test, X^2=4.39, df=5, P=0.6l). Although not statistically significant, only the territories in the distance classes greater than 150 m from the edge (151-200 m, 201-250 m, and

>250 m) reproduced more successfully than expected. By patch size class, reproduction differed significantly with distance to the edge only for large sites (X^2=13.68, df=5, P=0.019). The Chi-square total is driven by higher than expected reproduction in the 151-200 m distance class, but reproduction was higher than expected in every distance class except for the 0-50 m class. In both small and intermediate sized patches, warblers always reproduced less successfully than expected in all distance classes except for the >250 m class at intermediate sized sites, but in this case the sample size is insufficient (n=4) for a meaningful result.

Analyses of reproductive success relative to core areas revealed that the only significant difference occurred with the 50 m edge width. In this case, Golden-cheeked Warblers reproduced more successfully in sites with larger core areas than in sites with smaller core areas (Wilcoxon ranked sum test, P=0.047), Warbler reproductive success did not differ with core area using any edge widths greater than 50 m (100 m: P=0.11; 150 m: P=0.15; 200 m: P=0.59; and 250 m: P=0.33).

TABLE 3. Distribution of Golden-cheeked Warbler territories relative to the edge. Values are number of warbler territories within each distance class. Numbers in parentheses are expected numbers based on the total area contained in each distance class. P-values are based on Chi-square goodness-of-fit tests.

Distance (m)	Total	Small Sites	Intermediate Sites	Large Sites
0-50	91 (72.68)	15 (12.64)	5 (25.09)	31 (26.99)
51-100	124 (147.49)	23 (22.14)	56 (52.50)	45 (59.27)
101-150	115 (96.88)	8 (6.01)	48 (37.61)	59 (51.23)
151-200	76 (73.40)	3 (2.38)	39 (28.39)	34 (43.63)
201-250	63 (51.37)	0 (1.96)	22 (15.65)	41 (37.84)
>250	155 (182.18)	0 (3.88)	4 (54.77)	151 (142.04)
P-value:	0.003	0.32	<0.0001	0.21

TABLE 4. Reproductive success of Golden-cheeked Warbler territories relative to the edge. Territories with high reproductive success were those where young or adults carrying food were observed. Values are number of warbler territories falling within each distance class. Numbers in parentheses are expected values determined by applying overall reproductive success rate of 39.6% to each distance category. P-values are based on Chi-square goodness-of-fit test.

Distance	All Sites		Small Sites		Intermediate Sites		Large Sites	
(m)	High	Low	High	Low	High	Low	High	Low
0-50	34 (36.02)	57 (5498)	5 (5.94)	10 (9.06)	17 (17.81)	28 (27.19)	12 (12.27)	19 (18.73)
51-100	47 (49.08)	77 (74.92)	4 (9.10)	19 (13.90)	21 (22.16)	35 (33.84)	22 (17.81)	23 (2719)
101-150	39 (45.52)	76 (69.48)	3 (3.17)	5 (4.83)	12 (18.99)	36 (29.01)	24 (23.35)	35 (35.65)
151-200	36 (30.08)	40 (45.92)	0 (1.19)	3 (1.81)	13 (1544)	26 (23.56)	23 (13.46)	11 (2054)
201-250	25 (24.94)	38 (38.06)	0	0	7 (8.71)	15 (13.29)	18 (16.23)	23 (24.77)
>250	66 (61.35)	89 (93.65)	0	0	2 (1.58)	2 (242)	64 (59.77)	87 (91.23)
P-value:	0.61		[a]		0.46		0.02	

[a] Chi-square tests are invalid due to insufficient sample size

As shown in Table 5, Golden-cheeked Warblers did not differ in their selection of edge types nearest to their territorial centers (Chi-square test of homogeneity, X^2=0.735, df=l, P=0.39). Additionally, reproductive success of warbler territories did not differ by the edge type nearest to each territorial center (X^2=0.002, df=1, P=0.96).

The relationship of edge type to the various land use categories (Table 6) varied significantly (Chi-square test of homogeneity, X^2=152.45, df=12, P<0.001). Soft edges were associated with land uses that were natural in origin or reflected a low level of human disturbance. These include agriculture, forested non-warbler habitat, grassland, open water, and low-density residential development. Conversely, hard edges occurred more commonly with land uses associated with higher levels of human disturbance, such as medium-density residential development, medium-density transportation, high-density transportation, and utilities.

The distance to the edge from territorial centers (Table 7) varied by the edge type nearest to each territorial center only for large sites (t-test, t=2.60, P=0.010). Territories placed closest to hard edges were located farther from the edge than territories placed closest to soft edges. For both small and intermediate sized sites, the distances did not differ significantly.

LAND USES

The impact of different land uses as sources of fragmentation varied by land use category (Table 8), based both on the length of edge bordering each land use category and on the number of sites adjacent to each land use category. Length of edge for each land use category differed significantly between the occupied and unoccupied patches (Chi-square test of homogeneity, X^2=46902, df=13, P<0.0001). The significance is driven by differences in the edge length for

TABLE 5. Effects of edge type on Golden-cheeked Warbler site selection and reproductive success. Values for site selection are number of sites (Chi-square test of homogeneity, $X^2=0.735$, df=1, P=0.391). Selection "for" a site is based on the territory ratio (number of territories nearest to an edge type relative to total number of territories at a site) exceeding the edge ratio (length of edge for that edge type to the total edge length at a site), while selection "against" is when the edge ratio exceeds the territory ratio. Values for reproductive success are number of warbler territories (Chi-square test of homogeneity, $X^2=0.002$, df=l, P=0.963).

		Edge Type	
		Hard	Soft
Site Selection:	For	36	41
	Against	22	34
Reproductive Success:	High	88	159
	Low	135	242

TABLE 6. Relationship of edge types and land uses nearest to each Golden-cheeked Warbler territory. Partial Chi-square totals are from Chi-square test of homogeneity (X^2=152.45, df=l2, P<0.001).

	Edge Type		
Land Use	Hard	Soft	Partial X^2
Agriculture	15	51	4.86
Commercial	3	0	5.39
Entertainment	2	0	3.59
Forested non-warbler	7	27	3.39
Grassland	39	106	4.93
Industrial	7	13	0.005
Open water	0	41	22.80
Low-density residential	2	57	26.88
Medium-density residential	27	14	16.19
Low-density transportation	31	50	0.23
Medium-density transportation	61	32	36.09
High-density transportation	12	1	18.11
Utilities	17	9	9.95

TABLE 7, Distances from Golden-cheeked Warbler territories to different edge types. Values are mean ± standard error (n). P-values are based on t-tests.

	Edge Type	Distance to the Edge (m)	P-value
Large Sites	Hard	254.84 ± 150.62 (155)	0.010
	Soft	220.88 ± 142.61 (206)	
Intermediate Sites	Hard	104.46 ± 56.79 (56)	0.10
	Soft	125.25 ± 70.64 (158)	
Small Sites	Hard	69.17 ± 27.46 (12)	0.29
	Soft	87.84 ± 45.59 (37)	

TABLE 8. Impact of various land uses on occupation of patches by Golden-cheeked Warblers. Values are total edge length in contact with each land use and for the percentages of the number of sites adjacent to each land use. Differences in edge length were significant (Chi-square test of homogeneity, X^2=46902, df=13, P<0.0001). Numbers in parentheses are the actual number of sites. Warblers were found in 63 sites while 37 sites were unoccupied.

	Edge Length (m)		Number of Sites (%)	
Land Use	Occupied	Unoccupied	Occupied	Unoccupied
Agriculture	42528	0	20.63 (13)	0
Commercial	2520	3888	7.94 (5)	24.32 (9)
Entertainment	5784	2424	4.76 (3)	13.51 (5)
Forested non-warbler	25680	13608	34.92 (22)	40.54 (15)
Grassland	36744	6552	44.44 (28)	27.03 (10)
Industrial	5424	3480	14.29 (9)	18.92 (7)
Open water	15288	10632	17.46 (11)	32.43 (12)
Residential				
Low-density	11568	6528	25.40 (16)	35.14 (13)
Medium-density	8352	10392	12.70 (8)	32.43 (12)
High-density	0	3888	0	21.62 (8)
Transportation				
Low-density	25056	11328	33.33 (21)	32.43 (12)
Medium-density	29112	9600	31.75 (20)	51.14 (19)
High-density	8448	5664	20.63 (13)	32.43 (12)
Utilities	3696	0	9.52 (6)	0

agriculture, high-density residential development, medium-density residential development, and grassland. Agriculture and utilities did not border on unoccupied patches, while high-density residential development never abutted occupied sites. While agriculture and grassland may not normally be considered sources of fragmentation, their high edge lengths relative to other land uses at occupied patches indicate their compatibility with warbler presence.

By patch size classes (Table 9), the different land use categories differed significantly, based on edge length, between occupied and unoccupied patches for all size classes (large: $X^2=9373$, df=13, $P<0.0001$; intermediate: $X^2=14654$, df=13, $P<0.0001$; small: $X^2=31513$, df=13, $P<0.0001$). Since most unoccupied sites are small, comparisons of small sites seem most illustrative of the impacts of various land uses on warbler presence. Transportation accounts for 30.82% of edge length of occupied sites and 26.00% of unoccupied sites, while residential development accounts for 12.42 % of occupied and 29.91% of unoccupied patches. Agriculture and grassland combined amount to 41.33% of the edge for occupied sites but only 4.52% of the edge of unoccupied patches.

Golden-cheeked Warblers differentially selected land use categories that occurred closest to each territorial center (Table 10) (Chi-square test of homogeneity, $X^2=38.45$, df=11, $P<0.001$). Commercial development and entertainment were lumped for analysis due to small sample sizes. Warblers appear to be selecting for agriculture, grassland, and to a lesser extent industrial development, while selecting against commercial development, entertainment, forested non-warbler habitat, and high-density transportation.

Based on reproductive success of each territory, Golden-cheeked Warbler response to various land uses (Table 11) differed significantly between land use categories (Chi-square test of homogeneity, $X^2=22.12$, df=12, $P=0.036$). The significance was driven primarily by the low

TABLE 9. Impact of various land uses on occupation of patches by Golden-cheeked Warblers by patch size classes. Values are total edge length in contact with each land use (Part A) and for the percentages of the number of sites adjacent to each land use (Part B). Warblers were found in 63 sites while 37 sites were unoccupied. P-values are based on Chi-square test of homogeneity.

	Large Sites		Intermediate Sites		Small Sites	
	Occupied	Unoccupied	Occupied	Unoccupied	Occupied	Unoccupied
A. Based on Edge Length (m):						
Agriculture	23784	0	10704	0	8040	0
Commercial	1008	0	1104	888	408	3000
Entertainment	5784	0	0	1680	0	744
Forested non-warbler	3264	504	20664	4296	1752	8808
Grassland	5400	0	21264	4008	10080	2544
Industrial	1896	432	2400	672	1128	2376
Open water	5520	0	6912	3264	2856	7368
Residential						
Low-density	2640	0	6432	2352	2496	4176
Medium-density	3048	0	2352	1008	2952	9384
High-density	0	0	0	600	0	3288
Transportation						
Low-density	5856	504	15672	5784	3528	5040
Medium-density	9096	0	11376	4200	8640	5400
High-density	2904	720	4200	744	1344	4200
Utilities	1200	0	1872	0	624	0
P-values	<0.001		<0.001		<0.001	

TABLE 9. Continued.

	Large Sites		Intermediate Sites		Small Sites	
	Occupied	Unoccupied	Occupied	Unoccupied	Occupied	Unoccupied
B. Based on Number Of Sites (%):						
Agriculture	21.05	0	18.52	0	23.53	0
Commercial	5.26	0	11.11	22.22	5.88	25.93
Entertainment	15.79	0	0	22.22	0	11.11
Forested non-warbler	15.79	100.0	51.85	55.56	17.65	33.33
Grassland	21.05	0	48.15	33.33	52.94	25.93
Industrial	10.53	100.0	11.11	22.22	11.76	14.82
Open water	10.53	0	18.52	33.33	17.65	33.33
Residential						
Low-density	21.05	0	33.33	33.33	17.65	37.04
Medium-density	10.53	0	11.11	22.22	17.65	37.04
High-density	0	0	0	11.11	0	26.93
Transportation						
Low-density	21.05	100.0	40.74	44.44	29.41	25.93
Medium-density	21.05	0	37.04	55.56	35.29	51.85
High-density	10.53	100.0	22.22	22.22	29.41	33.33
Utilities	5.26	0	14.82	0	5.88	0

TABLE 10. Selection by Golden-cheeked Warblers of adjacent land uses by site. Sites selected "For" represent those sites where the proportion of edge available for each land use is less than the proportion of territories found closest to that land use for each site. Sites selected "Against" represent those sites where the proportion of edge is greater than the proportion of territories for each land use at each site. Commercial and entertainment were lumped for analysis. Partial Chi-square values represent each land uses' contribution to the overall Chi-square total. Commercial and entertainment were lumped for Chi-square test of homogeneity (X^2=38.45, df=11, P<0.001).

Land Use	Selection Against	Selection For	Partial X^2
Agriculture	7	16	4.73
Commercial and Entertainment	7	1	8.04
Forested non-warbler	17	5	5.17
Grassland	11	27	8.88
Industrial	3	8	2.94
Open water	6	9	1.03
Residential			
Low-density	11	12	0.25
Medium-density	4	3	0.05
Transportation			
Low-density	16	9	1.20
Medium-density	14	11	0.09
High-density	12	3	4.37
Utilities	8	3	1.71

reproductive success of territories located closest to forested non-warbler habitat. Warblers did not differ in pairing success relative to the various land use categories (X^2=12.78, df=12, P=0.38). The percentage of successful, paired males ranged from 93.75% closest to utilities to 45.45% closest to forested non-warbler habitat (Table 12).

By patch size classes, Golden-cheeked Warbler reproductive success differed between the land use categories located closest to each territorial centers (Table 13) only in intermediate sized patches (Chi-square test of homogeneity, X^2=16.95, df=7, P=0.018). Commercial development, low-density residential development, and high-density transportation were excluded from analysis due to small sample sizes. The significance was driven primarily by higher reproduction than expected next to low-density transportation and lower reproduction than expected next to forested non-warbler habitat. By land uses, warbler reproductive success differed between patch size classes only for open water (Fisher's exact test, P=0.047) with higher reproduction than expected for large sites and lower than expected for both small and intermediate sized sites.

The distance to the edge from territorial centers differed by land use category (Table 14) for large sites (ANOVA, F=2.83, P=0.005) and for intermediate sized sites (F=4.27, P=0.0002). Due to small sample sizes, commercial development, entertainment, and industrial development were omitted for analysis on the large sites, while commercial development, low-density residential development, and high-density transportation were omitted on the intermediate sized sites. Table 14 also shows the results of multiple comparison tests for large and intermediate sized sites. Distances to the edge from territorial centers did not differ significantly between high and low reproductive success territories for any of the land use categories.

TABLE 11. Effects of land uses on Golden-cheeked Warbler pairing and reproductive success. Values are the number of territories with high pairing success based on the presence of a female and high reproductive success based on the presence of young or adults observed carrying food. Partial Chi-square values represent each land uses' contribution to the overall Chi-square total based on Chi-square test of homogeneity (Pairing Success: $X^2=12.78$, df=12, P=0.38; Reproductive Success: $X^2=22.12$, df=12, P=0.036).

	Pairing Success			Reproductive Success		
Land Use	High	Low	Partial X^2	High	Low	Partial X^2
Agriculture	35	31	0.24	26	40	0.001
Commercial	2	1	0.33	1	2	0.05
Entertainment	0	2	2.00	0	2	1.31
Forested non-warbler	11	23	4.23	5	29	8.80
Grassland	67	78	0.83	55	90	0.17
Industrial	10	10	0	8	12	0.002
Open water	19	22	0.22	17	24	0.06
Residential						
Low-density	30	29	0.02	27	32	0.94
Medium-density	23	18	0.61	21	20	2.32
Transportation						
Low-density	39	42	0.11	34	47	0.19
Medium-density	51	42	0.87	30	63	2.09
High-density	9	4	1.92	8	5	2.62
Utilities	16	10	1.38	15	11	3.56

TABLE 12. Success rate of paired Golden-cheeked Warbler males relative to various land use categories. No paired males occurred in territories closest to entertainment.

Land Use	Success Rate (%)
Agriculture	71.43
Commercial	50.00
Entertainment	-
Forested non-warbler	45.45
Grassland	80.60
Industrial	80.00
Open water	89.47
Residential	
Low-density	90.00
Medium-density	91.30
Transportation	
Low-density	87.18
Medium-density	58.82
High-density	88.89
Utilities	93.75

TABLE 13. Reproductive success of Golden-cheeked Warbler territories by land use categories and patch size classes. Values are number of territories. P-values are based on Fisher's exact test except where noted. High reproductive success territories are those where young were observed or where adults were observed carrying food.

	Small Sites		Intermediate Sites		Large Sites		P-values
	High	Low	High	Low	High	Low	
Agriculture	4	11	5	10	17	19	0.34[a]
Commercial	-	-	1	1	0	1	1.00
Entertainment	-	-	-	-	0	2	
Forested non-warbler	1	2	4	27	-	-	0.39
Grassland	1	4	16	34	38	52	0.38
Industrial	2	4	5	7	1	1	1.00
Open water	0	3	6	14	11	7	0.047
Residential							
Low-density	0	1	1	1	26	30	1.00
Medium-density	0	2	5	3	16	15	0.46
Transportation							
Low-density	3	2	21	20	10	25	0.083
Medium-density	1	8	7	24	22	31	0.073[a]
High-density	-	-	1	1	7	4	1.00
Utilities	-	-	-	-	15	11	
P-values	0.67		0.018[a]		0.026[a]		

[a] Chi-square test of homogeneity

TABLE 14. Distance to the edge for Golden-cheeked Warbler territories relative to land uses. Values are mean ± standard error (n). P-values are based on analysis of variance of log-transformed distances. Groupings are from Student-Newman-Keuls multiple comparison test. Land uses not included in any groupings were omitted from analyses due to sample size.

	Distance to the Edge (m)	P-value
Large Sites:		0.0047
High-density transportation	401.8 ± 46.0 (11)	
Medium-density residential	291.6 ± 29.3 (31)	
Low-density residential	247.7 ± 16.5 (56)	
Grassland	240.7 ± 16.0 (90)	
Agriculture	233.9 ± 28.0 (36)	
Medium-density transportation	218.7 ± 16.5 (53)	
Low-density transportation	207.4 ± 27.5 (35)	
Utilities	199.6 ± 23.2 (26)	
Open water	155.6 ± 25.8 (18)	
Commercial	220.0 (1)	
Entertainment	105.0 ± 5.0 (2)	
Industrial	160.0 ± 10.0 (2)	
Intermediate Sites:		0.0002
Open water	162.0 ± 12.0 (20)	
Medium-density transportation	140.3 ± 11.4 (31)	
Medium-density residential	136.3 ± 21.0 (8)	
Industrial	123.3 ± 14.5 (12)	
Grassland	112.2 ± 8.2 (50)	
Forested non-warbler habitat	107.7 ± 12.2 (31)	
Low-density transportation	107.1 ± 12.5 (41)	
Agriculture	74.7 ± 13.5 (15)	
Commercial	150.0 ± 10.0 (2)	
Low-density residential	280.0 ± 50.0 (2)	
High-density transportation	80.0 ± 10.0 (2)	
Small Sites:		0.54
Industrial	116.7 ± 24.2 (6)	
Forested non-warbler habitat	90.0 ± 45.1 (3)	
Agriculture	80.0 ± 9.3 (15)	
Low-density transportation	78.0 ± 13.2 (5)	
Medium-density transportation	75.6 ± 11.3 (9)	
Grassland	64.0 ± 10.8 (5)	
Open water	50.0 ± 11.5 (3)	
Low-density residential	70.0 (1)	
Medium-density residential	150.0 ± 20.0 (2)	

Average territory size ranged from 3.68 ha for large sites to 7.28 ha for intermediate sized sites and to 9.75 ha for small sites. By individual land use categories, average territory size varied from a high of 23.15 ha for territories closest to entertainment to a low of 2.77 ha for territories closest to utilities (Table 15). With land use categories of increasing levels of human disturbance, average territory size tended to increase. Territory size for those territories closest to roads differed significantly between transportation densities (ANOVA, F=3.83, P=0.024). Territories closest to low-density transportation averaged 5.33 ha and were significantly smaller than territories closest to medium-density transportation (7.65 ha) and high-density transportation (8.76 ha). The same trend applied to territories closest to residential development, but the average territory sizes did not differ significantly (t-test, t=1.15, P=0.25). Territories nearest to low-density residential development averaged 3.95 ha in size while those nearest to medium-density residential development averaged 4.76 ha.

Some Golden-cheeked Warbler territories occurred near a second land use category along the edge which could potentially have influenced those territories, even though that secondary land use was not the closest land use category to the territorial center. The distance to the edge from territorial centers for the secondary land use categories (Table 16) differed significantly (ANOVA, F=2.38, P=0.011). Entertainment was excluded from the analysis due to small sample size. Distances from territorial centers to the edge were greatest for residential development and paved roads. Reproductive success of territories near a secondary land use category (Table 17) differed significantly for all patch sizes combined (Chi-square test of homogeneity, X^2=4.36, df=l, P=0.037), with the significance driven by the greater reproduction than expected for territories near rural land uses compared to territories near urban land uses. By patch size classes, reproduction differed for both intermediate sized sites and small sites (intermediate: X^2=6.19,

TABLE 15. Average Golden-cheeked Warbler territory size by land use. Values are territory size followed by sample size in parentheses.

Land Use	Territory Size (ha)
Agriculture	10.33 (64)
Commercial	14.07 (3)
Entertainment	23.15 (2)
Forested non-warbler	5.95 (33)
Grassland	3.51 (146)
Industrial	4.33 (20)
Open water	6.55 (41)
Residential	
Low-density	3.95 (59)
Medium-density	4.76 (41)
Transportation	
Low-density	5.33 (81)
Medium-density	7.65 (93)
High-density	8.76 (13)
Utilities	2.77 (26)

P=0.013; small: Fisher's exact test two-tailed, P=0.031). In both cases, the significance appears to reflect the greater than expected reproductive success for territories near the rural land uses compared to territories near the urban land uses.

Six land use categories occurred on the other side of the three transportation categories from my study sites: agriculture, commercial development, forested non-warbler habitat, grassland, low-density residential development and warbler habitat. Table 18 shows that warblers did not appear to select land use categories across roads when placing their territories within a patch, either for all roads lumped together or for each different road type. They tended to prefer placing territories near roads with warbler habitat across the road, particularly for low- and medium-density transportation, but not significantly more so than the other land use categories across roads. Reproductive success of territories nearest to roads did not differ significantly between the land use categories across the road for each of the three transportation land uses (Table 19), although the difference seen for medium-density transportation is marginal (Fisher's exact test, P=0.057). The difference in this case is driven by higher than expected success of territories across roads from forested non-warbler habitat.

ISOLATION

The smallest interpatch distance was 11 m. This slightly exceeds the minimum corridor width at which Rich et al. (1994) found significant differences in avifaunal distribution in forests adjacent to narrow corridors. Thus, all interpatch distances appear sufficiently large to potentially result in changes in avian distributions along patch boundaries. Site boundaries as I designated them seemed to be supported by the behaviors of the warbler in those patches. Even for the smallest interpatch distances, I was unable to lure warblers, using broadcast tape of territorial

TABLE 16. Reproductive success of Golden-cheeked Warbler territories and distance to the edge for secondary land uses. Values for distance to edge are mean ± standard error (n). Groupings are based on analysis of variance and Student-Newman-Keuls multiple comparison test of log-transformed distances. Land uses not included in groupings were omitted from analysis due to sample size.

	Reproductive Success		Distance to Edge (m)
	High	Low	
High-density transportation	3	6	387.78 + 70.1 (9)
Medium-density residential	3	5	373.75 + 39.4 (8)
Low-density residential	15	25	369.25 + 22.6 (40)
Medium-density transportation	17	33	336.20 + 18.1 (50)
Grassland	7	11	327.67 + 38.9 (18)
Commercial	5	8	316.15 + 43.8 (13)
Industrial	0	7	285.71 + 27.8 (7)
Open water	7	6	274.61 + 31.2 (13)
Agriculture	3	5	245.00 + 61.2 (8)
Low-density transportation	2	15	238.24 + 21.5 (17)
Forested non-warbler habitat	4	0	182.50 + 52.3 (4)
Entertainment	1	1	175.00 + 25.0 (2)

TABLE 17. Reproductive success of Golden-cheeked Warbler territories relative to secondary land uses. Rural land uses include agriculture, forested non-warbler habitat, grassland and open water. P-values are based on Chi-square test of homogeneity except where noted.

	All Sites		Large Sites		Intermediate Sites		Small Sites	
	High	Low	High	Low	High	Low	High	Low
Rural	21	22	6	8	12	10	3	4
Urban	46	100	29	38	17	49	0	13
P-value	0.037		0.98		0.013		0.031[a]	

[a] Fisher's exact test, 2-tailed

TABLE 18. Selection of land uses across roads from Golden-cheeked Warbler territories. Values are number of sites. P-values are based on Fisher's exact test, 2-tailed,

			Transportation					
	All Roads		Low-density		Medium-density		High-density	
Land Use	Against	For	Against	For	Against	For	Against	For
Agriculture	0	1	0	1	-	-	-	-
Commercial	4	3	-	-	0	2	4	1
Forested non-warbler	10	7	3	3	2	3	5	1
Grassland	6	3	3	1	2	2	1	0
Low-density residential	5	1	-	-	4	1	1	0
Warbler habitat	14	24	5	11	4	11	5	2
P-value	0.15		0.35		0.23		1.00	

song, to fly between patches. Individuals would move from site interiors to the edge, then move back and forth along the edge, but never cross the opening to a nearby patch. However, Golden-cheeked Warblers have been observed crossing openings somewhat wider than my minimum interpatch distance (K.A. Arnold, pers. comm). Of the few observations where warblers were seen crossing between patches during this study, their motivation did not appear to be territorial defense. All of these instances took place in May, during the time of renesting (Pulich 1976). It appeared that these males crossing between patches did so to either gain a mate, or possibly an extra-pair copulation, or to defend their mates from other males.

Comparisons of interpatch distances between warbler occupied patches and the nearest potential warbler patch reveal no statistically significant relationships (Table 20). The most reliable measurement of isolation is probably the interpatch distance at the nearest point and not the distance between patch centers. Golden-cheeked Warblers tend to breed more successfully in large patches, leading to the greater distances between patch centers for high reproductive success patches compared to low success patches as seen in Table 20. Additionally, the size of the nearest potential warbler patch did not differ based on the reproductive success of the occupied patch.

TABLE 19. Effects of land uses across roads on Golden-cheeked Warbler reproductive success. High reproductive success is based on the presence of young or observations of adults carrying food. P-values are based on Fisher’s exact test, 2-tailed.

	Transportation					
	Low-density		Medium-density		High-density	
	High	Low	High	Low	High	Low
Agriculture	4	1	-	-	-	-
Commercial	-	-	2	3	2	1
Forested non-warbler	3	11	4	1	0	1
Grassland	5	3	2	1	-	-
Low-density residential	-	-	0	2	-	-
Warbler habitat	22	31	22	56	6	3
P-value	0.08		0.057		0.71	

TABLE 20. Spatial configuration of Golden-cheeked Warbler patches within the landscape. Values are mean ± standard error. P-values are based on Wilcoxon ranked sum tests.

	Reproductive Success of Warbler Patch		
	High	Low	P-value
Distance to nearest patch:			
At closest point (m)	99.3 ± 18.8	92.0 ± 18.7	0.087
Between patch centers (m)	1144.4 ± 79.7	955.7 ± 69.0	0.069
Size of nearest patch (ha)	86.1 ± 18.6	101.6 ± 20.9	0.76

DISCUSSION AND CONCLUSION

FRAGMENTATION PATTERNS

Several different aspects of remnant patches need consideration before we can reach an understanding of the impacts of fragmentation on Golden-cheeked Warblers. These include characteristics of the patches such as size and shape, edge effects, the nature of the surrounding landscape matrix and the spatial configuration of the remnant patches. The first portions of this section look at the patterns observed in this study, while the last portions consider the possible processes which may have produced them.

Patch Characteristics

Relationships between species presence and patch size have been documented for a variety of species (Robbins et al. 1989) and the Golden-cheeked Warbler is no exception. Arnold et al. (1996) showed that warblers consistently occupied and reproduced in patches at least 23 ha in size. In this study, I found that warblers selected for sites larger than 100 ha and selected against all smaller sites. The results of Arnold et al. (1996) of 23 ha indicate that the minimum patch size for Golden-cheeked Warbler reproduction is several times the average territory size, which has been reported as ranging between 3.17 ha and 8.5 ha (Pulich 1976, Kroll 1980), but my findings of selection for sites larger than 100 ha reveal the minimum may be much larger than previously thought. The pattern of minimum patch sizes as several times greater than an average territory size has been documented for other species in different geographic regions, including birds of the eastern deciduous forest (Robbins et al. 1989) and sagebrush birds in the western United States (Knick and Rotenberry 1995), implying this result may hold for other area-sensitive species. However, determining the minimum area required to sustain a population for any species is difficult (Faaborg et al. 1995). Data on demography and dispersal must exist to determine whether a particular sized patch can maintain a population with some degree of probability over a period of time (Shaffer 1981). Unfortunately, those data do not exist for Golden-cheeked Warblers, so any minimum area estimates would be preliminary at best.

A vast literature exists on the effects of patch size on avian species diversity and on species presence/absence. but few studies have looked at the relationships between patch size and pairing success or reproductive success. Golden-cheeked Warblers showed a positive relationship between patch size and pairing success, similar to studies on Ovenbirds from the eastern United States. Gibbs and Faaborg (1990) found fewer Ovenbird males paired in small fragments (24% paired) than in larger control areas (75% paired). Similar results were obtained by Porneluzi et al. (1993) (47% paired in small patches compared to 67% in large patches) and Burke and Nol (1998) (0% paired in small patches, 100% in large patches). However, Gibbs and Faaborg (1990) failed to find any relationship between patch size and pairing success in Kentucky Warblers (*Oporornis formosus*), indicating this relationship may not be universal among species. One explanation might be that the relationship does exist for Kentucky Warblers, but the fragments used were greater than a threshold value for pairing in that species.

Pairing success in this study was only 50%. Certainly, this value is conservative due to the secretive behavior of female Golden-cheeked Warblers and probably underestimates the true rate of pairing success. The influence this may have on the relationship between patch size and pairing success is unknown; however, more time was spent, on average, in territories in small sites than in larger sites, although not statistically significantly more. Even though rates of pairing success may have been low, differences between patch sizes are probably consistent. In fact, our ability to find females and fledglings was probably greater in small sites due to the lower average canopy cover and greater number of small openings. I suspect the low pairing success in warbler populations also may reflect a male-biased sex ratio, a common occurrence in monogamous passerine birds (Breitwisch 1989). Working with Golden-cheeked Warblers on the wintering grounds, Vidal et al. (1994) also found a male-biased sex ratio and felt it may result from difficulties in finding females. They eventually rejected this explanation after testing it against a data set with experienced observers. Another possibility offered was the existence of sex-biased wintering locations with females wintering farther south than their study sites in Chiapas, Mexico, on the northern end of the Golden-cheeked Warbler wintering range. This study's success rate for paired males of about 80% is greater than average, based on the finding of Nice (1957) of an average reproductive success rate of 46% in 29 studies of open-cup nesting birds. This suggests that the low pairing success rate seen in Golden-cheeked Warblers may exert a greater influence on reproductive success than any factor associated with nest mortality.

Golden-cheeked Warblers exhibited greater reproductive success in large patches. Similarly, Porneluzi et al. (1993) found male Ovenbirds in small patches to reproduce less successfully (6% successful) than males in large patches (59%) with a 20 times increase in the number of young produced in large patches, although they did not differentiate as to whether this reduction in reproductive success was for all males encountered or just the paired males. Noojibail (1995) observed similar differences in Ovenbirds (25% successful in fragments compared to 77% in controls). We need research on other species to determine the universal nature of this pattern.

A look at perimeter-to-area ratios reveals a negative relationship between patch shape and Golden-cheeked Warbler reproductive success. Warblers exhibit greater success in patches with lower perimeter-to-area ratios than patches with higher ratios. Although perimeter-to-area ratios may accurately reflect variation in both size and shape (Laurence and Yensen 1991), these results appear to be strongly influenced by the relationship between patch size and reproductive success. Warbler reproductive success is greater in larger sites compared to smaller ones. The fractal dimension does not appear to change significantly across the range of patch sizes analyzed. This suggests that, across this range of patch sizes, the processes acting to create patch boundaries do not appear to change.

Edge Effects

Golden-cheeked Warblers occupy habitat that is essentially closed canopy forest (U.S. Fish and Wildlife Service 1992). This may be seen in the average canopy cover measurements from this study and that from Arnold et al. (1996) of around 80%. Thus, warbler habitat contains a number of small, natural openings. The effect these natural gaps have on warbler territory placement and reproductive success is potentially quite different than the effects of patch boundaries. This difference has been documented for other species. For example, Noss (1991) found that Hooded Warblers (*Wilsonia citrina*) were positively associated with natural gaps, but avoided patch boundaries. While fragmentation can occur through natural processes, changes in natural landscapes, including fragmentation, have resulted from widespread human activities occurring at rates far exceeding many species' abilities to adapt (Block and Brennan 1993). Thus, edge effects at patch boundaries are more important than effects at natural gaps in understanding a species vulnerability to fragmentation. The original vegetation in the Hill Country appears to have contained many openings, some large and some small (Weniger 1984), and so the Golden-cheeked Warbler probably evolved in a system with natural gaps. Therefore, I have considered edge effects only for patch boundaries and not for internal gaps.

Yahner (1988) feels that edge effects should be determined by species responses to edges and not by predetermined distances set by researchers. To do this for the Golden-cheeked Warbler requires viewing their responses to edge in two ways. The first deals with where warbler territories are placed relative to the edge and the amount of area available to them in each patch. The second concerns how successful those territories are, either by pairing success or reproductive success.

In this study, I looked at territorial placement by considering the location of approximate territorial centers. As expected, no territorial centers were located within 30 m of a boundary. However, more warbler territories were located between 30 m and 50 m of a boundary than expected by chance. Also, more territories were located between 100 m and 250 m than expected by chance. Thus, based on the amount of area available for territorial placement, warbler territorial distribution from the edge was bimodal with peaks at 30-50 m and 100-250 m. Since patch size relates positively to reproductive success, success relative to the edge at large sites seems important in determining edge effects on reproduction. Golden-cheeked Warblers did not reproduce better than expected until at least 100 m from the edge, and not significantly so until 150 m from the edge. Thus, there appears to be an edge effect of about 150 m when both territorial placement and reproductive success are taken into account (Tables 3 and 4).

The peak of territorial distribution seen between 30 and 50 m is for birds with lower reproductive success, so that the 50 m zone adjacent to the boundary may represent an ecological trap (Gates and Gysel 1978), however the results are equivocal. The core area analysis supports the ecological trap possibility. Size of the patch interior varied with reproductive success only with a 50 m edge zone. However, only 24% (11 out of 45) of paired males in the 50 m edge zone did not raise young, indicating the lower reproductive success seen in the 50 m edge zone results largely from low pairing rates and not an ecological trap regarding reproductive success.

Freemark and Collins (1992) define an edge species as typically using forest perimeters, nearby fields, or large clearings within a forest during the breeding season. They define a forest-interior species as nesting only within the interior of forests and rarely occurring near the edge. Assigning these definitions to the Golden-cheeked Warbler is not straightforward. Golden-cheeked Warblers use edges, particularly after young have fledged, but adults may be found singing or foraging near an edge at other times in the breeding season. Thus, by definition they are not strictly forest-interior. Conversely, they do not easily fit the definition of an edge species because their territories lie entirely within the largely closed canopy forest, although some authors have dubbed them as such (Kroll 1980).

The implications for management of the Golden-cheeked Warbler based on a simple forest-interior - edge dichotomy could be profound. If the Golden-cheeked Warbler is defined as an edge species, then management should favor the production of edges. However, if this is not done carefully, then one of the results would most likely be further fragmentation of warbler patches. Arnold et al. (1996) showed an area effect on warbler patch occupation, while I have shown an area effect not only on pairing success, but also reproductive success. Thus, management that favors edge and results in fragmenting warbler habitat into smaller patches could lead to local extinction in those patches. On the other hand, defining the Golden-cheeked Warbler as forest-interior could lead to the conclusion that only the larger patches are important because those are the ones in which warblers consistently reproduce successfully. Management that favors the large sites over the intermediate and small ones might allow the loss of those intermediate and small sites, but their role in Golden-cheeked Warbler population dynamics is unknown and their loss could lead to further population declines and possibly to local extinction.

I believe that the simple dichotomy of forest-interior versus edge breaks down with the Golden-cheeked Warbler and that a continuum between forest-interior and edge should be adopted. Freemark and Collins (1992) define a third type of species, one that is interior-edge. These species have territories entirely within the forest, but can also use the edge. Implicit in this definition is an indifference to the presence of edges. While Golden-cheeked Warblers do occur sometimes at edges, their reproductive success is greatest at distances farther than 150 m into a patch, leading to the conclusion that they are not indifferent to the presence of edge. In a review on the effects of edge on nest success, Paton (1994) concluded that edge effects occur primarily within 50 m of the forest edge, less than the 150 m edge effect seen in Golden-cheeked Warblers. By breeding best at distances greater than 150 m from the edge, yet relying on edges after young have fledged, the Golden-cheeked Warbler appears to be best described as being slightly forest-interior. While the definition of interior-edge might apply, I feel that reproductive success should be more heavily weighted than simple occurrences along edges, resulting in a description of the Golden-cheeked Warbler as slightly forest-interior. Since the reliance on edge appears to be more pronounced when young have fledged, the slight forest-interior nature of the Golden-cheeked Warbler may have more importance at earlier stages of breeding such as during pairing, incubation and the nestling phase.

The higher reproductive success at distances greater than 150 m from the edge may in part explain the low reproduction by Golden-cheeked Warblers in small patches. Based on patch sizes, few territories could be placed in small patches at distances greater than 150 m, and in fact only three territories in the small sites occurred at distances greater than 150 m (Table 3).

Land Use Effects

Adjacent land uses may impact Golden-cheeked Warbler patch use several ways. First, warblers returning from migration need to assess the suitability of a patch, and the surrounding landscape may influence their assessment (Hinsley et a1. 1995). Second, once a patch is deemed suitable, land uses may influence territorial placement within the patch. Last, adjacent land uses may also affect reproductive success (Wilcove 1985). Migrants appear more likely to make large-scale choices as to patch suitability than residents and may not settle in a patch that appears suitable if the surrounding landscape appears unsuitable (Hinsley et al. 1995). Different land uses may vary in their effects on patch suitability. Transportation is one of the most important aspects of modern infrastructure that leads to habitat fragmentation (Renman and Mortberg 1994). In western Travis County, transportation contributes to fragmentation of warbler habitat to a greater extent than any other land use (Table 8), but occupied and unoccupied patches differed little in the extent of edge for each of the transportation densities. Engels (1995) indicated that Golden-cheeked Warblers appear sensitive to residential development and that the number of houses within 500 m of his sample points influenced whether he recorded warblers on his surveys. Friesen et al. (1995) also found that as the number of houses near a site increased, the diversity and abundance of migrants decreased. Based on edge length, I found that residential development was more than twice as common at unoccupied sites compared to occupied sites. Medium-density residential development was approximately four times more common at unoccupied sites, while occupied sites never occurred adjacent to high-density residential development. Other land uses that were more common next to unoccupied patches consisted of commercial development, forested non-warbler habitat, and open water. Agriculture and grasslands abutted occupied patches more commonly than unoccupied patches by a factor of almost five. For small sites, the tendency was even more pronounced, with agriculture and grasslands being about 10 times more common next to occupied patches. In fact, agriculture was never encountered adjacent to an unoccupied patch. Therefore, it appears that the nature of the surrounding land uses does influence warbler patch occupation. Residential development, particularly high-density development, as well as agriculture and grassland, seem to exert the most influence. The effect of surrounding land uses on patch occupation based on associated levels of disturbance seems analogous to the variegated landscape as described by McIntyre and Lavorel (1994).

In terms of territorial placement within a patch, Golden-cheeked Warblers selected against commercial development, entertainment, forested non-warbler habitat, high-density transportation, and utilities (Table 10). Despite an apparent sensitivity to residential development (Engels 1995), warblers did not select for or against residential development. Once a warbler settled on a patch, placement of a territory was not based on the location of residential development next to the patch. Of the warbler territories placed closest to transportation, most were placed with warbler habitat across the road, although little influence on reproductive success was seen. The only land uses Golden-cheeked Warblers strongly selected for were agriculture and grasslands. Accounts of early explorers to the Hill Country indicate that grasslands were common and sign of American bison (*Bos bison*) were regularly encountered (Weniger 1984). Thus, agriculture and grasslands are probably the land uses most closely resembling the vegetation and disturbance patterns in the landscape matrix in which the Golden-cheeked Warbler evolved.

In addition to selection for various land uses, warbler territorial placement within a patch may also be assessed by the distance of territorial centers to the edge. In general, as the level of disturbance associated with a particular land use increased, the distance from the edge tended to increase. This was most easily seen with both transportation and residential development (Table 13). A similar phenomenon was reported by Watts and Bradshaw (1994) with Great Blue Heron (*Ardea herodias*) colonies, which were placed at greater distances from paved roads than from unpaved roads. Van der Zande et al. (1980) feel that the effects of a road *per se* are different than the effects of human activities on it, but these effects are not easily separated. In Travis County, the physical differences between transportation densities generally amount to wider corridors and a replacement of gravel and grass with asphalt and concrete. The most pronounced differences seem to be in the levels of vehicular traffic. It seems unlikely that a cause and effect relationship exists between corridor width and increased distances from the edge. Therefore, the differences in distance are most probably due to the levels of traffic, although corridor width may play a minor role.

Reijnen and Foppen (1994) found lower Willow Warbler reproductive success near a road compared to their control areas and concluded that differences in habitat quality were responsible for the patterns they saw. If this finding applies to the Golden-cheeked Warbler, one would expect decreasing reproductive success as transportation density increased. This pattern was not observed. Warbler reproductive success did not differ with transportation types. However, distance to the edge increased with increasing transportation density. Apparently, Golden-cheeked Warblers moved away from the edge as transportation density increased rather than settle next to a road and possibly suffer lower reproductive success. This may have been due to differences in vegetation, although I have no data to support or refute that possibility. Alternatives include possible differences in food availability (see section on Insect Availability) or insufficient population size to occupy all available habitat.

Spatial Configuration

The distance between patches could affect populations by limiting dispersal because of the amount of unfavorable habitat between patches (Faaborg et al. 1995), although the distance between patches may be less important for migrants who effectively “colonize” each patch every spring (Harris and Wallace 1984). The distance between warbler patches and the nearest potential warbler habitat did not affect reproductive success (Table 20). Additionally, the size of the nearest potential habitat patch did not appear to influence warbler reproductive success. Thus, in Travis County, the spatial configuration of warbler habitat patches relative to one another does not appear to affect Golden-cheeked Warbler reproductive success. However, this analysis effectively ignores the nature of the surrounding landscape matrix.

Robinson et al. (1995), working in the midwestern United States where forests were severely fragmented more than a century ago, found evidence for source-sink metapopulation structure with a variety of nearctic migrants, including Wood Thrush, Ovenbird, Kentucky Warbler, Hooded Warbler, and Scarlet Tanager (*Piranga olivacea*). Results by Donovan et al. (1995b) support the conclusion of a source-sink metapopulation structure for nearctic migrants in the midwestern United States. The data presented here on Golden-cheeked Warbler patch spatial configuration, although lacking data on dispersal rates and local extinction, do not seem to point to warbler populations as a source-sink metapopulation. The distance to the nearest patch and the size of the nearest patch did not appear to influence warbler reproductive success. However, one aspect of this data set does hint at source-sink metapopulation structure: differential reproductive success seen between small and large patches. Although patch size is irrelevant in determining metapopulation structure (Pulliam 1988), the key is that in some sites warblers do not reproduce successfully, while at others they do well. Whether the low reproductive success sites are maintained by a low rate of success within the patch, which may not have been effectively measured in this study, or by immigration remains unknown.

FACTORS INFLUENCING GOLDEN-CHEEKED WARBLERS

Vegetation

Although fragmentation seems to qualitatively change the remaining fragments (Temple and Wilcox 1986), the nature of the vegetation within a fragment does not seem to be affected (Keller and Anderson 1992). Askins et al. (1990) reviewed existing data on area-dependent differences in vegetation and could not detect any relationships between patch size and the habitat within a patch. Similarly, Arnold et al. (1996) found no significant differences in vegetation structure between Golden-cheeked Warbler occupied and unoccupied patches. I found no relationships of vegetative composition or structure with patch size or with warbler reproductive success. However, my vegetative measurements and those of Arnold et al. (1996) were made at the location of the first visual contact of a Golden-cheeked Warbler in each patch. Thus, the vegetation throughout each patch was not sampled. Biases could have been introduced several ways. Visual observations were easier to obtain in gaps and along edges. Many of the sites contained steep, rugged terrain and surveys tended to be conducted on flat terrain either above or below the steep slopes.

When selecting a territory, a bird needs to choose a location that will provide all of its requirements for survival and breeding, including nest sites, foraging areas, roosting sites and song perches (Sedgwick and Knopf 1992). Johnson (1980) described this selection process as hierarchical, defining first-order selection as selection for the physical or geographic range, second-order selection as selection for home ranges or territories, third-order selection as use of specific sites within the home range and fourth-order selection as the procurement of actual resources from those sites. Hutto (1985) concluded the first-order selection was probably innate and inflexible, but the second- and third-orders involved decision-making processes on the part of individuals, largely the result of food availability. Recent research has refined the selection process somewhat for second- and third-order levels. Other warblers, such as Black-throated Blue Warbler (*Dendroica caerulescens*) and Townsend's Warbler (*Dendroica townsendi*), appear to select habitat hierarchically, with selection for a patch based first on nesting habitat and secondarily on foraging habitat within a patch (Steele 1993, Matsuoka et al. 1997). Some evidence exists to support this hierarchical selection process by Golden-cheeked Warblers. Golden-cheeked Warblers breed in habitat that is a mixture of mature Ashe junipers and a variety of hardwoods (Pulich 1976, U.S. Fish and Wildlife Service 1992). During the breeding season, warblers do not occur outside this type of habitat, although they may occur along edges. Golden-cheeked Warblers are tied to this habitat type because females construct nests out of the peeling bark from mature Ashe junipers (Pulich 1976). After young have fledged, Golden-cheeked Warblers tend to move out of the closed canopy forest and into edges and gaps. Occasionally, family groups are found foraging in isolated trees in grasslands several hundred meters from the nearest closed canopy forest. Females usually build their nests in junipers, but may use any of a variety of hardwoods (U.S. Fish and Wildlife Service 1992). Thus, nest sites are probably not lacking, unlike the nest site limitation found with cavity nesters (Bock and Fleck 1995). Availability of water does not seem to be a problem for Golden-cheeked Warblers since they will leave their territories and travel long distances for water (Pulich 1976), and the distance to water does not influence warbler reproductive success (Arnold et a1. 1996). We lack data, but the number of roost sites is probably not limited. If food is limited, then selection should favor those birds with territories with better foraging opportunities (Kelly 1993). Presumably, territory size is related to habitat productivity (Kuitunen and Helle 1988) and birds have been shown to be able to adjust territory size based on resource availability (Whitcomb at al. 1981, Smith and Shugart 1987). Since territory size for Golden-cheeked Warblers appears inversely related to reproductive success, as seen by the use of smaller territories at large sites where they exhibit the highest reproductive success, habitat productivity maybe related to reproductive success. If so, the relationship is probably such that reproductive success is based on food availability and foraging opportunities. Thus, it appears that Golden-checked Warblers may select territories within a patch based on foraging opportunities.

Insect Availability

The abundance of resources, primarily food, provides the ultimate check on population numbers (Newton 1993). In temperate forests, food appears to be the most important factor in reproductive success, and its availability frequently, and perhaps regularly, limits reproductive output (Holmes et al. 1986). Although nest predation is the largest single source of nest mortality (Martin 1992), it primarily serves to reduce population levels below what resources would allow (Newton 1993). Many of the patterns seen in nearctic migrants in fragmented forests of the eastern and midwestem United States have been attributed to predator avoidance; however, at least some of those patterns may actually be based on food abundances (Robinson 1998). Some of the patterns seen in this study may support a food abundance hypothesis for explaining Golden-cheeked Warbler distribution and reproductive success, although direct evidence is lacking.

Upon their return to the breeding grounds, migratory birds must assess the suitability of potential territories. This must be done quickly in order to compete for the highest quality breeding sites. However, assessing the food supply quickly may be difficult for an insectivore relying on a complex food supply (Tye 1992). Instead insectivores might assess a potential territory by features correlated with the breeding season food supply such as vegetation structure or foliage density as indirect indices of resource abundance (Smith and Shugart 1987, Tye 1992). The study by Folkard and Smith (1995) supports this idea: they observed increased bird densities following nitrogen fertilization on their study sites. Although plant biomass increased, insect production did not, indicating that selection for territories was probably not based on direct assessments of the food supply, but on vegetative characteristics.

Vegetative structural diversity tends to correlate with insect productivity (Webb 1989, Tye 1992). Although foliage density does not directly measure insect abundance, it can serve as a measure of abundance because foliage density directly measures the availability of feeding substrates for insects (Blake and Hoppes 1986). Many insects favor plants in sunlight over those in shade and lepidopteran larvae prefer plants in gaps (White 1984), apparently due to higher nutrient levels (Harrison 1987). Several studies have documented increased insect diversity and abundance in areas with higher foliage density. Hansson (1983) found that edge trees support a richer insect fauna than interior trees, while Blake and Hoppes (1986) observed significantly more insects in forest gaps than in the forest understory. Invertebrates occurred at higher densities with lower distances from the edge and were positively correlated with the density of saplings along the edge (Helle 1986). However, Folkard and Smith (1995) failed to find an increase in insect production following nitrogen fertilization, although both plant biomass levels and bird density increased. Areas of high insect abundances may serve as profitable foraging areas by reducing the search effort (Blake and Hoppes 1986) and, as would be expected, Helle (1986) found higher densities of foliage insectivores along edges compared to interiors.

If these findings hold for Golden-cheeked Warblers, I would expect them to select territories based on vegetative characteristics and not direct assessments of insects. Circumstantial evidence indicates this may be true. The Golden-cheeked Warbler returns from migration in early to mid-March (Pulich 1976), probably before the availability of food is apparent. Wharton et al. (1996) found arthropod levels in warbler habitat increased from early March to peak in late April, corresponding to a peak in warbler breeding activity (Pulich 1976). Beardmore (1994) documented a shift in foraging patterns through the breeding season. In May and June, after young had fledged (Pulich 1976), Golden-cheeked Warblers used a more diverse group of broad-leaved trees than in March and April. Thus, assessments of territorial suitability may be based more on the abundance and distribution of hardwoods than on insect abundances, although direct assessments at the time of territory establishment cannot be ruled out.

Golden-cheeked Warblers often use edges and gaps for foraging after young have fledged, indicating the presence and quality of those edges and gaps may be important in determining reproductive success. Therefore, I would expect them to select territories based on the number and types of edges as an index to food availability later in the breeding season. Golden-cheeked Warblers selected for land uses, such as agriculture and grassland, which are associated with soft edges (Tables 6 and 10), while selecting against land uses more closely associated with hard edges, such as commercial development and high-density transportation. While warbler selection of land uses may have been based on edge types, it could also have been based on the types of disturbances. By definition, hard edges are those with abrupt changes between vegetation types, while soft edges show a graded change between vegetation types (Hawrot and Niemi 1996). Hard edges thus exhibit lower amounts of structural diversity than soft edges. Although no data exist for warbler habitat, the lower structural diversity of hard edges probably results in lower insect diversity and abundance. Wharton et al. (1996) found somewhat higher insect abundances in low vegetation height classes, precisely the height classes in which Beardmore (1994) most often observed foraging females and young. Additionally, Golden-cheeked Warblers occurred significantly farther from hard edges at large sites than from soft edges. Therefore, agriculture and grassland may have less detrimental influences on insects than other land uses. These two land uses more closely resemble the land uses adjacent to warbler habitat prior to man's impact in the region (Weniger 1984).

The suitability of a patch for breeding may be impacted by the surrounding landscape (Hinsley et al. 1995), but the influences of adjacent land uses on insects as food for an insectivorous bird like the Golden-cheeked Warbler are poorly known. Land uses probably differ in their effects on insects based on the associated levels of human disturbance. This pattern is best seen with the transportation land uses. Transportation may impact Golden-cheeked Warbler food supply in several ways. Exhaust gases reduce the abundances and diversity of insects in the vicinity of roads (Przybylski 1979), most likely by lowering fecundity (Coleman and Jones 1988). For herbivorous insects, food supplies may be reduced as a result of premature senescence of leaves on trees and shrubs near roads (Fluckiger et al. 1979), decreased foliage quality which necessitates increased leaf consumption (Coleman and Jones 1988), and declines in leaf size of deciduous trees (Koricheva et al. 1996). Thus, roads appear to affect hardwood vegetation most strongly. This potentially could result in lower foliage density and, consequently, lower abundances of insects near roads. Since Beardmore (1994) found a greater reliance by female and fledgling Golden-cheeked Warblers on a diversity of hardwood trees in May and June, females and fledglings may feel these effects more strongly than males. Additionally, the amount of pollutants from exhaust gases are positively correlated with traffic volume (Martel 1995), implying that effects from transportation should be more pronounced as the density of traffic increases. As a result of possible lowered insect levels, territories placed farther from a road should contain natural gaps less impacted by that road than territories placed nearer the road, and greater distances should be seen as traffic density increases. The same effect could be seen with both commercial and residential development because of exhaust from traffic associated with these land uses. If this scenario exists in warbler habitat, then I would expect to see two patterns of territorial placement relative to land uses. Golden-cheeked Warblers would be expected to select against those land uses. Warblers that settle nearest one of those land uses should place their territories farther from the edge than for other land uses. This pattern appears somewhat with Golden-cheeked Warblers. They selected against both high-density transportation and commercial development (Table 10). In addition, only one large site was unoccupied, and it was long and narrow with high-density transportation along its longest side. Additionally, the distances to the edge for warbler territories near these land uses tended to be greater than for land uses without these potential effects (Tables 13 and 15). One alternative explanation is the presence of differences in vegetation between areas near the edge and those in the interior. My vegetative measurements are insufficient to test this possibility; however, any differences in vegetative structure may still correlate with differences in insect abundances.

Birds appear capable of adjusting territory size based on food availability (Whitcomb et al. 1981, Burke and Nol 1998), with smaller territories occurring in areas of greater food abundances. If land uses impact insects as hypothesized above, then Golden-cheeked Warbler territory sizes would be expected to increase with increasing levels of human disturbance. This pattern was seen in residential development, but was most pronounced with the three transportation land uses (Table 15). Thus, warblers appear to have compensated for reduced insect abundances by increasing their territory size. However, increasing territory size did not seem to affect reproductive success as seen by a lack of significant differences in success among territories closest to the two residential development categories and the transportation categories. Apparently, birds moved away from the edge and increased territory size in order to be successful. One alternative exists to explain the differences in territory size. Based on my method of determining average territory size, selection against a land use would result in larger territory sizes for that land use. Conversely, if territory size increased due to reduced food availability, fewer territories could be placed next to a land use, giving the appearance of warbler selection against that land use. This possibility seems more plausible and offers a reasonable mechanism for increasing territory size with levels of human disturbance than just simply selection against one or more land uses.

The only land which significantly affected Golden-cheeked Warbler reproductive success was forested non-warbler habitat. This land use category consists primarily of a monoculture of young, “Christmas-tree like” junipers and few hardwoods. As a result, forested non-warbler habitat probably has lower insect diversity and abundances than the adjacent warbler habitat, while simultaneously lacking the hardwood diversity used for foraging by fledgling warblers (Beardmore 1994). Other researchers have found lower avian diversity in coniferous forests than nearby or adjacent deciduous forests (James and Warner 1982, Turchi et a1. 1995). Seitz and Zegers (1993) concluded those differences were not due to predation, but likely associated with other factors such as a difference in food supply. The same may be true for forested non-warbler habitat with the more diverse warbler habitat supporting more insects than the less-diverse forested non-warbler habitat.

Fragmentation may result in a loss of habitat heterogeneity within the remaining fragments (Faaborg et al. 1995), possibly translating into a reduced food supply. Howe and Jones (1977) found that insectivorous foliage gleaners disappeared from small, isolated fragments. One explanation may be food limitation on smaller patches, resulting in lowered reproductive success and ultimately in species loss (Blake 1991). Also, young produced in small patches may have lower body masses, implying that food abundances in small patches might be lower than in larger patches (Lens and Dhondt 1994). Wylie and Currie (1993) found that species-energy theory predicts species richness better than species-area relationships because it appears to incorporate factors that directly affect species abundance and distribution. The amount of energy available in a given area limits species richness and reflects such site characteristics as biomass levels, habitat diversity, and food resource levels.

Many researchers have investigated the effects of fragmentation on birds without quantitatively considering the effects of fragmentation on resources needed by the birds. Insects could be affected by fragmentation in ways similar to that seen in birds. Reduced patch size would result in lower population size and increased isolation would reduce rates of dispersal between patches. These could combine to increase the risk of local extinction. Indeed, several studies have documented a patch size effect on various arthropods (Muhlenberg et al. 1977, Faeth and Kane 1978, Jaenike 1978, Burke and Nol 1998). Additionally, Roland (1993) found differences in insect abundances and distributions with large-scale fragmentation. Taken together, these studies indicate the food supply for insectivorous birds may vary with both patch size and the nature of the surrounding landscape.

The mechanisms which would produce patch size effects on insect populations are not well understood. One possibility is the influence of the surrounding land uses. As stated before, roads impact insect diversity and abundance through exhaust gases (Przybylski 1979). Paved roads constitute about 23% of the surrounding landscape matrix for small sites, but only 17% for large sites. Residential development decreases from 12% at small sites to 8% at large sites. Also, edge effects should be felt more strongly in small patches because edge affects a greater proportion of the area in a small site than in a large one (Robinson and Wilcove 1994). Thus, the potential exists for edge effects on insects, resulting in lower levels of warbler food availability in small sites.

The observed patterns of patch size effect on Golden-cheeked Warbler pairing and reproductive success may result from patch size effects on their food supply. Female birds may select sites based on their needs for reproduction, while males may select for features that enhance mate attraction and territorial defense (Sedgwick and Knopf 1992, Burke and Nol 1998). Small patches of warbler habitat have more edge and a higher number of gaps, potentially leading to more song perches for males, although no significant differences in tree height or canopy density exist between patch size classes. Thus, smaller patches may be more suitable for males, resulting in the lower pairing and reproductive success rates in small patches.

Burke and Nol (1998) provided the first real test of the importance of food for explaining the patterns of nearctic migrants in a fragmented setting, although the results may not be completely applicable to Golden-cheeked Warblers. Ovenbirds are ground foragers and edge effects on food were documented, probably due to desiccation of leaf litter along edges. Since the Golden-cheeked Warbler is a foliage gleaner (Pulich 1976), edge effects potentially could be just the opposite. Lepidopteran larvae, a preferred food of the Golden-cheeked Warbler (Pulich 1976, Wharton et al. 1996), may be more abundant along edges due to greater foliage diversity and volume as a result of increased solar radiation along edges (Saunders et al. 1991). If this were true, then Golden-cheeked Warbler pairing and reproductive success should be higher in small sites due to greater amounts of edge. However, the opposite is true, indicating some mechanism is acting to lower the suitability of small patches for both pairing and reproduction. The most likely probability is the influence of the surrounding land uses (Hobbs 1993). Burke and Nol (1998) used study sites in a predominantly agricultural setting, effectively controlling for differences in landscape effects, whereas I have shown differences in both warbler distribution and reproduction relative to various land uses. Since Golden-cheeked Warblers appear to base territorial distribution within a patch on foraging opportunities, differences in food should relate to differences in adjacent land uses. Edge effects on food from the land uses would then be felt most strongly in small patches, leading to patch size effects on food, similar to the conclusions of Burke and Nol (1998).

Several Golden-cheeked Warbler behaviors observed during this study appear to be based on food availability. Golden-cheeked Warbler broods split upon fledging with one or more young tended exclusively by each parent, a phenomenon known as brood division (Smith 1978). Other warblers exhibit this behavior, including Black-throated Green Warbler (*Dendroica virens*) (Morse 1993), the Golden-cheeked Warbler's closest relative (Mengel 1964). Several hypotheses have been put forth to explain brood division in birds and include optimizing the ability of adults to provision young and reducing the risk of predation (McLaughlin and Montgomerie 1985). Few tests of these hypotheses exist, but Anthonisen et al. (1997) concluded that Bluethroats (*Luscinia svecica*) divide their broods to optimize adult foraging to feed young. Lastly, anecdotal data indicate that Black-and-white Warblers (*Mniotilta varia*) may compete with Golden-cheeked Warblers during periods of food limitation. Although Black-and-white Warblers primarily forage on bark, they will also glean insects from folage (Kricher 1995).

During 1994, a year of lowered insect production (Wharton et al. 1996), Black-and-white Warbler family groups were observed driving off Golden-cheeked Warbler adults and young on two occasions. Also, a Black-and-white Warbler adult male responded swiftly and agitatedly to broadcast tapes of Golden-cheeked Warbler song. These behaviors were not seen during 1993 or 1995.

Alternative hypotheses exist to explain the difference in pairing success and reproductive success with patch size. Females may select against males in small patches for several reasons. Small sites have lower canopy cover, although not significantly lower. Female Golden-cheeked Warblers may require minimum areas with high cover and so select against males in small sites because of the lower canopy cover in small sites. Higher cover may confer several advantages. Females and nests would experience less exposure to predators and brood parasites. Nest sites and nesting material would be more plentiful. Alternately, females may select for males in large sites because of the higher density of males. This would give them greater opportunities to evaluate male quality before selecting a mate. It would also give them more opportunities for extra-pair copulations or males for "divorce", a common occurrence following a failed nesting attempt (Breitwisch 1989).

Another explanation is a difference in rates of predation with patch size. Wilcove (1985) found higher rates of nest predation in smaller patches in Maryland using artificial nests and suspected that most of the predation came from Corvids. However, within warbler habitat, avian predators generally were more likely to occur in large sites over small ones (Arnold et al. 1996). Also, higher numbers of predators were found in sites with Golden-cheeked Warblers than in sites without Golden-cheeked Warblers, while warbler presence was positively related to patch size (Arnold et al. 1996).

A fourth explanation is noise from adjacent land uses. Reijnen and Foppen (1994) noted that Willow Warbler males near roads had trouble attracting and keeping females, possibly due to stress from traffic noise resulting in avoidance by females of areas near roads. However, Benson (1995) could not find any relationship between Golden-cheeked Warbler occurrences and highway noise, although his study was based solely on singing males and failed to consider pairing rates or reproductive success. I found that roads, both paved and unpaved, amounted to 31% of the edge bordering small sites compared to 25% for large sites. Combined with residential development, those edge totals go up to 43% for small sites and 32% for large sites. Sound attenuates with distance, so noise effects should be edge related. Since small sites have more edge and less interior than large sites, it seems possible that females select against males in small sites due to noise-related stress, although this possibility needs additional research.

Some evidence exists that Golden-cheeked Warbler population size at a site may depend on the previous year's reproduction. Several study sites were monitored for multiple years and the overall trend was for more territories in 1994 than in either 1993 or 1995. The highest reproductive success rate occurred in 1993 (44% successful) while the lowest rate occurred in 1994 (35%). Of the six sites with more than five territories, four sites reflected this overall trend, while two did not. For example, one site had six territories in 1993, 10 in 1994, and six in 1995. Reproduction was high in 1993 at this site with 83.3% of the territories successful while only 10% were successful in 1994. Arthropod abundances at this site were higher in 1993 than in 1994 (Wharton et al. 1996), with a scarcity of lepidopteran larvae in 1994 compared to 1993. In a re-evaluation of Golden-cheeked Warbler gizzard contents, Wharton et al. (1996) supported the conclusion of Pulich (1976) that lepidopteran larvae represent an important dietary component for the Golden-cheeked Warbler. Thus, this trend supports the possibility that population size is based on the previous year's reproduction. Holmes et al. (1986) found similar patterns elsewhere for different species and concluded that food availability was one of the strongest possibilities. Predation might also explain the pattern observed between years, but based on potential avian predators, Arnold et al. (unpublished data) did not find a difference in the abundances of nest predators between years.

Nest Mortality

Several processes may serve to reduce nest success, including nest predation, brood parasitism, competition, starvation, disease and nest destruction. Of these, nest predation and brood parasitism are often viewed as the most important factors affecting nearctic migrant bird populations (Robinson and Wilcove 1994). However, care must be exercised in relating causes of mortality to population trends of migrant birds. Confirmed sources of mortality are not necessarily causes of population regulation (James and McCulloch 1995). In fact, Robinson and Wilcove (1994) could not relate the effects of nest predation and brood parasitism directly to population changes. Predation and parasitism can never completely account for a given population size because neither mortality nor recruitment depend entirely on predation or parasitism (Newton 1993). In fact, loss of eggs or chicks is less likely to affect population trends than loss of breeding adults.

Nest predation accounts for the majority of nest losses in passerine birds (Martin 1992). However, Holmes et al. (1986) reported food as more important in governing reproductive success, with predation adding to its variability. Many studies in recent years have documented rates of nest predation in areas of high fragmentation, primarily on artificial nests (Wilcove 1985, Andren 1992), but also with real nests (Donovan et al. 1995b, Robinson et al. 1995). Several generalizations have arisen from these studies, but none appears universal. Rates of nest predation are generally higher in smaller fragments than large ones (Wilcove 1985) and higher near edges, usually within 50 m (Paton 1994). However, rates of predation appear strongly tied to the species composition of the predator assemblage (Andren 1992, Telleria and Santos 1992, Leimgruber et al. 1994, Harmon and Cotterill 1998) and the nature of the surrounding landscape matrix (Andren 1992, Donovan et al. 1995b). The majority of the studies on nest predation have been conducted in Europe and eastern and midwestem United States, presumably with predator assemblages and landscapes that differ from those found within the range of the Golden-cheeked Warbler. Therefore, extrapolating rates of nest predation from those studies may not yield actual rates of nest predation on Golden-cheeked Warblers.

Life history traits can provide an indirect indication of the role of nest predation in the evolutionary history of a species (Martin 1992). Species that evolved with low predation rates typically have large clutches, few brood attempts per year and high adult survival (Martin 1988, Martin and Li 1992). The problem for these species in the face of fragmentation is a lowered ability to compensate for increased mortality, and not just a greater vulnerability to predation. The Golden-cheeked Warbler seems to fit this model with clutch sizes averaging about four eggs and one nesting attempt per season, although renesting with failure of the first clutch does occur (Pulich 1976). However, adult survival rates are not known, but are probably comparable to the 67% yearly adult survivorship seen for Black-throated Green Warbler (Morse 1993). Pulich (1976) documented one female surviving to at least 13 years old, although sufficient demographic data to determine survival rates do not exist. Thus, the Golden-cheeked Warbler probably evolved with low nest predation pressure.

One adaptation to nest predation may be nest construction and placement (Martin 1988). Golden-cheeked Warbler nests are made from Ashe juniper bark and often placed along the main trunk of junipers, although many species of nest trees have been documented (U.S. Fish and Wildlife Service 1992). Nest concealment may significantly affect nest success (Angelstam 1986), especially concealment from below (Kelly 1993). Golden-cheeked Warbler nests are difficult to locate, in large part due to the nest material and placement. Although I was not actively searching for nests, none were located during the three years of this study. I am aware of only one case of nest predation having been documented in the literature. Pulich (1976) observed a rat snake having depredated Golden-cheeked Warbler nestlings.

Several of the patterns observed in this study might be based on nest predation. The Golden-cheeked Warbler is essentially forest-interior species and an edge effect on reproductive success was observed. Since nest predation is highest in the 50 m closest to the edge (Paton 1994), the lower reproductive success nearer the edge could be due to nest predation. Small sites have higher perimeter-to-area ratios, so edge effects should be more strongly felt in small sites than in large sites. Therefore, small sites should show lower reproductive success than large sites. This is indeed the case. Controlling for differences in pairing success yields the same conclusion. The percentage of paired males without young to all paired males decreases as patch size increases. For small sites, 47.8% of paired males did not reproduce successfully, while 27.3% and 15.3% were unsuccessful in intermediate sized sites and large sites, respectively.

Despite possibly explaining the relationship between reproductive success and patch size, nest predation does not appear to account for other patterns seen in this study. Although overall reproductive success was only 39.6%, the success of paired males was 79.2%. The failure of paired males to reproduce successfully may be due to several factors and nest predation is only one of those. So, at most, nest predation affects about one nest in every five. Golden-cheeked Warblers selected against high-density transportation and the territories which were placed closest to this land use at large sites were significantly farther from the edge than for other land uses. If selection against high-density transportation was based on nest predation, then I would expect high-density transportation to support a predator assemblage that is richer or denser than other land uses. This seems unlikely, and in fact, abundances of avian predators near high-density transportation appears lower than for other land uses (Arnold et al. unpublished data).

Engels and Sexton (1994) implicated the Blue Jay (*Cyanocitta cristata*) in the absence of Golden-cheeked Warblers near urbanization, with an emphasis on residential development (Engels 1995). Arnold et al. (1996) found a strong relationship between Blue Jays and residential development. If Blue Jays affect Golden-cheeked Warblers by depredating nests, then high rates of nest loss should occur closest to residential development. However, percentages of unsuccessful paired males for territories closest to residential development were low: 10% for low-density residential and 8.7% for medium-density residential development (Table 12). Several other land uses had much higher percentages of unsuccessful paired males, with rates of 54.5% for forested non-warbler habitat, 28.6% for agriculture, and 19.4% for grassland. Additionally, Golden-cheeked Warblers did not select against residential development as would be expected if Blue Jays affected warbler territorial placement. Regarding patch site suitability, Golden-cheeked Warblers did not occupy patches adjacent to high-density residential development, but this land use category only occurred next to small and intermediate size sites, which warblers selected against. Thus, Golden-cheeked Warbler absence in sites next to high-density residential development may not be due to the presence of that land use of Blue Jays associated with it, but instead may relate to patch size, possible patch size effects on insects, or other mechanisms associated with patch size.

Brood parasitism has often been considered a major factor affecting nest loss in migratory passerines (Brittingham and Temple 1983, Robinson and Wilcove 1994, Faaborg et al. 1995). Although Pulich (1976) reported a cowbird parasitism rate of over 57% (19 out of 33 nests parasitized), both Beardmore (1994) and Arnold et al. (1996) found low rates of parasitism (8.3% and 0.55%, respectively). Also, while concentrating almost exclusively on Golden-cheeked Warbler reproduction, Arnold et al. (unpublished data) found an equal number of parasitized hosts of other species (two Painted Buntings [*Passerina ciris*], one Blue-gray Gnatcatcher [*Polioptila caerulea*] and one Northern Cardinal [*Cardinalis cardinalis*]). Several explanations exist for these discrepancies between Pulich (1976) and other Golden-cheeked Warbler studies. Land uses near host breeding areas affect rates of cowbird parasitism (Brittingham and Temple 1983) and Pulich (1976) did not describe the land uses in the vicinity of his study site or of levels of cowbirds in the area. The two study sites used by Beardmore (1994) were also used by Arnold et al. (1996). All four cases of parasitism reported by Arnold et al. were in patches either adjacent to or near agricultural areas. Timing of nesting attempts may also affect parasitism rates. Early nesting warblers in Travis County were not parasitized, but all four cases reported in Arnold et a1. (1996) were for late nesting attempts (Catherine Gibbons, unpublished data). Since they were not monitoring nests, Arnold et al. (1996) may have missed a few cases of parasitism is a parasitized nest was abandoned prior to hatching, although this probably would not have had a significant effect on their reported rates of parasitism. Thus, while the potential for impacts exists, further data, at different locations and under differing landscape scenarios, are needed to assess the role brood parasitism plays on Golden-cheeked Warbler reproductive success.

POTENTIAL PROBLEMS

Several shortcomings of this study exist. I would like to mention each shortcoming briefly and discuss its possible effect on my results and conclusions. First no adequate controls were used. Studies on fragmentation in the eastern United states have generally used controls of >10,000 ha. Unfortunately, no contiguous blocks of >1,000 ha in Travis County were available to me, and in fact, few if any blocks of that size exist. In some respects, that is a reflection on the extent of anthropogenic fragmentation in Travis County, but also of the naturally fragmented and discontinuous nature of warbler habitat.

The three-year length of this study makes it something of a “snapshot in time”, and as such, species composition and population density in each site may not have reached equilibrium. This should have underestimated fragmentation effects by the inclusion of small sites that have become isolated only recently, yet still support Golden-cheeked Warblers. Given sufficient time, these sites may eventually no longer support Golden-cheeked Warblers. Also, effects of land uses on edge of sites may not have been fully expressed if a change in land use occurred recently. A good example of this possibility was the ongoing growth of medium-density residential development at the edge of one of the large sites.

Vegetation measurements were taken at the point of first visual occurrence of a Golden-cheeked Warbler at each site. These points were biased somewhat toward male singing perches and so may not be representative of each site. Additionally, only one point per site was sampled, with the effect of possibly overlooking differences in vegetative composition or structure, both within and between sites.

Because adults split broods, both reproductive success and cowbird parasitism may have been underestimated. However, begging cowbirds are very noisy and I doubt many were missed.

Since more time was spent in smaller sites, patch size effects were probably underestimated and the effects shown here are therefore conservative. Additionally, this study was biased toward males with high reproductive success by the exclusion in the analyses of all males encountered on only one visit. Thus, the effects on floaters and males with very large territories were not included.

I did not determine stocking rates for agriculture. Variation in stocking rates may indeed affect Golden-cheeked Warblers breeding closest to agriculture. I would anticipate greater stocking rates would result in less vegetative foliage density on edges and consequently have more detrimental effects on Golden-cheeked Warblers. Also, I often did not have access to adjacent properties, so areas of low stocking rates may have been classified as grasslands.

For mapping purposes, I used approximate territorial centers. In some territories I did not have many observations, so I may not have adequately determined territorial centers. As such, the distances to the edge and nearest land use may have been incorrect. The use of maps at 1:24000 scale may have produced smoothed contours of actual patch boundaries, affecting the perimeter and area measurements, and as a result, the perimeter/area ratios and fractal dimension. This could have obscured any potential differences in fractal dimension with patch size.

FUTURE RESEARCH

The patterns seen in this study suggest several avenues of research on Golden-cheeked Warblers and other migrant birds in the future. The most appropriate would be the testing of patterns and processes prior to, during, and after fragmentation. Unfortunately, this may not be practical with the Golden-cheeked Warbler because of its endangered status. The mechanisms suggested in this study, principally food availability and the impact of adjacent land uses, should be tested, although the endangered status of the Golden-cheeked Warbler and the required spatial scale make testing those mechanisms logistically difficult. The usefulness of small patches, and to a lesser extent intermediate sized patches, for Golden-cheeked Warblers need to be evaluated. Possibilities to be considered should include, but not be limited to, their value as migratory stopover habitat or as metapopulation sinks which serve to remove excess individuals from large sites to prevent overcrowding and possible reproductive failure in the large sites as a result.

Sources of nest mortality, particularly nest predation, and their relative effects on reproductive success need evaluation. Various Golden-cheeked Warbler demographic parameters, such as juvenile survivorship, adult survivorship, and lifetime reproductive effort, are largely unknown. Knowledge of these would be useful in producing reliable population viability analyses to assess the factors associated with long-term declines for Golden-cheeked Warblers.

MANAGEMENT RECOMMENDATIONS

I would propose the following management guidelines for the Golden-cheeked Warbler, keeping in mind that proper conservation requires managing the landscape and not just a few select elements in that landscape (Harris 1984):

1. Minimize further fragmentation of warbler habitat, particularly fragmentation of large patches. If any habitat loss is allowed, it would be most beneficial for the population within the site if it occurred only on the edges of patches and not result in additional fragmentation.

2. As much as possible, minimize the types of land uses occurring adjacent to a patch.

3. Buffer zones adjacent to warbler patches would be beneficial for warblers occupying those patches. Preferably, the buffer zones would be maintained as grassland, particularly between patches and those land uses associated with higher levels of human disturbance. Width of the buffer zone would need to be determined by additional research.

4. Minimize the extent of edges so patches contain as much interior habitat as possible.
5. Encourage soft edges as opposed to hard edges.

CONCLUSION

In summary, I found the Golden-cheeked Warbler to be an area-sensitive species, having documented area effects on both pairing and reproductive success. The warbler is slightly forest-interior, relying on edges for foraging after young have fledged but with its greatest reproduction occurring in the interior. Additionally, warblers appear affected by the nature of the surrounding landscape, primarily in terms of patch suitability and territorial placement within a patch. Evidence suggests that food availability, as possibly affected by patch size and influences from the surrounding landscape, may be the most important factor determining Golden-cheeked Warbler distribution and reproductive success. Therefore, to conserve the Golden-cheeked Warbler, management which would be most beneficial to the bird would take into account factors such as patch size, the amount of edge, and the type and extent of land uses in the surrounding landscape matrix.

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VITA

Cade Lawrence Coldren was born on 3 February 1960 and is married to the former Mary Kathleen Orr. They have one son, Ethan Cooper. Cade's permanent address is P.O. Box 818, Throckmorton, Texas 76483. Cade received his B.S. in electrical engineering from Texas A&M University in December 1982 and his M.S. in wildlife and fisheries sciences from Texas A&M University in December 1992.