

THE RELATIVE IMPORTANCE OF NESTING AND FORAGING SITES IN SELECTION OF BREEDING TERRITORIES BY TOWNSEND'S WARBLERS

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ABSTRACT.—We investigated habitat selection by the Townsend's Warbler (*Dendroica townsendi*), a Neotropical-Nearctic migrant that breeds primarily in mature coniferous forests. From 1993 to 1994, we compared the features of habitat selected for nest sites and foraging sites with those selected for territories in mature, mixed coniferous-deciduous forests in south-central Alaska. We also tested the prediction that large conifers are selected for nesting and foraging sites. Females placed nests in relatively large white spruce (*Picea glauca*) and consistently chose nest trees that were within areas of higher densities of large white spruce than were generally available. Nesting areas also had a higher density of small white spruce than was generally available, which may have been important in concealing nests from predators. Vegetation features selected for foraging differed from those selected for nesting and varied seasonally. Foraging was concentrated in medium-sized white spruce during the pre-hatching stage and became more generalized across coniferous and deciduous vegetation during the posthatching stage. Adults foraged in large white spruce in direct proportion to their availability on the study areas. Territories, which encompassed both nesting and foraging areas, were heterogeneous in vegetation structure and floristics. Areas selected for territories clearly reflected availability of the large white spruce selected for nest sites but did not reflect selection of medium white spruce for foraging. Characteristics of habitats varied with specific resource needs, but the distribution of Townsend's Warblers was most strongly related to specific habitat requirements for nest sites. Received 29 July 1996, accepted 5 May 1997.

BIRDS OFTEN ARE ASSOCIATED with specific habitats, presumably through the evolution of behavioral affinities for habitat features that are linked to resources necessary for reproduction and survival (Hildén 1965, Fretwell 1972, Steele 1993). Although habitat selection in birds has been widely studied, much of the literature has documented correlations between the distribution of birds and specific features of habitat without identifying the causes of these associations (Holmes 1981, Martin 1992). Examining the selection of multiple resources that influence reproduction and survival enables a

more comprehensive understanding of ecologically relevant factors that influence the choice of habitats in birds (Martin 1992, Steele 1993).

For many passerines, the breeding territory encompasses all resources required during most of the breeding season. Breeding territories must provide song perches, suitable places to obtain food and raise young, and shelter from predators and inclement weather. Therefore, territories may reflect selection for several resources that enhance reproduction and survival, all of which may not be maximized at the site (Petit et al. 1988, Sedgwick and Knopf 1992).

Availability of suitable nest sites may influence choice of breeding territories by open-nesting passerines (Martin 1988b, 1992). The selection of nest sites has a direct effect on fitness through its influence on the production of young (Martin and Roper 1988). Predation is the primary source of nest failure among many

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species of open-nesting passerines (Ricklefs 1969; Martin 1992, 1993), including many breeding at northern latitudes (Goossen and Sealy 1982, Rogers 1994, Briskie 1995). Thus, vegetative features that conceal nests from predators may play an important role in determining reproductive success (Wray and Whitmore 1979, Martin and Roper 1988, Martin 1992, Kelly 1993). The availability of such features in turn may exert a strong influence on choice of territories during the breeding season (Martin 1992, Steele 1993).

Availability of food also may influence the selection of breeding territories. Several species of birds forage preferentially on particular species of plants or foliage types (Emlen and DeJong 1981; Holmes and Robinson 1981; Mannan and Meslow 1984; Parrish 1995a, b). Access to suitable substrates for foraging and associated food resources may have a strong influence on individual fitness (Martin 1987, Simons and Martin 1990, Holmes et al. 1992, Rodenhouse and Holmes 1992). Vegetation structure and floristics affect where food may be obtained and thus may determine the habitats a species will occupy (Robinson and Holmes 1982; Parrish 1995a, b).

The Townsend's Warbler (*Dendroica townsendi*) is a Neotropical-Nearctic migrant that is strongly associated with mature coniferous and mixed coniferous-deciduous forests throughout its breeding range (Bent 1953, AOU 1983, Curson et al. 1994). Little is known, however, about resource requirements that determine habitat use by this species. We investigated habitat selection by Townsend's Warblers breeding in mature, mixed coniferous-deciduous forests in south-central Alaska. First, we identified the structural and floristic characteristics of habitat associated with the selection of territories, nest sites, and foraging sites. Because Townsend's Warblers occur primarily in mature coniferous forests (Spindler and Kessel 1980, Mannan and Meslow 1984, Kessler and Kogut 1985, Hejl et al. 1995), we then tested the hypotheses that large coniferous trees were used selectively for nesting and foraging. Finally, we compared features of habitats selected for nest sites and foraging sites with those selected for territories to determine the relative importance of these two resources in the selection of breeding territories.

STUDY AREA AND METHODS

We selected two study areas in the Campbell Creek drainage (61°08'N, 149°43'W) near Anchorage, south-central Alaska. The areas were about 2 km apart and were within a large expanse of boreal forest along the lower slopes of the Chugach Mountains. The study areas contained mature, mixed coniferous-deciduous forests in which Townsend's Warblers had access to both deciduous and coniferous trees. We chose study areas that differed in coniferous cover and total cover of the tree canopy to examine selection under a range of different microhabitats.

The first study area was 140 to 220 m in elevation and consisted of 26 ha of closed-canopy mixed-forest habitat (Viereck et al. 1992). The mature-forest overstory was dominated by white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*). The understory consisted of saplings of overstory species, Sitka alder (*Alnus sinuata*), thinleaf alder (*A. tenuifolia*), high-bush cranberry (*Viburnum edule*), Pacific red elder (*Sambucus racemosa*), devil's club (*Oplopanax horridus*), American red raspberry (*Rubus idaeus*), rusty menziesia (*Menziesia ferruginea*), and Alaska spirea (*Spiraea beauverdiana*). The second study area was 320 to 400 m in elevation and consisted of 35 ha of subalpine open-canopy mixed-forest (Viereck et al. 1992). This mature, open forest was similar in plant species composition to the study area in the closed forest but included large open areas where bluejoint grass (*Calamagrostis canadensis*) and thinleaf alder were the dominant species.

Delineation of breeding territories.—Between 10 May and 2 June 1994, we searched the study areas on alternate days to locate newly arrived male Townsend's Warblers, which we captured in mist nets with the aid of song playbacks. In each study area, female and additional male Townsend's Warblers were captured in an array of 15 mist nets in a centrally located 10-ha area. Each warbler was measured, examined for breeding condition, and fitted with an aluminum U.S. Fish and Wildlife Service leg band and a unique combination of three colored leg bands.

We used spot-mapping (International Bird Census Committee 1970, Bibby et al. 1992) to delineate territories in 1994. We censused both study areas seven times between 1 May and 7 July. Censusing began at sunrise and lasted approximately 3 to 4 h. During each census, we mapped the movements and behavior (singing, foraging, mate-guarding, fighting, preening, roosting) of each male for as long as it remained in sight or until it had been in the same area for approximately 2 min. We also mapped locations of all territorial disputes and countering males. We supplemented spot-map censuses with observations of marked males that we mapped while searching for and monitoring nests. At the end of the nesting season, we compiled all observations of males on a single acetate overlay for each study area. We iden-

tified territories by delineating areas in which males were observed during three or more spot-mapping visits (Marchant 1983, Bibby et al. 1992). We used resightings of marked individuals to help distinguish adjacent territories in which observations of the males were tightly clustered.

Nest locations and foraging observations.—During 1993 and 1994, we searched both study areas every two to five days between 10 May (when females first arrived) and 11 July (when active nests were no longer observed). Nest searches began 15 min before sunrise and continued until we had searched a route passing within 50 m of all points within the study area.

We recorded the foraging behavior of males and females during the pre- and posthatching stages of the nesting cycle in 1994. The prehatching period included observations during nest building, egg laying, and incubation from 2 to 10 June. During the posthatching period from 19 to 28 June, we restricted observations to individuals carrying food for nestlings or newly fledged young. We recorded observations of foraging birds throughout the day to minimize sampling bias due to diurnal variation in foraging behavior (Holmes et al. 1978, Sherry 1979, Morse 1990). To help assure statistical independence, we recorded one bout of foraging per individual during each period of the nesting cycle. Individuals were identified by color-band combinations or by association with a particular territory or nest site.

Observations of foraging bouts ranged from 1 to 5 min, during which we recorded the vegetative stratum used for foraging at 10-s intervals. We classified foraging strata by plant species (alder, paper birch, white spruce, other) and stem diameter at breast height (dbh) class (1 to 2 cm, 3 to 7 cm, 8 to 14 cm, 15 to 22 cm, 23 to 37 cm, 38 to 53 cm, and >53 cm).

Vegetation sampling.—We sampled habitat characteristics of study areas, territories, and nest sites between mid-July and mid-August using a modified version of the circular-plot method (0.04 ha) described by James and Shugart (1970). Within each circular plot, we measured 24 structural and floristic characteristics, including slope, percent canopy cover, density of shrub stems, and 21 classes of tree stems. Tree stems were counted by species and dbh class as for foraging observations (but without the class 1 to 2 cm).

We sampled characteristics of available habitat in 1994 following a two-stage, stratified random sampling procedure (Scheaffer et al. 1990). In the first stage, we measured canopy cover of conifers between 29 April and 19 May, before deciduous foliage had emerged, at each of 118 evenly spaced grid points in the closed forest and 165 grid points in the open forest. For each point we calculated the average of four spherical-densitometer measurements (Lemon 1957) of coniferous canopy cover sampled in the cardinal compass directions. We then classified each

grid point into one of three strata of coniferous cover (0 to 9%, 10 to 29%, or >30%) and estimated the proportion of each stratum for both study areas. In the second stage, we selected a stratified random sample of 42 grid points from each study area, with the number of points allocated to each stratum proportionately to its size. Intensive sampling of the circular plots was conducted at each of the stratified random sampling points as described above.

In 1994, we sampled habitat characteristics at two sites within each of the territories of 21 males in the closed forest and 19 males in the open forest study areas. We located our samples near mapped observations of males in order to avoid sampling large unused areas within territories (Odum and Kuenzler 1955, Sedgwick and Knopf 1992). For each male, we randomly selected two dates on which it had been observed during the breeding season. We then randomly selected one of the locations where it had been mapped on each date, excluding first locations to reduce the bias associated with sampling first detections. Centers of circular habitat plots were placed at a random direction and distance (0 to 10 m) from the mapped observation point.

We sampled habitat characteristics at 23 nest sites in the closed forest and 10 nest sites in the open forest study areas during 1993 and 1994. Vegetation characteristics were measured within a single 0.04-ha circular plot centered at each nest. To determine if nest trees were larger than a random selection of non-nest trees, we measured dbh and mean crown width of the nest tree and the nearest tree (dbh >8 cm) not used for nesting that occurred within a randomly selected quarter-circle centered on the nest. We restricted measurements to white spruce because Townsend's Warblers had been found to nest only in conifers (Mannan et al. 1983).

Statistical analyses.—We examined data on habitat using descriptive statistics and Spearman rank correlations. Several size classes of trees occurred infrequently on the sampling plots, so we collapsed adjacent categories into larger classes. In other instances, the numbers of tree species in adjacent size classes were highly correlated ($r \geq 0.545$), so we collapsed the classes to eliminate redundant variables. Because tree species other than white spruce, paper birch, and alder were rare and relatively invariant in occurrence, we eliminated their densities from further analysis. We retained 10 of 24 habitat variables for final analyses of selection of territories and nest sites and 7 of 24 habitat classes for analysis of selection of foraging sites (Table 1). We performed all statistical analyses using SAS (SAS Institute, Inc. 1988) or SPSS (Norusis 1994) statistical packages. Significance levels for all tests were set at $P < 0.05$; means are reported ± 1 SD.

A single 0.04-ha circular plot habitat sample taken from within the bounds of a breeding territory generally is inadequate to represent the habitat occupied

TABLE 1. Definitions of habitat variables used in analyses of habitat selection.

Circular plots^a
Slope: Maximum slope (in degrees) measured with a clinometer over a 10-m distance crossing the sampling circle center.
Total canopy cover: Average % canopy cover from four spherical-densimeter measurements in each of the 4 cardinal compass directions at the center of the sample circle.
Shrub: Number of woody plant stems 1 to 3 cm at 1 m height in two 22.6 × 1.2-m transects.
Alder: Number of alder stems >3 cm dbh.
Small birch: Number of paper birch 3 to 15 cm dbh.
Medium birch: Number of paper birch 15 to 38 cm dbh.
Large birch: Number of paper birch ≥38 cm dbh.
Small spruce: Number of white spruce 3 to 15 cm dbh.
Medium spruce: Number of white spruce 15 to 38 cm dbh.
Large spruce: Number of white spruce ≥38 cm dbh.
Nesting trees^b
dbh: Diameter at breast height (cm)
Crown: Mean of four distance measurements (m) taken from the tree bole to distal end of the longest branch in each of four quarters defined by the cardinal compass directions.
Foraging strata
Alder: Alder stem 1 to 15 cm dbh.
Small birch: Paper birch 1 to 15 cm dbh.
Medium birch: Paper birch 15 to 38 cm dbh.
Large birch: Paper birch ≥38 cm dbh.
Small spruce: White spruce 1 to 15 cm dbh.
Medium spruce: White spruce 15 to 38 cm dbh.
Large spruce: White spruce ≥38 cm dbh.

^a Habitat variables measured in 0.04-ha circular plots at stratified random sites, territory sites, and nest sites.

^b Habitat variables measured at trees used for nesting and adjacent trees not used for nesting.

(Holmes 1981), so several samples within a territory often are collected to characterize the habitat (e.g. Noon 1981, Craig 1985, Conner et al. 1986, Wenny et al. 1993). Statistical treatment of multiple samples from individual territories can result in pseudoreplication (Hurlbert 1984), and averaging samples may produce numerical values for habitat components that individuals do not use or even encounter.

We used a resampling method that employed stepwise logistic regression to identify and confirm features of habitat important in the selection of male territories. We used logistic regression in favor of other statistical techniques (e.g. multivariate analysis of variance [MANOVA] or discriminant function analysis) because of the lack of assumptions in logistic regression concerning multivariate normality and homoscedasticity (Hosmer and Lemeshow 1989, Norusis 1994) and because it models a selection

probability instead of simply comparing sample means (Manly et al. 1993).

In the first step of the resampling procedure, we randomly selected one of the two habitat samples collected from each territory. We then used stepwise logistic regression to identify the combination of habitat variables that best separated the set of randomly selected territory samples from the stratified random samples of available habitat. An indicator variable for study site was added to the list of potential variables for inclusion in the stepwise models to determine if selection of territories varied between study areas. The criterion for entry of a variable into the stepwise logistic regression model was $\alpha = 0.10$ for the score statistic and, for removal from the model, $\alpha = 0.15$ for the log-likelihood ratio statistic (Hosmer and Lemeshow 1989, Norusis 1994). We resampled one of the two habitat samples from each territory with replacement for a total of 100 stepwise logistic regression iterations. We constructed a predictive model using the mean coefficients from the most commonly recurring model and used the Hosmer-Lemeshow (1989) goodness-of-fit test to assess the fit of the model for a random sample of territory sites. The number of times each habitat variable entered during the 100 stepwise logistic regression iterations was used to confirm its importance in modeling selection of territories (Johnson and Wichern 1992). Because the sampling fractions of used and available habitats were unknown, the resulting logistic regression models measured relative rather than absolute probabilities of habitat selection (Manly et al. 1993).

We also used stepwise logistic regression to identify combinations of habitat characteristics that best distinguished nest sites from random samples of available habitat. We used one-tailed, paired-sample *t*-tests to determine if trees used for nesting had greater dbh or crown width than adjacent trees not used for nesting.

For each foraging bout, we calculated the proportion of observations occurring in each tree species by diameter class. Because not all bouts were of equal length, we weighted proportions by:

$$w = \sqrt{n_i / N_{\max}}, \quad (1)$$

where n_i = the total number of 10-s intervals in the i^{th} bout and $N_{\max} = 30$, the maximum number of 10-s intervals recorded in a bout. We transformed the weighted proportions to ranks and used a full-factorial MANOVA on the ranked proportions to test for differences in the use of foraging strata by sex, breeding stage, and study area. A Bonferroni multiple-comparisons test was performed to identify specific differences in mean foraging strata use.

To determine the availability of foraging strata, we estimated the proportion of vegetative basal area (m^2) in each stratified random sample occupied by each foraging stratum. We then compared the mean

TABLE 2. Habitat features of territories, nest sites, and stratified random sites in south-central Alaska, 1994. Values are $\bar{x} \pm SD$.

Variable ^a	Territory (n = 40)	Nest site (n = 33)	Random site (n = 84)
Slope	15.23 ± 11.49	15.42 ± 14.77	8.82 ± 8.22
Shrub	49.01 ± 37.22	55.58 ± 36.18	54.90 ± 38.44
Alder	21.67 ± 20.89	22.42 ± 36.61	36.61 ± 41.60
Small birch	2.19 ± 3.68	4.82 ± 8.23	2.43 ± 4.73
Medium birch	2.15 ± 1.91	2.21 ± 2.25	1.46 ± 1.94
Large birch	0.39 ± 0.70	0.27 ± 0.63	0.42 ± 0.85
Small spruce	4.20 ± 6.92	9.88 ± 25.28	3.77 ± 6.45
Medium spruce	3.63 ± 3.69	3.18 ± 3.39	2.23 ± 3.73
Large spruce	1.21 ± 1.22	1.00 ± 1.09	0.60 ± 0.91
Total canopy cover	56.55 ± 23.31	63.50 ± 20.48	52.00 ± 32.25

^a See Table 1.

proportion of foraging strata used to that available using MANOVA on the ranked proportions to test for selection of foraging strata. A Bonferroni multiple comparisons test was used to identify specific group-mean differences between foraging strata use and availability.

RESULTS

Selection of territories.—Areas used by territorial males were characterized by steeper slopes, higher densities of large spruce, and lower densities of alder than those available on the study areas (Table 2). These three variables comprised the most commonly recurring logistic regression model distinguishing territories from random sites (53 of 100 iterations; Table 3). They also occurred together in 17 models in which additional habitat variables were selected.

Using the mean coefficients from the most commonly recurring model (Table 3), the predicted probability of an area being selected for a territory was:

$$P(x) = \frac{1}{1 + e^{-[-1.42 + 0.07(\text{Slope}) + 0.46(\text{Large spruce}) - 0.02(\text{Alder})]}}$$

(2)

under the assumption of equal sampling fractions of used and available habitat (Manly et al. 1993). This model was highly significant, based on the Hosmer-Lemeshow goodness-of-fit statistic ($C = 4.36$, $df = 8$, $P > 0.75$). Forty-three percent of the areas used by territory-holding males had predicted probability values of ≥ 0.5 of being classified as a territory based on this model, and 90% of the random sites had predicted probability values < 0.5 , for an overall correct classification rate of 75%.

The relative importance of slope, large spruce, and alder in distinguishing areas used by territorial males from those available was confirmed by the high frequencies with which these variables were selected during the 100 re-sampling iterations. Slope was included in 99%, large spruce in 96%, and alder in 73% of the models generated (Table 4). All other variables were included in less than half of the iterations. The indicator variable for study area entered only once, suggesting that habitat features selected for territories were similar between the two areas.

Selection of nest sites.—Townsend's Warblers typically nested in areas with higher densities of large and small spruce and steeper slopes relative to availability (Table 2). The stepwise logistic regression model incorporating these variables effectively discriminated nest sites from random samples of habitat ($C = 8.42$, $df = 8$, $P > 0.25$; Table 5). The indicator variable for study area did not enter the stepwise logistic regression model, suggesting that habitat features selected for nest sites were similar be-

TABLE 3. The most frequently occurring territory-selection model for Townsend's Warblers nesting in south-central Alaska, 1994. Values based on stepwise logistic regression (100 iterations). Coefficient means and SDs calculated from the 53 iterations in which model was selected.

Variable	Coefficient mean	SD	Minimum	Maximum
Intercept ^a	-1.42	0.20	-2.14	-0.94
Slope	0.07	0.01	0.05	0.10
Large spruce	0.46	0.08	0.31	0.69
Alder	-0.02	0.03	-0.21	-0.01

^a Includes unknown ratio of sampling fractions of used and available habitat.

TABLE 4. Frequency of occurrence of habitat variables from stepwise logistic regressions (100 iterations) comparing habitat within Townsend's Warbler territories with available habitat, south-central Alaska, 1994. Coefficient means and SDs calculated from models in which the variable occurred.

Variable	Frequency	Coefficient			
		mean	SD	Minimum	Maximum
Slope	0.99	0.07	0.01	0.04	0.10
Large spruce	0.96	0.53	0.13	0.31	0.91
Alder	0.73	-0.02	0.02	-0.21	-0.01
Medium birch	0.41	0.23	0.05	0.09	0.36
Small spruce	0.17	0.06	0.01	0.05	0.10
Shrub	0.03	-0.01	<0.01	-0.01	-0.01
Study site	0.01	-1.13			
Large birch	0.01	0.46			
Small birch	0.00				
Medium spruce	0.00				
Total canopy cover	0.00				

tween the two study areas. Overall, 77% of the sites were correctly classified by the model, including 30% of the nest sites and 95% of the random sites.

Thirty-two of 33 nests (97%) were in white spruce; one nest in the closed forest was located in a paper birch. White spruce used for nesting were larger in diameter ($\bar{x} = 30.15 \pm 14.8$ cm) than adjacent white spruce not used for nesting ($\bar{x} = 24.1 \pm 13.4$ cm; $t = 1.94$, $df = 31$, $P = 0.031$) and also had greater crown width ($\bar{x} = 2.8 \pm 1.2$ m) than neighboring trees not used for nesting ($\bar{x} = 2.3 \pm 0.8$ m; $t = 1.74$, $df = 31$, $P = 0.047$).

Use of foraging habitats.—During 97 foraging bouts ($n = 1,391$ observations), Townsend's Warblers foraged more frequently in white spruce, less frequently in paper birch and alder, and only once in willow. Time spent foraging in each habitat stratum did not differ significantly between sexes or study areas but did differ significantly between the prehatching and

posthatching stages (Wilks' Lambda = 0.70, $F = 5.15$, $df = 7$ and 83, $P < 0.001$). Before nestlings hatched, adults foraged primarily in medium spruce and very little in alder or paper birch (Fig. 1). During the posthatching period, foraging declined significantly in medium spruce and increased in alder and medium birch (Fig. 1).

Townsend's Warblers used foraging habitats nonrandomly during the prehatching (Wilks' lambda = 0.13, $F = 132.83$, $df = 7$ and 135, $P < 0.001$) and posthatching (Wilks' Lambda = 0.32, $F = 34.16$, $df = 7$ and 114, $P < 0.001$) pe-

TABLE 5. Habitat characteristics distinguishing Townsend's Warbler nest sites from available habitat, south-central Alaska, 1993 to 1994. Variables presented in order of selection by logistic regression model. Model $\chi^2 = 19.51$, $df = 3$, $P < 0.001$. Intercept $B_0 = -2.40$, which includes unknown ratio of sampling fractions of used and available habitat.

Variable	B	SE	Log likelihood		
			Log likelihood	-Log LR	P
Slope	0.06	0.02	-64.28	8.86	0.003
Small spruce	0.08	0.03	-64.41	9.12	0.003
Large spruce	0.45	0.22	-61.85	4.01	0.045

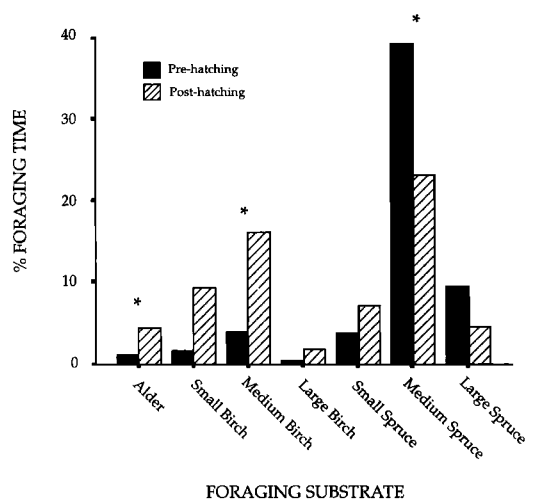


FIG. 1. Seasonal variation in the percentage time spent in different habitat strata by foraging Townsend's Warblers in south-central Alaska, 1994. Asterisks denote significant ($P < 0.05$) differences between prehatching ($n = 38$ males, 21 females) and posthatching periods ($n = 19$ males, 19 females).

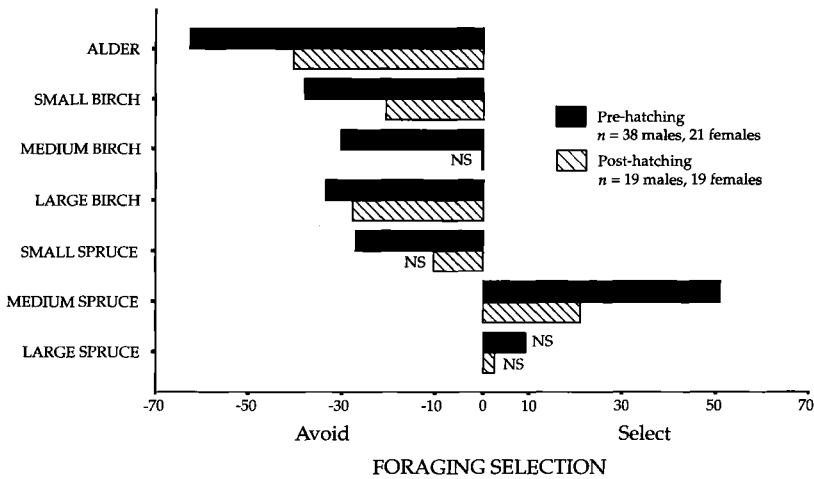


FIG. 2. Selection of foraging habitat strata by Townsend's Warblers during the prehatching and posthatching stages of the nesting cycle in south-central Alaska, 1994. Foraging selection (mean proportion of stratum use - mean proportion of stratum availability) was based on ranked data. All graphed values represent significant differences between use and availability ($P < 0.05$) except those denoted by "NS."

riods. Males and females foraged significantly more in medium spruce than expected throughout the nesting season, despite a decline in use during the posthatching period (Fig. 2). Warblers foraged in large spruce in proportion to availability during both periods of the nesting cycle. Alder, paper birch, and small spruce were used less frequently than expected or in proportion to availability during both periods.

DISCUSSION

Our results suggest that the affinity of Townsend's Warblers for mature coniferous forest is based more on selection of nest sites than on choice of foraging sites. Within mixed forests of deciduous and coniferous trees, Townsend's Warblers nested primarily in large white spruce and consistently chose trees that occurred within areas of relatively high densities of large white spruce. Nests also were placed in forest patches with relatively high densities of small white spruce, suggesting that the selection of nest sites is not based solely on the distribution of large spruce. All of the Townsend's Warbler nests reported from Montana (Silloway 1906), Washington (Bowles 1908, Decker and Bowles 1923), and Oregon (Mannan et al. 1983) have been in conifers, suggesting that the selection of conifers for nesting is widespread. The single nest that we found in

paper birch is the first record of this species nesting in a deciduous tree.

Characteristics of Townsend's Warbler nest sites influence the production of young in that nests in large white spruce have lower rates of predation than those in smaller white spruce (Matsuoka et al. 1997). Greater foliage volume of large white spruce probably helps make nests and adults moving near nests less conspicuous to predators (Matsuoka et al. 1997). Additionally, the long branches associated with nest trees may enable warblers to nest farther out on limbs away from arboreal predators. Nesting in patches with relatively high densities of large white spruce may further reduce the risk of predation by increasing the number of potential nest sites in the surrounding area that must be searched by predators (cf. Martin 1988a, Martin and Roper 1988).

Selection of steep slopes may have been related to selection of large white spruce, because steep slopes provide optimum growing conditions for white spruce (Viereck and Little 1972). Large white spruce were not restricted to steep slopes, however, and their density was not correlated with slope ($r_s = 0.05$, $df = 84$, $P = 0.65$). The placement of nest sites on steep slopes may have facilitated defense of territories or mates, provided a favorable microclimate for the production of arthropods, or aided in the thermoregulation of adults and nestlings.

Although large white spruce were used selectively for nesting, medium-sized spruce were used selectively by both males and females for foraging, particularly during the pre-hatching stage. The seasonal decline in time spent foraging in white spruce and the concomitant increase in use of deciduous strata suggest that Townsend's Warblers respond to seasonal changes in food availability within their territories. Temporal changes in foraging behavior have been documented in a number of bird species (Hejl and Verner 1990, Petit et al. 1990, Sakai and Noon 1990, Lovette and Holmes 1995), suggesting that behavioral responses to changes in resource demand and distribution of food resources are common in birds (Recher 1990).

Experimental studies have shown that parulines have intrinsic preferences for specific microhabitats for foraging (Emlen and DeJong 1981; Whelan 1989; Parrish 1995a, b), but use of preferred strata can be reversed by greater availability of insect prey on less-preferred strata (Whelan 1989, Parrish 1995b). The preferred use of white spruce for foraging by Townsend's Warblers may have reflected an intrinsic preference for coniferous foliage. If so, the shift to use of alder and paper birch during the posthatching period may have been a functional response to increased abundance of insect larvae on deciduous foliage later in the breeding season (Keast 1990, Petit et al. 1990), decreased abundance of insect larvae on coniferous foliage because of foraging (Holmes et al. 1979), increased resource demands associated with provisioning young (Weathers and Sullivan 1989, 1991), or some combination of these factors.

Vegetation structure and floristics were heterogeneous on Townsend's Warbler territories, as indicated by high variability in the models of territory selection resulting from resampling analyses. For those bird species in which territories encompass most of the activities of adults during the breeding season, patches of habitat with varied vegetation structure and floristics may be selected to simultaneously fulfill different resource demands (Petit et al. 1988). Vegetation features associated with nesting (i.e. high densities of large and small white spruce) and foraging (i.e. medium-sized white spruce) were nonoverlapping, suggesting that territories with heterogeneous habitat provid-

TABLE 6. Concordance for selection of habitat features for territories, nest sites, and foraging sites by Townsend's Warblers, south-central Alaska. Within rows, similar symbols^a indicate shared patterns of selectivity; dissimilar symbols indicate potential conflicts in resource needs.

Habitat feature	Territory	Nest site	Foraging sites	
			Pre-hatching	Post-hatching
Large spruce	+	+	0	0
Medium spruce	0	0	+	+
Small spruce	0	+	-	0
Large birch	0	0	-	-
Medium birch	0	0	-	0
Small birch	0	0	-	-
Alder	-	0	-	-
Steep slope	+	+	N	N

^a +, feature selected; -, feature avoided; 0, feature included in <70% of models (territories), not included in model (nest sites), or used in proportion to availability (foraging sites); N, not measured.

ed distinctive habitat requirements for these resources (Martin and Roper 1988, Petit et al. 1988, Steele 1993).

Comparisons of the habitat features selected for nest sites and foraging sites with those selected for territories provided insights into how different resource requirements may have influenced the selection of territories. For example, selection of territories containing relatively high densities of large white spruce and steep slopes corresponded to selection of such areas for nest sites. Patches of large white spruce were not used preferentially for foraging, however (Table 6). Selection of territories with low densities of alders may have been related to the avoidance of alders by foraging adults.

Other components of the vegetation were selected or avoided for nest sites or foraging sites but not for territories. This lack of concordance was most evident in the use of medium-sized white spruce for foraging even though they were not abundant within territories (Table 6). The relationship between selection of foraging sites and territories may have been weak because the abundance of insect prey in different vegetation types was difficult for birds to predict at the time of territory selection (Holmes 1988). Consequently, birds may have selected territories based on the availability of more predictable resources, such as nest sites, and subsequently selected vegetation for foraging sites based on the local distribution of arthropods within territories. Alternatively, if food re-

sources are abundant in highly seasonal environments at high latitudes (see Ashmole 1963, Ricklefs 1980), then food availability may not have had a strong influence on the selection of territories by Townsend's Warblers breeding near the northern limit of their range.

Habitat characteristics associated with nest sites and foraging sites were not equivalent predictors of habitats selected for territories. Selection of breeding territories by Townsend's Warblers was more closely associated with selection of nest sites than with selection of foraging sites, similar to Steele's (1993) finding for Black-throated Blue Warblers (*Dendroica caerulescens*). These findings suggest that the distribution of breeding Townsend's Warblers is strongly related to their specific habitat requirements for nest sites.

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