FORAGING ECOLOGY OF KIRTLAND'S WARBLERS IN MANAGED AND NATURAL BREEDING HABITAT

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By

Jennifer Lynn Fussman, B.A.

* * * * *

The Ohio State University
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Master's Examination Committee:

Dr. Thomas C. Grubb, Jr., Adviser

Dr. Richard A. Bradley

Dr. Deanna J. Stouder

Dr. Carol I. Bocetti

Approved by

Thomas C. Grubb, Jr.

Adviser
Department of Zoology

ABSTRACT

This study examines prey availability as a factor influencing breeding habitat selection by Kirtland's Warblers *(Dendroica kirtlandii)*, and characterizes the foraging behavior of this endangered species. Kirtland's Warblers nest on the ground in early-successional jack pine forests in northern Lower Michigan. The species may reject old jack pine stands for nesting due to decreased prey density in lower branches and ground vegetation of old stands. Insects were captured in young and old nesting habitat and in mature jack pine too old to be attractive for breeding, and birds were observed foraging in young and old nesting habitat. Insect biomass in low vegetation was less in old nesting habitat than in young nesting habitat, and was much less in mature habitat. Kirtland's Warblers in old nesting habitat did not forage higher than those in young nesting habitat, suggesting that the decrease in insect biomass in old nesting habitat is not great enough to affect the birds. Managed plantations and natural wildfire-regenerated jack pine stands were very similar in terms of insect abundance, diversity, and distribution, and warbler behavior. Warblers foraged most often on jack pines, but also used ground vegetation and pin oak trees as foraging substrates. The proportion of foraging attempts in oak varied widely among stands, suggesting that warblers use oak in proportion to its availability.

Female Kirtland's Warblers foraged significantly lower than males, following a general trend for species of parulid warblers.

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VITA

December 7, 1973.....Born - Pontiac, Michigan

1993 - 1995.....Research Fellow and Mentor, Howard Hughes Medical Institute/Ohio Wesleyan University Grant Program

1995.....B.A. Zoology, Ohio Wesleyan University

1995 - 1996.....Field Technician and Team Leader, National Biological Service, Kirtland's Warbler Banding Program

1996 - present.....Graduate Teaching Associate, The Ohio State University

PUBLICATIONS

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INTRODUCTION

The habitat of species is often spatially heterogeneous at various scales (Meffe and Carroll 1994). At the landscape scale, the environment consists of a mosaic of favorable and unfavorable areas. Conspecifics of a given population often exist in relatively close proximity to each other, but in habitat of differing quality. At a smaller scale, individual home ranges can contain high quality and low quality patches. The environment can also be temporally heterogeneous - habitat availability and food levels often vary from year to year due to factors such as disturbance and succession (Morrison et al. 1992).

Habitat heterogeneity influences the diversity of species assemblages, the distribution of species, and demography of populations. In forests, both vegetative height diversity (MacArthur and MacArthur 1961) and plant species heterogeneity (Wiens and Rotenberry 1981, Rotenberry 1985, Wiens 1985) are correlated with diversity of bird assemblages. The regional distribution of species has been shown by early ecologists to be related to specific components of the habitat within patchy environments (Grinnell 1917, Lack 1937, Svardson 1949). Habitat heterogeneity also results in high and low quality patches being occupied by individuals of a population. Individuals in rich patches often have higher survivorship and reproductive success than individuals in poor habitat

(VanHorne 1983). The distribution of patches of favorable habitat within the landscape may also influence the success of dispersers. Populations with high reproductive output in favorable patches may serve as "sources" of dispersing individuals to lower quality habitat that is a "sink" in terms of recruitment (Pulliam 1988) The effects of habitat heterogeneity on distribution have been studied on a variety of taxa including mammals (e.g., Vaughan 1954, Bowers and Smith 1979) fish (e.g., Norton 1991, Benson and Magnuson 1992, Poizat and Pont 1996), and birds (e.g., Collins et al. 1982, Cody 1985).

For birds, spatial and temporal heterogeneity in habitat affects the distribution of important resources, such as foraging sites, nesting sites, singing and roosting perches, and cover from predators (Wiens 1989, Sharpe 1996). Birds may increase their individual fitness by choosing to nest in areas where these resources are abundant. For example, Holmes et al. (1996) found the Black-throated Blue warblers (*Dendroica caerulescens*) nesting in forest patches with a dense shrub layer (presumably providing cover from predators) had a higher reproductive output than warblers in areas of low shrub density.

Within breeding habitat of birds, stage of succession is an important component of heterogeneity. The age of habitat affects structure and vegetative height diversity which may be important to birds for nest and foraging sites (MacArthur and MacArthur 1961). Studies have shown changes in bird species assemblages with succession of habitat in grasslands and forests (e.g., Johnston and Odum 1956, Moss et al. 1979, Bollinger 1995). For many species, a given area of habitat is only suitable for nesting during a certain successional stage. For example, in grasslands, Grasshopper Sparrows (*Ammodramus savannarum*) require very young fields with low vegetation, and are not found in older

fields with accumulated litter depth (Herkert 1994, Delisle and Savage 1997). Certain forest birds also require habitat of a specific age. Northern Spotted Owls (*Strix occidentalis caurina*) nest and forage exclusively in old growth forests of the Pacific Northwest (Carey et al. 1990, Bart and Forsman 1992). Red-cockaded Woodpeckers (*Picoides borealis)* also require mature forests for breeding habitat, in this case old growth pines in the Southeast United States (Jackson 1994). Bachman's Sparrows (*Aimophila aestivalis*) have slightly different stand age requirements such that they breed in very young and very old pine forests, but are not found in stands of intermediate ages (Dunning and Watts 1990).

In many cases, the habitat age requirements of birds conflict with human activity. In agricultural landscapes, the availability and distribution of young grasslands varies widely both spatially and temporally depending on agricultural practices (Warner 1994). Old growth forests have been extensively reduced in size and fragmented by timber harvesting. For Red-cockaded Woodpeckers, small patches of forest may not provide enough space for foraging, and fragmentation may lower the birds' ability to locate conspecifics for mating (Conner and Rudolph 1991). Managers of rare species need to provide suitably aged habitat to allow for sufficiently high survivorship and reproductive success in populations of rare species. This can be a challenge for species such as Bachman's Sparrow, which require a mosaic of pine stands of different ages (Pulliam et al. 1992, 1994). A similar challenge exists for management of Kirtland's Warblers (*Dendroica kirtlandii*), which nest in early-successional jack pine stands between 5 and 20 years of age (Mayfield 1992).

For many rare species, the specific breeding habitat requirements are known, but it is not understood why or how the species chooses this particular habitat. The factors influencing habitat selection in birds are often difficult to discern, even when bird density can be correlated with structural habitat components such as vegetation type or density (Cody 1985, Vickery and Hunter 1995, Petit and Petit 1996, Sharpe 1996). When choosing breeding habitat, birds may be responding to abiotic factors such as moisture level or temperature, or biotic factors such as vegetation density, food supply, intraspecific and interspecific competition or predation (Morse 1985). Combinations of these factors may represent trade-offs to birds. For instance, the nesting habitat offering the best cover from predation may not be in an area of maximum prey abundance. By selecting favorable nesting habitat, birds may benefit from decreased risk of nest predation and starvation of young, leading to increased reproductive success and fitness (Cody 1985).

For insectivorous warblers, favorable nesting sites and foraging areas had been suggested as two important components of breeding habitat (Knopf and Sedgewick 1992, Martin 1992, Steele 1992, 1993). Breeding birds could choose habitat that provided suitable vegetative cover to conceal their nests from potential predators. Knopf and Sedgewick (1992) found that Yellow Warblers (*Dendroica petechia*) appeared to select nest sites based on vegetation components of the surrounding area, a response presumably lowering the risk of nest predation or brood parasitism. Similarly, Steele (1992, 1993) determined that the presence of dense shrubs influenced the choice of nest sites by Black-throated Blue Warblers. Bocetti (1994) showed that Kirtland's Warbler nest sites had a

higher proportion of low shrubby vegetation than randomly selected points, indicating a preference for greater nest cover.

Birds could also choose nest sites near areas of high arthropod prey density. Petit and Petit (1996) showed that when equal numbers of artificial nest boxes were available, Prothonotary Warblers (*Protonotaria citrea*) preferentially nested in areas of greater arthropod density.

In this study, I explore the importance of prey abundance to habitat selection of Kirtland's Warblers during the breeding season. Kirtland's Warblers nest primarily in a 120 x 160 km area covering 13 counties in the AuSable River drainage system of northern Lower Michigan (Mayfield 1992; Figure 1). In recent years, the species has begun to nest in similar habitat in the Upper Peninsula of Michigan. These small areas constitute the entire breeding range for this federally endangered species.

The restricted nature of the birds' breeding range seems to be due to their specificity for nesting habitat (Mayfield 1983). Kirtland's Warblers are insectivorous ground-nesters. They place their nest in thick cover in large tracts of early-successional (6 - 21 year-old) jack pine (*Pinus banksiana*; Mayfield 1992). The warblers glean small flying and crawling arthropod adults and larvae from jack pines, interspersed pin oak (*Quercus ellipsoidalis*), and ground vegetation (Mayfield 1992).

Jack pine barrens exist in northern Michigan in a region of dry soil known as Grayling Sand (Walkinshaw 1983). These trees have serotinous cones which require

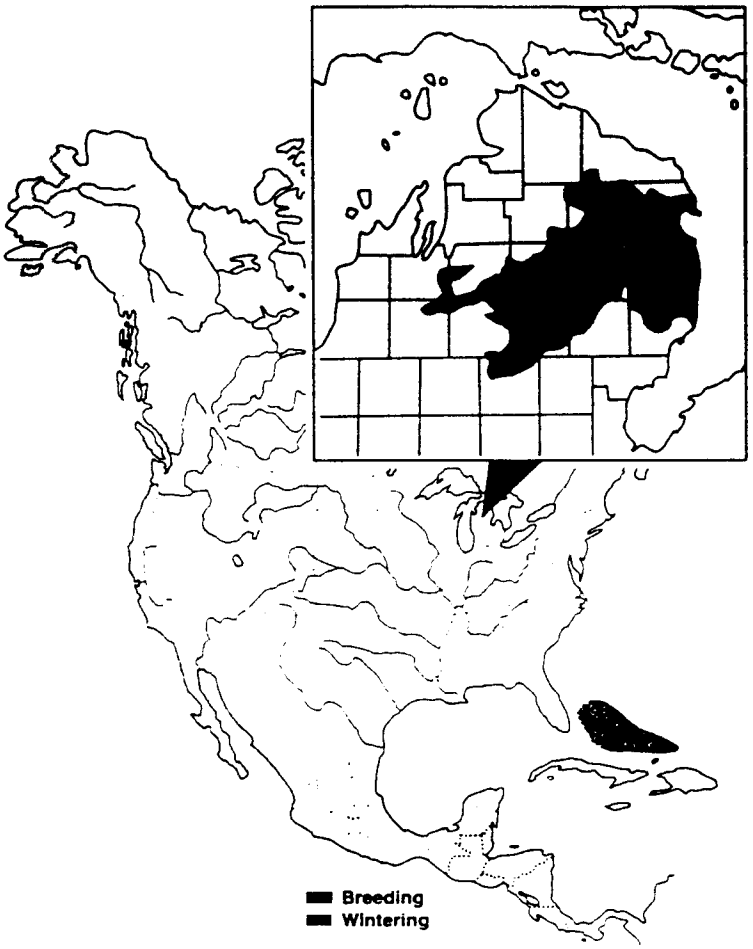

Figure 1. Map of breeding and wintering ranges of Kirtland's Warblers (from Mayfield 1992).

high temperatures to open and propagate. Historically, large patches of young jack pine forest regenerated in this area as a consequence of frequent wildfires, resulting in consistently available nesting habitat for Kirtland's Warblers. With the onset of modern fire suppression, breeding habitat for the warbler became scarce (Mayfield 1992).

Managers attempting to increase the numbers of this endangered species have focused on two approaches: 1) controlling the Brown-headed Cowbird (*Molothrus ater*) nest parasitism that has had a serious impact on the population size (Walkinshaw 1983), and 2) providing sufficient nesting habitat. Cowbird parasitism has been practically eliminated since 1972 due to intensive trapping and removal of adult cowbirds (Kelly and DeCapita 1982). In the past, management for nesting habitat has included prescribed burning of jack pine stands followed by natural regeneration. Currently, most habitat is created by systematically rotating the planting and harvesting of jack pine. Typically, plantations are harvested for pulp when the trees are 50 years old, so that the stand exists for approximately 30 years after it has become too old for Kirtland's Warbler nesting habitat. The goal is to provide a consistent acreage of young jack pine at all times. Plantations resemble naturally fire-regenerated habitat because seedlings are planted in high density strips following sine wave patterns that reverse periodically. This method creates thickets interspersed with small openings similar to those existing after wildfires. Kirtland's Warblers often place their nests on the edges of such openings (Bocetti 1994).

It is unclear what factors influence Kirtland's Warblers' preference for nesting habitat in early successional jack pines. One factor may relate to the changes that occur in the vegetative structure of jack pines as they age. Very young trees (5-6 years old) have

thick lower branches that extend to the ground layer of lush blueberry (*Vaccinium angustifolium*), grasses (*Andropogon* spp., *Danthonia spicata*) and sedge (*Carex pennsylvanica*) (Walkinshaw 1983). Jack pines on Grayling Sand are slow-growing trees, reaching a height of approximately 8 meters in 20 years. By this age, the needles on the shaded lower branches have dropped off, leaving bare branches near the ground. This loss of needles and the accompanying thinning of the ground vegetation (Walkinshaw 1983) may cause older jack pine stands to become unsuitable for the ground-nesting Kirtland's Warblers.

Many studies have shown that male warblers tend to forage higher in the vegetation than females (e.g., Nolan 1978, Busby and Sealy 1979, Morse 1980, Franzreb 1983, Steele 1993). If male Kirtland's Warblers forage higher than females, the thinning of lower branches in older jack pines and any resulting change in prey availability in this zone may be especially important to females. Although both males and females feed nestlings, only females incubate the clutch. Females that nest in older habitat may have to forage higher in the trees (farther from the nest) during the incubation period, leaving their nest unattended for longer intervals. Such females could therefore have a higher risk of nest failure than females nesting in younger habitat. If such a selection pressure exists, however, it does not translate into different pairing success in young and old stands. Bocetti (1994) showed that stand age did not affect density of females.

Fewer suitable nest sites and fewer arthropod prey have both been suggested as the primary reasons for Kirtland's Warblers rejection of mature jack pine forests for nesting habitat. The sparse lower branches and ground vegetation in a mature jack pine stand may

not provide enough concealing cover for nests. The height of the first live branch at nest sites is lower than at random sites, suggesting that vegetation structure above the ground may be important to habitat choice (Bocetti 1994). Alternatively, the thinner low vegetation may not support a favorable prey base for the ground-nesting warblers (Probst and Weinrich 1993). Both of these factors may contribute to habitat selection by this species, although neither has been explored.

This study had three objectives. The first objective was to test the hypothesis that young jack pine forests were chosen by nesting Kirtland's Warblers because prey availability in low vegetation was greater in this habitat than in mature jack pine. Two predictions were made from this hypothesis. First, arthropod populations may differ in abundance and/or distribution between young and old jack pine forests. Second, within occupied nesting habitat, foraging behavior may differ as the habitat aged and the arthropod community changed. Other parulid warblers were shown to shift foraging behavior with altered habitat structure and food resources (Maurer and Whitmore 1981, Robinson and Holmes 1984). Thus, as foliage on the lower branches thinned, Kirtland's Warblers might be expected to shift their foraging to higher zones in the trees.

The second objective was to examine differences in behavior between male and female Kirtland's Warblers. Morse (1980) attributed sexual differences in warbler foraging height to reproductive activities. By foraging high in a tree, a male could remain conspicuous to nearby males, allowing him to defend his territory. By foraging low, a female can remain near a nest, especially during the energetically demanding incubation period. Mayfield (1992) observed that female Kirtland's Warblers usually forage near the

nest. Attracting or searching for extra-pair copulations could be an additional motive for an intersexual difference in foraging height.

My third objective was to test the null hypothesis that plantations and wildfire-regenerated stands of the same age did not differ in the arthropod communities they supported and in the foraging behavior of resident Kirtland's Warblers. Currently, the majority of stands in the breeding range are managed plantations, but stands also exist that have regenerated naturally following wildfires. Bocetti (1994) found that warblers nested in higher density in wildfire stands than in plantation stands. She also suggested that a more abundant prey base may exist in wildfire stands due to a greater density of trees and ground cover as compared to plantations. A difference in prey availability could make wildfire areas more attractive to warblers.

METHODS

Study Area

The study area included 31 jack pine stands in six counties (Alcona, Crawford, Iosco, Oscoda, Ogemaw, and Roscommon) in the northern Lower Penninsula of Michigan. A stand was defined as an area of contiguous, even-aged jack pine forest subject to the same management practice (plantation or wildfire). Stands were classified into one of three age categories: young nesting habitat (6-13 years), old nesting habitat (14-21 years), and mature (> 21 years). The two nesting habitat age categories were determined by dividing in half the age range of stands currently occupied by Kirtland's Warblers. Nineteen of the stands visited contained Kirtland's Warbler nesting habitat, and the remaining 12 contained mature jack pine forest (Table 1).

In 1995, seven nesting habitat stands were chosen from among those stands that had been used earlier in the season for a separate banding study. In 1996, 17 nesting habitat stands were chosen from all of the stands that had been occupied by Kirtland's Warblers the previous year. I first randomly chose six plantations of each age category from all the plantations in the breeding range. Too few wildfire stands existed to choose six stands from each nesting habitat age category, so all of the available wildfire stands

Table 1. Number of individual Kirtland's Warblers observed and number of arthropod samples taken in various types of jack pine stands in 1995 and 1996.

	Management Practice			
Stand Age	Plantation		Wildfire	
Young nesting habitat (6-13 years)	Stands visited:	8	Stands visited:	2
	Birds observed:	20	Birds observed:	11
	Mean observations per bird:	8	Mean observations per bird:	8
	Arthropod samples:	18	Arthropod samples:	18
Old nesting habitat (14-21 years)	Stands visited:	6	Stands visited:	3
	Birds observed:	13	Birds observed:	14
	Mean observations per bird:	10	Mean observations per bird:	9
	Arthropod samples:	18	Arthropod samples:	18
Mature (>21 years)	Stands visited:	6	Stands visited:	6
	Arthropod samples:	18	Arthropod samples:	18

were used. In 1996, I also randomly chose 6 mature plantations and 6 mature wildfire stands from all the mature stands (21-50 years) in the breeding range.

Arthropod sampling

Arthropods were collected from young and old nesting habitat and from mature jack pine stands (Table 1) in order to compare density, diversity and distribution as a function of stand age. Arthropod samples were collected from 27 May through 9 July, 1996. I collected three sets of samples during each visit to a nesting stand, on the same day that bird observations were taken. Three sets of samples were also taken during each visit to a mature jack pine stand.

Each set of arthropod samples included four jack pine branch segments and one sweep-net sample from ground vegetation. The branch-clipping technique described by Cooper and Whitmore (1990) was used to sample insect populations in jack pine trees. Samples were taken from each of the four vertical zones of the vegetation at the outer third of the branch, from four different trees of uniform height that were surrounding a small opening. The segments of branches were inserted into plastic bags and clipped off, and the bags were sealed and frozen until processed. The ground vegetation sample was collected by 25 sweeps of a sweep-net on the edge of a small opening. Insect data from all three sets of samples were averaged to obtain mean number of individuals, number of families (using Borror et al. 1989) and biomass per sample in each stand.

Although Kirtland's Warblers diets may not include diet all of the arthropod taxa I collected, I assume that the density of their prey was positively correlated with the density

of arthropods I recorded. This assumption is based on the observation by other researchers that Kirtland's Warblers are generalists with respect to arthropod prey (Walkinshaw 1983, Mayfield 1992), and the fact that two sampling techniques were used to collect a wide variety of arthropods.

Numerous non-insects of the Phylum Arthropoda (primarily spiders) were present in the samples. All collected arthropods were identified to family, with the following exceptions: 1) spiders, mites, and millipedes were classified by order, 2) Lepidoptera were classified as adult or larvae. The length of each arthropod was measured to the nearest millimeter, and length-weight regressions at the level of order (Rogers, et al. 1977) were used to calculate biomass.

Bird observations

Foraging Kirtland's Warblers were observed in plantations and wildfires of both age categories (Table 1), during all stages of nesting from incubation through fledgling. Birds were observed from 17 June to 7 July, 1995 and from 27 May through 9 July, 1996. In 1995, 14 male and 9 female warblers were observed, and in 1996, 24 males and 11 females were observed.

I collected data on each bird during a single observation period. Due to the scarcity of wildfire stands, these stands were visited more than once throughout the season. However, individual territories within the stands were visited only once. Also, three wildfire stands were visited both in 1995 and 1996. However, no territory within a stand was visited in both years. During the 1996 season, I rejected any territories that had

been visited in 1995 or that were immediately adjacent to territories visited in 1995. By following this procedure, I lowered the chances of collecting data on the same birds during both years, since adult male Kirtland's Warblers are likely to use the same territory from year to year. Some of the birds studied in 1995 were color-banded, and I also referred to these band combinations to help avoid visiting any birds twice.

Visits to different habitat categories were rotated such that all categories had been visited once before any were visited a second time. I attempted to visit at least two territories at a single site per day. Visits were made both in the morning and afternoon. At each territory I located the male by following his song, and followed him until I located the female and approximate nest area. Remaining in that location, I observed one member of the pair for 1 h, then the other member for 1 h. Separating the observations temporally allowed me to avoid recording data on the male and female simultaneously when their behavior may have been dependent on each other. Due to the difficulty of finding females, it was not always possible to collect data on both members of a pair.

Each time I observed a bird attempting to capture a prey item, I recorded the following data: 1) type of vegetation the bird was in (jack pine, oak, cherry, ground vegetation, dead wood on the ground, or snag), 2) horizontal and vertical position if in a jack pine, 3) height of the tree, 4) substrate the bird foraged on (branch, needles, tip of new growth), 5) foraging maneuver (glean, sally), 6) prey identity when possible, and 7) how the prey was handled after capture (consumed or loaded to be fed to nestlings or female). The vertical position was defined as the lower, lower-middle, upper-middle, or

upper quarters of the tree. The horizontal zones corresponded to the inner, middle, and outer thirds of the tree from the trunk to the tips of the branches.

In the interest of minimizing disturbance to this endangered species, prey loading behavior was used to classify reproductive stage instead of directly examining nests. A female loading prey indicated the nestling or fledgling period. A male loading prey might have indicated the incubation stage as well as the nestling or fledgling stages, since males deliver food to incubating females.

A sequence of foraging attempts was recorded for each bird. Because warblers often moved out of sight during the observation period, these sequences did not represent continuous bouts of foraging behavior. The mean number of observations per bird was calculated for warblers in different habitat types (Table 1).

Data Analysis

The location of foraging Kirtland's Warblers and the abundance, diversity, and distribution of arthropods were compared between plantations and wildfires, and among stand of different ages. Multivariate Analysis of Variance (MANOVA) was used for all tests, with the significance level of $\propto = .05$.

I compared arthropod communities among habitat types as an index to prey availability to Kirtland's Warblers. For any species, available prey include only those items that the predator actually encounters and is able to use (Holmes and Schultz 1988, Raphael and Maurer 1990). We do not have detailed information on the composition of prey species in the diet of Kirtland's Warblers because gut contents and fecal samples have

not been analyzed. However, the warblers feed their young predominantly larvae (Walkinshaw 1983, pers. obs.). Therefore, for data analysis I employed both total arthropod abundance and abundance of lepidopteran and hymenopteran (F. Diprionidae) larvae, the latter hereinafter referred to simply as larvae.

I first used a one-way Multivariate Analysis of Variance (ANOVA) model to test for effects of individual stand on number of individual arthropods, number of larvae, number of arthropod families, total arthropod biomass, and larval biomass. A second model tested for a relationship between these dependent variables and management practice and stand age. Two additional models tested for effects of management practice and stand age on 1) total arthropod biomass and 2) larval biomass sampled from ground vegetation. Two final models tested for relationships between the independent variables and both total arthropod biomass and larval biomass in the vertical zones of jack pines.

The data on foraging behavior were in the form of sequences of foraging attempts for each bird. Because the foraging events in a sequence were not independent from one another, the bird was considered to be the primary sampling unit (Noon and Block 1990, Hejl et al. 1990). Birds in the same stand were assumed to be statistically independent from one another for the purposes of analysis, and stand was used as a factor in all analyses to test this assumption. For each sequence, I calculated the proportion of observations falling into each category (Aerially and Barrett 1985) of vegetation type (jack pine, oak, cherry, ground vegetation, dead wood on the ground, or snag), vertical position in jack pine (Lower, lower-middle, upper-middle, or upper-quarter), and horizontal position in jack pine (inner, middle, or outer third). Sequences with less than five

foraging attempts were discarded in order to avoid giving too much weight to a single foraging event (Hejl et al. 1990).

For statistical analysis of warbler foraging locations, proportional use of vegetation types, vertical zones, and horizontal zones were considered three separate groups of dependent variables. For each group, one-way MANOVA tests were run with the individual stand as the only factor. Then, I used MANOVA tests to search for relationships of each aspect of foraging location with six factors and their interactions. The factors were management practice of the stand (plantation, wildfire); stand age (young, old), deciduous component of the territory ($\leq$10% deciduous, >10% deciduous), sex of the bird (male, female), year of the study (1995, 1996), and prey loading behavior (consuming prey, loading prey).

All two-way interactions were also included in the models. After each successive run of a MANOVA model, the interaction effect with the largest non-significant p-value ($p > .05$) was removed, and the model was rerun to obtain a better fit (M. Irwin, pers. comm.). This process of elimination and reiteration was repeated until all remaining interaction effects had p-values less than .05 or until all interaction effects had been eliminated. All main effects remained in the models, regardless of their p-values.

RESULTS

Arthropod abundance and diversity was similar between plantations and wildfires, and among stands of different ages. However, vertical distribution of arthropod biomass in jack pines may have been influenced by stand age. Kirtland's Warblers of both sexes foraged most often from the upper half of jack pine trees, but also used oak and ground vegetation as foraging substrates. Neither proportional use of vegetation types nor proportional use of horizontal zones in jack pines were affected by any of the habitat factors tested. Proportional use of vertical zones in jack pine was related to sex and prey-loading behavior of the bird, and to management practice and deciduous composition of the habitat.

Arthropod samples

Although arthropod abundance in branch samples and sweep-net samples can not be compared directly due to the different techniques, diversity appeared to be higher in ground vegetation than on jack pine. Branch samples contained mostly crawling insects, while sweep-net samples contained many more flying insects of the orders Diptera and Hymenoptera (Table 2).

Table 2. Arthropod taxa collected in samples from jack pine branches and ground vegetation.

Taxon	Jack pine	Ground vegetation
C. Arachnida	X	X
O. Araneae	X	X
O. Opiliones		X
O. Acari	X	
C. Diplopoda		X
C. Hexapoda	X	X
O. Odonata		X
F. Coenagrionidae		X
O. Orthoptera	X	X
F. Tetrigidae		X
F. Acrididae	X	X
F. Tettigonidae		X
O. Hemiptera	X	X
F. Miridae	X	X
F. Nabidae		X
F. Aradidae		X
F. Corimelaendiae		X

(continued)

Table 2 (continued).

Taxon	Jack pine	Ground vegetation
F. Pentatomidae	X	X
Nymphs	X	X
O. Homoptera	X	X
F. Membracidae		X
F. Cicadellidae	X	X
F. Delphacidae		X
F. Eriosomatidae	X	
F. Chermidae	X	X
Nymphs	X	X
O. Neuroptera		X
F. Hemerobiidae		X
O. Coleoptera	X	X
F. Carabidae	X	X
F. Cantharidae	X	X
F. Dermestidae	X	
F. Lycidae		X
F. Cleridae		X
F. Elateridae	X	X
F. Byrrhidae		X

(continued)

Table 2 (Continued)

Taxon	Jack pine	Ground vegetation
F. Coccinellidae	X	X
F. Alleculidae	X	X
F. Melandryidae	X	
F. Scarabaeidae	X	X
F. Chrysomelidae	X	X
F. Curculionidae		X
F. Scolytidae	X	
Larvae	X	X
O. Mecoptera		X
F. Panorpidae		X
O. Diptera	X	X
F. Tipulidae	X	X
F. Culicidae	X	X
F. Chironomidae		X
F. Simuliidae	X	X
F. Mycetophilidae		X
F. Tabanidae		X
F. Rhagionidae		X

(continued)

Table 2 (continued)

Taxon	Jack pine	Ground vegetation
F. Therividae		X
F. Asilidae		X
F. Dolichopidae		X
F. Pipunculidae		X
F. Syrphidae		X
F. Tephritidae		X
F. Sepsidae		X
F. Lauxaniidae		X
F. Clusidae		X
F. Lonchaeidae		X
F. Chloripidae		X
F. Drosophilidae		X
F. Anthomyiidae		X
F. Muscidae	X	X
F. Tachinidae		X
Acalyptrate Muscoid		X
O. Lepidoptera	X	X
Larvae	X	X
Adult	X	X

(continued)

Table 2 (Continued)

Taxon	Jack pine	Ground vegetation
O. Hymenoptera	X	X
F. Tenthredinidae		X
F. Braconidae	X	X
F. Ichneumonidae	X	X
F. Chalcididae		X
F. Perilampidae		X
F. Formicidae	X	X
F. Sphecidae		X
F. Colletidae		X
F. Halictidae		X
F. Apidae		X
F. Anthophoridae		X
F. Diprionidae (Larvae)		X
Total number of orders	9	11
Total number of families	11	61

A total of nine orders and 11 families of arthropods were collected on jack pine branch segments, while 11 orders and 61 families were collected on ground vegetation (Table 2). Lepidopteran adults and larvae were also collected on both types of vegetation. The total number of arthropods captured peaked on approximately 30 June (Figure 2), as did total arthropod biomass and biomass of larvae (Figure 3). Overall, both mean arthropod biomass and mean larval biomass per branch sample were greatest in the upper half of jack pine trees, and were least in the lowest quarter of the trees (Figure 4). The effect of stand was explored individually prior to other analyses (Table 3), and it did not significantly affect arthropod abundance or diversity ($F_{(25,9)} = .758$, $p = .882$), or vertical distribution (total arthropods: $F_{(25,9)} = .772$, $p = .841$; larvae: $F_{(25,9)} = .519$, $p = .994$).

Abundance, diversity, and distribution of arthropods were analyzed for effects of the stand age, management practice (plantation or wildfire), and the interaction between stand age and management practice (Table 3). Only stand age had a nearly significant effect on the vertical distribution of arthropod biomass in jack pines ($F_{(2,29)} = 2.000$, $p = .063$; Table 3). The mean biomass of arthropods in the upper three quarters of a tree increased from young nesting habitat (6-13 years) to old nesting habitat (14-21 years), while biomass in the lowest quarter of the tree was similar in both age classes. Biomass in the lowest quarter decreased from old nesting habitat to mature jack pine, while biomass in the upper three quarters of the tree remained relatively constant (Figure 5). The same trends existed for biomass of larvae, although the differences were not significant. In this case, the biomass of larvae was zero in the lowest quarter of mature jack pine trees

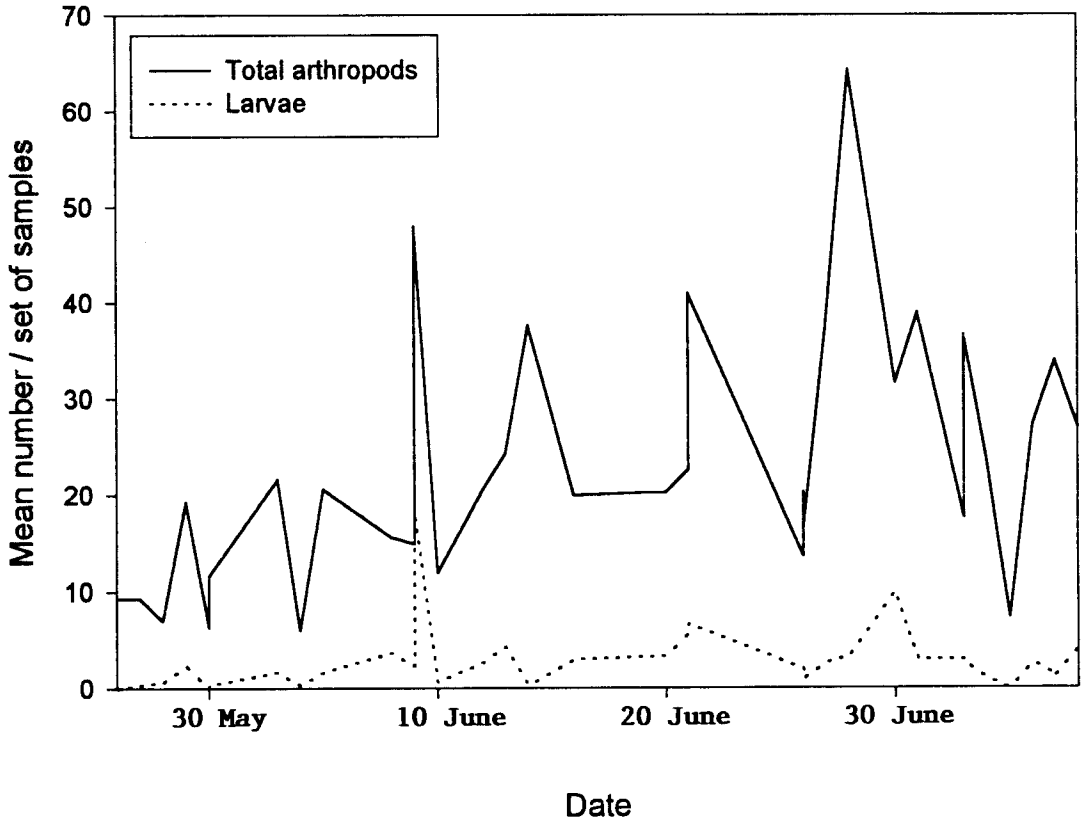

Figure 2. Distribution of arthropods across samples collected in 1996. "Larvae" include Orders Lepidoptera and Hymenoptera (F. Diprionidae).

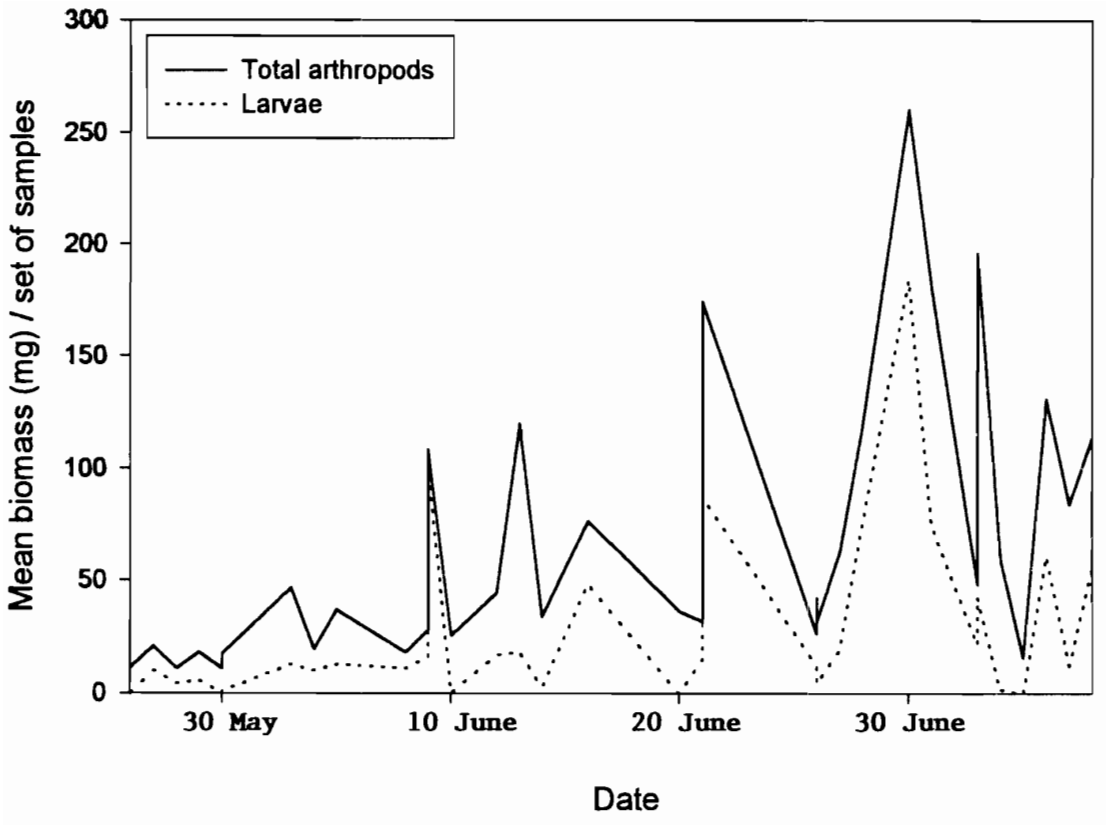

Figure 3. Distribution of arthropod biomass across samples collected in 1996. "Larvae" include Orders Lepidoptera and Hymenoptera.

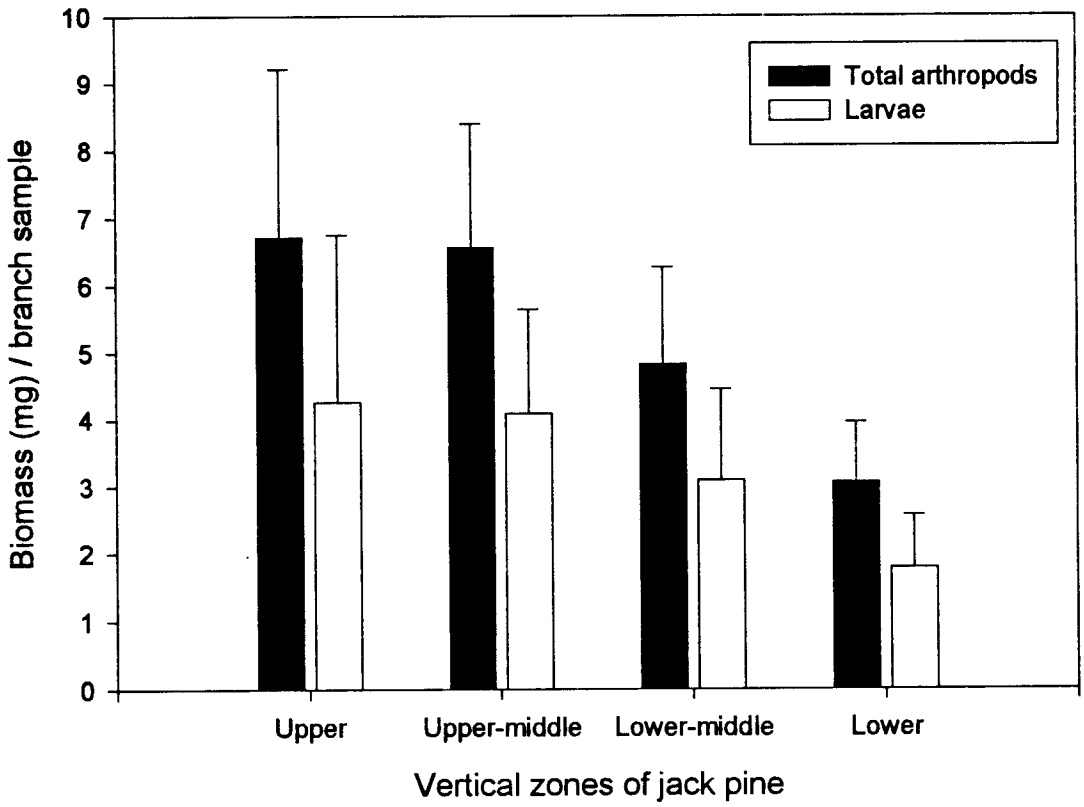

Figure 4. Mean (± SE) biomass of arthropods per branch sample in vertical zones of jack pines. "Larvae" include Orders Lepidoptera and Hymenoptera.

Table 3. MANOVA analysis of arthropod abundance and distribution

	Independent variables							
	Stand		Stand age		Management practice		Stand age X management practice	
	$F_{(25,9)}$	p	$F_{(2,29)}$	p	$F_{(1,29)}$	p	$F_{(2,29)}$	p
Abundance								
Multivariate MANOVA	.758	.882	.823	.608	.241	.941	1.010	.449
Univariate ANOVA								
Number of arthropods	.500	.917	.121	.886	.001	.970	.181	.834
Number of larvae	2.137	.118	1.344	.277	.569	.457	.062	.940
Number of taxa	1.359	.327	.464	.633	.069	.795	2.181	.131
Biomass of arthropods	.659	.790	.911	.413	.002	.961	1.267	.297
Biomass of larvae	.564	.876	1.362	.272	.006	.938	.848	.439

(continued)

Table 3 (continued).

	Independent variables							
	Stand		Stand age		Management practice		Stand age X management practice	
	$F_{(25,9)}$	p	$F_{(2,29)}$	p	$F_{(1,29)}$	p	$F_{(2,29)}$	p
Distribution								
Multivariate MANOVA	.772	.841	2.000	.063	.024	.999	1.040	.417
Univariate ANOVA								
Biomass in zone 1[a]	.499	.918	.877	.427	.000	.985	1.568	.226
Biomass in zone 2	.941	.578	1.752	.191	.001	.978	2.760	.080
Biomass in zone 3	.402	.965	1.399	.263	.021	.886	.442	.647
Biomass in zone 4	.303	.991	1.921	.165	.011	.919	.317	.731

(continued)

Table 3 (continued).

	Independent variables							
	Stand		Stand age		Management practice		Stand age X management practice	
	$F_{(25,9)}$	p	$F_{(2,29)}$	p	$F_{(1,29)}$	p	$F_{(2,29)}$	p
Multivariate MANOVA	.519	.994	1.660	.129	.290	.882	1.030	.424
Univariate ANOVA								
Larvae biomass in zone 1[a]	.527	.901	.668	.520	.107	.747	1.913	.166
Larvae biomass in zone 2	.612	.841	1.281	.293	.169	.684	1.976	.157
Larvae biomass in zone 3	.495	.920	1.406	.261	.011	.918	.903	.416
Larvae biomass in zone 4	.200	.999	1.326	.281	.095	.760	.513	.604
Multivariate MANOVA	1.710	.106	.325	.860	.053	.948	1.110	.362
Univariate ANOVA								
Arthropod biomass on ground vegetation	1.939	.151	.537	.590	.017	.897	.934	.404
Larval biomass on ground vegetation	1.727	.199	.611	.550	.092	.764	.018	.982

[a]zone 1 = upper quarter of jack pine, zone 2 = upper-middle quarter, zone 3 = lower-middle quarter, zone 4 = lower quarter.

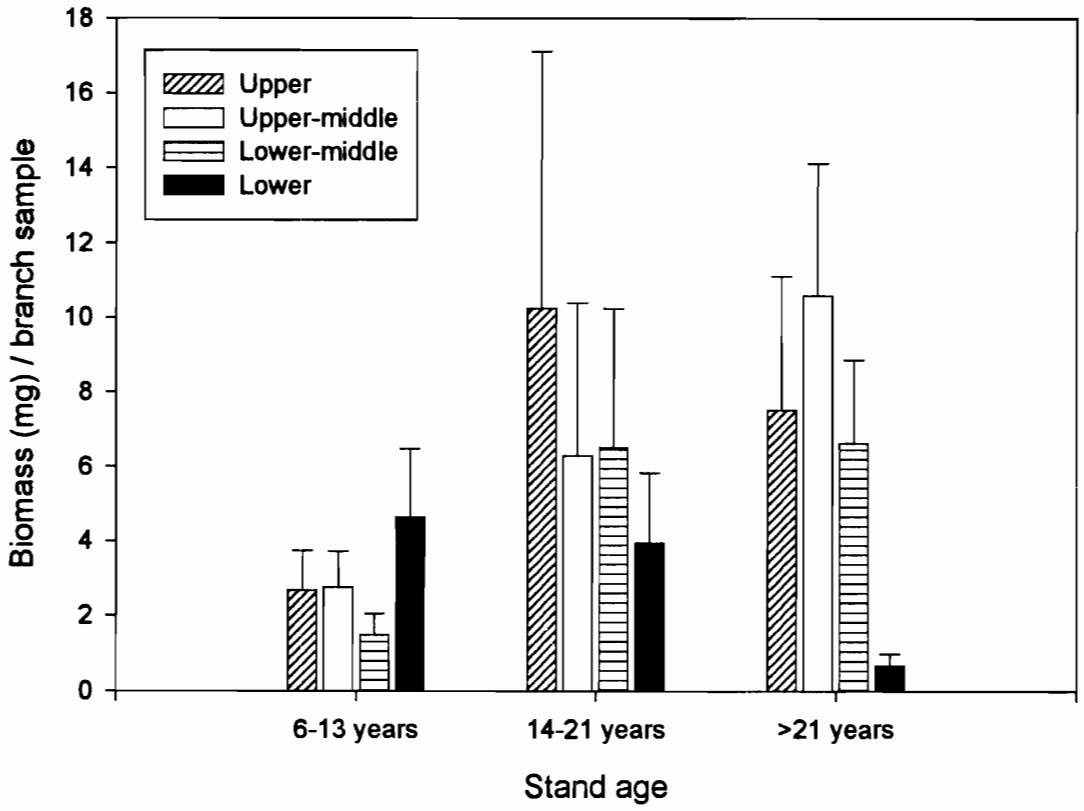

Figure 5. Mean (± SE) arthropod biomass per branch sample in vertical zones of jack pines in stands of different age.

(Figure 6). No significant differences in biomass on ground vegetation existed among stands of different ages (Figure 7).

Management practice did not significantly affect any of the dependent variables (Table 3). In fact, the arthropod communities in plantations and wildfires were extremely similar in terms of diversity (Figure 8), abundance (Figures 9 and 10), and distribution (Figures 11 and 12). Variability around the means was high in the arthropod data, as is often the case with this type of sampling (Cooper and Whitmore 1990).

Foraging behavior

Kirtland's Warblers were observed capturing a wide variety of prey items, including various types of larvae, moths, flies, beetles, grasshoppers, ants, aphids, and spittlebugs. Larvae appeared to be the most common prey items carried by parent birds.

Overall, 83% of observed foraging attempts by Kirtland's Warblers of both sexes combined were in jack pine trees, 10% of the attempts were in ground vegetation, 4% were in oak trees, and the other 3% in cherry trees, dead wood on the ground, and snags (Figure 13). Only jack pine, ground vegetation, and oak were considered in further analyses because of the relative rarity of foraging in the other vegetation types. While in jack pine trees, male and female warblers foraged most often in the middle half of the tree (63%) and less often in the upper and lower quarters (36%; Figure 14).

The proportions of foraging attempts in different vegetation types, vertical zones in jack pines, and horizontal zones in jack pines were analyzed for effects of stand, stand age, management practice, habitat composition, sex, prey-loading behavior, year of the

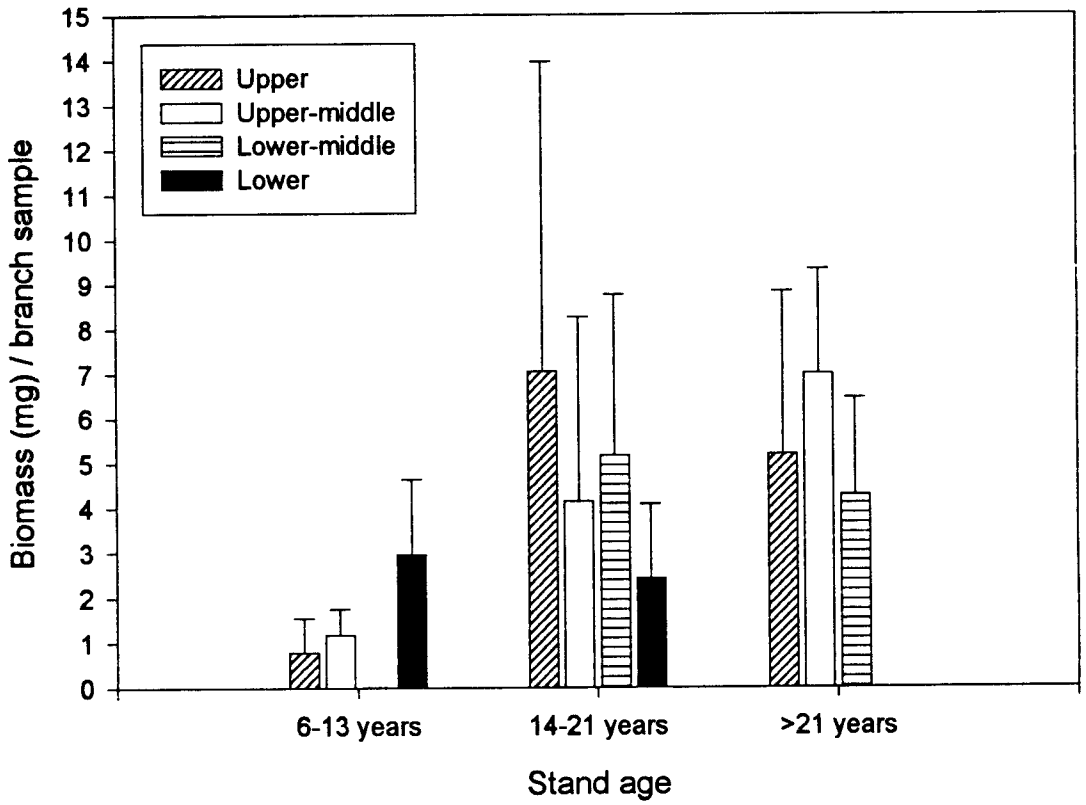

Figure 6. Mean (± SE) biomass of larvae per branch sample in vertical zones of jack pines in stands of different age.

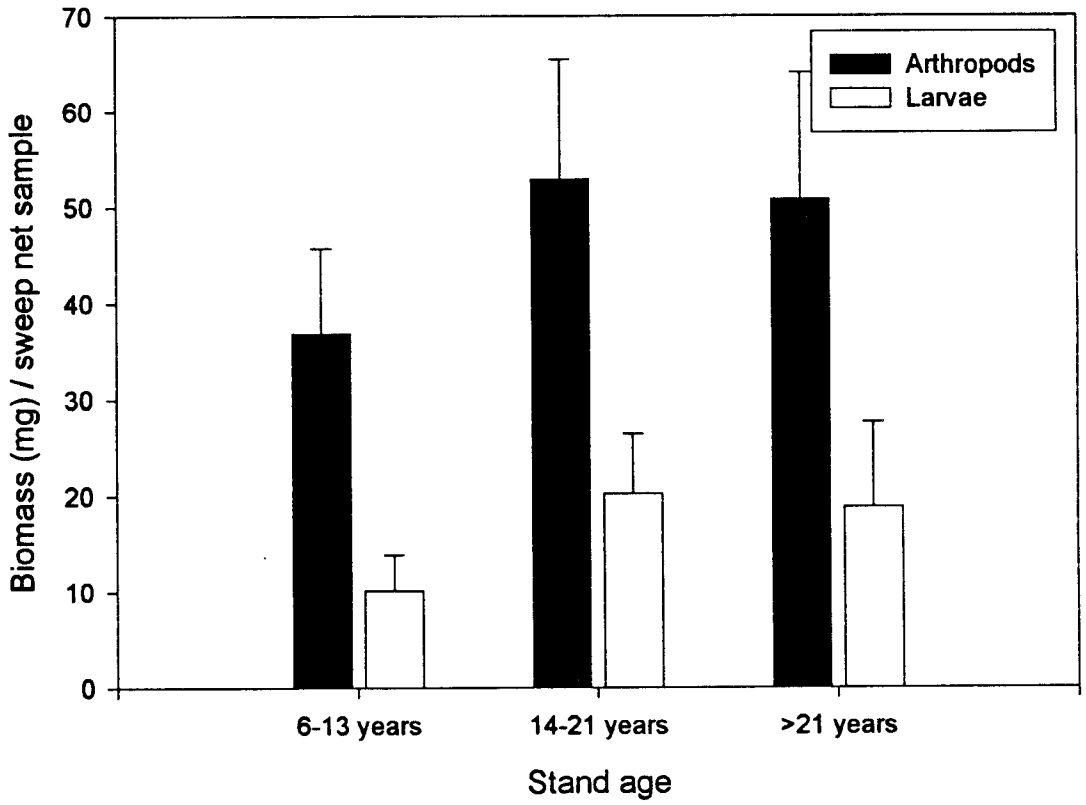

Figure 7. Mean (± SE) biomass of arthropods and larvae in sweep net samples of ground vegetation in stands of different age.

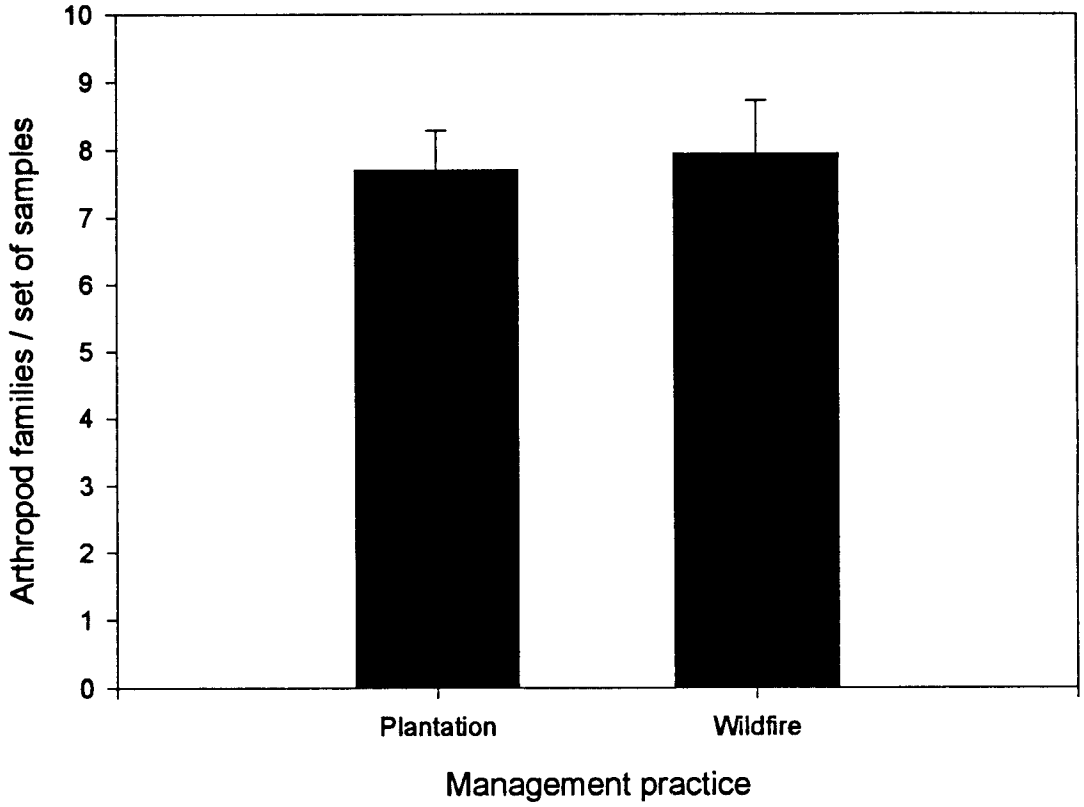

Figure 8. Mean (± SE) number of arthropod families per set of samples in plantations and wildfire stands.

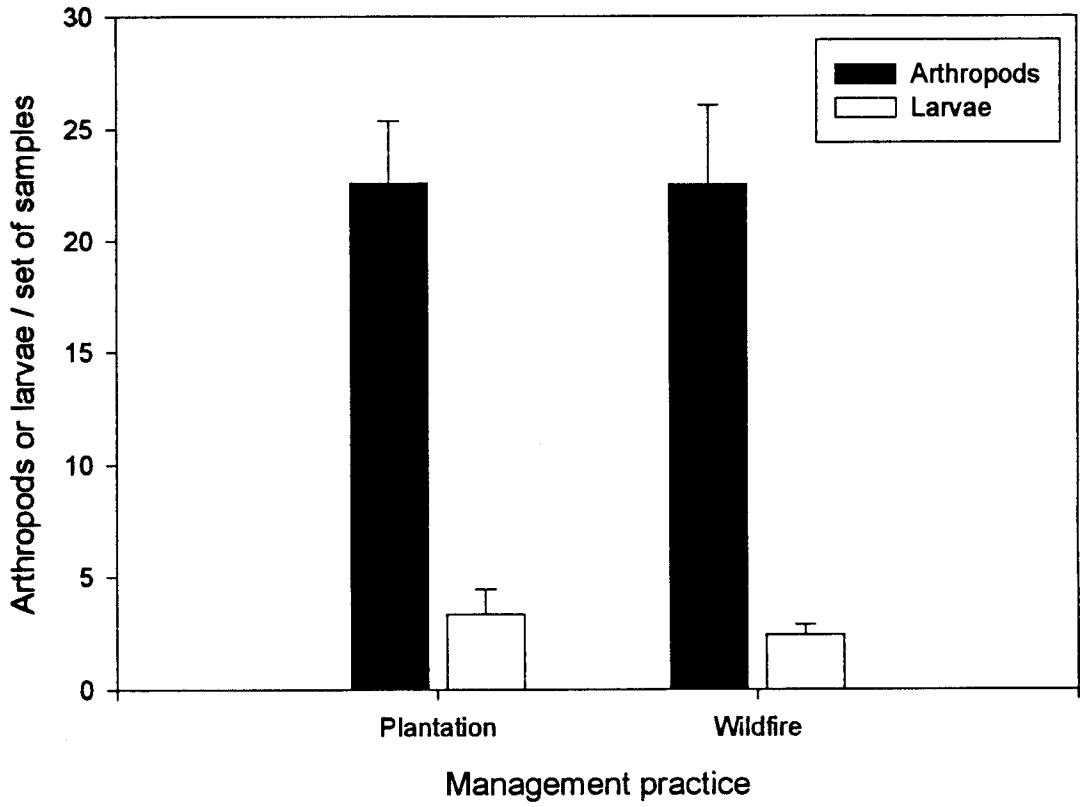

Figure 9. Mean (± SE) number of arthropods and larvae per set of samples in plantations and wildfire stands.

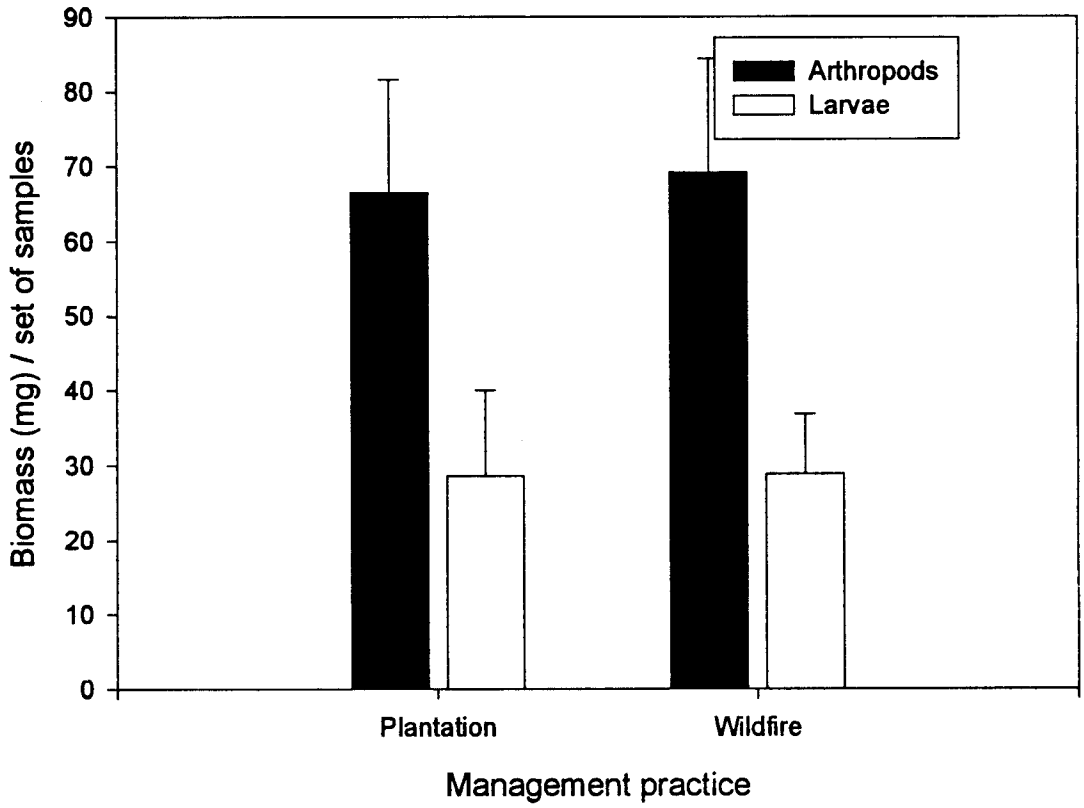

Figure 10. Mean (± SE) biomass of arthropods and larvae per set of samples in plantations and wildfire stands.

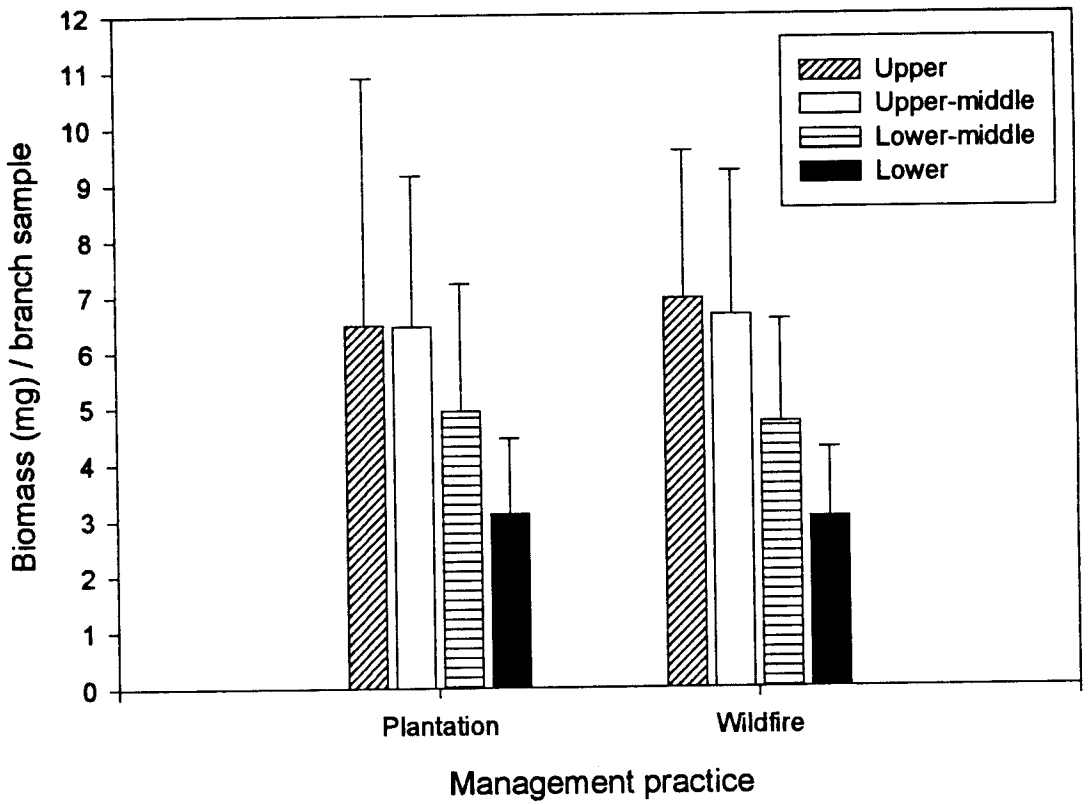

Figure 11. Mean (± SE) biomass of arthropods in vertical zones of jack pines in plantations and wildfire stands.

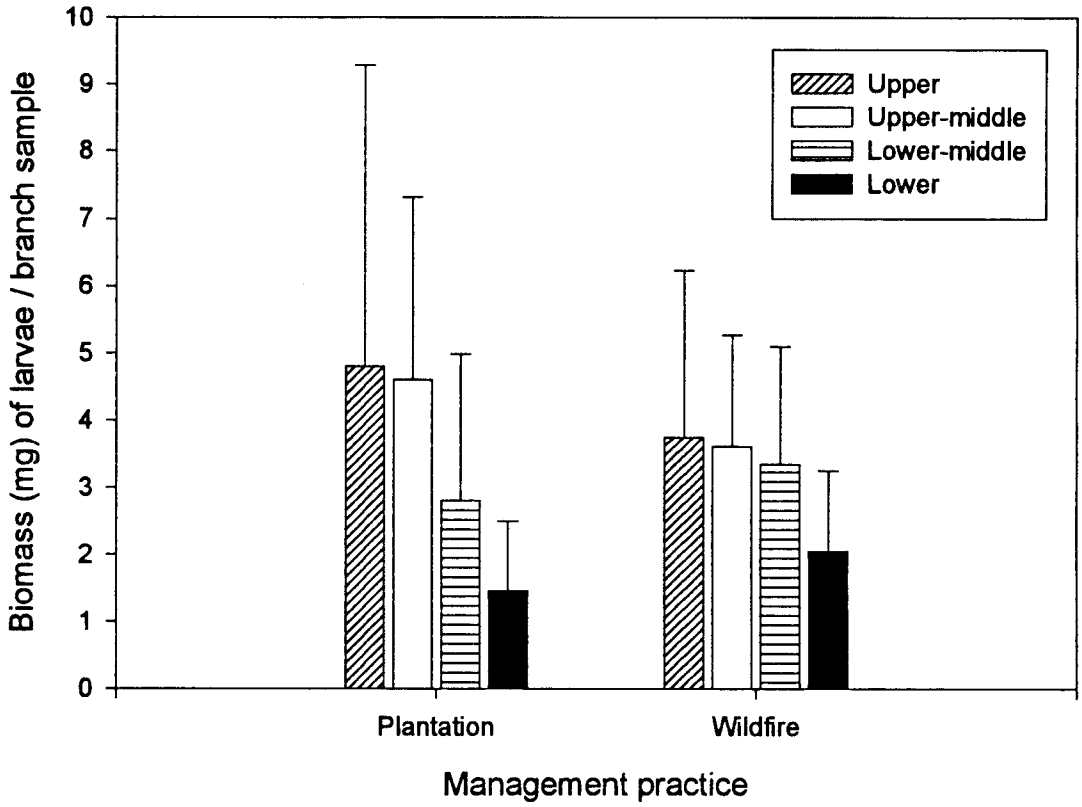

Figure 12. Mean (± SE) biomass of larvae in vertical zones of jack pines in plantations and wildfire stands.

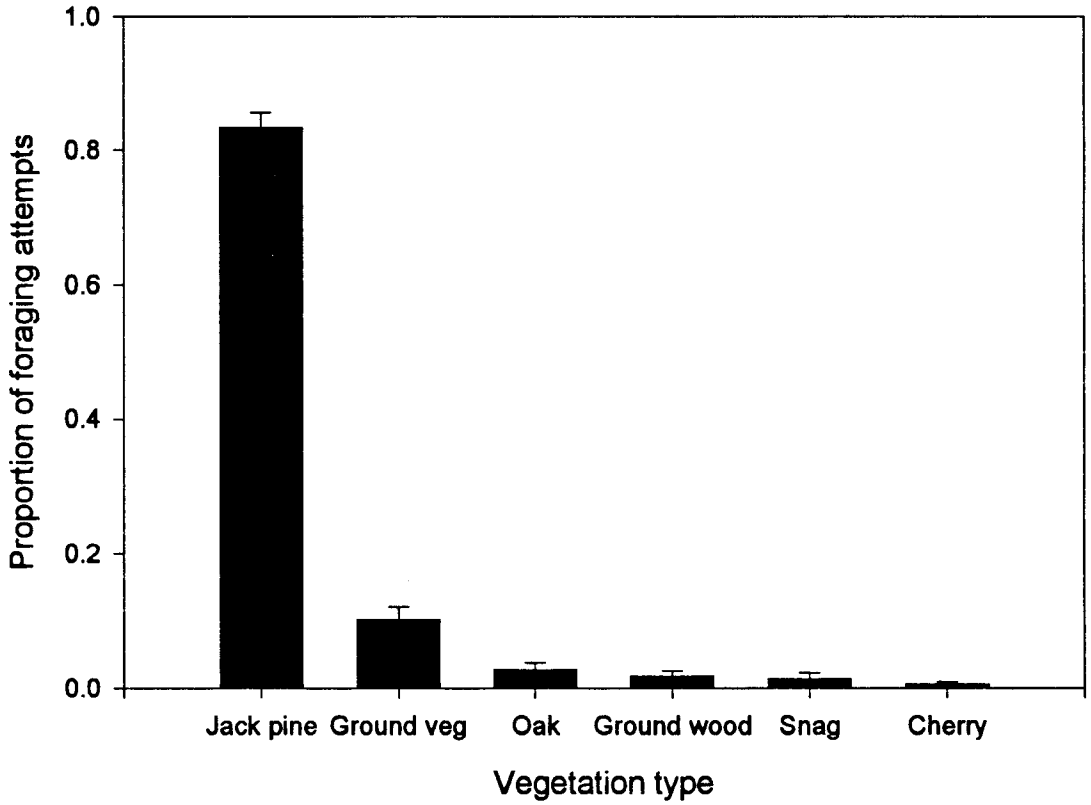

Figure 13. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in different vegetation types.

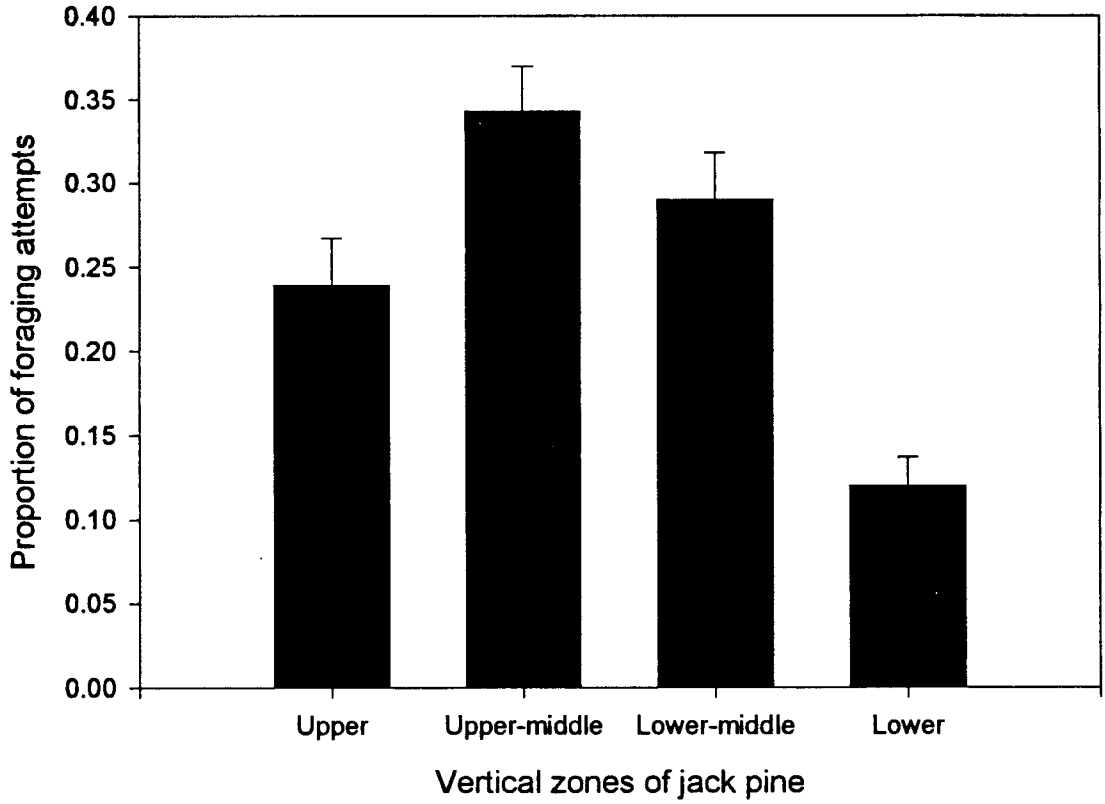

Figure 14. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in vertical zones of jack pines.

study, and all possible two-way interactions (Table 4). The effect of stand was analyzed individually prior to other analyses. While the stand had no effect on the frequency of foraging in vertical or horizontal zones of jack pine (Table 4), it did have a significant relationship with the proportion of foraging attempts in different vegetation types ($F_{(17,40)}$ = 1.562, p = .025) and, in particular, foraging attempts in oak ($F_{(17,40)}$ = 5.586, p < .001) (Table 4). The proportion of foraging attempts in oak was highly variable from stand to stand, ranging from 0 to .43 (Figure 15, Appendix A). However, very few birds were observed in some stands (Appendix A), and results for these stands should be interpreted cautiously.

The proportion of foraging attempts in various vegetation types also appeared to be related to deciduous component and year of the study. Although the proportion of deciduous trees in a stand (≤ 10% or > 10%) did not have a significant effect on the Multivariate MANOVA (Table 4), the univariate ANOVA for oak and trends in the data suggested that across all stands with a deciduous component, warblers foraged about 5% of the time in oak, and they foraged more often from ground vegetation (12%) in stands with mostly jack pine than in stands with many deciduous trees (8%; Figure 16). Year had a nearly significant effect on the extent of foraging in the various vegetation types ($F_{(1,49)}$ = 2.585, p = .064), in particular on jack pine ($F_{(1,49)}$ = 5.850, p = .019) and on ground vegetation ($F_{(1,49)}$ = 6.467, p = .014; Table 4). In 1996, warblers foraged less often from jack pine and more often from ground vegetation than in 1995 (Figure 17).

The proportion of foraging attempts in the vertical zones of jack pines was the variable most affected by habitat and bird characteristics. Vertical foraging position was

Table 4. MANOVA analysis of proportion of Kirtland's Warbler foraging attempts in various vegetation types, vertical zones of jack pines, and horizontal zones of jack pines. Significant p values are shown in boldface.

	Independent Variables													
	Stand		Stand age		Sex		Year		Management practice		Habitat composition		Prey-loading behavior	
	$F_{(17,40)}$	p	$F_{(1,49)}$	p	$F_{(1,49)}$	p	$F_{(1,49)}$	p	$F_{(1,49)}$	p	$F_{(1,49)}$	p	$F_{(1,49)}$	p
Vegetation type														
Multivariate MANOVA	1.562	**.025**	.419	.740	1.990	.128	2.585	.064	1.947	.128	1.710	.178	1.287	.290
Univariate ANOVA														
Jack pine	1.276	.256	.618	.436	.073	.789	5.850	**.019**	2.190	.145	.423	.519	.484	.490
Oak	5.586	**.000**	.036	.849	.887	.351	1.126	.294	.707	.404	4.794	**.033**	.068	.796
Ground vegetation	.759	.725	.008	.950	1.690	.200	6.467	**.014**	.464	.501	.441	.510	.421	.519

(continued)

Table 4 (continued).

	Independent Variables													
	Stand		Stand age		Sex		Year		Management practice		Habitat composition		Prey-loading behavior	
	$F_{(17,40)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p
Vertical zones														
Multivariate MANOVA	.975	.537	.988	.425	6.620	**.000**	1.662	.177	3.663	**.012**	3.378	**.018**	5.434	**.001**
Univariate ANOVA														
Upper	.983	.494	.192	.663	3.830	.057	.858	.359	1.261	.267	.105	.748	1.211	.277
Upper-middle	.869	.611	2.215	.144	.013	.910	3.116	.084	.751	.391	1.388	.245	1.039	.314
Lower-middle	1.428	.174	.834	.366	2.129	.152	1.950	.170	4.977	**.031**	5.175	**.028**	.123	.728
Lower	1.614	.106	3.252	.078	1.766	.191	5.777	**.021**	6.233	**.016**	.493	.486	.001	.980

(continued)

Table 4 (continued)

	Independent Variables													
	Stand		Stand age		Sex		Year		Management practice		Habitat composition		Prey-loading behavior	
	$F_{(17,40)}$	p	$F_{(1,48)}$	p	$F_{(1,48)}$	p	$F_{(1,48)}$	p	$F_{(1,48)}$	p	$F_{(1,48)}$	p	$F_{(1,48)}$	p
Horizontal zones														
Multivariate MANOVA	.870	.708	.247	.863	.251	.860	.414	.744	1.935	.137	.359	.783	.768	.518
Univariate ANOVA														
Inner	.863	.616	.017	.897	.000	.994	.414	.744	5.374	**.025**	.696	.408	1.917	.173
Middle	1.181	.322	.666	.419	.585	.448	.757	.389	3.225	.079	.004	.950	.181	.672
Outer	.888	.591	.449	.506	.552	.461	.348	.558	.320	.574	.605	.441	.946	.336

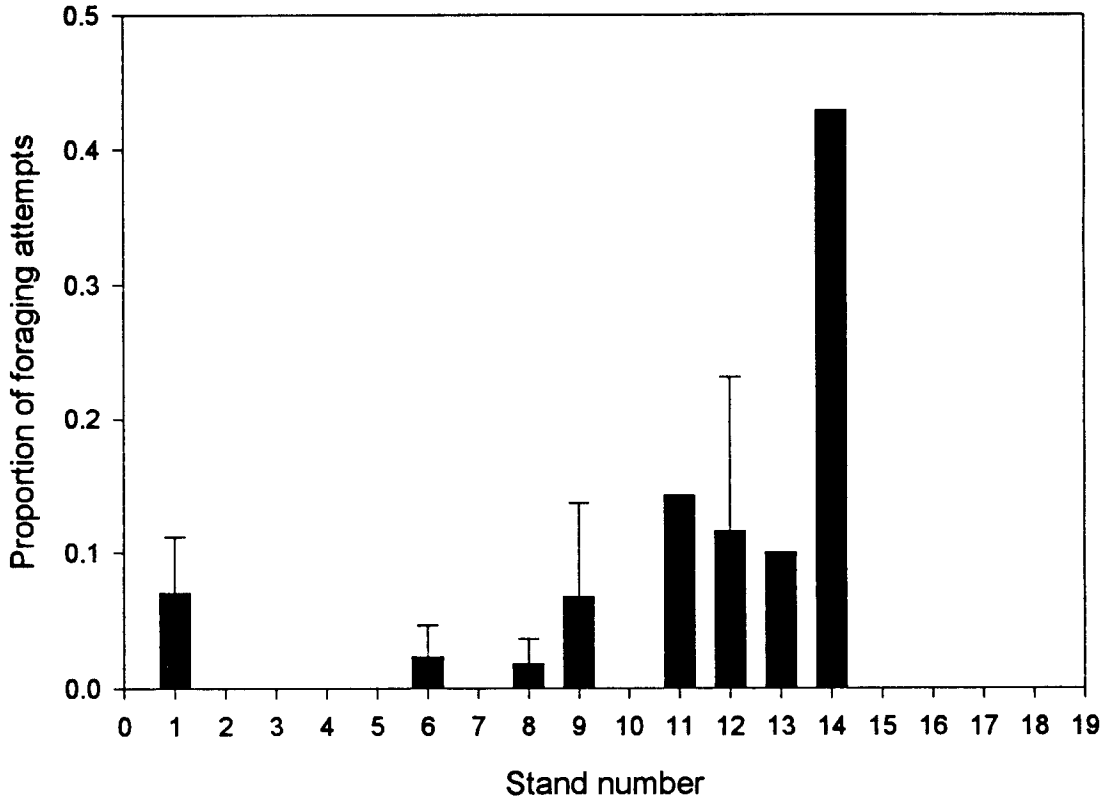

Figure 15. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in oak in different stands. Stands are identified in Appendix A.

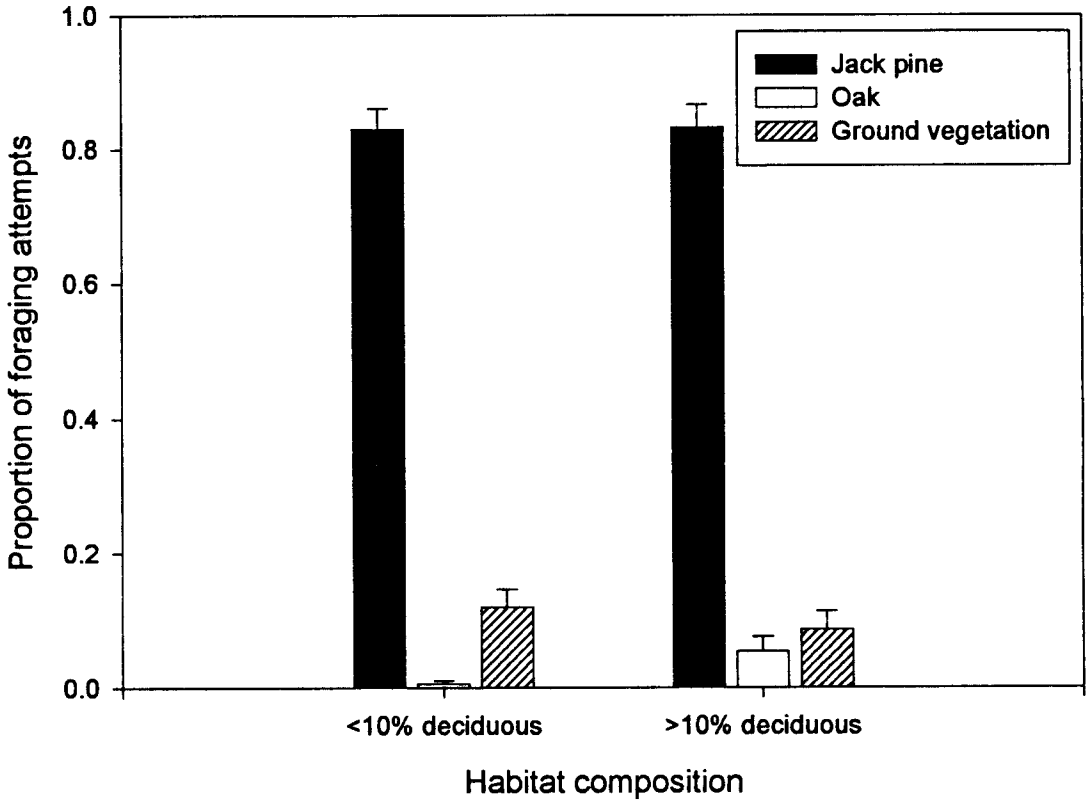

Figure 16. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in various vegetation types in stands of different deciduous components.

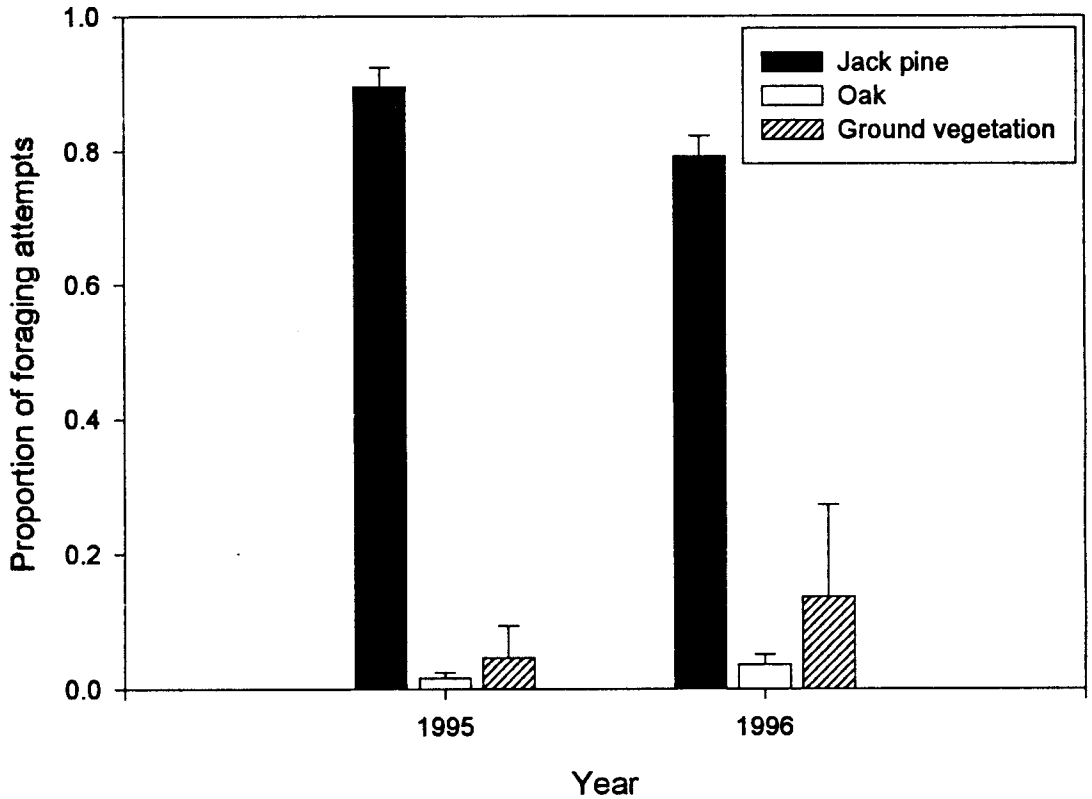

Figure 17. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in various vegetation types in 1995 and 1996.

significantly related to several factors, including sex ($F_{(1,44)} = 6.620$, $p = .000$), prey-loading behavior ($F_{(1,44)} = 5.434$, $p = .001$), management practice ($F_{(1,44)} = 3.663$, $p = .012$), and habitat composition ($F_{(1,44)} = 3.378$, $p = .018$); (Table 4). Female Kirtland's Warblers foraged less from the upper quarter of the tree (18%) than males (27%), and this univariate test was nearly significant ($F_{(1,44)} = 3.830$, $p = .057$); (Table 4, Figure 18).Combining sexes, Kirtland's Warblers carrying prey appeared to forage more often from the upper half of the tree (61%) than birds not carrying prey (56%), although the effects of this variable are difficult to interpret visually (Figure 19). Univariate ANOVAs indicated significant differences in foraging behavior in relation to management practice and habitat composition. In terms of management practice, trends in the data suggested that Kirtland's Warblers in wildfire stands foraged more often from the middle half of the trees (72%) than did those in plantations (57%), and less often from the top and bottom of the trees (29%) than birds in plantations (42%); (Figure 20). Differences between proportions of foraging attempts in the lower-middle quarter ($F_{(1,44)} = 4.997$, $p = .031$) and lower quarter ($F_{(1,44)} = 6.233$, $p = .016$; Table 4) were statistically significant. Stand age did not have a significant effect on foraging in vertical zones (Table 4). Kirtland's Warblers did not forage proportionally higher in old nesting habitat than in young nesting habitat (Figure 21).

The univariate ANOVA for habitat composition indicated a difference in the proportion of foraging in the lower-middle quarter of jack pines between birds in essentially pure jack pine stands (i.e., $\leq 10\%$ oak) and birds in mixed deciduous stands

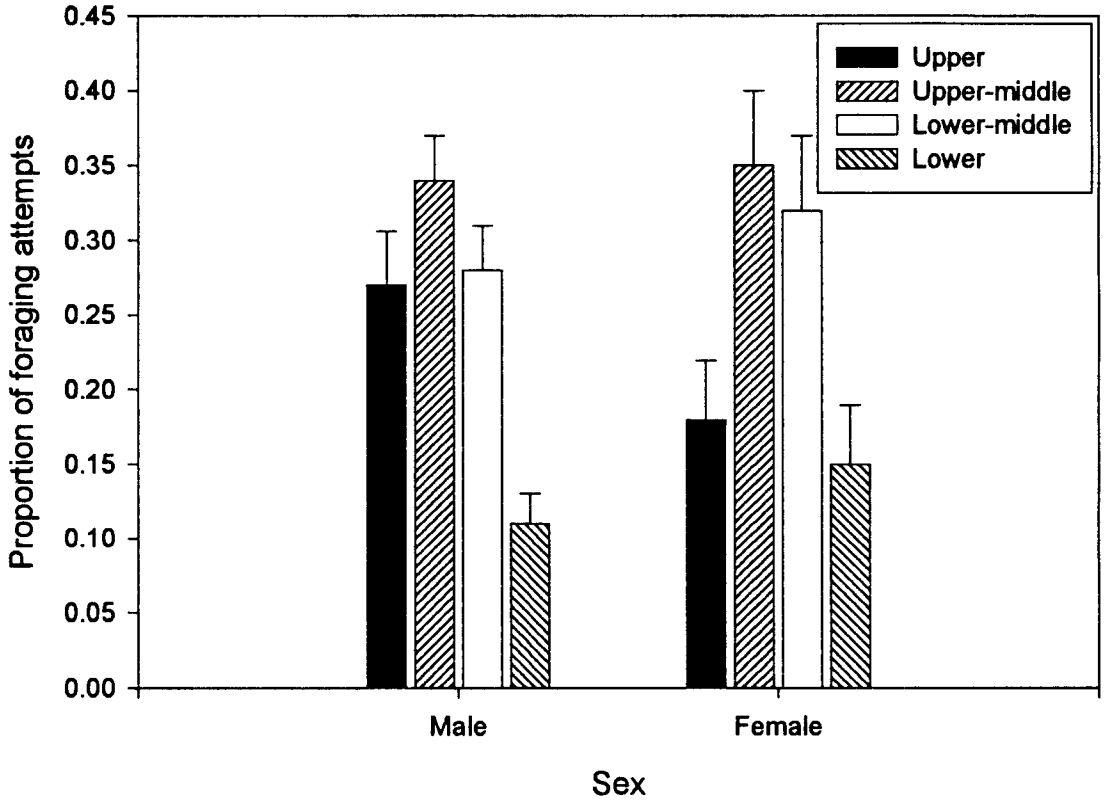

Figure 18. Mean (± SE) proportion of foraging attempts by male and female Kirtland's Warblers in vertical zones of jack pines.

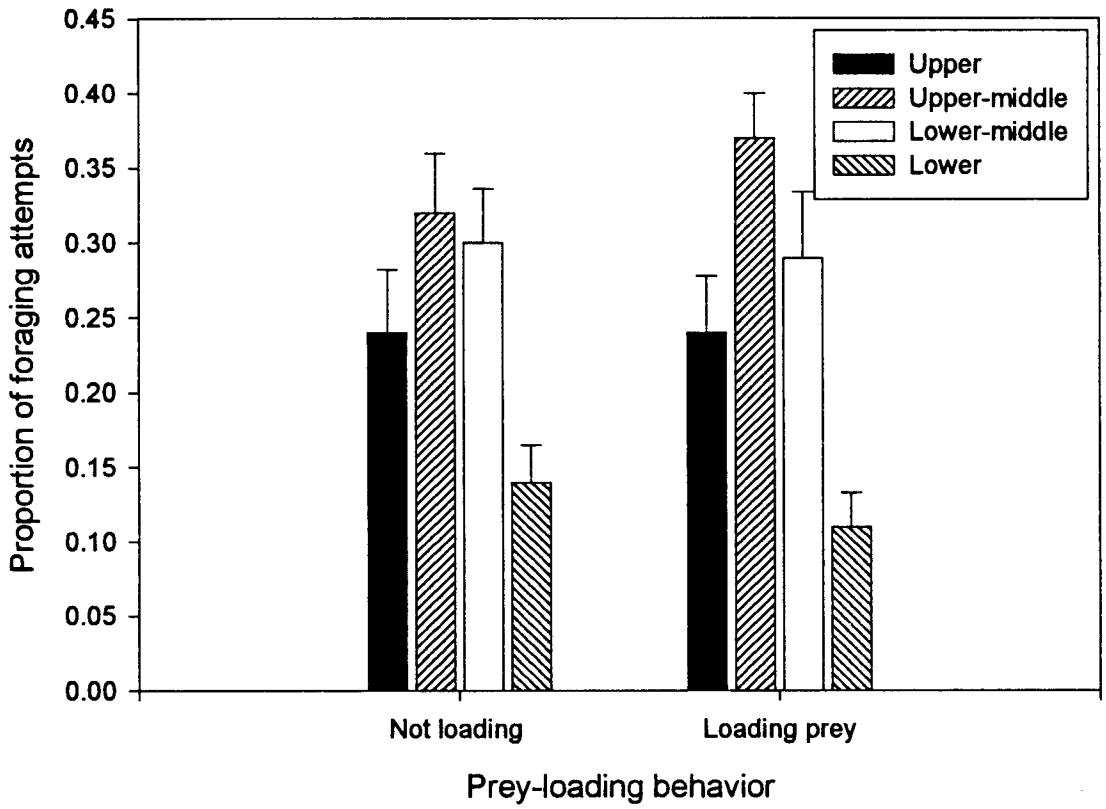

Figure 19. Mean (± SE) proportion of foraging attempts in vertical zones of jack pines by Kirtland's Warblers loading prey or not loading prey.

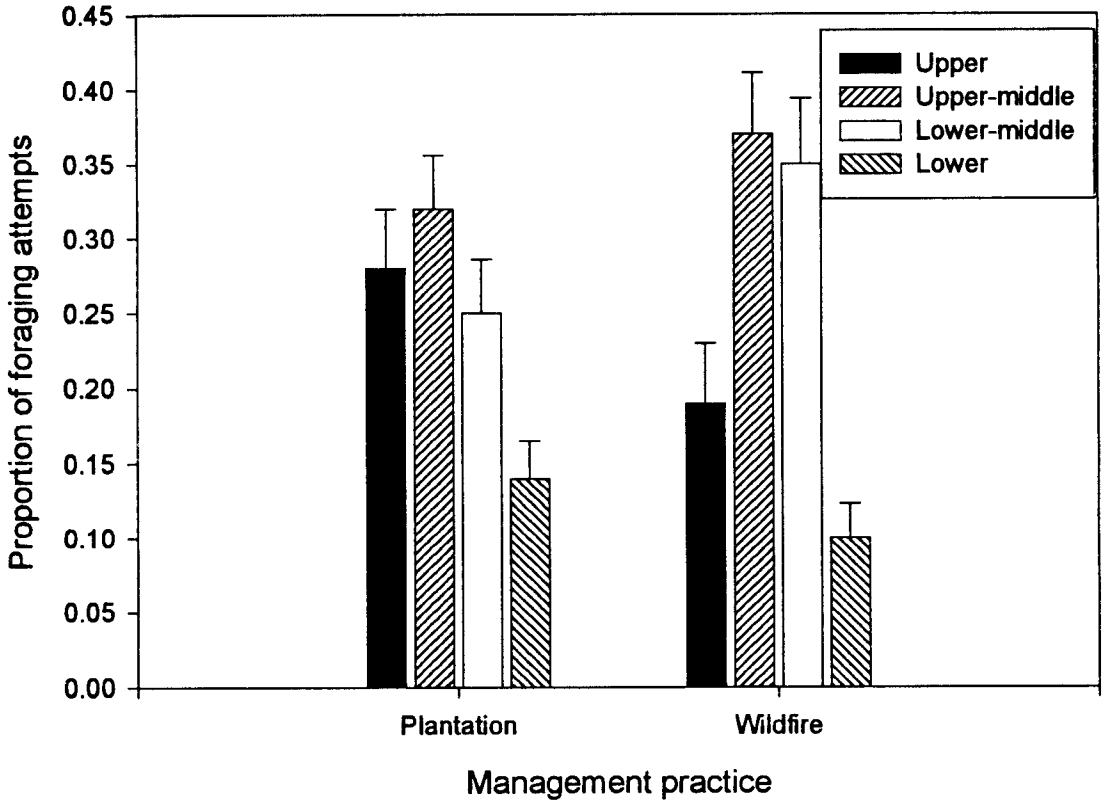

Figure 20. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in vertical zones in jack pines in plantations and wildfire stands.

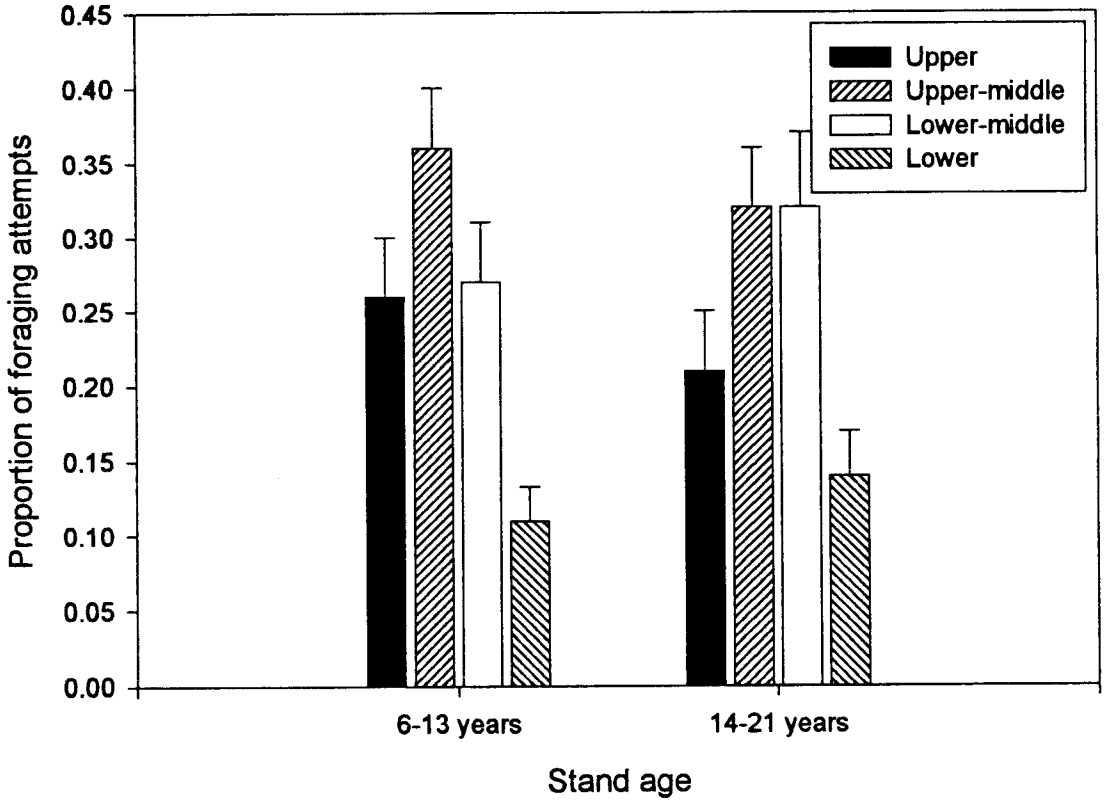

Figure 21. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in vertical zones of jack pines in young and old nesting habitat.

($F_{(1,44)} = 5.175$, $p = 0.028$; Table 4). However, the direction of this effect is difficult to interpret (Figure 22).

Five two-way interactions of factors were associated with significant differences in vertical foraging (Table 5). These included the interaction of prey-loading behavior with sex, habitat composition with management practice, habitat composition with prey-loading behavior, habitat composition with sex, and habitat composition with year. The first two interactions were significantly related to the proportion of foraging attempts in the lower-middle quarter of a tree. First, males loading prey foraged less in this zone than males not loading prey (Figure 23), while female prey-loaders foraged more in this zone than females not prey-loading (Figure 24). Second, birds in mixed-deciduous wildfire stands foraged more often from the lower-middle zone than birds in mixed-deciduous plantations.

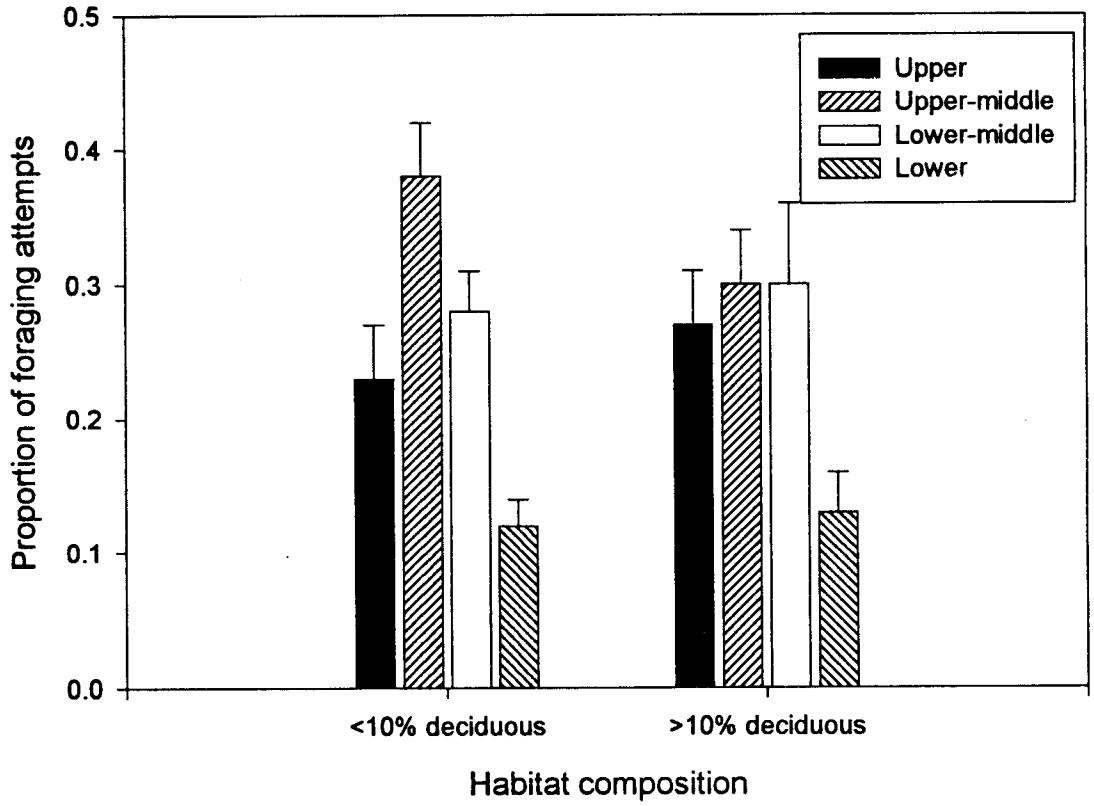

Figure 22. Mean (± SE) proportion of Kirtland's Warbler foraging attempts in vertical zones of jack pines in stands of different deciduous components.

Table 5. MANOVA analysis of interaction effects on proportion of Kirtland's Warbler foraging attempts in vertical zones of jack pines. Significant p values are shown in boldface.

	Interaction									
	Prey-loading behavior X sex		Habitat composition X management practice		Habitat composition X prey-loading behavior		Habitat composition X sex		Habitat compositon X year	
	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p	$F_{(1,44)}$	p
Multivariate MANOVA	4.207	**.006**	4.063	**.007**	3.511	**.015**	4.625	**.004**	3.858	**.009**
Univariate ANOVA										
Upper zone	2.212	.144	.835	.366	.583	.449	.176	.677	.573	.453
Upper-middle zone	.882	.353	3.116	.084	1.064	.308	.662	.420	2.570	.116
Lower-middle zone	4.527	**.039**	14.014	**.001**	2.970	.092	.057	.812	1.424	.239
Lower zone	1.388	.245	.779	.382	.386	.538	.006	.938	8.233	**.006**

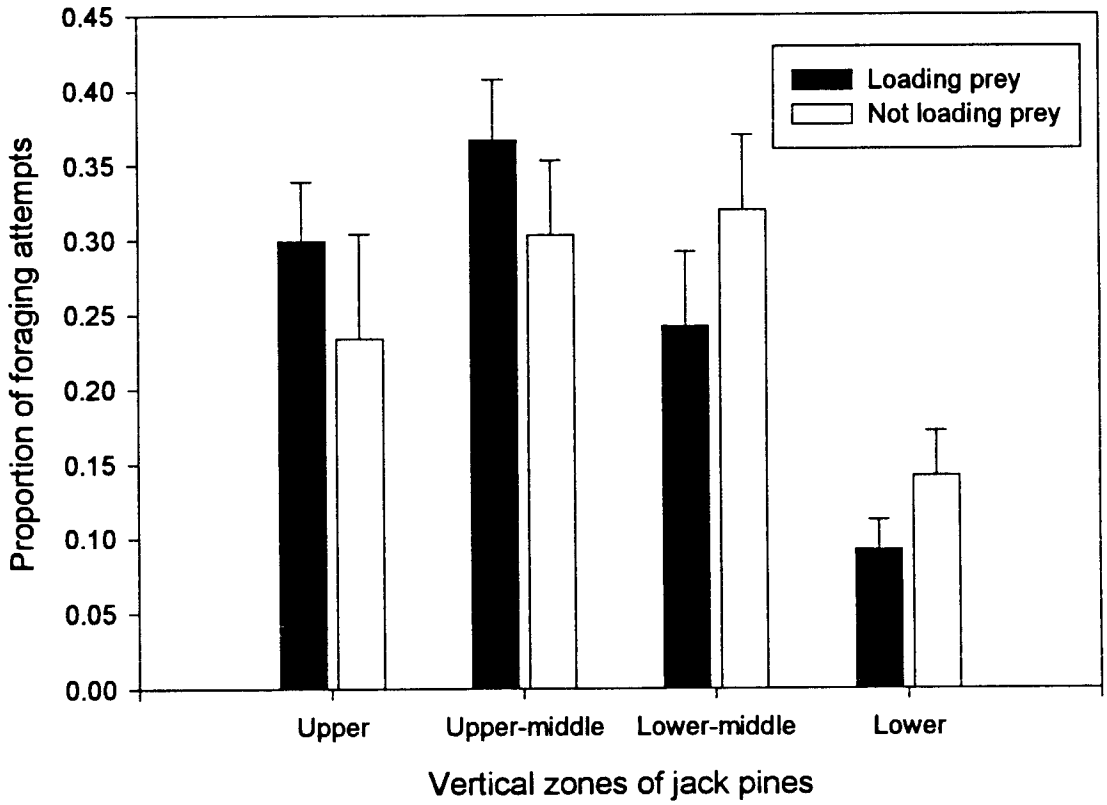

Figure 23. Mean (± SE) proportion of foraging attempts in vertical zones of jack pines by Kirtland's Warbler males loading prey or not loading prey.

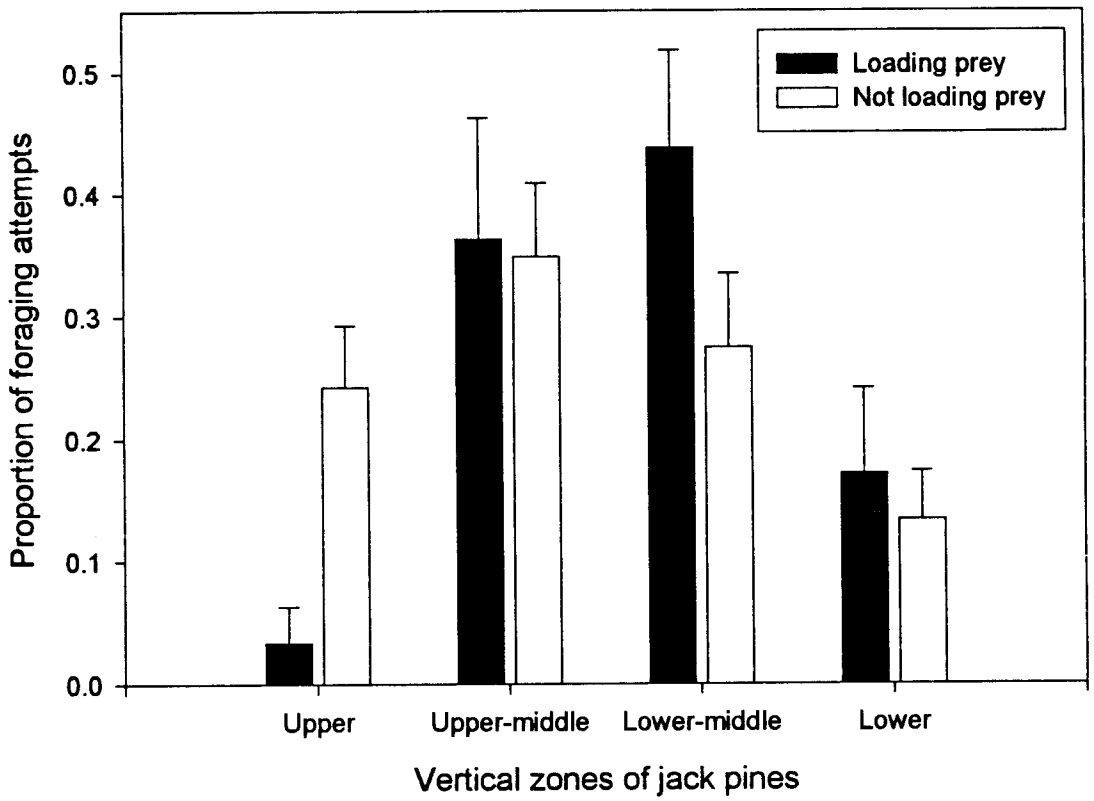

Figure 24. Mean (± SE) proportion of foraging attempts in vertical zones of jack pines by Kirtland's Warbler females loading prey or not loading prey.

DISCUSSION

This study provided some support, although equivocal, for the hypothesis that Kirtland's Warblers reject mature jack pine for nesting due to low prey availability in the lower zones of vegetation. Insect biomass did vary, both in abundance and distribution, among habitat age categories, although insignificantly. Overall, arthropod biomass was similar between old nesting habitat and mature stands, however, arthropod biomass was much lower in the lower quarter of mature trees as compared to jack pines in nesting habitat. This trend was especially clear for larvae, which were never present in the lower quarter of mature trees. Biomass on ground vegetation was similar in stands of all three age categories. These trends suggest that mature stands furnish a high prey availability to the warblers overall, but very low availability, especially of larvae, in the lowest quarter of the tree. Because larvae are important food for nestling warblers, their absence in the lower reaches of mature jack pines could force warbler parents to forage further from the nest, possibly decreasing their vigilance ability or incubation time if they were to nest in mature habitat. However, the presence of larvae in ground vegetation would seem to contradict such an interpretation.

This research did not indicate that Kirtland's Warblers foraged higher in older habitat than in young habitat. In old nesting habitat, a higher proportion of the total

arthropod biomass was present in the upper three quarters of the trees as compared to young nesting habitat. However, warblers did not respond to this difference in arthropod abundance by foraging higher in older habitats.

It is possible that lack of prey in the lower vegetation does cause rejection of mature habitat, but that the comparison of foraging behavior in young nesting habitat and old nesting habitat did not reveal this influence. First, the height and structural differences may not have been great enough within the age range of nesting habitat. Jack pine trees in nesting habitat range from 1.5 m to 5 m in height. Foraging in the upper quarter of a 5m-tall tree may not increase time away from the nest as compared to foraging high in a 1.5m-tall tree. In contrast, foraging high in mature jack pines (reaching 8 m in height) could impact vigilance ability. Second, the proportional decrease in arthropod abundance in the lower zone of old nesting habitat may not be significant enough to decrease the rate of prey intake by warblers. The reduction in arthropod abundance in this zone is much more pronounced in mature stands, in which the lower quarter of the tree encompasses much more space than it does in the shorter trees of nesting habitat.

Female Kirtland's Warblers foraged significantly lower than males in jack pine nesting habitat, supporting the general trend for sex-specific foraging heights in parulid warblers (Morse 1980). This result also suggested that the lack of prey in the lower quarter of mature jack pine trees could impact rate of prey intake by females more than males. The interaction between sex of the bird and food carrying behavior showed that females carrying food foraged lower than those not feeding nestlings, and males carrying food foraged higher than those not feeding nestlings or females. These patterns might

reflect conflicting strategies on the part of males and females. Males carrying food had active nests, while males not carrying food might have been non-territorial. Territorial males may benefit from foraging high in the tree and remaining visible to neighboring males, thereby limiting intrusions (Morse 1980). Females, on the other hand, might benefit by foraging near the nest. This pressure appeared to be strong, because females with the high prey demand of nestlings foraged low, even though the upper halves of the trees were richer in arthropod abundance.

When measuring foraging behavior of birds, there was always the risk of two biases. These included a discovery bias, in which birds behaving in conspicuous ways were included in the data more often than others, and an observability bias, in which obvious behaviors were over-represented in the data set (Wiens 1969, Bradley 1985). The methodology and habitat structure involved in this study reduced the influence of these biases in several ways. First, there was usually a delay between the first location of an individual and the first observed foraging event, during which time the bird moved within the habitat. Because I recorded data on individuals where they actively foraged rather than where they were first located, discovery bias probably did not greatly influence the data. Secondly, because of the short trees in Kirtland's Warbler breeding habitat, birds were not foraging much above eye-level where many foraging maneuvers would be difficult to see. Observability could have been a factor, however, in recording data on birds foraging in the ground vegetation. When birds were not loading prey, it was not always possible to observe how many times they foraged in the thick ground cover. Thus,

my estimates of the proportional use of ground vegetation as a foraging substrate were generally conservative.

Over all habitat types the number of sampled arthropods peak at approximately 30 June, which corresponds to the time when most first broods reach the fledging stage (Walkinshaw 1983). This peak may have been slightly later in 1996 than in other years due to the cold, damp spring and late summer. The nearly significant effect of year on foraging frequency in jack pine and ground vegetation also suggests a difference in vegetation density or prey distribution between 1995 and 1996, however, I am unable to address this matter directly.

This study also provides insight into how spatial heterogeneity of habitat affects the foraging ecology of Kirtland's Warbers at two levels: at the landscape scale and within stands. First, the landscape of nesting habitat of the warbler exists in a mosaic of young and old jack pine stands, which differ in the structure of low vegetation. Although old stands have proportionally lower insect abundance low in the trees, they support a greater density of arthropod biomass per branch than young stands. This result, combined with the greater foliage volume due to height in old trees, suggests that 14-21-year-old stands may be much richer in prey availability for Kirtland's Warblers than 6-13 year old stands.

The landscape also consisted of a patchwork of managed plantations and natural wildfire-regenerated stands. These two habitat types appeared to be extremely similar in both arthropod populations and foraging behavior of the warblers. Plantations and wildfires had a similar number of arthropod taxa, total biomass, and vertical distribution of biomass. However, the arthropod samples were taken from similar microhabitats in each

type of stand, perimeters of openings. Plantations and wildfire stands might differ in the proportion of such microhabitats, and/or their use by warblers as foraging areas. For instance, wildfire stands contained more dense thickets than do plantations (Bocetti 1994) and in this study thickets were not sampled for arthropods.

The distribution of microhabitats such as thickets, gaps, and edge is an important component of within-stand habitat heterogeneity. These microhabitats may offer varying quality in terms of nest sites and foraging sites. The propensity of Kirtland's Warblers to nest in microhabitats on the edge of openings may be related to density of nest cover, or to prey abundance. The extra sunlight and warmth in openings may cause arthropods to be more active, and warblers nesting on the edges of openings may be able to take advantage of this rich prey source while still maintaining vigilance or incubation of the nest. Such an increase in activity of arthropods in forest gaps created by fallen trees is known to influence the foraging behavior of other birds (Smith and Dallman 1996, Sharpe 1996).

Another component of within-stand spatial heterogeneity is the distribution of vegetation types such as jack pine, oak, and ground cover. Although Kirtland's Warblers forage predominantly from jack pines, they do use other types of vegetation, especially ground vegetation and oak. Even though these substrates are used less often, they may be important to the warbler. In pure jack pine stands, warblers forage more often from ground vegetation than in mixed-deciduous stands, and in mixed-deciduous stands they forage more often from pin oak trees. That is, when oak is available they use it, and when it is not available they spend more time foraging in the blueberry, sedges, and grasses of

the ground layer. These substrates may harbor different arthropod taxa than are present on jack pines.

Although this study focuses on the very specific jack pine ecosystem, the results relate to broad goals of conservation biology in two ways. First, managers of rare species are increasingly recognizing the importance of adaptive management (Walters 1986, Lee 1993, Haney and Power 1996). This process involves continually evaluating management techniques to determine whether they are meeting goals, altering methods when necessary. My study evaluates the effectiveness of managed plantations in meeting the goal of replicating natural habitat from the perspective of prey availability to Kirtland's Warblers. The evidence suggests that the current technique used in plantations is effective in mimicking natural arthropod communities in the jack pine ecosystem.

Second, in order to effectively manage rare species the reasons for habitat requirements need to be understood, including what factors define habitat suitability. For Kirtland's Warblers, the reasons for rejection of forests older than 20 years are not yet clear. This study provides some evidence that prey availability may influence this habitat choice. Other hypotheses, including the possible limitation of nest cover in mature forests, need to be tested in the future.

Management recommendations

Plantations appear to be successful in replicating the effects of wildfires on prey availability to Kirtland's Warblers, at least in the vicinity of the edges of openings where warblers nest. Vegetation types other than jack pine may be important foraging substrates

for the warbler, particularly ground vegetation and pin oak. These non-pine substrates support a more diverse arthropod community and may provide different taxa of prey than the relatively few taxa available on jack pine. Because the warblers did not seem to select against oak, but used it when present in the habitat, oak does not seem to be harmful to the birds and may actually be beneficial. It does not appear necessary to remove interspersed oak from nesting habitat.

Future research needs

Arthropod sampling from microhabitats other than openings, such as jack pine thickets, along with sampling from pin oak trees would provide a more complete picture of arthropod communities in jack pine habitat.

There is a limit to the quantity of information on diet composition gained by visual observations of foraging Kirtland's Warblers. Analysis of Kirtland's Warbler fecal samples collected while banding the birds would be very important to quantifying the diet of the species. To identify and quantify food brought to nestlings, temporary neck ligatures could be used at a small number of nests. Both of these techniques would greatly increase our knowledge of diet selection in this endangered species.

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Appendix A. List of jack pine stands occupied by Kirtland's Warblers that were visited in 1995 and 1996.

Stand #	Stand name	Habitat Category	Number of warblers observed
1	Pine River Unit 1 s 20	Young plantation	4
2	Beaver Lake Burn	Young wildfire	6
3	Bald Hill Flats s 28	Old wildfire	5
4	Fletcher, Crawford Co.	Old plantation	5
5	Perry Holt Burn	Young wildfire	5
6	Hippie Plantation	Old plantation	4
7	Perry Holt East s14, 23	Young plantation	2
8	Mack Lake	Old wildfire	8
9	Muskrat Lake	Young plantation	3
10	Damon	Old plantation	2
11	Bald Hill Northwest	Old wildfire	1
12	Big Creek Mapes Road	Young plantation	2
13	Eldorado Rock Cemetery s 14	Young plantation	1
14	Wurtsmith Air Force Base	Old plantation	1
15	Big Creek Union Corners	Young plantation	3
16	McKinley Roadhouse	Young plantation	1
17	Mack Lake Crane Lake Unit	Old plantation	1
18	Big Creek County Line	Old plantation	4