



FORAGING ECOLOGY OF YELLOW-RUMPED WARBLERS IN AN ALASKAN
BOREAL FOREST FOLLOWING A SPRUCE BEETLE OUTBREAK

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FORAGING ECOLOGY OF YELLOW-RUMPED WARBLERS IN AN ALASKAN
BOREAL FOREST FOLLOWING A SPRUCE BEETLE OUTBREAK

A
THESIS

Presented to the Faculty
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By

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ABSTRACT

I examined the foraging ecology of the Yellow-rumped Warbler (*Dendroica coronata*) several years after an outbreak of spruce beetles (*Dendroctonus rufipennis* [Kirby]) in the Copper River Basin, Alaska. With increased beetle-induced mortality of white spruce (*Picea glauca*), a preferred foraging substrate, we predicted warblers would respond through: (1) decreased overall use of white spruce, (2) increased selectivity of live white spruce that remained, and (3) reduced foraging efficiency, reflected by a greater proportion of time spent foraging and lower prey attack rates. We examined warbler foraging behavior and arthropod biomass on commonly used foraging substrates, and in stands with low-moderate (< 40%) and heavy (> 40%) spruce mortality. Live and dead white spruce, quaking aspen, and willow were the most commonly used foraging substrates, and selection of coniferous versus deciduous tree types varied by breeding stage. Yellow-rumped Warblers foraged extensively on dead spruce in stands with heavy spruce mortality, although they avoided it in stands with low-moderate spruce mortality. Dead spruce supported significantly lower arthropod biomass than any other tree type except black spruce, and warblers that foraged in dead spruce tended to have lower prey attack rates than when they foraged in live white spruce.

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FORAGING ECOLOGY OF YELLOW-RUMPED WARBLERS IN AN ALASKAN BOREAL FOREST FOLLOWING A SPRUCE BEETLE OUTBREAK¹

Introduction

In the boreal forests of the Copper River Basin, Alaska, spruce beetles (*Dendroctonus rufipennis* [Kirby]) ravaged over 200,000 hectares of mature white spruce (*Picea glauca*) forest during an outbreak between 1989 and 1998 (Wesser and Allen 1999; Wittwer 2002). Large-scale beetle attack causes numerous structural changes within a forest. Spruce beetles selectively attack and kill larger-diameter trees (Veblen et al. 1991; Holsten 1995 et al.; Wesser and Allen 1999; Matsuoka et al. 2001; Doak 2004), thus releasing smaller spruce from growth suppression (Veblen et al. 1991), or stimulating the growth of understory vegetation by providing gaps in the forest canopy (Stone and Wolfe 1996). In these forests, spruce beetle epidemics may eventually influence the composition of canopy species if black spruce (*Picea mariana*) or deciduous trees replace beetle-killed white spruce (Wesser and Allen 1999). In response to landscape-level changes in forest type and successional stage, we expected changes in the foraging opportunities and behaviors of birds, especially among those species that forage on white spruce.

Availability of food is an important factor limiting bird populations and breeding success (Lack 1954; Martin 1987; Wiens 1989; Burke and Nol 1998). Occupation of suitable foraging habitats and acquisition of food resources may influence individual

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fitness (Martin 1987; Simons and Martin 1990; Holmes et al. 1992; Rodenhouse and Holmes 1992; Wiehn and Korpimaki 1997). For insectivorous forest birds, habitat changes affecting preferred foraging substrates (Robinson and Holmes 1982, 1984; Peck 1989; Whelan 2001) and prey distribution and abundance (Robinson and Holmes 1982; Holmes and Schultz 1988) may influence food availability. Within an altered environment, individuals must adjust to novel or reduced foraging opportunities, or leave in search of better habitat if preferred foraging substrates become limited (Morrison 1981). To quantify the availability of food for birds we must examine both the foraging patterns of a bird species and the distribution and abundance of its potential prey (Hutto 1990; Wolda 1990). For breeding birds, estimates of food availability must also account for temporal variations in prey densities and prey species composition (Werner 1983; Holmes and Schultz 1988; Hutto 1990; Van Horne and Bader 1990), as well as the foraging behavior of birds (Sakai and Noon 1990; Petit et al. 1990a; Matsuoka et al. 1997; Dobbs and Martin 1998). Because the foraging patterns of breeding birds may differ for males and females (Morse 1968, 1980; Steele 1993), foraging behavior should also be examined by sex.

The Yellow-rumped Warbler (*Dendroica coronata*) is one of the most common Neotropical migrants in the boreal forest of Alaska. During the breeding season in Alaska, this species generally resides in mixed coniferous-deciduous forests (Kessel 1998). Breeding Yellow-rumped Warblers forage primarily on arthropods (Bent 1953; Morse 1989) that they either glean from tree foliage or capture in flight (Morse 1968; Sabo 1980; Franzreb 1983; Airola and Barrett 1985; Block 1990; Petit et al. 1990b).

Throughout their breeding range, Yellow-rumped Warblers use coniferous tree species for foraging more often than deciduous trees (MacArthur 1958; Kilgore 1971; Morse 1973; Franzreb 1978; Szaro and Balda 1979; Airola and Barrett 1985; Block 1990; Kirk et al. 1996; Simon et al. 2002). We assumed that Yellow-rumped Warblers in Alaska would also depend highly on white spruce for foraging and that increased beetle-induced mortality of white spruce would likely result in reduced food available to these birds. In this study we tested the predictions that the warblers would respond to spruce mortality through: (1) decreased overall use of white spruce, (2) increased selectivity of live white spruce that remained, and (3) reduced foraging efficiency, reflected by a greater proportion of time spent foraging and lower prey attack rates. An accompanying study examined responses in density (Matsuoka et al. 2001) and breeding success (Matsuoka and Handel, *Unpubl.*), both of which should decline as availability of white spruce declined but found no significant effects on Yellow-rumped Warblers. This study examines more subtle adverse effects of reduced availability of white spruce in beetle-killed stands by comparing the foraging behavior of warblers and food abundance among their foraging substrates and between stands with different levels of spruce mortality.

Methods

With the onset of the spruce beetle outbreak in the Copper River Basin, Wrangell-St. Elias National Park land managers became interested in its influence on the structure and composition of forests and wildlife communities. This study was undertaken to better understand the impacts of spruce beetle infestation on boreal forest songbirds in this region and was conducted in conjunction with a community-level comparison of

songbird breeding density, nesting productivity and vegetation structure in areas of varying spruce mortality (Matsuoka et al. 2001). We investigated the behavior of Yellow-rumped Warblers in forests in which spruce had been attacked and killed by spruce beetles approximately 3-5 years earlier but were usually still standing (KBR pers. obs.).

Study area

We conducted fieldwork in 1998 within the boreal forests of the Copper River Basin, Alaska. The study area extended from the town of Copper Center south to Tonsina Lake and east towards McCarthy (Fig. 1). The dominant tree species in the region were white spruce, quaking aspen (*Populus tremuloides*), birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), willow (*Salix spp.*) and alder (*Alnus spp.*) on drier sites and on south-facing slopes. Black spruce dominated the low-lying, water-saturated areas (Gallant et al. 1995).

Level of spruce mortality from spruce beetles was characterized as low (0-10%), moderate (11-40%) and heavy (> 40%) based on maps (Wittwer 1998) and visual estimation. These categories matched levels of spruce mortality used in studies of spruce beetle-disturbance on the Kenai Peninsula, Alaska (Reynolds and Holsten 1996). Using maps with the level of spruce mortality overlaid, we randomly selected study plots from regions that met the following criteria: (i) supported spruce stands of at least 50 ha; (ii) were within 5 km of a road or trail; and (iii) had land owners who permitted access (Matsuoka et al. 2001). Six 36 ha (600 m x 600 m) plots were situated on flat or gently rolling terrain that ranged in elevation from 420 to 900 m ASL.

Behavioral observations

We recorded observations of foraging Yellow-rumped Warblers during three stages of the breeding season: pre-breeding, incubation, and nestling. When the breeding stage of a focal bird could not be determined from its behavior or association with a nest, we assigned the observation to the modal breeding stage for known nesting pairs on that date: pre-breeding (17 May to 25 May), incubation (26 May to 10 June), and nestling (11 June to 5 July). Whenever possible we banded birds and used unique color-combinations to identify individuals.

Behavioral observations were conducted on male and female warblers on each plot every other day between 0400h-1400h Alaska Daylight Time (ADT). Observers walked through a plot systematically until they encountered a Yellow-rumped Warbler. At this time a continuous record of bird behavior and foraging substrate was dictated into a portable recorder. Every time a bird switched substrates, the time and new substrate were recorded. Individuals were observed for as long as possible (maximum = 25 min). Observations of females were conducted only when they were away from the nest. We transcribed recorded observations into The Observer (Noldus Information Technology 1991), a behavioral data-recording program that provided a time-stamp for each recorded behavior and substrate.

We examined the foraging efficiency of Yellow-rumped Warblers using each of 18 possible substrates (Appendix A) in stands with varying levels of spruce mortality. We used two measures of behavior that have been shown to vary predictably in response to prey availability (Robinson and Holmes 1982; Davies and Lundberg 1985; Hutto 1990;

Lovette and Holmes 1995). The first was *time spent foraging*, defined as the proportion of time a bird foraged out of the total amount of time it was observed. We considered a bird to be foraging if it was actively scanning the surface of substrates or the sky for prey. We expected the proportion of time a bird spent foraging to increase during periods of high energetic demands or low prey availability (Davies and Lundberg 1985). The second was *prey attack rate*, the number of times a bird lunged towards prey items divided by the amount of time it was observed foraging (Holmes et al. 1982; Lovette and Holmes 1995). In the field we further distinguished prey attacks as either “surface” (attacking prey on the foraging substrate) or “aerial” (attacking prey in the air, often using the substrate as a perch). The type of attack may indicate a difference in type of prey available (i.e. stationary vs. flying prey) (Lovette and Holmes 1995). Prey attack rates provide a relative measure of how often prey are encountered (Thiollay 1988; Hutto 1990; Lovette and Holmes 1995) and illustrate the intensity of foraging effort.

To minimize the chance of treating repeated observations of individual unbanded birds as independent observations, thereby introducing pseudoreplication (Hurlbert 1984), we conducted observations across a broad area (within plot boundaries) and identified unbanded individuals through territory mapping and nest monitoring. If a banded or otherwise known individual was observed more than once within a breeding stage, observations were combined for analyses. Observations with <10 s of foraging were excluded from analyses.

We retained eight substrates for analyses (Appendix A), excluding those substrates used < 3% of the time during all breeding stages, except for balsam poplar and

paper birch, which we included to compare with data collected on arthropod biomass from branch-clippings.

Vegetation sampling

Habitat characteristics of each study plot were sampled between 15 July and 15 August using systematic random sample of 20 m x 20 m subplots ($n = 18$) within each plot (as described in Matsuoka et al. 2001). Within subplots we counted the number of each tree species in each diameter class (2.5-7, 8-14, 15-22, 38-53, > 53 cm) measured at breast height (~1.7m). Spruce trees were categorized as live, dead, or dying. If a spruce was dying or dead it was further examined for the cause of morbidity (spruce beetle, fire, etc.) through external cues or by removing a segment of bark to examine damage to the cambium. Spruce beetle-caused mortality was identified by the presence of adult spruce beetles or egg and larval galleries beneath the bark (Holsten et al. 1985). Because a related study on our plots had shown that vegetation in stands with low and moderate spruce mortality were similar in post-infestation structure and composition (Matsuoka et al. 2001), we combined these stand types for analyses and compared them to stands with heavy mortality for analyses. We estimated the basal area of each tree type within a subplot by multiplying the number of trees of each species and size class by the average diameter of the size class. We then summed the basal area of each size class to estimate the total basal area for a given tree species (James and Shugart 1970). We estimated the original basal area of live spruce on each plot before infestation of spruce beetles by summing the basal area of live and beetle-killed spruce.

Arthropod sampling

Because Yellow-rumped Warblers obtain most of their prey by gleaning insects from the surface of tree leaves and branches rather than from shrubs or herbaceous vegetation, we sampled insects on branch-clippings from the tree types most commonly used by the warblers (Werner 1983; Cooper and Whitmore 1990). We sampled arthropods twice on each plot, once each during the incubation and nestling stages from two randomly selected individuals of seven tree types (live white spruce, dead white spruce, black spruce, quaking aspen, balsam poplar, paper birch, and willow). Alder was not sampled because we initially observed infrequent use compared to other tree types. We selected trees for sampling by dividing plots into 100 m x 100 m sections ($n = 36$) and then randomly selecting two sections. From each of the two 1-ha sections we haphazardly selected one tree of each species. If a tree species was not found within that section we sampled the next closest individual.

A 1-m-long branch was collected from three heights (within range of 0-7 m) from each sampled tree (following Werner 1983). To prevent arthropods from dislodging, one person quickly covered selected branches with a 1-m-long opaque cloth sack attached to an adjustable pole. A second person clipped the branch into the sack using a pole-pruner. After each branch was clipped, it was carefully transferred into a plastic garbage bag and sprayed with insecticide. At the end of the day we extracted arthropods from each sample and placed them in 70% ethanol for preservation. Immediately following arthropod extraction, all branches were weighed to the nearest gram using a Pesola spring scale.

In the laboratory, we counted arthropods and identified them to order and family when possible. Following identification, we placed arthropods in tared drying tins, separated by branch-clip sample and taxon, and placed them in a drying oven at 60 ° C for 24 hours. We measured the dry biomass of arthropods to the nearest mg using an electrobalance.

Statistical analyses

To examine whether foraging Yellow-rumped Warblers altered their relative use of coniferous trees for foraging in stands with heavy spruce mortality, we classified each foraging bout as either coniferous or deciduous, depending on tree type predominately used, since warblers used only a single tree type during most (60%) of the bouts. We used logistic regression (PROC LOGISTIC, SAS Institute, Inc. 1999) to test if use of coniferous trees depended on the level of spruce mortality (low-moderate vs. heavy), sex, or breeding stage (pre-breeding, incubation, nestling). We compared full and reduced models with main effects and interactions using an information-theoretic approach, choosing the most parsimonious model based on Akaike's Information Criterion modified for small samples (AICc; Burnham and Anderson 1998). Models within 2 AICc units of the best model were considered to have substantial support (Burnham and Anderson 1998).

We also examined the warblers' use of foraging substrates in relation to availability to determine whether the birds exercised selection for foraging substrates and if the level of spruce mortality influenced their selectivity. We defined selection as the use of a foraging substrate beyond its availability, and avoidance as use less than its

availability. To examine selection of tree types for foraging, we calculated selection ratios for each bird by dividing the proportion of time it spent in each tree type by the relative proportion of each tree type available to that bird (following Manly et al. 2002). Individual birds were treated as replicate sampling units and the foraging substrates available to each individual were those on the plot it inhabited, as measured by the mean basal area across the 18 vegetation subplots on each plot. The standard error of the average selection ratio for each foraging substrate was calculated for each level of spruce mortality and breeding stage as the square root of the variance of the individual selection ratios (Manly et al. 2002). We constructed simultaneous Bonferroni confidence intervals for each mortality level and breeding stage using Z -values corrected for the number of tree types being compared (Manly et al. 2002). If the 95% confidence level included 1, we concluded that warblers used that tree type in proportion to its availability. Avoidance was indicated by an upper 95% confidence limit <1 , and selection by the lower 95% confidence limit >1 .

To examine patterns of arthropod abundance, each tree sample (3 branches per tree) served as a unit of replication. For each sample, we counted the number of individual arthropods and calculated biomass (mg arthropod (dry-weight) kg^{-1} vegetation (wet-weight)) for each taxon. Because Yellow-rumped Warblers consume a wide variety of prey types and sizes (Hunt and Flaspohler 1998), we considered all arthropods (including arthropod eggs and pupae) to be potential food. We used total arthropod biomass as a direct measure of food abundance. Prior to analysis we log-transformed biomass to correct for non-normality of data. To avoid taking a log of 0 for those few

samples in which no insects were found, we added a small constant (0.001) to all values before data transformation. We used ANOVA (PROC GLM) on the transformed data to test for differences in total arthropod biomass by tree type, level of spruce mortality, and breeding stage (incubation and nestling) and all interaction factors. Student-Newman-Keuls (SNK) test was used for post-hoc comparisons of mean biomass by substrate (Zar 1996).

We analyzed prey attack rates to determine if they varied among different tree types or by level of stand mortality, breeding stage, or sex. For each foraging bout in a given tree type, we calculated the number of prey attacks per minute. Observations with < 30 s total foraging or <1 prey attack were excluded from analysis. We log-transformed the rates to meet assumptions of normality. We used ANOVA (PROC GLM) to test for differences in prey attack rates on the eight most heavily used tree types (live white spruce, dead white spruce, black spruce, aspen, willow, balsam poplar, and alder), testing for effects of breeding stage, sex, and the interaction of stage and sex. Data were insufficient to test for differences among all individual substrates by level of stand mortality. The SNK test was used for post-hoc comparisons of mean prey attack rates among tree types.

At the stand level, we tested whether the proportion of time spent foraging or prey attack rate varied by level of mortality (low-moderate vs. heavy), breeding stage (pre-breeding, incubation, nestling), or sex, including all two-way interactions of these factors. Prior to analyses, we arcsine-transformed proportions and log-transformed prey attack

rates were to meet assumptions of normality. For both tests, we used ANOVA (PROC GLM) on the transformed data, and SNK test for post-hoc comparisons.

We performed all statistical procedures using SAS statistical software (SAS Institute, Inc. 1999).

Results

Composition of trees in relation to spruce mortality

Variability in basal area of live spruce (white and black) was much higher among our six study plots before the spruce beetle outbreak than after the outbreak within both levels of spruce mortality (Fig. 2). Black spruce was generally uncommon in our study area, and it suffered relatively low mortality from spruce beetles. In contrast, basal area of live white spruce after the infestation was reduced to $11.50 \pm 1.25 \text{ m}^2 \text{ ha}^{-1}$ (mean \pm SE) in stands with low-moderate spruce mortality, and to $4.25 \pm 0.50 \text{ m}^2 \text{ ha}^{-1}$ in stands with heavy spruce mortality (Fig. 2).

The relative composition of tree species varied between stands suffering low-moderate and heavy spruce mortality (Fig. 3). Basal areas of black spruce and balsam poplar were higher in stands with low-moderate spruce mortality than in stands with heavy spruce mortality, while basal areas of quaking aspen and willow were greater in stands with heavy spruce mortality than in stands with low-moderate mortality (Fig. 3). The total average basal area of all tree types, which could reflect the amount of substrate available to birds for foraging, was similar in stands with low-moderate spruce mortality ($37.0 \pm 3.5 \text{ m}^2 \text{ ha}^{-1}$) and in stands with heavy spruce mortality ($35.5 \pm 5.0 \text{ m}^2 \text{ ha}^{-1}$).

Use of substrates for foraging

During the pre-breeding and incubation stages, Yellow-rumped Warblers spent most of their time foraging in deciduous trees, but during the nestling period they spent more time foraging in coniferous trees (Table 1). Warblers foraged infrequently in small shrubs or on the ground (3-9%) throughout the breeding season (Table 1). Quaking aspen was the deciduous species most frequently used during all breeding stages, regardless of the level of spruce mortality, but willows were also used often, particularly in stands with low-moderate spruce mortality. Warblers regularly used both live and dead white spruce, with use varying by breeding stage and level of spruce mortality (see below); they rarely foraged in black spruce.

The proportion of foraging bouts predominantly in coniferous trees differed between stands with low-moderate and heavy spruce mortality; these differences varied with breeding stage but not sex. The most parsimonious model included spruce mortality and breeding stage, and the interaction between these factors ($P < 0.0001$, $\chi^2 = 26.67$, $df = 5$, $AICc = 306.40$, $-2 \text{ Log-likelihood} = 294.03$). All other candidate models had considerably less support, with $\Delta AICc > 5$. On plots with low-moderate spruce mortality, the percent of foraging bouts predominately in coniferous trees increased from 14% during the prebreeding stage to 33% during incubation and 71% in the nestling stage. In contrast, use of coniferous trees on plots with heavy spruce mortality was much less variable, predominating in 44%, 38%, and 51% of the foraging bouts during the three breeding stages, respectively. These patterns were mirrored closely by the average percent total foraging time spent in coniferous trees (Table 1).

Selection of foraging substrates

Yellow-rumped Warblers selectively used or avoided particular tree types for foraging, relative to their availability, as evidenced by selection ratios significantly greater or less than one, respectively (Table 2). Resource selection varied significantly both by breeding stage and level of spruce mortality (Fig. 4, Table 2). In areas with low-moderate spruce mortality, Yellow-rumped Warblers avoided live white spruce during the pre-breeding period, foraged in it in proportion to its availability during incubation, but selected it heavily during the nestling period. In these stands the warblers either avoided or used dead white spruce in proportion to its availability. In stands with heavy spruce mortality, warblers foraged in both live and dead spruce in proportion to their availability. In both types of stands, warblers tended to avoid black spruce, balsam poplar, and paper birch as foraging substrates; alder was either avoided or used in proportion to its availability. In contrast, Yellow-rumped Warblers selected quaking aspen more consistently than any other tree type; birds selected aspen three times more often than expected in stands with low-moderate mortality during the pre-breeding period and two-three times more than expected in heavy-mortality stands during the incubation and nestling periods (Table 2). Willow was also selected in the stands with low-moderate mortality, being used three times more than expected during both the pre-breeding and incubation periods (Table 2).

Abundance of arthropods on trees

We examined arthropods on 145 branch clip samples from seven tree species commonly used by Yellow-rumped Warblers for foraging. We counted 6144 individuals

from two non-insect orders, Acari (mites) and Aranae (spiders), and 13 insect orders (Appendix B). Aphids (Aphididae) comprised the greatest number of individuals, followed by spiders and leaf miners (Lepidoptera: Gracillariidae). Leaf rollers (Lepidoptera: Tortricidae) made up 53% of the total arthropod biomass. Other Lepidopterans (larvae and adults) and spiders also contributed greatly to overall estimates of biomass. For the tree species sampled, spiders alone accounted for the greatest biomass in white spruce (49%), dead spruce (59%), and black spruce (69%) (Fig. 5). Lepidoptera larvae contributed the greatest arthropod biomass of any single arthropod group in quaking aspen (91%), balsam poplar (44%), paper birch (50%), and willow (41%) (Fig. 5).

Food abundance, as measured by geometric mean arthropod biomass, varied significantly among tree types ($F_{1,119} = 6.73$, $P < 0.0001$; Fig. 6a). Biomass among tree types was not influenced by breeding stage ($F_{6,119} = 0.63$, $P = 0.71$) or by the level of spruce mortality ($F_{5,119} = 0.76$, $P = 0.58$). Arthropod biomass was highest on deciduous trees, with biomass on paper birch significantly higher than that on any coniferous tree type (SNK test, $P < 0.05$; Fig. 6a). Conversely, biomass on dead white spruce was significantly lower than that on any other tree type except black spruce (SNK test, $P < 0.05$, Fig. 6a).

Warbler foraging behavior

Yellow-rumped Warblers obtained 88% of their prey from the surface of foraging substrates (i.e., tree leaves, branches and bole) and 12% using aerial maneuvers ($n = 1350$ total prey attacks). Warblers used aerial maneuvers more often on deciduous trees than

on coniferous tree types (12% and 8% respectively), and the percent of surface (93%) versus aerial prey attacks (7%) by warblers was the same on both live and dead white spruce.

The rates at which Yellow-rumped Warblers attacked prey while actively foraging did not vary significantly among substrates ($F_{6,223} = 1.68$, $P = 0.13$, Fig. 6b), although there was a significant interaction between sex and breeding stage ($F_{2,223} = 10.97$, $P < 0.0001$), with higher attack rates by males during the pre-breeding stage ($F_{12,223} = 4.31$, $P < 0.0001$, Fig. 7). We found little apparent relationship between arthropod biomass and prey attack rates across substrates (Fig. 6a and b).

At the stand level (low-moderate vs. heavy spruce mortality), we found no differences in the foraging efficiencies of Yellow-rumped Warblers, as measured by the proportion of time warblers spent foraging and their prey attack rates. Although the proportion of time the warblers spent foraging did not differ with respect to the level of spruce mortality ($F_{1,194} = 1.87$, $P = 0.17$), it did differ significantly among breeding stages ($F_{2,194} = 5.16$, $P = 0.007$) and between sexes ($F_{1,194} = 69.14$, $P < 0.001$), with a significant interaction between breeding stage and sex ($F_{2,194} = 3.20$, $P = 0.04$) (Fig. 8). Throughout the breeding season females spent a greater proportion of time foraging than males (0.59 ± 0.02 , $n = 84$, 0.34 ± 0.02 , $n = 122$, respectively; Fig. 8). Males spent more time foraging during the incubation and nestling stages than during pre-breeding, and females spent significantly more time foraging during incubation than during the nestling stage (SNK test, $P < 0.05$, Fig. 8). Prey attack rates measured at the stand level did not differ

significantly between levels of spruce mortality ($F_{1,192} = 0.39$, $P = 0.53$), but there was a significant interaction between sex and breeding stage, as previously described.

Discussion

We were surprised that Yellow-rumped Warblers foraged extensively on dead spruce in stands that had suffered heavy spruce mortality, although they avoided it in areas with low-moderate spruce mortality. Dead spruce supported significantly lower arthropod biomass than any other substrate except black spruce, which the warblers consistently avoided in all stands. Contrary to our predictions, warblers did not spend significantly more time foraging in stands with heavy spruce mortality, but there may be a cost in foraging efficiency through lower prey attack rates when foraging on dead spruce compared to live white spruce. Though we found no statistical difference in prey attack rates between live and dead white spruce when we examined pairwise-comparisons on a full ANOVA model (included all substrates, sex, and breeding stage); figure 6b illustrates higher attack rates on live white spruce than on dead white spruce that may be significant biologically. High densities of dead white spruce in the heavy mortality stands may have swamped search efforts for better foraging substrates, or perhaps arthropods associated with mature white spruce were preferred foods for the warblers and these arthropods were still available on beetle-killed trees. By using dead spruce as a foraging substrate, the warblers may have balanced a trade-off between search time and success rate in acquiring prey (Stephens 1990).

In this study we found that white spruce (live and dead) was an important foraging substrate for Yellow-rumped Warblers, which further corroborates the

preference of these warblers for foraging on coniferous trees across their breeding range (MacArthur 1958; Kilgore 1971; Morse 1973; Franzreb 1978; Szaro and Balda 1979; Airola and Barrett 1985; Kirk et al. 1996; Simon et al. 2002). However, in the Copper River Basin, Yellow-rumped Warblers exhibited a seasonal pattern of foraging in deciduous trees (especially quaking aspen and willow) during pre-breeding and incubation stages, and strong selection of coniferous trees during the nestling period. In our study area, deciduous trees also supported greater arthropod biomass than coniferous trees throughout the breeding season. Although some researchers have observed Yellow-rumped Warblers foraging on deciduous tree species proportionally more than on coniferous trees, especially when conifers were less available (Franzreb 1978; Block 1990; Folkard 1990), the seasonal pattern of substrate use we observed has not been previously described for this species. However, temporal shifts in substrate use within the breeding season have been observed in Prothonotary Warblers (*Protonotaria citrea*) (Petit et al. 1990a) as well as Black-throated Gray Warblers (*Dendroica nigrescens*) (Keane and Morrison 1999) and were directly related to changes in food abundance.

Arthropods and foraging behavior

In the boreal forests of Interior Alaska, several hundred kilometers north of our study area, measures of arthropod biomass in the same tree species we sampled nearly mirrored our findings, with the greatest biomass in birch, followed by aspen, balsam poplar, white spruce, and black spruce (Werner 1983; see Fig. 6a). This similarity in arthropod biomass across tree types further indicates that the abundances we recorded were probably typical levels, and warbler foraging in deciduous trees was not likely an

anomaly due to a Lepidoptera outbreak. Deciduous trees harbored higher arthropod biomass and prey types with larger than average body mass (e.g., Lepidoptera larvae, KBR pers. obs.) than conifers, and may explain why aspen and willow were frequently selected as foraging substrates. Aspen also provided the greatest proportion of Lepidoptera larvae of any tree type (Fig. 5). However, in our study area, selection of foraging substrates was not simply correlated with abundance of arthropods. The warblers consistently avoided paper birch and balsam poplar despite relatively high arthropod biomass in each species, including a large proportion of Lepidoptera larvae, and no obvious differences in the Lepidoptera community among deciduous tree species. Yellow-rumped Warblers in our study area may have avoided paper birch and balsam poplar because of competition with other insectivorous species that use similar foraging substrates, such as the Ruby-crowned Kinglet (*Regulus calendula*), but this scenario seems unlikely because Kinglet breeding densities were 4-10 times lower than the warblers in our study area (Matsuoka et al. 2001). We suspect that the warblers avoided these tree species for foraging because stored compounds in paper birch (Sunnerheim et al. 1988) and balsam poplar (Henriksson et al. 2003) rendered prey unpalatable to birds. Because of the differences we found among tree types in prey abundance and use for foraging, we caution researchers to examine inter-specific differences among trees before lumping them into general categories such as deciduous and coniferous species.

In this study, seasonal variation in the Yellow-rumped Warblers' use of tree species further supports that prey abundance alone does not dictate the selection of tree species by birds (Busby and Sealy 1979; Holmes and Shultz 1988). Because deciduous

trees supported higher arthropod biomass than coniferous trees throughout the breeding season, we suspect prey type, rather than abundance *per se*, was driving selection for white spruce (for foraging) during the nestling stage. In our branch-clippings, spiders comprised the greatest biomass of any one arthropod group in all spruce types (Fig. 5). Though Lepidopteran larvae have been shown to be an important component of the diet of nestlings and adult songbirds (Bent 1953; MacArthur 1959; Holmes and Shultz 1988), several studies have recorded a large proportion of spiders in the diets of nestlings (Royama 1970, van Balen 1973, Cowie and Hinsley 1988). These studies found that adult preference for provisioning nestlings with spiders was not related to variation in spider abundance; rather, spiders were thought to be selected for the unique nutritional value they offered nestlings during the early stages of development. Ramsay and Houston (2003) suspected that taurine, an amino acid found at high levels in spiders, was critical in post-natal development of young birds. If this prey type is necessary for the growth of nestlings, then lower prey abundance in dead spruce and the eventual loss of those trees might have a significant negative effect on nestling growth or productivity.

We also observed seasonal variations in the foraging behavior of males and females that were expected due to sex-specific differences in duties associated with the reproductive effort (Morse 1980; Walsberg 1983). Throughout the breeding season, the proportion of time females foraged was greater than that for males (Fig 8). However, we question whether our data are appropriate for making this comparison. Differences between males and females in daily activities and general conspicuousness may influence the proportion of time we observed foraging. Males were easier to observe throughout

the day than females because they engaged in noticeable behaviors such as singing and territorial aggression. For females, the proportion of time spent foraging excluded time spent on the nest incubating eggs or brooding young and thus could not be compared directly to that of males. During pre-breeding, males spent a lesser proportion of time foraging than during incubation or nestling stages (Fig. 8), but their prey attack rates were highest, suggesting that they foraged more intensively during this period of significant energetic demand (i.e., post-migration, courtship, territoriality) (Ricklefs 1974; Walsberg 1983). Contrary to our expectations, females spent proportionally more time foraging during incubation than during the nestling stage, a time adults must feed themselves as well as their young (Morse 1980; Walsberg 1983).

Impacts of habitat change and plasticity of foraging behavior

Yellow-rumped Warblers are often characterized as foraging generalists because they can use a variety of resources and exhibit plastic foraging behavior (MacArthur 1958; Greenberg 1983; Ehrlich et al. 1988; Block 1990; Simon et al. 2003), which implies flexibility in the face of change (Greenberg 1990). The boreal forest of the Copper River Basin is a region currently undergoing marked change due to spruce beetle infestations. The warblers in that area have demonstrated foraging plasticity by switching from live to dead white spruce in response to increasing beetle-induced spruce mortalities with no negative effects on their breeding densities. The Ruby-crowned Kinglet, on the other hand, a species considered more stereotyped (less flexible) in its foraging behavior than Yellow-rumped Warblers (Franzreb 1978) suffered decreasing breeding densities as spruce mortality increased in our study area (Matsuoka et al. 2001).

In Arizona, Yellow-rumped Warblers switched to aspen for foraging after ponderosa pine, a preferred foraging substrate, had been selectively removed from the forest (Franzreb 1978).

With the eventual loss of dead white spruce from the forests in the Copper River Basin, alders are expected to benefit from the opening canopies (Wesser and Allen 1999; Matsuoka et al. 2001), leading to a significant shift in habitat across the landscape. Because Yellow-rumped Warblers generally avoided alder as a foraging substrate in our study area, they will likely suffer higher costs in foraging efficiency, either by traveling farther in search of suitable foraging substrates, or else by a reduction in prey attack rates. If mature white spruce forest is converted to early successional stages of coniferous forest, or pure hardwood stands as predicted (Wesser and Allen 1999), this warbler species will likely become much less common in this region (Quinlan 1978; Holmes et al. 1986; Parker et al. 1994).

Plasticity probably has its limits for Yellow-rumped Warblers. In the Copper River Basin, these warblers appeared to select territories encompassing a habitat mosaic, where nesting sites were often in live and dead white spruce trees (S. Matsuoka and C. Handel unpubl.) in close proximity to stands of quaking aspen (KBR pers. obs.). Though Yellow-rumped Warblers have plastic foraging behaviors, they were found to be rather inflexible in their nesting and habitat requirements in Ontario, Canada (Simon et al. 2003). Throughout their breeding range, these warblers nest almost exclusively in conifers (Hunt and Flaspohler 1998). The habitat mosaics available in our study area might provide the necessary combination of nesting and foraging habitats for these

warblers. However, if spruce mortality exceeds a particular ceiling, or dead trees are no longer available, nesting sites and prey types necessary for Yellow-rumped Warblers may become limited, and subsequent breeding densities and reproductive success of this species may be reduced.

Future considerations

Besides this study there is little information on the effects of spruce-beetle-caused habitat disturbance on birds (but see Lance and Howell 2000; Matsuoka et al. 2001). Future studies in the Copper River Basin could examine the foraging behavior of birds and prey abundance over time in infested stands and specifically on dead spruce trees, to determine if there is a ceiling beyond which warblers cannot compensate behaviorally. Examination of stomach contents or fecal samples would bridge the gap between measures of prey abundance and actual prey taken by the warblers. We recommend that land managers weigh the importance of dead spruce trees as foraging and nesting sites for birds when making decisions about salvage-logging or cutting dead spruce for fire prevention.

It is important that we better understand the dynamic effects of spruce beetle outbreaks on forests and wildlife. With evidence of significant climatic changes in Alaska, including warmer air and soil temperatures (Hinzman et al. 2004, *In press*), and increased drought-stress in white spruce trees (Barber et al. 2000), we will likely observe increasing frequency and intensity of spruce beetle outbreaks in the future (Malmstrom and Raffa 2000; Volney and Fleming 2000; Werner et al. 2004, *In press*).

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Table 1. Percent time (mean \pm SE) Yellow-rumped Warblers foraged in common tree types within stands suffering low-moderate and heavy spruce mortality during each breeding stage in the Copper River Basin, Alaska.

Breeding period	Level of spruce mortality	N ^a	Mean % time spent foraging									Total Coniferous	Total Deciduous
			White spruce live	White spruce dead	Black spruce live	Quaking aspen	Balsam poplar	Paper birch	Willow	Alder	Other ^b		
Pre-breeding													
	Low-moderate	36	12 \pm 5	2 \pm 1	0 \pm 0	41 \pm 8	4 \pm 3	0 \pm 0	31 \pm 7	2 \pm 2	9 \pm 4	14 \pm 5	77 \pm 6
	Heavy	39	22 \pm 6	21 \pm 5	1 \pm 1	27 \pm 6	0 \pm 0	2 \pm 2	12 \pm 4	9 \pm 4	6 \pm 2	44 \pm 7	50 \pm 7
Incubation													
	Low-moderate	48	22 \pm 5	7 \pm 4	1 \pm 1	32 \pm 7	1 \pm 1	0 \pm 0	31 \pm 6	2 \pm 2	4 \pm 2	30 \pm 6	65 \pm 6
	Heavy	37	15 \pm 5	23 \pm 6	0 \pm 0	35 \pm 6	4 \pm 1	0 \pm 0	17 \pm 7	3 \pm 1	3 \pm 1	37 \pm 7	56 \pm 7
Nestling													
	Low-moderate	28	60 \pm 4	4 \pm 4	6 \pm 4	13 \pm 6	1 \pm 1	0 \pm 0	12 \pm 5	0 \pm 0	5 \pm 2	70 \pm 8	25 \pm 7
	Heavy	49	16 \pm 4	31 \pm 5	0 \pm 0	34 \pm 6	0 \pm 0	0 \pm 0	8 \pm 3	2 \pm 1	9 \pm 3	47 \pm 6	44 \pm 6

^aNumber of birds observed.

^bIncludes those substrates used infrequently, such as small shrubs and ground litter.

Table 2. Selection ratios and Bonferroni confidence intervals examining selectivity of tree types for foraging by Yellow-rumped Warblers in stands with different levels of spruce mortality and among breeding stages in the Copper River Basin, Alaska.

Low-moderate spruce mortality								
Breeding stage	Tree type ^a	N ^b	w ^c	SE(w)	Z-value ^d	Bonferroni		Avoid (-) ^e
						LCI	UCI	Select (+)
Pre-breeding								
	WSL	36	0.45	0.15	2.64	0.06	0.84	-
	WSD	36	0.20	0.17	2.64	0.00	0.64	-
	BSL	36	0.00	0.00				-
	QA	36	3.06	0.70	2.64	1.22	4.89	+
	BP	36	0.31	0.19	2.64	0.00	0.81	-
	BI	36	0.00	0.00				-
	WI	36	2.91	0.66	2.64	1.16	4.66	+
	AL	36	0.13	0.13	2.64	0.00	0.46	-
Incubation								
	WSL	48	0.64	0.18	2.69	0.16	1.11	
	WSD	48	1.19	0.63	2.69	0.00	2.88	
	BSL	48	0.44	0.38	2.69	0.00	1.46	
	QA	48	2.11	0.46	2.69	0.87	3.35	
	BP	48	0.10	0.07	2.69	0.00	0.30	-
	BI	48	0.00	0.00				-
	WI	48	2.98	0.61	2.69	1.35	4.62	+
	AL	48	0.12	0.12	2.69	0.00	0.45	-
Nestling								
	WSL	28	2.35	0.42	2.74	1.22	3.49	+
	WSD	28	0.24	0.22	2.74	0.00	0.83	-
	BSL	28	0.22	0.13	2.74	0.00	0.58	-
	QA	28	0.77	0.36	2.74	0.00	1.75	
	BP	28	0.06	0.04	2.74	0.00	0.17	-
	BI	28	0.02	0.02	2.74	0.00	0.07	-
	WI	28	1.34	0.57	2.74	0.00	2.90	
	AL	28	0.00	0.00	2.74	0.00	0.01	-

(cont'd)

Heavy spruce mortality

Breeding stage	Tree type ^a	N ^b	w ^c	SE(w)	Z-value ^d	Bonferroni		Avoid (-) ^e Select (+)
						LCI	UCI	
Pre-breeding								
	WSL	39	1.13	0.30	2.69	0.33	1.93	
	WSD	39	0.79	0.19	2.69	0.28	1.31	
	BSL	39	29.45	26.68	2.69	0.00	101.24	
	QA	39	1.86	0.48	2.69	0.58	3.14	
	BP	39	0.00	0.00				-
	BI	39	0.14	0.14	2.69	0.00	0.52	-
	WI	39	0.75	0.30	2.69	0.00	1.56	
	AL	39	1.78	0.80	2.69	0.00	3.94	
Incubation								
	WSL	37	0.77	0.27	2.64	0.07	1.47	
	WSD	37	1.01	0.29	2.64	0.26	1.76	
	BSL	37	0.00	0.00				-
	QA	37	2.83	0.68	2.64	1.03	4.64	+
	BP	37	0.55	0.43	2.64	0.00	1.69	
	BI	37	0.00	0.00				-
	WI	37	0.98	0.34	2.64	0.09	1.87	
	AL	37	0.51	0.26	2.64	0.00	1.19	
Nestling								
	WSL	49	0.90	0.24	2.64	0.27	1.54	
	WSD	49	1.43	0.26	2.64	0.75	2.11	
	BSL	49	0.00	0.00				-
	QA	49	2.34	0.44	2.64	1.19	3.50	+
	BP	49	0.03	0.03	2.64	0.00	0.10	-
	BI	49	0.00	0.00				-
	WI	49	0.58	0.20	2.64	0.07	1.10	
	AL	49	0.59	0.39	2.64	0.00	1.62	

^aWSL = white spruce live, WSD = white spruce dead, BSL = black spruce live, QA = quaking aspen, BP = balsam poplar, BI = paper birch, WI = willow, AL = alder.

^bNumber birds observed.

^cw = selection ratio = proportion use / proportion available

^dValues vary depending on number of substrates (1-8) used by birds within each level of spruce mortality and breeding stage.

^eIf CI : includes 1 than use is proportional to availability;
if UCI < 1 than substrate is avoided (-);
if LCI > 1 than substrate is selected (+)

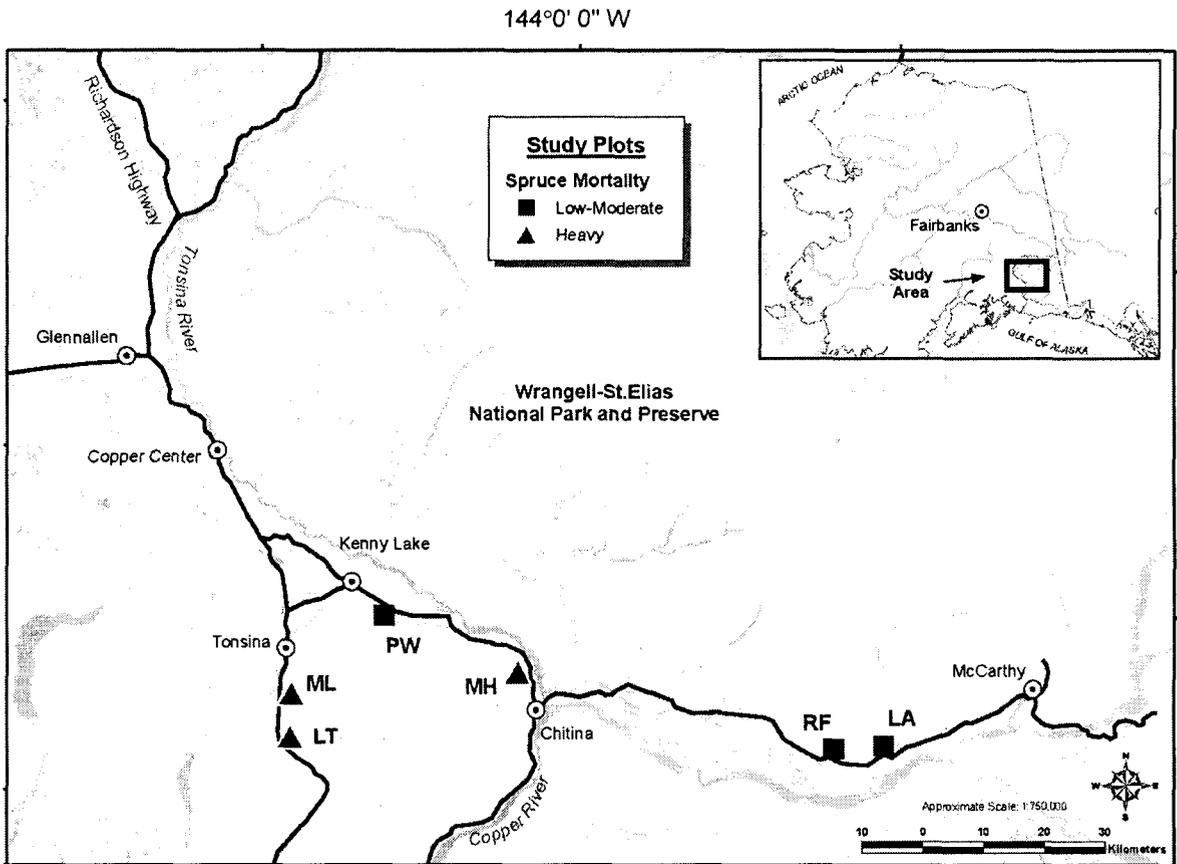


Fig 1. Location of study plots and the level of spruce mortality caused by spruce beetles (*Dendroctonus rufipennis*) in the Copper River Basin, Alaska (map courtesy of D. Dissing). Two-letter codes indicate study plots.

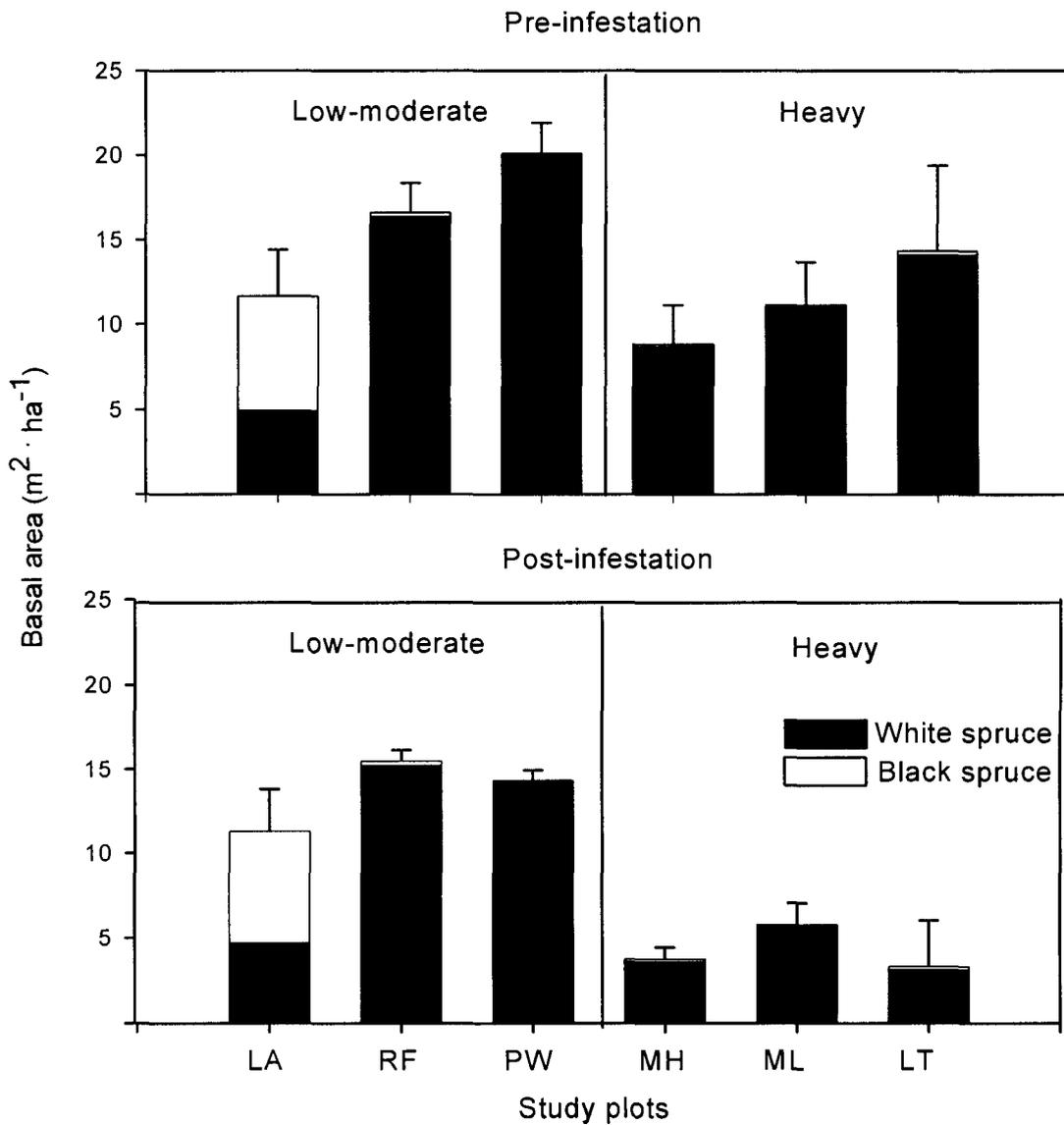


Fig 2. Basal area (mean \pm SE) of live spruce (black and white) before and after an infestation of spruce beetles, on six 36-ha plots within stands of low-moderate (0-40%) and heavy (> 40%) spruce mortality in the Copper River Basin, Alaska. See Fig. 1 for locations of plots.

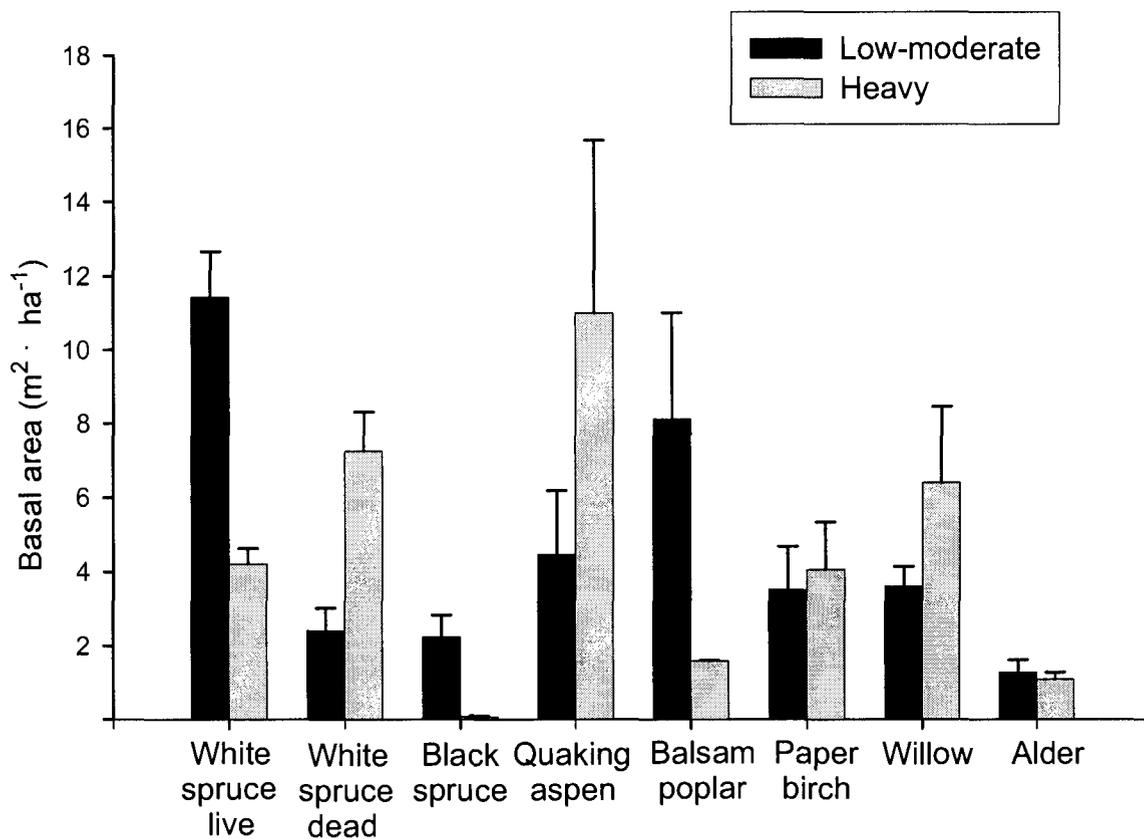


Fig. 3. Mean basal area of tree species (\pm SE) in stands that suffered low-moderate (0 - 40%) or heavy (> 40%) mortality of spruce following an infestation of spruce beetles in the Copper River Basin, Alaska.

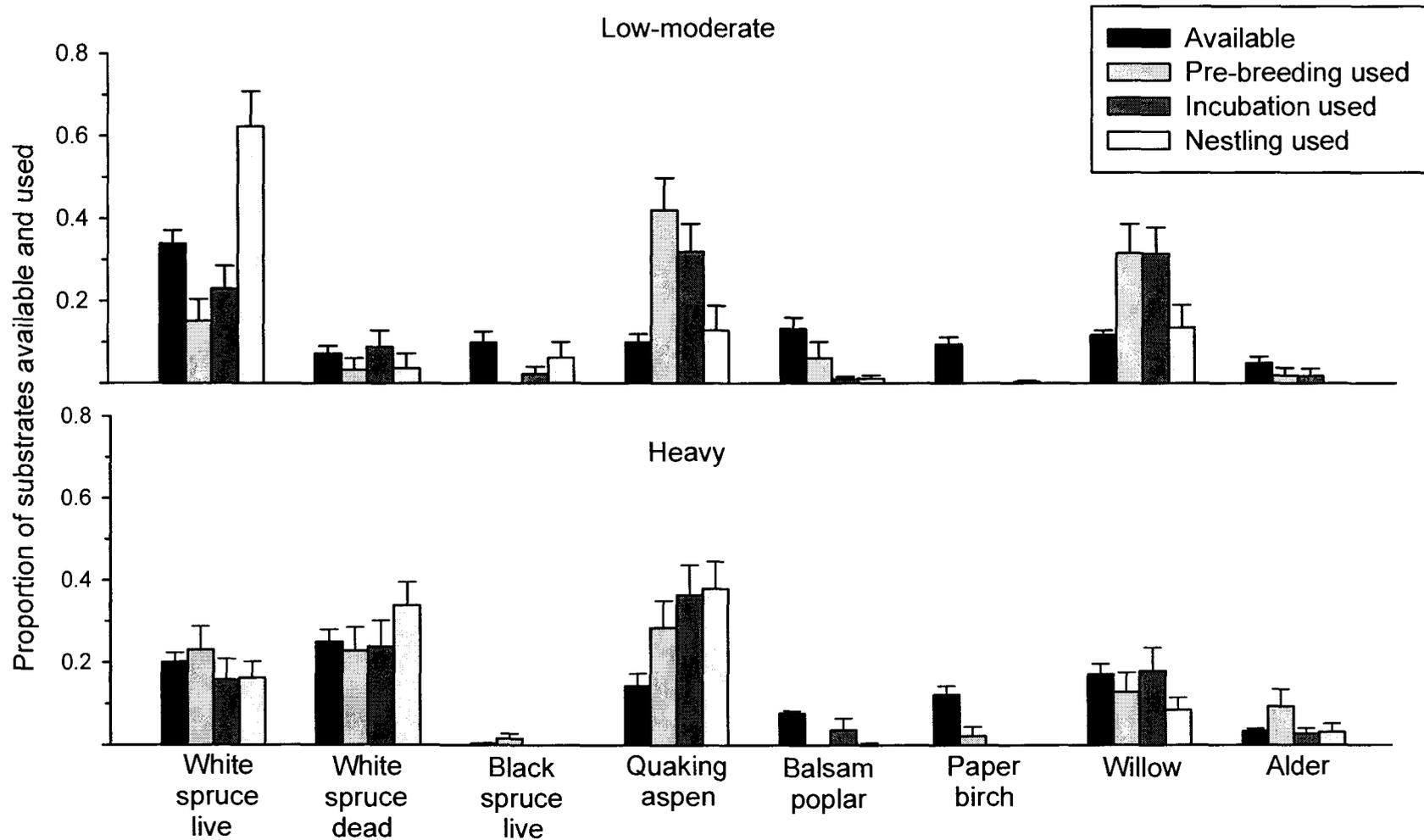


Fig 4. Proportional use of eight common tree types used as foraging substrates by Yellow-rumped Warblers during three breeding stages in comparison to the relative basal area of each tree type available in stands with low-moderate or heavy spruce mortality. Data presented as mean \pm SE. Proportions exclude other substrates used infrequently.

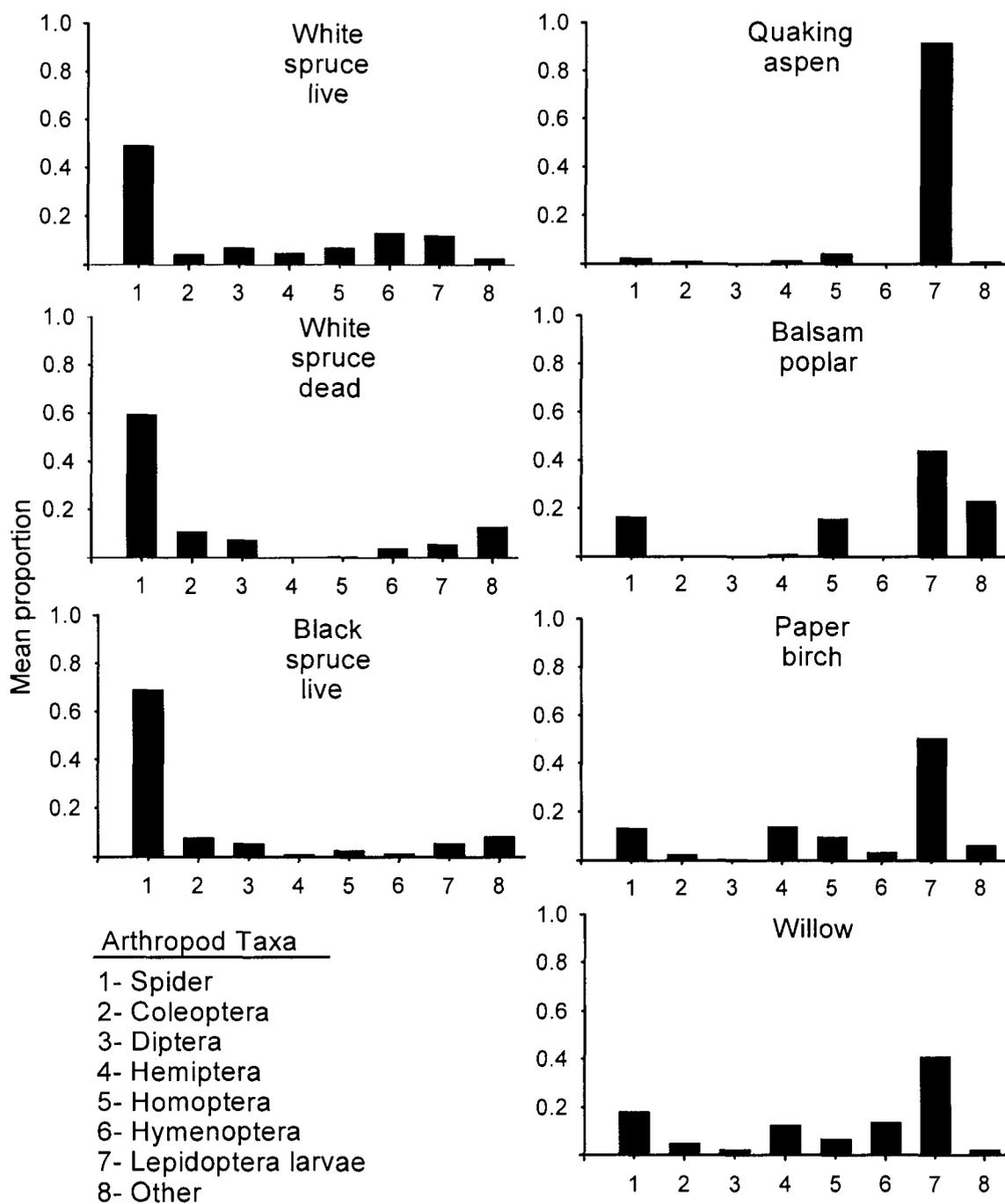


Fig 5. Proportion of major arthropod groups (biomass: mg arthropod (dry-weight) kg⁻¹ vegetation (wet-weight)) on seven tree types common in the Copper River Basin, Alaska.

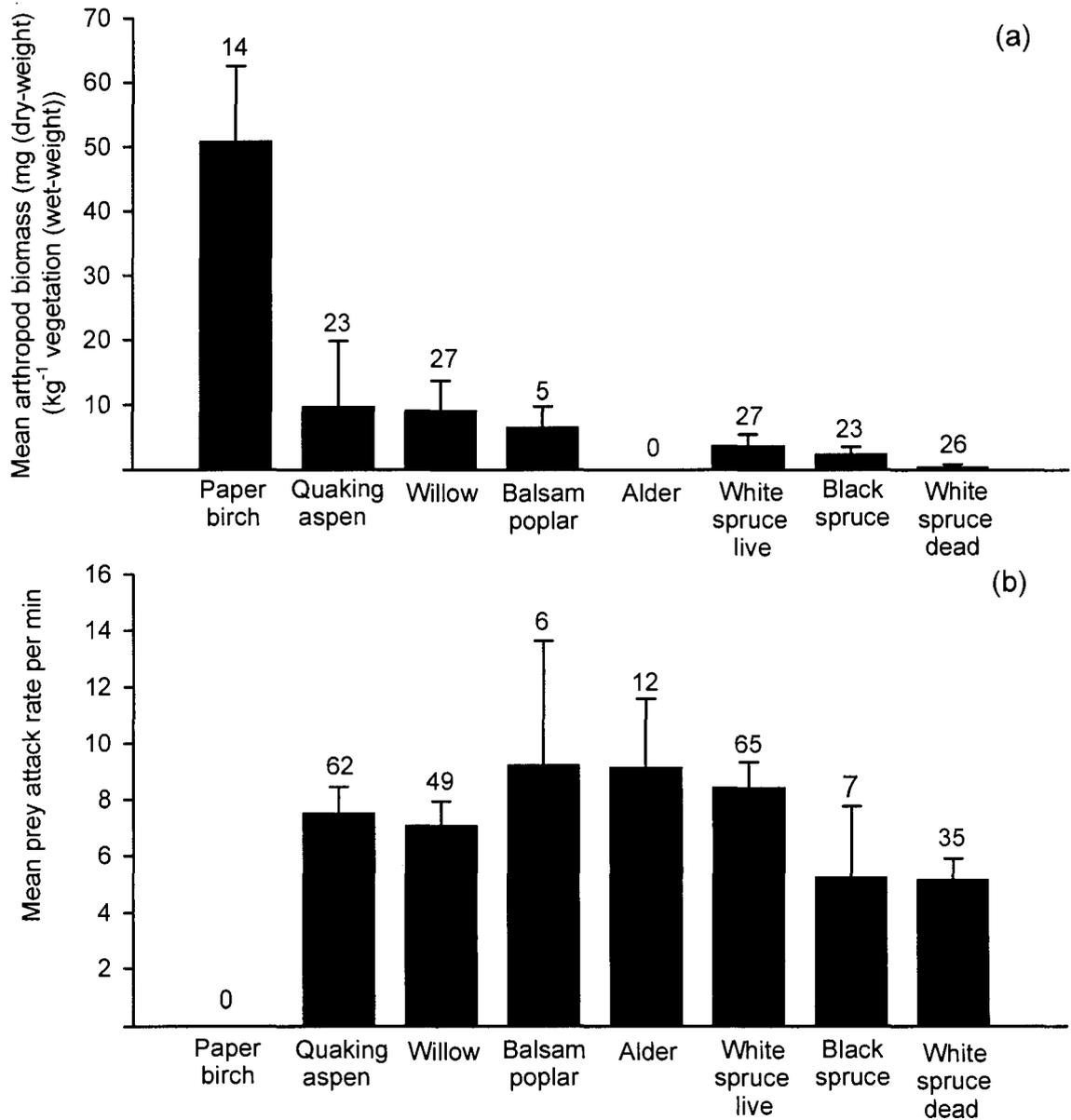


Fig. 6. Comparison of (a) distribution of arthropods (mean biomass \pm SE) sampled in common tree types in the Copper River Basin, Alaska, and (b) attack rate (mean \pm SE) by Yellow-rumped Warblers in the same tree types. Sample size is shown above the error bars.

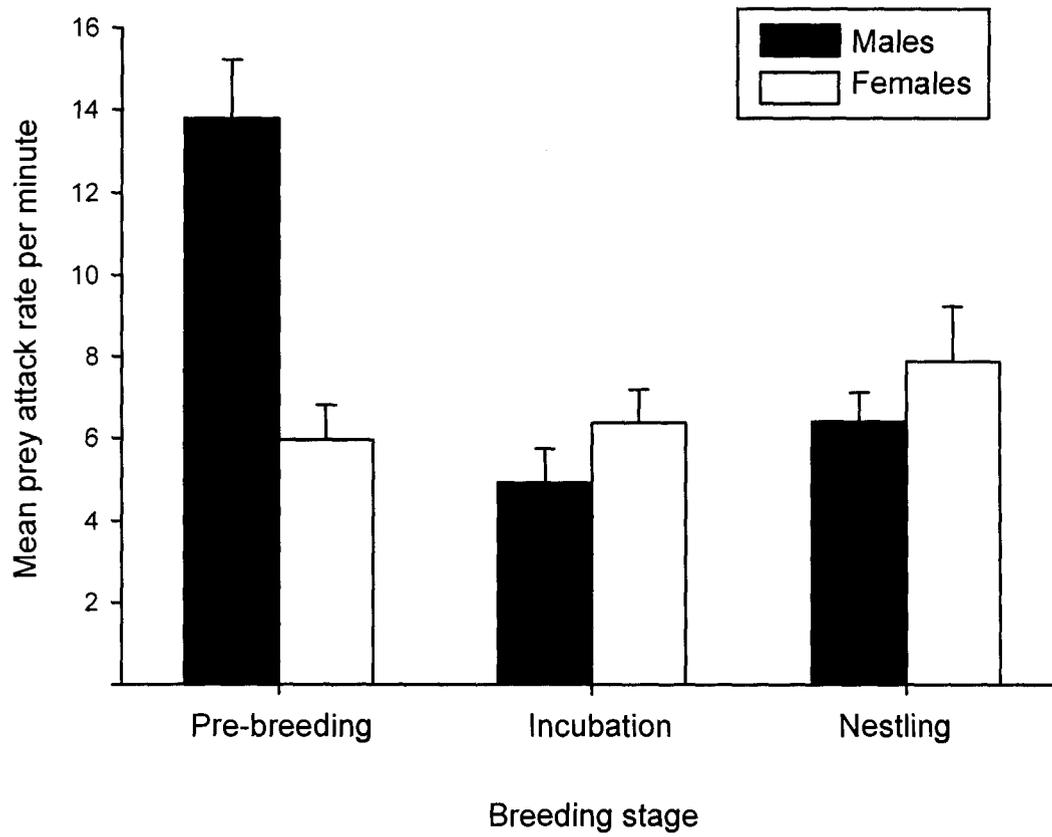


Fig 7. Prey attack rates (mean \pm SE) by male and female Yellow-rumped Warblers among breeding stages in the Copper River Basin, Alaska.

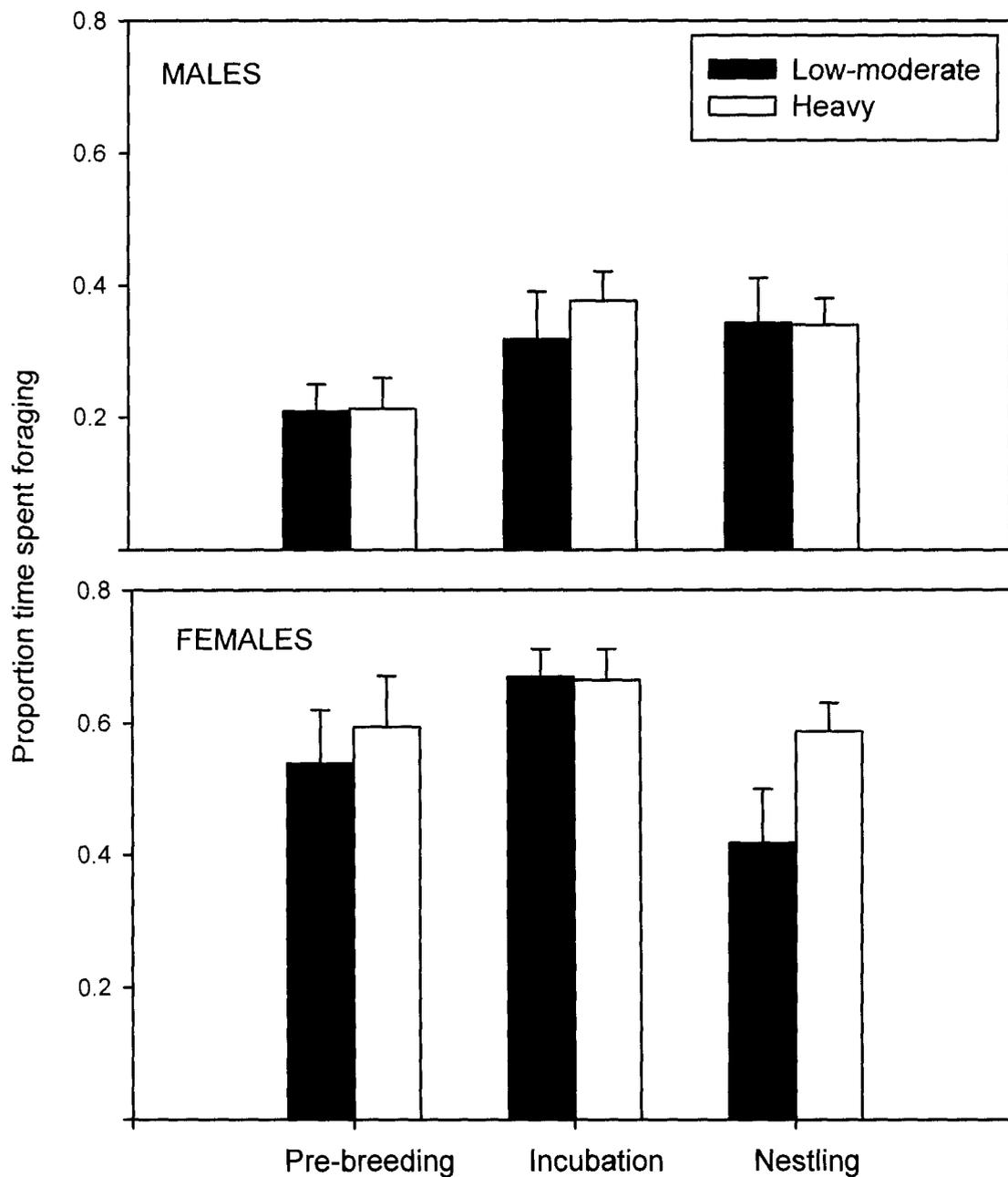


Fig. 8. Proportion of time (mean + SE) male and female Yellow-rumped Warblers spent foraging in stands with low-moderate and heavy spruce mortality during each stage of the breeding season in the Copper River Basin, Alaska.

Appendix A. Substrates used by Yellow-rumped Warblers for foraging. Eight substrates in bold type were retained for analyses.

Foraging substrate

White spruce live

dying

dead

Black spruce live

dying

dead

Unidentified spruce (*Picea spp.*)

dying

dead

Quaking aspen

Balsam poplar

Paper birch

Willow

Alder

Shrub

Ground/herb

Deadfall

Unknown

Appendix B. Numbers of individuals and biomass of arthropods collected from branch clippings within areas of low (L) or high (H) spruce mortality in the Copper River Basin, Alaska, 1998.

Order	Family ^a	N	Arthropod biomass mg(dry-wt.) kg ⁻¹ veg (wet-wt.)	Level of spruce mort. (L,H)	Tree species ^b
Non-Insecta					
Acari		5	2.7	H	BS, QA
Arachnida		799	556.0	L, H	WSL,BS,WSD,QA,BP,PB,WI
Insecta					
Coleoptera	Carabidae	9	2.4	H	WSL,BS,WSD,PB,WI
	Chrysomelidae	5	17.8	H	QA,PB
	Cleridae	5	9.3	H	BS,QA,PB
	Coccinellidae	7	7.6	L,H	WSL,QA,PB
	Curculionidae	4	12.4	L,H	BS,PB,WI
	Elateridae	14	30.5	L,H	WSL,BS,WSD,QA,PB,WI
	Scolytidae	14	1.8	L,H	BS,WSD
	Staphylinidae	1	5.68 x 10 ⁻⁵	H	PB
	Other	15	11.4	L,H	WSL,BS,WSD,QA,WI
Collembola	Isotomidae	51	1.9	L,H	WSL,BS,WSD,BP,PB,WI
Diptera	Culicidae	7	3.3	H	WSL,WSD,QA,WI
	Mycetophilidae	114	18.6	L,H	WSL,BS,WSD,QA,BP,WI
	Other	124	26.2	L,H	WSL,BS,WSD,QA,PB,WI
Ephemeroptera		1	4.2	H	WSD
Hemiptera	Lygaeidae	1	1.1	H	WI
	Miridae	44	9.7	L,H	WSL,BS,BP,PB,WI
	Nabidae	2	0.8	H	BS,WI
	Pentatomidae	151	232.8	L,H	WSL,BS,WSD,QA,PB,WI
	Other	52	6.6	L,H	WSL,BS,PB,WI
Homoptera	Adelgidae	239	10.7	L,H	WSL,BS,QA,BP
	Aphididae	2097	117.7	L,H	WSL,BS,QA,BP,PB,WI
	Cicadellidae	73	48.2	L,H	WSL,WSD,QA,BP,PB,WI
	Psocidae	86	2.6	L,H	WSL,BS,WSD
	Psyllidae	431	61.6	L,H	WSL,BS,PB,WI
	Other	17	3.6	L,H	WSL,BS,PB
Hymenoptera	Formicidae	41	23.0	L,H	WSL,BS,WSD,QA,PB,WI
	Orussidae	36	13.6	L,H	WSL,BS,WI
	Tenthredinidae	23	67.9	L,H	WI

Appendix B. Continued.

Order	Family ^a	N	Arthropod		Tree species ^b
			biomass mg(dry-wt.) kg ⁻¹ veg (wet-wt.)	Level of spruce mort. (L,H)	
Hymenoptera	Other	28	64.7	L,H	WSL,BS,WSD,QA,PB,WI
Lepidoptera	Geometridae	28	61.1	L,H	WSL,WSD,QA,PB,WI
	Gracilariidae	570	316.3	L,H	PB,WI
	Lycanidae	3	4.0	L	WI
	Plutellidae	1	3.9	H	BS
	Thyatiridae	1	4.6	L	QA
	Tortricidae	134	2930.0	L,H	WSL,QA,BP,PB,WI
	Other larvae	10	27.0	H	QA
	Other adult	173	650.0	L,H	WSL,BS,WSD,QA,PB,WI
Neuroptera	Chrysopidae	270	36.1	L,H	WSL,BS,WSD,QA,BP,PB,WI
Psocoptera	Psocidae	91	1.8	L,H	WSL,BS,WSD,BP
Strepsiptera	Halictophagidae	20	3.0	L,H	WSL,QA,PB,WI
Thysanoptera	Phalaeothripidae	11	0.5	H	WSL,QA,PB
Miscellaneous eggs		281	46.7	L,H	WSL,BS,PB
Miscellaneous pupae		16	23.3	L,H	BS,QA,PB,WI
Miscellaneous other		39	5.3	L,H	WSL,BS,WSD,QA,BP,PB,WI
Total		6144	5484.2	L,H	WSL,BS,WSD,QA,BP,PB,WI

^aNot all individuals within a family may have been recognized. This is especially true when several lifeforms were represented within a family.

^bWSL= white spruce live, BS = black spruce, WSD = white spruce dead, QA=quaking aspen, BP = balsam poplar, PB = paper birch, WI= willow.