

NESTING ECOLOGY OF TOWNSEND'S WARBLERS IN RELATION TO HABITAT CHARACTERISTICS IN A MATURE BOREAL FOREST¹

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Abstract. We investigated the nesting ecology of Townsend's Warblers (*Dendroica townsendi*) from 1993-1995 in an unfragmented boreal forest along the lower slopes of the Chugach Mountains in southcentral Alaska. We examined habitat characteristics of nest sites in relation to factors influencing reproductive success. Almost all territory-holding males (98%, $n = 40$) were successful in acquiring mates. Nest success was 54% ($n = 24$ nests), with nest survivorship greater during incubation (87%) than during the nestling period (62%). Most nesting failure (80%) was attributable to predation, which occurred primarily during the nestling period. Fifty-five percent of nests containing nestlings were infested with the larvae of bird blow-flies (*Protocalliphora braueri* and *P. spenceri*), obligatory blood-feeding parasites. The combined effects of *Protocalliphora* infestation and inclement weather apparently resulted in nestling mortality in 4 of the 24 nests. Nests that escaped predation were placed in white spruce with larger diameter than those lost to predation; nests that escaped blow-fly parasitism were located higher in nest trees and in areas with lower densities of woody shrubs than those that were infested. The availability of potential nest sites with these key features may be important in determining reproductive success in Townsend's Warblers.

Key words: *bird blow-flies, Protocalliphora, nest success, predation, nesting ecology, habitat, Townsend's Warbler, Dendroica townsendi, Alaska.*

INTRODUCTION

Identification of habitat features that influence the occurrence, density, and distribution of birds is a major goal in avian ecology (Holmes 1981). Numerous studies have documented significant relationships between the location or density of birds and specific habitat features, but these correlations do not always help identify those factors that shape patterns of habitat selection (Holmes 1981, Martin 1992). An understanding

of the ecological factors that influence habitat use among birds is important not only in providing insight into the ecological and evolutionary processes that shape life-history strategies, but also in providing critical information upon which to base sound decisions regarding land management (Holmes 1981, Martin 1992).

Choice of nest sites has a direct effect on individual fitness through its influence on reproductive success (Martin and Roper 1988, Martin 1992). Choice of nest sites is presumably influenced by a number of abiotic and biotic factors that can affect the survival of both young and adults tending young. Nest sites with specific microclimates may be selected to provide protection from inclement weather, as well as favorable conditions for the thermoregulation of eggs and developing young (Calder 1973, Walsberg 1985). The proximity of the nest to an adequate food supply also may influence repro-

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ductive output (Simons and Martin 1990, Holmes et al. 1992, Rodenhouse and Holmes 1992). Concealment from potential predators may influence the selection of nest sites (Martin 1992) because predation is commonly the main source of nest failure among open-nesting birds (Ricklefs 1969, Martin 1992, 1993). Lastly, factors that affect the prevalence of brood parasites (Gates and Gysel 1978, Brittingham and Temple 1983, Robinson 1992) and nest ectoparasites (Loye and Zuk 1991) also may influence the choice of nest sites.

The Townsend's Warbler (*Dendroica townsendi*) is a long-distance migratory passerine associated with mature coniferous and mixed coniferous-deciduous forests throughout its breeding range, which extends from east-central Alaska and the Yukon Territory to the Pacific Northwest as far south as Oregon, Idaho, and Wyoming (AOU 1983). Near the northern limit of its breeding range in central Alaska, the Townsend's Warbler is found almost exclusively in forests dominated by mature white spruce (*Picea glauca*) (Spindler and Kessel 1980). In northeastern Oregon, the species is largely restricted to unmanaged, old-growth forests dominated by grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) (Mannan and Meslow 1984). The few nests that have been described (Silloway 1906, Decker and Bowles 1923, Bent 1953, Mannan et al. 1983) have all been in coniferous trees.

Because of this strong habitat association, breeding populations of Townsend's Warblers may be deleteriously affected by timber harvest in mature and old-growth forests (Mannan and Meslow 1984, Wetmore et al. 1985, Hejl et al. 1995), which is currently occurring throughout the Pacific Northwest and is expanding through southcentral and central Alaska. Knowledge of habitat features that influence the ability of Townsend's Warblers to reproduce successfully is necessary to guide decisions concerning forest management. Virtually no information on reproductive ecology exists for this species, other than the length of the incubation and nestling periods for a single nest (Mannan et al. 1983).

In this study we examined the reproductive ecology of Townsend's Warblers in relation to habitat characteristics in southcentral Alaska. Our main objectives were to identify the primary factors influencing reproductive success and to test the hypothesis that sites of successful nest-

ing attempts differed in specific habitat features from those of unsuccessful attempts.

STUDY AREA

We conducted field research in the South Campbell Creek drainage (61° 08' N, 149° 43' W) on the outskirts of Anchorage, Alaska. Breeding Townsend's Warblers were studied on two areas that differed in canopy closure and were approximately 2 km apart within a large expanse of boreal forest along the lower slopes of the Chugach Mountains of southcentral Alaska. The study area in the closed forest was 140–220 m in elevation and consisted of 26 ha of closed canopy mixed forest (Viereck et al. 1992) with an average total canopy cover of 66% and an average coniferous canopy cover of 21%. The study area in the open forest was 320–400 m in elevation and consisted of 35 ha of subalpine open canopy mixed forest (Viereck et al. 1992) with an average total canopy cover of 38% and an average coniferous canopy cover of 12%. The mature forest overstory in both study areas was dominated by white spruce and paper birch (*Betula papyrifera*). The understorey consisted of saplings of the overstorey species, Sitka alder (*Alnus sinuata*), thinleaf alder (*A. tenuifolia*) and a variety of shrub species. Black cottonwood (*Populus trichocarpa*) and balsam poplar (*P. balsamifera*) occurred along a narrow riparian zone in the closed forest study area. The open forest study area was a natural mosaic of forest patches and large open areas dominated by blue-joint grass (*Calamagrostis canadensis*) and thinleaf alder.

Potential nest predators in the study areas included Gray Jay (*Perisoreus canadensis*), Steller's Jay (*Cyanocitta stelleri*), Black-billed Magpie (*Pica pica*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), least weasel (*Mustela nivalis*), short-tailed weasel (*M. erminea*), mink (*M. vison*), marten (*Martes americana*), and black bear (*Ursus americanus*).

METHODS

Most of our field efforts were concentrated in 1994 when we gathered information on breeding chronology, mate pairing success, nesting success, and habitat characteristics of nest sites. This information was augmented by information on arrival dates in 1993 and 1995, and on nest-site characteristics in 1993. Each year we cen-

sused the study areas every 5 days beginning the third week of April to determine the approximate date of spring arrival for Townsend's Warblers. In 1994, we captured, color-banded, and followed individual males throughout the breeding season. A territorial male was considered to be paired if there was a nest in his territory, a female was observed repeatedly within the boundaries of the defended territory, or the male was observed provisioning young with food.

We systematically searched both study areas for nests every 3–5 days in 1993 and every 2–3 days in 1994 between mid-May, when the first females arrived, and mid-July, when active nests were no longer observed. Nest searches began 15 min before local sunrise and continued until a route passing within 50 m of all points in the study area had been searched. We varied the starting point for each nest search sequentially among four points within each study area to reduce potential diurnal-related biases in detection of nesting females. Nests were located by visually following females that were carrying nesting materials or returning to the nest following an incubation break, or adults provisioning young with food.

We monitored nests at regular intervals in 1994 to determine the status of each nesting attempt. Each nest was examined by observing the activity of adults around the nest or by climbing the nest tree and inspecting the nest contents with a mirror mounted on a telescopic fiberglass pole. Nests could not be inspected using a mirror pole from below the nest because of dense foliage. During egg-laying and incubation, we visited nests every 1–3 days to determine approximate date of clutch initiation, clutch size, approximate onset of incubation, and survival. Nests were examined daily from 8 days after clutch completion until hatch to determine duration of the incubation period and the number of eggs hatched. We visited nests every 2–4 days after hatch to determine nestling survival. At 6–7 days post hatch, nestlings were fitted with a U. S. Fish and Wildlife Service aluminum leg band, weighed with an electronic balance (± 0.1 g), and measured for wing chord length (mm). Thereafter, we examined nests daily to determine the date of fledging. Nest contents were not inspected directly after day 8 in order to avoid causing premature fledging. Instead, we determined the activity in nests by observing feeding behavior of parents at the nest with the

aid of binoculars. After nest failure or fledging, we continued to observe adults in the nesting area to determine if renesting occurred.

We classified a nesting attempt as successful if adults were observed feeding one or more newly fledged young in the nesting area. Nest failures were classified as depredated if the entire contents of the nest disappeared before nestlings had adequate time to fledge (minimum = 8 days following completion of hatch), abandoned if a clutch of cold eggs was discovered before the estimated time of hatch, or weather-induced if a brood of dead nestlings was discovered following a period of cold, wet weather. We further classified nests as either infested or uninfested by the ectoparasitic larvae of bird blowflies, *Protocalliphora* (Diptera: Calliphoridae). Infestation was identified by finding larvae of bird blowflies attached to nestlings during banding or puparia of bird blowflies in nests, which were all collected in mid-July after active nests were no longer observed in the study areas. We kept in petri dishes the larvae collected from nestlings, and kept in paper bags the nests containing puparia until the adult stages emerged. Adult specimens, puparia, and puparia cases were preserved for identification. We compared the growth of young from parasitized and nonparasitized nests with analysis of variance, testing the effects of parasitism on nestling mass and wing chord, controlled for age.

We used the Mayfield method (Mayfield 1961, 1975) as modified by Johnson (1979) and Bart and Robson (1982) to calculate maximum-likelihood estimates of average daily nest survival and nest success. To test for differences in average daily nest survival between the study areas and between the incubation and nestling stages of the nesting cycle, we calculated a Z-test statistic based on the standard deviation of the pooled data (Bart and Robson 1982). Nest survivorship for the entire nesting period was calculated by multiplying nest survivorship during the incubation period by that during the nestling period (Mayfield 1961).

After the breeding season, we sampled habitat characteristics at each nest site. Variables included species of nest tree, diameter at breast height, dbh (cm), height of nest tree (m), height of nest (m), distance from the nest to tree bole (m), and the concealment of the nest by foliage from 1 m above and from the sides (0–25%, 26–50%, 51–75%, or 76–100% concealment),

which was estimated visually. We also sampled the structural and floristic characteristics within a 0.04-ha circular plot surrounding the nest ("nest area") following methods described by James and Shugart (1970) and modified by Matsuoka et al. (unpubl. data). Nest-area variables included maximum slope (degrees) over a 10-m distance centered on the nest, percent canopy cover, number of woody stems (1–3 cm in diameter) at 1-m height along two 22.6-m \times 1.2-m transects, and the number of alder (*Alnus* sp.), paper birch, and white spruce within the 0.04-ha circle in each of three diameter classes: 3–14 cm, 15–37 cm, and \geq 38 cm.

We used stepwise logistic regression to identify habitat characteristics that best separated successful nests from depredated nests, and uninfested nests from those infested with blow flies. An indicator variable for the two study areas was included in the set of potential variables for inclusion in the logistic-regression models. The criterion for adding a variable into the models was $\alpha = 0.10$ for the score statistic and, for removing a variable from models, $\alpha = 0.15$ for the log-likelihood ratio statistic (Hosmer and Lemeshow 1989, Norusis 1994). We used variables with significant log-likelihood ratio statistics ($P < 0.05$) as evidence for group separation.

The heights of nests and nest trees were compared with those recorded for Townsend's Warblers nesting in northeastern Oregon (Mannan et al. 1983). Variances of the two samples were tested for homogeneity using an F -statistic (Ostle and Malone 1988). Means were compared using a t -test with pooled variance when homogeneous and approximate t^* -test when not (Ostle and Malone 1988).

We performed all statistical analyses using the SPSS Statistical Package (Norusis 1994). Significance levels for statistical tests were set at $P < 0.05$, unless otherwise noted. Means are presented \pm SD.

RESULTS

SPRING ARRIVAL

Males were first observed on the study areas on 10 May 1993, 27 April 1994, and 4 May 1995. Upon arrival, males engaged in active song display and began establishing territories. Females were first observed on the study areas between 15 and 17 May all three years and paired with males within days, possibly hours following ar-

rival. Eighteen of 19 territory-holding males in the open forest and all males in the closed forest ($n = 21$) paired with females for an overall pairing success rate of 98%. Among nests located during the first day of construction ($n = 7$), nest-building lasted approximately 3–4 days. The female built the nest unaided by the male in all nests observed during the construction period ($n = 17$).

NESTS AND NEST SITES

Nests ($n = 25$) were constructed of white spruce and paper birch branchlets, white-spruce needles, dried bluejoint grass, lichens, moss, horsetail (*Equisetum* sp.), and seed hairs from fireweed (*Epilobium angustifolium*). All nests were lined with fine grasses and moose (*Alces alces*) hair. Dimensions of nests ($n = 25$) were: outside diameter = 10.0 ± 0.8 cm, height = 6.8 ± 0.9 cm, inside cup diameter = 6.1 ± 0.8 cm, and cup depth = 3.7 ± 0.8 cm.

Thirty-two of the 33 nests (97%) located in 1993 and 1994 were in white spruce; one nest was in a paper birch. Nest trees ranged from 3.4–23.4 m in height ($\bar{x} = 14.6 \pm 5.3$ m) and 6–55 cm in dbh ($\bar{x} = 30.7 \pm 13.5$ cm). These trees were shorter ($t_{46} = 8.30$, $P < 0.001$) than the grand fir, Douglas-fir, and Engelmann spruce (*Picea engelmannii*) trees ($\bar{x} = 27.3 \pm 3.9$ m, $n = 15$) used for nesting in Oregon (Mannan et al. 1983). Nine percent of nests ($n = 33$) were placed in the lower quarter of the nest tree, 88% in the middle two quarters, and one nest (3%) was in the upper quarter. Nest height ranged from 1.8–11.8 m above the ground ($\bar{x} = 6.7 \pm 2.9$ m), lower than those in larger trees in Oregon ($\bar{x} = 11.0 \pm 4.6$ m, $n = 15$; $t^*_{19,1} = 2.60$, $P < 0.05$; Mannan et al. 1983). There was no correlation between nest-tree height and nest height ($r_s = 0.32$, $P = 0.07$). Distance of the nest from the tree bole ranged from 0–2.3 m ($\bar{x} = 0.6 \pm 0.7$ m) and was positively related to dbh of the nest tree ($r_s = 0.51$, $P < 0.01$). The single nest found in a paper birch was placed 7.1 m above the ground in a dense cluster of foliage approximately 1.5 m from the tree bole. The mature paper birch was 16.5 m in height and 42 cm in dbh.

Nest sites were characterized by high densities of foliage within 1 m of the nest. From above, 81% of nests ($n = 31$) were concealed more than 75% by foliage, 13% were 51–75% concealed, 6% were 26–50% concealed, and no

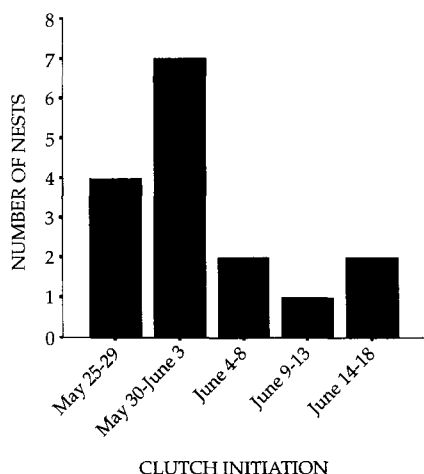


FIGURE 1. Chronology of clutch initiation among Townsend's Warblers in southcentral Alaska, 1994.

nest was $\leq 25\%$ concealed. From the sides, 39% of nests ($n = 31$) were concealed $> 75\%$ by foliage, 48% were concealed 51–75%, 10% were concealed 26–50%, and only one nest was $\leq 25\%$ concealed.

NEST CHRONOLOGY AND SUCCESS

Clutch initiation ranged from 25 May to 17 June in 1994, but most nests (69% of 16 nests) were initiated between 25 May and 3 June (Fig. 1). One egg was laid each day ($n = 12$ nests) until clutch completion. Among 15 nests monitored through the incubation period, modal clutch size was 6 eggs ($n = 9$ nests), but 5 nests had 5 eggs and 1 nest had 7 eggs (overall $\bar{x} = 5.7 \pm 0.6$ eggs). Females were not observed incubating until the last egg was laid. The incubation period (from laying of the last egg to hatching of the last egg) had a mode of 12 days and ranged from 11–14 days ($\bar{x} = 12.5 \pm 0.9$, $n = 13$). The hatching period had a mode of 1 day and ranged from 1–2 days ($\bar{x} = 1.2 \pm 0.4$, $n = 13$). Males were

never observed approaching the nest during incubation. The nestling period (from hatching of the first egg to departure of the last nestling) had a mode of 10 days and ranged from 9–10 days ($\bar{x} = 9.9 \pm 0.4$ days, $n = 7$ nests). Both males and females provisioned nestlings and fledglings with food ($n = 22$ nests). We observed no behavioral evidence of polygyny or reneating. All clutches had been initiated by the time the first nest failure or fledging was noted on the study areas.

In the closed forest, 59% of 17 pairs successfully fledged one or more young; 5 nests (29%) were lost to predation, 1 clutch (6%) was abandoned, and 1 brood was lost to inclement weather (6%). In the open forest, 57% of 7 nesting attempts were successful and 3 nests (43%) were lost to predation. Although nest predation was prevalent in both study areas, only one predation event, by an adult red squirrel on nestlings, was observed during this study. Adults were observed scolding Gray Jays in the vicinity of nests on two occasions.

No differences in the average daily rates of nest survival were detected between the two study areas during the incubation ($Z = 0.69$, $P = 0.49$) or nestling ($Z = 0.15$, $P = 0.88$) periods. With data from the two study areas combined, the average daily rate of nest survival during incubation (0.988) was significantly higher than that during the nestling period (0.948; $Z = 2.02$, $P = 0.04$; Table 1). A single nest was lost to inclement weather or abandonment in each period, but 7 of 8 depredated nests were lost during the nestling period. Predation accounted for 80% of nest failures ($n = 10$) and inclement weather and abandonment each accounted for another 10%.

Nest survivorship for the entire nesting period was estimated at 54% (Table 1). Based on the Mayfield method, nest mortality due to preda-

TABLE 1. Townsend's Warbler nesting success in southcentral Alaska, 1994.

Period	Number survived	Number lost	EXP ^a	DSR ^b	Success ^c
Incubation ^d	14	2	175 (16)	0.988 (0.981–0.994)	0.865
Nestling ^e	14	8	138 (22)	0.948 (0.926–0.967)	0.618
Overall nest success					0.535

^a Exposure days over which (n) nests were observed.

^b Average daily survival rate (95% confidence interval).

^c Nest survival probability for incubation period (12 days) and nestling period (9 days).

^d Period from laying of last egg to hatching of last egg.

^e Period from hatching of last egg to fledging of last nestling.

TABLE 2. Habitat characteristics distinguishing successful Townsend's Warbler nests from those lost to predation, and nonparasitized nests from those infested with the larvae of bird blow-flies in southcentral Alaska, 1994. Values are presented as $\bar{x} \pm SD$ (n).

Habitat characteristic	Successful	Depredated	<i>t</i>	<i>P</i>
Nest tree diameter (cm)	36.1 \pm 12.9 (14)	15.9 \pm 8.2 (8)	3.98	<0.001
Shrub density ^a	34.3 \pm 17.9 (9)	69.2 \pm 18.6 (11)	4.23	<0.001
Nest height (m)	8.7 \pm 6.0 (9)	2.1 \pm 3.02 (11)	2.27	<0.05

^a Number of woody stems (1–3 cm in diameter) per 27 m² within 0.04-ha circular plot centered on nest.

tion was 38% and mortality due to abandonment and weather combined was 8%. Viability of individual eggs and young within successful nests was high. Within 14 nests that survived the incubation period, 98% of 86 eggs successfully hatched. Within 14 nests that successfully fledged young, 95% of 78 nestlings survived to day 8 post-hatching, for an estimate of 3.5 \pm 2.7 fledglings/nest and 5.3 \pm 1.0 fledglings/successful nest. Nestlings banded on day 6 post-hatch had a mean mass of 8.4 \pm 1.0 g and wing chord of 25 \pm 2 mm (n = 32 nestlings from 6 nests). Those banded on day 7 (n = 27 nestlings from 6 nests) had greater mass (\bar{x} = 9.2 \pm 1.2 g; $F_{1,58}$ = 7.31, P < 0.01) and longer wing chord (\bar{x} = 29 \pm 3 mm; $F_{1,58}$ = 36.12, P < 0.001) than those banded on day 6.

NEST PARASITES

On the two study areas combined, 55% of 22 nests with nestlings and 50% of 14 nests that fledged young were infested with the larvae of bird blow-flies, which were identified as *Protophthora braueri* and *P. spenceri* (T. L. Whitworth, pers. comm.). The larvae of both species are obligatory blood-feeding parasites (Sabrosky et al. 1989). Infestation occurred in 50% of 6 nests in the open forest and 64% of 14 nests in the closed forest. All 12 infested nests contained *P. braueri*, whereas only 25% contained *P. spenceri*. In each infested nest all nestlings had *P. braueri* larvae embedded in subcutaneous cavities. These occurred primarily along the shafts of the remiges, but *P. braueri* larvae were observed embedded in most regions of the body except the tarsi. No *P. spenceri* larvae were observed attached to nestlings. Our only observations of *P. spenceri* were from puparia and adults recovered from nests following nest failure or fledging. Infested nests contained an average of 18.3 \pm 16.6 larvae per brood. The maximum number of larvae observed in a nest was

51 *P. braueri*, collected as puparia from a nest containing six young. These estimates of parasite loads per nest are conservative because it was unlikely that we recovered all larvae or pupae associated with each nest. For example, some *P. braueri* larvae were lost during banding of nestlings, when larvae emerged from subcutaneous wounds in their hosts. Additional larvae were probably lost from nests during predation of nestlings.

Nestlings suffering from severe *P. braueri* infestation appeared jaundiced and displayed overall reduced vigor. Parasitism did not appear to affect growth rates, however, since infested nestlings (n = 34 nestlings from 6 nests) did not differ from uninfested nestlings (n = 25 nestlings from 6 nests) in either mass ($F_{1,58}$ = 3.45, P = 0.07) or wing chord ($F_{1,58}$ = 0.74, P > 0.1) after controlling for age of nestling. The single brood that was lost following a bout of cold, wet weather contained nestlings that were heavily infested with *P. braueri* larvae. In three other nests that were infested with *P. braueri* larvae, a total of 4 nestlings died but the remaining brood members fledged. In each of these instances, inclement weather could not be ruled out as the cause of mortality; no nestling mortality could be unequivocally attributed to *Protophthora* parasitism.

NESTING SUCCESS IN RELATION TO HABITAT CHARACTERISTICS

Pairs that fledged young nested in white spruce that were greater in diameter than those used by pairs that lost all eggs or nestlings to predation (Table 2). Nest-tree diameter was the only habitat characteristic that entered the stepwise logistic regression model distinguishing successful from depredated nests (-2 Log likelihood = 16.40, G = 11.50, P < 0.001). Nests free of blow-fly parasitism were located in areas with lower densities of woody shrubs and were

placed higher in trees than infested nests (Table 2). Shrub density was the single most important variable in the logistic regression model distinguishing nonparasitized from parasitized nests ($-2 \text{ Log likelihood} = 15.10$, $G = 12.43$, $P < 0.001$). Nest height also entered into the model but was not significant ($G = 3.35$, $P = 0.065$) with density of shrubs already included. When density of shrubs around the nest was removed from the model, nest height contributed significantly to the difference between nonparasitized nests and parasitized nests ($-2 \text{ Log likelihood} = 22.49$, $G = 5.04$, $P = 0.025$), with nests placed higher in trees experiencing a lower incidence of blow-fly infestation than those placed lower. The indicator variable for study area did not enter into any of the stepwise logistic regression models, suggesting that habitat features that contributed to nesting success did not differ between the two study areas.

DISCUSSION

The reproductive ecology of Townsend's Warblers breeding in an unfragmented boreal forest was similar in many respects to that of most open-nesting passerines breeding in temperate forests, but also showed some disparities that were primarily related to latitudinal differences in seasonality and predation regimes. Predation was the main source of nesting failure among Townsend's Warblers, which conforms with the pattern reported for 28 of 32 species of open-nesting, Neotropical-Nearctic migrant passerines (Martin 1992). Predation was responsible for a 38% reduction in nesting success, close to the mean rate of loss (43%, range 11–67%) reported for open-nesting passerines (Martin 1992). Another important source of loss for most open-nesting passerines, parasitism by Brown-headed Cowbirds (*Molothrus ater*), was not a factor because our study areas are beyond the current breeding range of this brood parasite (AOU 1983; D. D. Gibson, pers. comm.).

Comparisons with studies of other migrant parulines breeding in unfragmented temperate forest tracts suggest that patterns of predation were similar in some respects but differed in others. Among Townsend's Warblers, nesting success (54%) and percent nest failure due to predation (80%) were similar to those of American Redstarts (*Setophaga ruticilla*; 48% and 90%, respectively; Sherry and Holmes 1992) and Black-throated Blue Warblers (*Dendroica caerules-*

cens; 63% and 79%, respectively; Holmes et al. 1992). Several of the potential nest predators encountered in boreal forests by Townsend's Warblers are the same species or ecologically similar to species recorded in the north temperate forest where both warbler studies were conducted (red squirrel, northern flying squirrel, black bear, Blue Jay *Cyanocitta cristata*; Reitsma et al. 1990, Holmes et al. 1992). Such parallels in nesting success likely reflected similar predation pressures on these boreal and north temperate warbler populations.

The seasonal pattern of nest predation, however, was different from that of the Black-throated Blue Warbler (Holmes et al. 1992), the American Redstart (Sherry and Holmes 1992), and most temperate breeding passerines, which typically experience constant rates of predation or a greater proportion of predation during the incubation period (Martin 1992). Predation on Townsend's Warbler nests was concentrated during the nestling period, potentially due to the increased odors, noise, and activity around the nest site that predators may use to detect nests (Kelly 1993, Morton et al. 1993). The seasonal pattern of predation suggests that our nest checks had little effect on predation rates, because predation was extremely low during the incubation period when we checked nests most frequently. High predation rates during the nestling period suggest that predation regimes on our study areas differed in some way from those encountered by open-nesting passerines breeding in more southern latitudes, and point to the need for studies of seasonal interactions between nesting passerines and nest predators in different regions.

Because predation occurred late in the nesting cycle, it may have precluded renesting. All clutches were initiated within a 24-day period, with no evidence of renesting following nest failure or successful fledging. Abiotic factors associated with the short breeding season at high latitudes (Keast 1990) may have placed time constraints on reproduction that not only favored relatively synchronous breeding (cf. Briskie 1995) but also precluded renesting following successful fledging of young (Nolan 1978, Holmes et al. 1992) or nest failure late in the nesting cycle.

Pairing success by male Townsend's Warblers (98%) was much higher than that of Black-throated Blue Warblers (87%; Holmes et al.

1992), Ovenbirds (*Seiurus aurocapillus*; 55–75%; Gibbs and Faaborg 1990, Porneluzi et al. 1993, Van Horn et al. 1995), and Kentucky Warblers (*Oporornis formosus*; 67%; Gibbs and Faaborg 1990) nesting in large temperate forest tracts. Such disparities may have arisen from differences in nesting densities, sex ratios, or mating strategies. The apparent absence of polygyny among Townsend's Warblers, which may have been precluded by latitudinal related time constraints, would likely contribute to higher pairing success among males.

Other aspects of the nesting ecology of Townsend's Warblers also may be adaptive at high latitudes. The modal clutch size was 6 eggs in this study, high when compared with the 3–5 eggs reported for Townsend's Warblers breeding at more southern latitudes (Mannan et al. 1983) and also higher than most parulines breeding in the Temperate Zone (Bent 1953, Morse 1989). Also, nests in this study were greater in both outside diameter and cup diameter than those reported from British Columbia (Bent 1953), Montana (Silloway 1906), and northeastern Oregon (Mannan et al. 1983), suggesting possible adaptation to larger brood size and cooler climate in Alaska. These findings are consistent with the pattern of increased clutch size at higher latitudes (Kulesza 1989), which is thought to occur in response to greater food abundance in highly seasonal, high-latitude environments (Ashmole 1963, Ricklefs 1980) or to longer days during which adults can provision young with food (Lack 1968, Hussel 1985). Comparative studies of reproductive parameters of Townsend's Warblers in relation to seasonal food availability at northern and southern latitudes would provide a test of these hypotheses.

We did not expect to find bird blow-fly infestation in this study. Parasitism by *Protocalliphora* was undocumented in Townsend's Warblers, and the findings of this study represent a northern range extension for *P. spenceri* and a new locality in Alaska for the more ubiquitous *P. braueri* (Sabrosky et al. 1989; T. L. Whitworth, pers. comm.). The rarer *P. spenceri* was not found attached or embedded subcutaneously in any nestling, which is consistent with the little that has been reported on the occurrence of this species (Sabrosky et al. 1989). The subcutaneous burrowing we observed by the more prevalent *P. braueri* larvae has been documented for many other passerine species but with varying

degrees of harm (Sabrosky et al. 1989, Whitworth and Bennett 1992). Infestation by the larvae of *Protocalliphora* was common in nests with nestlings (55%), but the direct effects of blow-fly parasitism on nestlings were not clear. Infestation apparently had no effect on nestling mass or body size, as measured from wing chord, similar to the findings for Sage Thrashers (*Oreoscoptes montanus*; Howe 1992) and House Wrens (*Troglodytes aedon*; Eastman et al. 1989, but see Johnson et al. 1991). Howe (1992), however, reported 26.5% mortality in Sage Thrasher nestlings infected with *P. braueri*, compared with 3.7% mortality in nonparasitized nestlings. Cold, wet weather apparently exacerbated the effects of *P. braueri* on nestling Sage Thrashers and increased parasite-associated mortality (Howe 1992). Our results suggest that this combination of factors also reduced survival of nestling Townsend's Warblers. Although parasite-associated mortality of nestlings was not pronounced during the single year in which nests were monitored in this study, *P. braueri* may reduce reproductive success more during years that have more inclement weather during the nestling period.

Several Townsend's Warbler nests that fledged young contained nestlings that were infested with *P. braueri* larvae, but their fate after leaving the nest was not determined in this study. Although the effects of *Protocalliphora* infestation on post-fledging survival remain unknown (Sabrosky et al. 1989), these blood-feeding parasites may impair the physical condition of nestlings through the reduction of hematocrit and hemoglobin levels (Whitworth and Bennett 1992) and through secondary bacterial infection of subdermal wounds (Warren 1994). If Townsend's Warbler nestlings could not recover from the effects of *P. braueri* infestation prior to fledging, impaired physiological condition may have lowered post-fledging survival.

Our study suggests that selective pressures of both predation and blow-fly parasitism may influence patterns of nesting habitat selection among Townsend's Warblers. Nests of Townsend's Warblers placed in larger white spruce were less likely to suffer predation and more likely to fledge young than nests placed in smaller white spruce. Townsend's Warblers selected white spruce for nesting that were larger in diameter than neighboring white spruce not used for nesting (Matsuoka et al., unpubl. data). Fur-

thermore, territories and nest sites were located in areas with higher densities of large white spruce than were generally available.

Several studies have reported that increased amounts of foliage immediately concealing nests was associated with reduced nest predation (Wray and Whitmore 1979, Martin and Roper 1988, Kelly 1993). We observed no association, however, between nest predation and the amount of foliage within 1 m of the nest, suggesting that reduced depredation of nests in large white spruce was because of factors other than direct nest concealment. Large white spruce had greater numbers of densely foliated tree boughs than smaller white spruce (Matsuoka, pers. observ.), which may have helped conceal adult activities around the nest from nest predators. High densities of foliage, when used for nesting, can decrease predator efficiency by increasing the number of potential nest sites a predator must search (Martin 1988, Martin and Roper 1988). The greater relative foliage volume of large white spruce compared to small spruce may have reduced predation risk in a similar manner. In addition, nests situated in larger spruce were placed farther out on limbs and may have been afforded additional protection from arboreally searching predators.

Different habitat characteristics were associated with lower rates of blow-fly parasitism. Nests in areas with low densities of woody shrubs and nests placed high in nest trees experienced lower incidence of *P. braueri* infestation. Little is known about factors that influence infestation, but most documented cases of *P. braueri* in eastern North America have been in ground- and shrub-nesting birds (Bennett and Whitworth 1992). Infestation may be higher in microhabitats associated with densely vegetated forest openings or the forest understory. Because activity of adult *Protocalliphora* is positively related to ambient temperature (Bennett and Whitworth 1991), nests in areas that are more exposed to the sun may be encountered by adult females and infested at higher rates than nests in less exposed areas. Factors such as low ambient temperature and exposure to rain and wind may restrict adult *Protocalliphora* to particular microhabitats and thereby influence spatial patterns of infestation.

Comparisons of characteristics of Townsend's Warbler nest sites in Alaskan boreal forests with those described from old-growth mixed-conif-

erous forests in northeastern Oregon (Mannan et al. 1983) suggest that this species is selecting sites in relation to what is available within the local landscape, rather than according to absolute criteria. Although the white spruce and paper birch trees used for nesting in Alaska were larger than those generally available on the study areas (Matsuoka et al., unpubl. data), they were shorter than the various coniferous trees used for nesting in Oregon. Similarly, the nests themselves were situated lower in trees used for nesting in Alaska than in the larger trees in Oregon.

Within the old-growth forests in Oregon, Townsend's Warblers nested on sites that had high canopy volumes of grand fir and Douglas-fir compared with what was generally available (Mannan and Meslow 1984). This supports the idea that relative foliage volume of coniferous trees used for nesting may be an important factor in the selection of nesting areas throughout the species' range. The relatively high percentage of shrubby ground cover surrounding nesting sites in Oregon suggests either that parasitism of Townsend's Warbler nestlings by *Protocalliphora* is relatively unimportant in influencing the selection of nest sites there or that its incidence is unrelated to the density of shrubs in old-growth forests.

The availability of suitable nest sites has not traditionally been viewed as a limiting factor for open-nesting passerines (Lack 1971). More recently, however, this view of unlimited availability has been challenged based on the observed high degree of specificity in nest-site choice (MacKenzie et al. 1982, Martin and Roper 1988), the high rates of nest predation among many species of open-nesting passerines (Martin 1992), and the search tactics of nest predators in relation to habitat features, both at the nest site and in the area surrounding the nest site (Martin 1988, 1992; Martin and Roper 1988). When these factors are taken into consideration, high-quality sites for nests may not be as widely available as generally thought (Martin and Roper 1988, Martin 1992). Our findings suggest that both nest predators and perhaps larvae of parasitic blow flies are important factors influencing reproductive success of Townsend's Warblers near the northern limit of their breeding range. Productivity was increased by using habitats with key features—large nesting trees and a sparse shrub layer—that were associated with

reduced nest predation and parasitism, respectively. Changes to the structure of mature and old-growth forests in the Pacific Northwest and Alaska, particularly the loss of larger conifers and proliferation of shrubs, are likely to result in decreased reproductive success of Townsend's Warblers.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. American Ornithologists' Union, New York.
- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:456-473.
- BART, J., AND D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078-1090.
- BENNETT, G. F., AND T. L. WHITWORTH. 1991. Studies on the life history of some species of *Protocalliphora* (Diptera: Calliphoridae). *Can. J. Zool.* 69: 2048-2058.
- BENNETT, G. F., AND T. L. WHITWORTH. 1992. Host, nest, and ecological relationships of species of *Protocalliphora* (Diptera: Calliphoridae). *Can. J. Zool.* 70:41-61.
- BENT, A. C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.
- BRISKIE, J. V. 1995. Nesting biology of the Yellow Warbler at the northern limit of its range. *J. Field Ornithol.* 66:531-543.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31-35.
- CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology* 54:127-134.
- DECKER, F. R., AND J. H. BOWLES. 1923. Bird notes from Chelan County, Washington. *Murrelet* 4:16.
- EASTMAN, M. D., L. S. JOHNSON, AND L. H. KERMOTT. 1989. Ectoparasitism of nestling House Wrens, *Troglodytes aedon*, by larvae of the blow fly *Protocalliphora braueri* (Diptera: Calliphoridae). *Can. J. Zool.* 67:2358-2362.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- GIBBS, J. P., AND J. FAABORG. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. *Conserv. Biol.* 4:193-196.
- HEIL, S. J., R. L. HUTTO, C. R. PRESTON, AND D. M. FINCH. 1995. Effects of silvicultural treatments in the Rocky Mountains, p. 220-244. In T. E. Martin and D. M. Finch [eds.], *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*. Oxford Univ. Press, New York.
- HOLMES, R. T. 1981. Theoretical aspects of habitat use by birds, p. 33-37. In D. E. Capen [ed.], *The use of multivariate statistics in studies of wildlife habitat*. USDA For. Serv. Tech. Rep. RM-87.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETTIT. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321-333.
- HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York.
- HOWE, F. P. 1992. Effects of *Protocalliphora braueri* (Diptera: Calliphoridae) parasitism and inclement weather on nestling Sage Thrashers. *J. Wildl. Diseases* 28:141-143.
- HUSSEL, D. J. T. 1985. Clutch size, day length, and seasonality of resources: comments on Ashmole's hypothesis. *Auk* 102:632-634.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- JOHNSON, L. S., M. D. EASTMAN, AND L. H. KERMOTT. 1991. Effects of ectoparasitism by larvae of the blow fly *Protocalliphora parorum* (Diptera: Calliphoridae) on nestling House Wrens, *Troglodytes aedon*. *Can. J. Zool.* 69:1441-1446.
- KEAST, A. 1990. The annual cycle and activity on the breeding grounds in a Canadian broadleaved deciduous forest bird community, relationship to the prey resource base, p. 197-214. In A. Keast [ed.], *Biogeography and ecology of forest bird communities*. SPB Academic Publishing, The Hague, The Netherlands.
- KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in a timber pine-juniper woodland. *Condor* 95:83-93.
- KULESZA, G. 1989. An analysis of clutch-size in New World passerine birds. *Ibis* 132:407-422.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LACK, D. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, MA.
- LOYE, J. E., AND M. ZUK. 1991. Bird-parasite interactions: ecology, evolution, and behavior. Oxford Univ. Press, Oxford.
- MACKENZIE, D. I., S. G. SEALY, AND G. D. SUTHERLAND. 1982. Nest site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. *Can. J. Zool.* 60:2212-2223.
- MANNAN, R. W., B. S. HALE, AND M. L. MORRISON. 1983. Observations of nesting Townsend's Warblers in northeastern Oregon. *Murrelet* 64:23-25.
- MANNAN, R. W., AND E. C. MESLOW. 1984. Bird pop-

- ulations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. *J. Wildl. Manage.* 48:1219-1238.
- MARTIN, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proc. Natl. Acad. Sci.* 85:2196-2199.
- MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management?, p. 455-473. *In* J. M. Hagan III and D. W. Johnston [eds.], *Ecology and conservation of Neotropical migratory landbirds*. Smithsonian Inst. Press, Washington, DC.
- MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* 141:897-913.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest site selection of a western population of the Hermit Thrush. *Condor* 90:51-57.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- MORSE, D. H. 1989. *American warblers: an ecological and behavioral perspective*. Harvard Univ. Press, Cambridge, MA.
- MORTON, M. L., K. W. SOCKMAN, AND L. E. PETERSON. 1993. Nest predation in the Mountain White-crowned Sparrow. *Condor* 95:72-82.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.
- NORUSIS, M. J. 1994. *SPSS advanced statistics*. SPSS Inc., Chicago.
- OSTLE, B., AND L. C. MALONE. 1988. *Statistics in research: basic concepts and techniques for research workers*. 4th ed. Iowa State Univ. Press, Ames, IA.
- PORNELUZI, P., J. C. BEDNARZ, L. J. GOODRICH, N. ZAWADA, AND J. HOOVER. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conserv. Biol.* 7:618-622.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375-380.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1-48.
- RICKLEFS, R. E. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97:38-49.
- ROBINSON, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape, p. 408-418. *In* J. M. Hagan III and D. W. Johnston [eds.], *Ecology and conservation of Neotropical migratory landbirds*. Smithsonian Inst. Press, Washington, DC.
- RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357-372.
- SABROSKY, C. W., G. F. BENNETT, AND T. L. WHITWORTH. 1989. Bird blow flies (*Protocalliphora*) in North America (Diptera: Calliphoridae), with notes on the Palearctic species. Smithsonian Inst. Press, Washington, DC.
- SHERRY, T. W., AND R. T. HOLMES. 1992. Population fluctuations in a long-distance Neotropical migrant: demographic evidence for the importance of breeding season events in the American Redstart, p. 431-442. *In* J. M. Hagan III and D. W. Johnston [eds.], *Ecology and conservation of Neotropical migratory landbirds*. Smithsonian Inst. Press, Washington, DC.
- SILLOWAY, P. M. 1906. Among the Flathead birds. *Condor* 8:109-110.
- SIMONS, L. S., AND T. E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology* 71:869-876.
- SPINDLER, M. A., AND B. KESSEL. 1980. Avian populations and habitat use in interior Alaska taiga. *Syesis* 13:61-104.
- VAN HORN, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112:98-106.
- VIERECK, L. A., C. T. DYRNESS, A. R. BATTEN, AND K. J. WENZLICK. 1992. The Alaska vegetation classification. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-286. Portland, OR.
- WALSBERG, G. E. 1985. Physiological consequences of microhabitat, p. 389-413. *In* M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, Orlando, FL.
- WARREN, Y. 1994. *Protocalliphora braueri* (Diptera: Calliphoridae) induced pathogenesis in a brood of Marsh Wren (*Distothorus palustris*) young. *J. Wildl. Diseases* 30:107-109.
- WETMORE, S. P., R. A. KELLER, AND G. E. J. SMITH. 1985. Effects of logging on bird populations in British Columbia as determined by a modified point-count method. *Can. Field-Nat.* 99:224-233.
- WHITWORTH, T. L., AND G. F. BENNETT. 1992. Pathogenicity of larval *Protocalliphora* (Diptera: Calliphoridae) parasitizing nestling birds. *Can. J. Zool.* 70:2184-2191.
- WRAY, T., II, AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. *Auk* 96:802-805.