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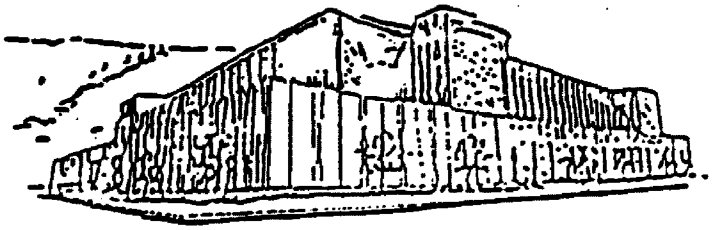

THE INFLUENCE OF PREY DENSITY ON POST-FIRE HABITAT USE OF THE BLACK-BACKED WOODPECKER

by

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B.A., Huntingdon College, 1990

Presented in partial fulfillment of the requirements

for the degree of

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ABSTRACT

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The influence of prey density on post-fire habitat use of the Black-backed Woodpecker

Advisors: Richard L. Hutto RLH
Sallie J. Hejl SJH

Fire suppression and salvage logging of burned forests have combined to reduce the amount of available post-fire habitat for the Black-backed Woodpecker (*Picoides arcticus*). Detailed knowledge of habitat requirements within recently burned forests could aid conservation of this species. I studied the habitat use of Black-backed Woodpeckers in relation to prey density in two post-fire forests of the northern Rocky Mountains. I measured diet to ensure that prey sampling methods were directed at the appropriate set of prey insects. To measure prey, I developed and tested a bark-sampling method that produced a ranking of insect abundance that could be compared among trees (Chapter I). I used this method to index insect abundance among tree species, between used and unused trees, and at one site, among patches of trees (Chapter II).

Although trees that birds foraged upon contained more prey than trees selected at random, prey densities in separate patches of a burn did not appear to determine where Black-backed Woodpeckers foraged or nested. Both insect abundance among tree species and tree species use differed between sites. Without knowledge of prey density, tree species use would have appeared inconsistent between the two sites and when compared to previously published reports. This suggests that the foraging value of a particular tree species depends on the number of insects it contains and may differ among sites. Therefore, prey density appears to be an important variable to include when evaluating the importance of habitat components. Moreover, at one site, only one of the two most prey-rich tree species was used more than expected on the basis of availability, suggesting that prey density is not the only factor affecting tree use by foraging Black-backed Woodpeckers.

I compare foraging data from this study with previously published reports, and then discuss two hypotheses for the basis of habitat selection in Black-backed Woodpeckers. Finally, because of the importance of bark and wood-boring beetles to woodpeckers in post-fire forests and the paucity of detailed studies on them, I summarize trends affecting insect populations in post-fire forests from the entomological literature and from data collected in this study.

ACKNOWLEDGEMENTS

I thank the members of my committee for guidance throughout this project. My advisors, Dick Hutto and Sallie Hejl, were very helpful during the planning and writing of this thesis. Dick Hutto was instrumental in my thinking about how to measure food availability, how to sample systematic-randomly, and how to construct adjectives properly. Sallie Hejl provided insight and immense logistical support, and made funding (especially for the second field season and the writing phase) materialize out of the thin Montana air. Diana Six taught me about bark and wood-boring beetles, and how to identify sub-bark insect larvae. Doug Emlen made helpful suggestions about sampling designs, data analysis, and presentation of results.

More than 700 trees were sampled for insects in the course of this study. Such an effort would not have been possible without the unflagging and cheerful help of David Jachowski and Adam Ehmer. Thanks are due also to Forest Service employees in the West Fork District, particularly Maria and Chicken Guts; the Plains District, Tricia O'Connor and Polly Weinbrenner; the Superior District, Beth Kennedy; the Lolo National Forest, Mike Hillis; and the Region 1 office, Skip Kowalski. At Warrior's Face, Scott Story, Jason Beason, Seth Britch, and Dina Roberts helped greatly, especially at dusk on 12 June 1998, when I found I had miscut 12 tree-trunk sections and had to shave another 15 cm off each one with a crosscut saw. Mary McFadzen provided logistical assistance, color-banded some of the Warrior's Face birds, and selflessly volunteered for winter surveys for Black-backed Woodpeckers in Canada. A final thanks to the Greene/Hutto lab: K. Short, A. Cilimburg, J. Young, B. Walker, and J. Jolivette, and to my family, especially Emma Elizabeth Powell, for their support.

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CHAPTER I

A GROUND-BASED BARK-SAMPLING METHOD FOR COMPARING WOOD-BORING BEETLE (COLEOPTERA: BUPRESTIDAE, CERAMBYCIDAE) ABUNDANCE AMONG FIRE-KILLED TREES

INTRODUCTION

In avian studies, food availability is a desirable but difficult quantity to measure (Smith and Rotenberry 1990). For a measurement of food availability to be realistic, it must account for the diet of the study animal and the abundance and distribution of its prey throughout the habitat, among other variables (Hutto 1990). Once the diet is known (methods reviewed in Rosenberg and Cooper 1990), finding an appropriate method for measuring prey populations can be troublesome, especially in the case of insectivores. Insects are diverse and often patchily distributed, their populations can change size rapidly, and they tend to occupy a range of microhabitats that no single sampling technique can capture (Cooper and Whitmore 1990). Sampling designs must, therefore, be carefully matched to the foraging behavior of a particular study animal (Wolda 1990).

While studying the foraging behavior of the Black-backed Woodpecker (*Picoides arcticus*) in burned forests of Idaho and Montana, I needed a technique for sampling its prey. Black-backed Woodpeckers eat primarily wood-boring beetles (Coleoptera: Buprestidae, Cerambycidae) contained in the bark, phloem, and xylem of standing dead trees (Beal 1911, Murphy and Lehnhausen 1998). Because no standard method existed for estimating wood-boring beetle populations in trees, I adapted a method from established techniques for estimating within-tree bark beetle (Coleoptera: Scolytidae) populations (Pulley et al. 1977, McClelland et al. 1978, Coulson et al. 1979, DeMars et al. 1986).

Precise estimation of within-tree insect numbers requires more effort than most studies can expend (Schowalter et al. 1982), making it important to find an estimation method that captures the true distribution of the target insect while remaining feasible to apply in the field (Coulson et al. 1979). This problem has received considerable attention in bark beetle systems, and techniques have been developed that estimate within-tree population size from a small number of bark samples (Pulley et al. 1977, Schowalter et al. 1982, Dahlsten et al. 1990).

For my comparison of trees as foraging sites for Black-backed Woodpeckers, I needed to rank insect density among trees, rather than precisely estimate within-tree populations. Therefore, I looked for a sampling technique that was (1) precise enough to provide rankings of trees based on their wood-borer abundance; and (2) limited enough to be conducted by two field workers sampling > 250 trees per three-month field season. Climbing trees to sample bark, a common component of bark-beetle sampling methods, is time-consuming; therefore, a usable sampling design should employ bark samples taken near ground level. With these conditions in mind, I chose a sampling design that used two bark samples (one each from the north and south sides of each tree) at a height of 1.7 m (eye level).

Because conclusions about wood-borer abundance hinged on the results of this sampling design, I conducted a test of its reliability. For a subset of trees at each site, I sampled eight pieces of bark per tree from two sampling heights. For these trees, I measured the correlation between tree rankings produced by the two-sample design and the larger, eight-sample design (hereafter, the full sample). A strong correlation between the rankings produced by each sampling method would support the idea that the smaller bark sample provided an index of insect abundance that was nearly as accurate as a sample that required more than four times the effort.

As an extension of this test, I investigated the increase in accuracy and precision of tree rankings afforded by increasing the amount of bark sampled. I did this by comparing the agreement of rankings produced by one, two, three, and four eye-level bark samples to rankings from the full eight samples. This information may be useful for refining the sampling technique for future studies.

This paper assesses the reliability of ground-based bark sampling for ranking levels of wood-borer abundance among trees, concentrating on four specific objectives: (1) testing the reliability of the north-south, eye-level sampling method (hereafter, the standard sample; Figure 1); (2) assessing the reliability of the sampling method when using two different measures of potential prey; (3) comparing the accuracy and precision of estimates provided by taking up to four eye-level bark samples per tree; and (4) testing for a consistent effect of tree side or sampling height on the number of wood-borers in bark samples.

METHODS

Study areas. I tested the technique at two study sites in the Intermountain West. In 1998, I studied the two-year-old Warrior's Face burn in the Selway-Bitterroot Wilderness of Salmon County, Idaho (45° 43′ N, 114° 38′ W). The site was dominated by Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), with ponderosa pine (*Pinus ponderosa*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and grand fir (*Abies grandis*) present in smaller numbers. The following year, I studied the one-year-old Boyer Creek burn near Plains, Mineral County,

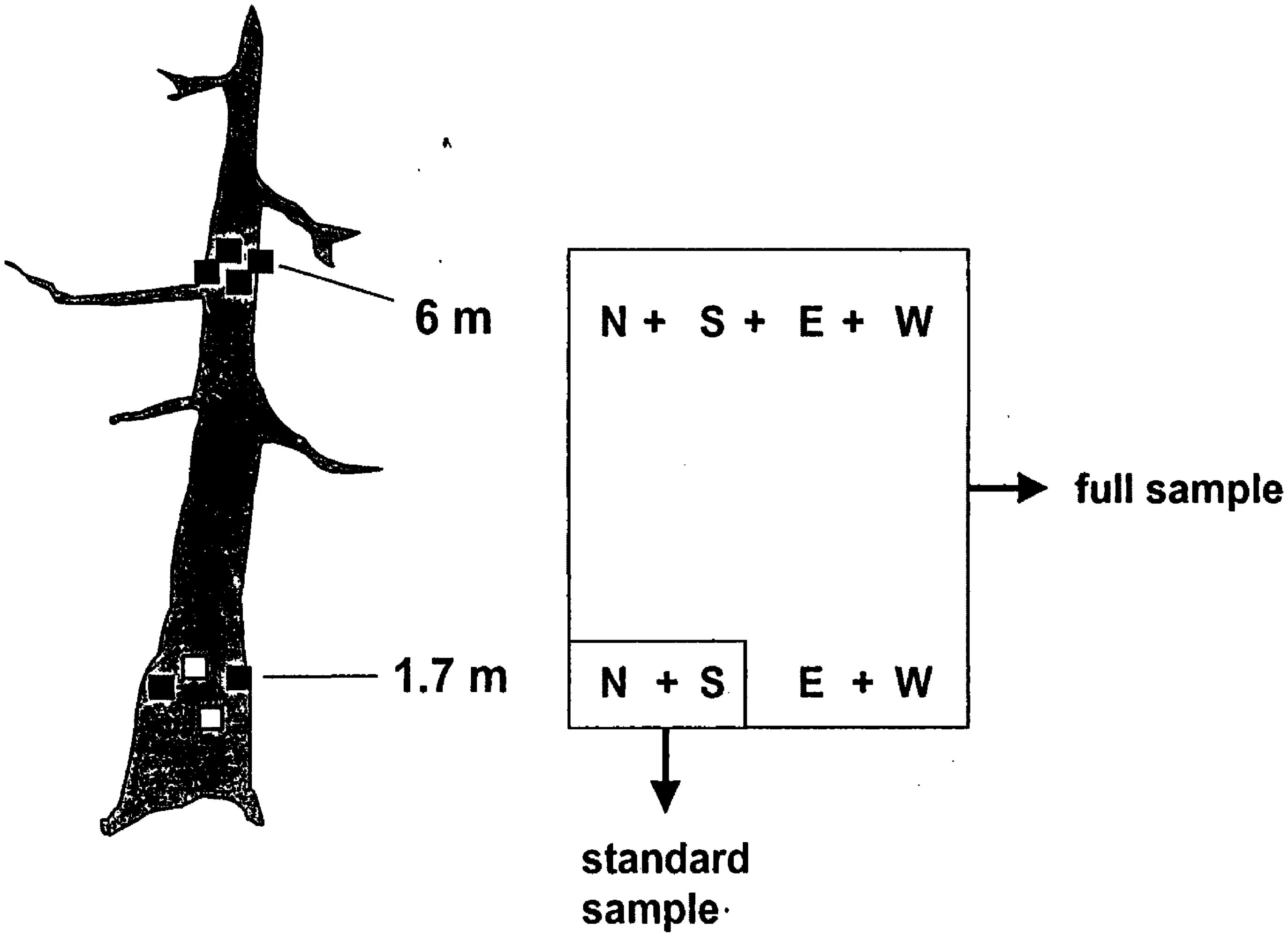

Figure 1. Sampling scheme for the expanded-sample trees. The reliability of the standard sample (white squares) was evaluated by calculating the correlation between the total number of insects in the standard sample and the full sample (white + black squares).

Montana (47° 27′ N, 114° 46′ W), about 230 km north of the Warrior's Face burn. At Boyer, the most common tree was Douglas-fir, followed by ponderosa pine, western larch (*Larix occidentalis*), grand fir, and rarer lodgepole pine and western red cedar (*Thuja occidentalis*). Elevation and aspect at both sites were similar, ranging from 1500 m to 1850 m on generally southward aspects.

Insect sampling. I sampled the three most numerous tree species at each site. At Warrior's Face, I sampled 32 trees: 14 Douglas-firs, 9 ponderosa pines, and 9 lodgepole pines. At Boyer, I sampled 33 trees: 11 Douglas-firs, 11 ponderosa pines, and 11 western larches. I sampled trees systematically, by locating a point at a random bearing and distance within 50 m of gridpoints spaced at regular intervals (100 m for Warrior's Face; 80 m for Boyer) across the sites. At each point, I chose the closest tree of the appropriate species and size. I sampled trees of a consistent size to eliminate any confounding effect of tree size on insect colonization level. The target tree size was 40 ± 5 cm diameter at breast height (dbh) at Warrior's Face and 30 ± 5 cm dbh at Boyer, reflecting a difference in tree-size distribution between the two sites.

Using a hammer and chisel, I removed eight, 15 x 15-cm squares of bark and phloem from each tree. Bark squares were located, one each, on the north, south, east, and west sides of the trunk, at heights of 1.7 m and 6 m (see Figure 1). Because wood-borer density tends to be positively correlated with bark thickness and tree diameter (Linsley 1961, Hughes and Hughes 1982, Zhang et al. 1993), I assumed that sampling at these two heights captured the part of the tree containing the greatest wood-borer density. These sampling heights also represent typical Black-backed Woodpecker foraging heights; 65% of foraging observations during this study were recorded at heights of 10 m or less (unpubl. data). Trees were climbed using a belt and climbing spurs.

I dissected the bark samples and counted all insects > 5 mm in length and all wood-borers and bark beetles of any size. Larvae were identified to family using Raske (1968), and placed into four size categories, based on length: < 5 mm (small), 5-10 mm (medium), 10-20 mm (large), and > 20 mm (extra large).

One difficulty with using bark samples to estimate wood-borer abundance is that wood-borers spend a portion of their developmental period in galleries in the xylem. However, phloem tissue is more nutritious than xylem, and late-instar wood-borers feeding in xylem are known to return to the phloem or bark to feed and pupate (Rose 1957). While collecting bark, I checked xylem gallery entrances for wood-borers and recorded any larvae I found. I then assumed that the total number of wood-borers found in bark, phloem, and xylem gallery entrances was close to the total number of wood-borers in the part of the tree I was sampling.

Data analysis. I measured two subsets of insects that represented potential prey for Black-backed Woodpeckers: *all wood-borers* and *all large insects* (including extra-large; i.e. all insects > 10 mm in length). The all-wood-borer count included many wood-borer larvae that were not in the large or extra-large size classes. The all-large insect count included large and extra-large wood-borers and large, non-wood-boring insects: mainly Coleoptera (Cleridae, Trogositidae, and Staphylinidae) or, at Boyer, parasitic Hymenoptera. Large non-wood-borers accounted for less than 20% of the large-insect total, and I considered this grouping to be an appropriate measure of potential prey for Black-backed Woodpeckers, based on a concurrent study of their diet (see Chapter II). I had intended to evaluate the usefulness of this technique in assessing scolytid abundance, but the very low incidence of scolytids in sample trees precluded calculating meaningful correlations.

Insect counts from bark samples contained many zero values and approached the negative binomial distribution (Fowler and Cohen 1990, White and Bennetts 1996). Therefore, non-parametric tests were used to evaluate correlations and to test the effects of sampling height and side. For correlations between subsets of bark samples, I calculated Spearman's rank correlation coefficient (r_s) (Sokal and Rohlf 1995; SPSS, Inc. 1998).

I tested the usefulness of the standard sample (north and south sides, 1.7-m high) against the full sample, for each tree (see Figure 1). I also calculated correlations for each of the possible combinations of one, two, three, and four 1.7-m samples and the full sample. This analysis yielded four one-sample, six two-sample, four three-sample, and one four-sample correlations. To assess accuracy and precision of potential sampling designs, I calculated the mean and standard deviation for all correlations at each of the four levels of effort. Accuracy and precision should increase as more samples are added. When variance is large (i.e. at low levels of effort), certain combinations of sampling sides may be expected to be higher than others; these combinations might prove more valuable as a standardized sampling method than the north-south, 1.7-m sample. To investigate this possibility, I graphed the range of correlations for each sampling effort and looked for tree-side combinations that were consistently high.

I calculated correlations between subsamples and the full sample for all tree species lumped at each site. However, the possibility exists that consistent, large differences in colonization levels among tree species might mask inconsistency in insect counts between subsamples and the full sample, which would result in false confidence in the sampling method. Therefore, I also calculated the same set of correlations separately for each tree species at each site.

I tested for an effect of tree side on the number of insects at each sampling height, using Friedman's method for randomized blocks (Sokal and Rohlf 1995; SPSS, Inc. 1998). I then tested the effect of sampling height using Wilcoxon's signed-ranks test on the mean number of insects for all four samples at each height (Sokal and Rohlf 1995; SPSS, Inc. 1998). For both tests, individual trees were considered blocks, and I assumed there was no interaction between blocks, tree side, and sampling height.

For side and height effects, I tested each tree species separately to allow for differences in insect colonization rates among tree species. Because I was conducting three statistical tests on the same effect, I used a Bonferroni adjustment to determine the appropriate α-level ($\alpha = .05/3 = .0167$).

Decision rule for useful correlations. Statistical significance testing of a correlation coefficient depends entirely on the α-level and the sample size (Rohlf and Sokal 1995). Sample sizes in this study were limited by available time, and in some cases, small sample sizes yielded high *p*-values despite a fairly strong measured correlation. However, high *p*-values indicate only that the correlation could be due to chance; they do not imply that the correlation is less than the measured strength. In identifying reliable correlations, I concentrated on identifying an appropriate effect size, rather than testing a null hypothesis that a correlation was different from zero (Cherry 1998, Johnson 1999).

I assumed that the measured correlations were reasonably accurate (i.e. that sampling error was minor), and then decided on the strength of correlation needed to rank trees adequately. This assumption is supported by similarly high correlations in larger sample sizes (all tree species combined for a site, n = 32 or 33; Figure 2). I examined scatterplots of hypothetical datasets with predetermined correlation coefficients to decide what level of association was acceptable for ranking insect abundance among trees. From these examinations, I designated a correlation of 0.600 as a reliable indication of overall insect abundance. This r_s-value corresponds to p-values between 0.06 (for n = 9) and less than 0.01 (for n = 32).

RESULTS

Correlation of the standard sample with the full sample. At Warrior's Face, Douglas-fir and lodgepole pine standard samples were strongly correlated with the full sample. The correlations were higher for measures of wood-borers (Douglas-fir, r_s = 0.918; lodgepole pine, r_s = 0.793; Table 1) than for large insects (Douglas-fir, r_s = 0.518; lodgepole pine, r_s = 0.694; Table 1). However, ponderosa pine standard samples reflected overall tree colonization poorly (r_s = 0.192 for counts of large insects, r_s = 0.287 for counts of wood-borers).

At Boyer, all three tree species tested had the standard sample highly correlated with the full sample for counts of large insects (Table 1). The correlations were slightly poorer for counts of wood-borers, and for western larch the correlation was less than the 0.600 cutoff (r_s = 0.557; Table 1).

Prey measures. With all tree species lumped at each site (Figure 2), the differences between the two insect measures appear slight. However, when tree species

Table 1. Spearman's rank correlation coefficients (r_s) for standard samples compared to the full sample, for each tree species at each site. The best-correlated insect metric differed between the two study sites. Large insects includes all insects > 10 mm in length.

		Wood-borers		**Large insects**	
	n	**r_s**	**p**	**r_s**	**p**
Warrior's Face					
Douglas-fir	14	**0.918**	**< 0.001**	0.518	0.058
Ponderosa pine	9	**0.287**	**0.011**	0.192	0.038
Lodgepole pine	9	**0.793**	**0.453**	0.694	0.621
Boyer					
Douglas-fir	11	0.786	0.004	**0.807**	**0.003**
Ponderosa pine	11	0.822	0.002	**0.877**	**< 0.001**
Western larch	11	0.557	0.075	**0.953**	**< 0.001**

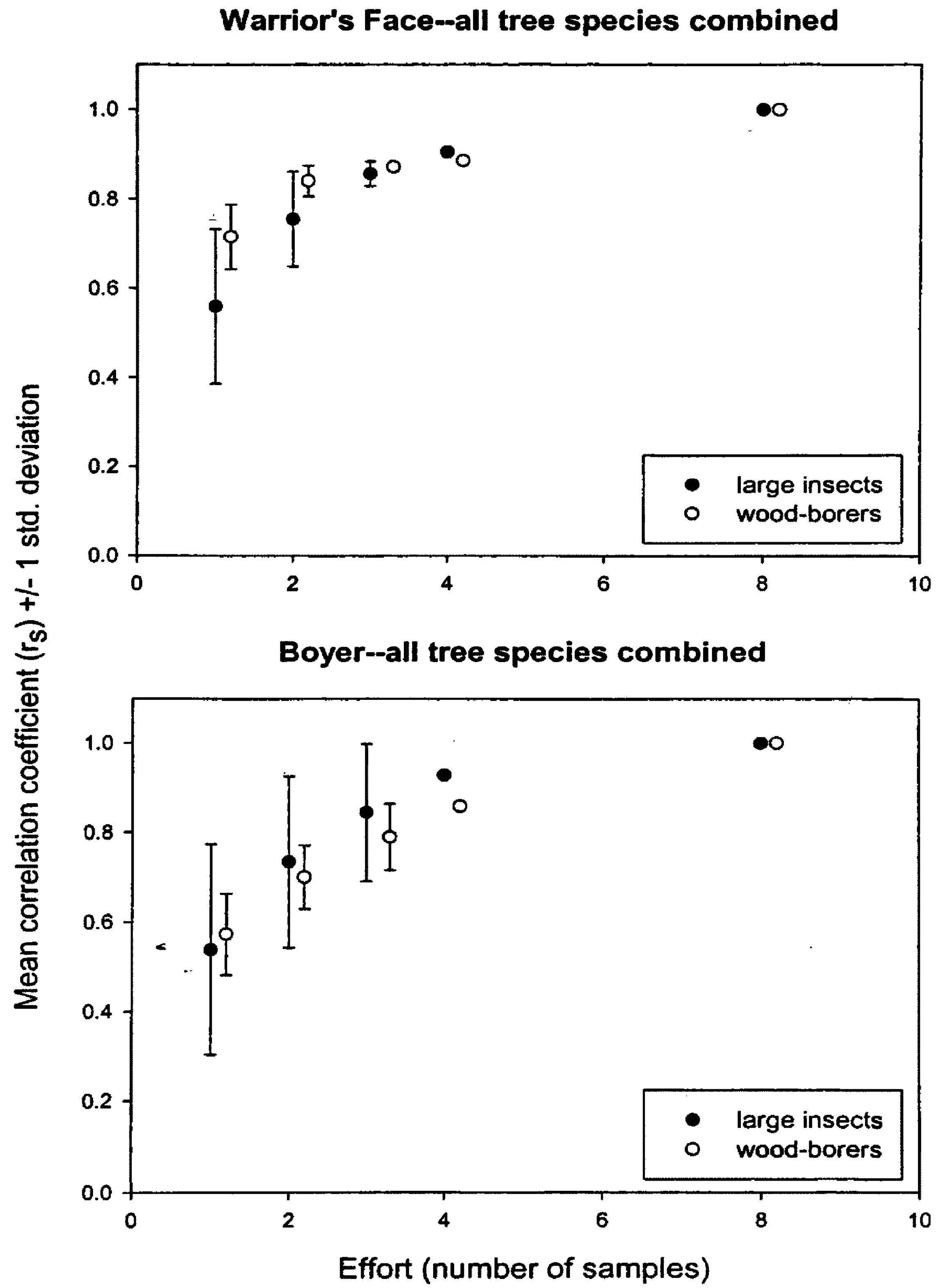

Figure 2. Mean correlation coefficients calculated for all combinations of one, two, three, and four eye-level bark samples against the full sample, for two insect measures, with all tree species combined at each site. As effort increased, mean correlation strength increased and variance decreased.

are analyzed separately, it is apparent that at Warrior's Face, counts of large insects yielded poorer correlations than counts of wood-borers for lodgepole pines (Figure 3). Conversely, at Boyer, counts of wood-borers for western larch are substantially more poorly correlated than counts of large insects (Figure 4). Correlations using counts of wood-borers contained substantially less variance than correlations using large insects, indicating that wood-borers tended to be distributed in trees more uniformly than were large insects. In general, counts of wood-borers were most reliable at Warrior's Face, but counts of large insects were most reliable at Boyer (Figure 2).

Accuracy and precision over a range of sampling efforts. As expected, the correlation between a subsample and the full sample increased with the size of the subsample. As sampling effort increased from one to four bark samples, the mean correlation strength increased and variance decreased (Figures 2, 3, 4), indicating that accuracy and precision of tree rankings improves as more samples are taken. In general, mean correlation strength exceeded the 0.600 cutoff when the sampling effort included at least two bark samples (Figure 2). For ponderosa pine at Warrior's Face, however, mean correlation strength remained weak at all sampling levels up to four samples per tree (Figure 3)

Correlations for specific tree-side combinations. These results indicate that, in general, increasing sampling effort yielded better estimates of insect abundance in trees. The problem remains to identify the particular bark samples that provided the most reliable estimate for a particular sampling effort. For a level of effort of two samples per tree, the best combinations were north+south for Douglas-fir, north+east for ponderosa pine, and north+west for lodgepole pine at Warrior's Face; and south+west for Douglas-

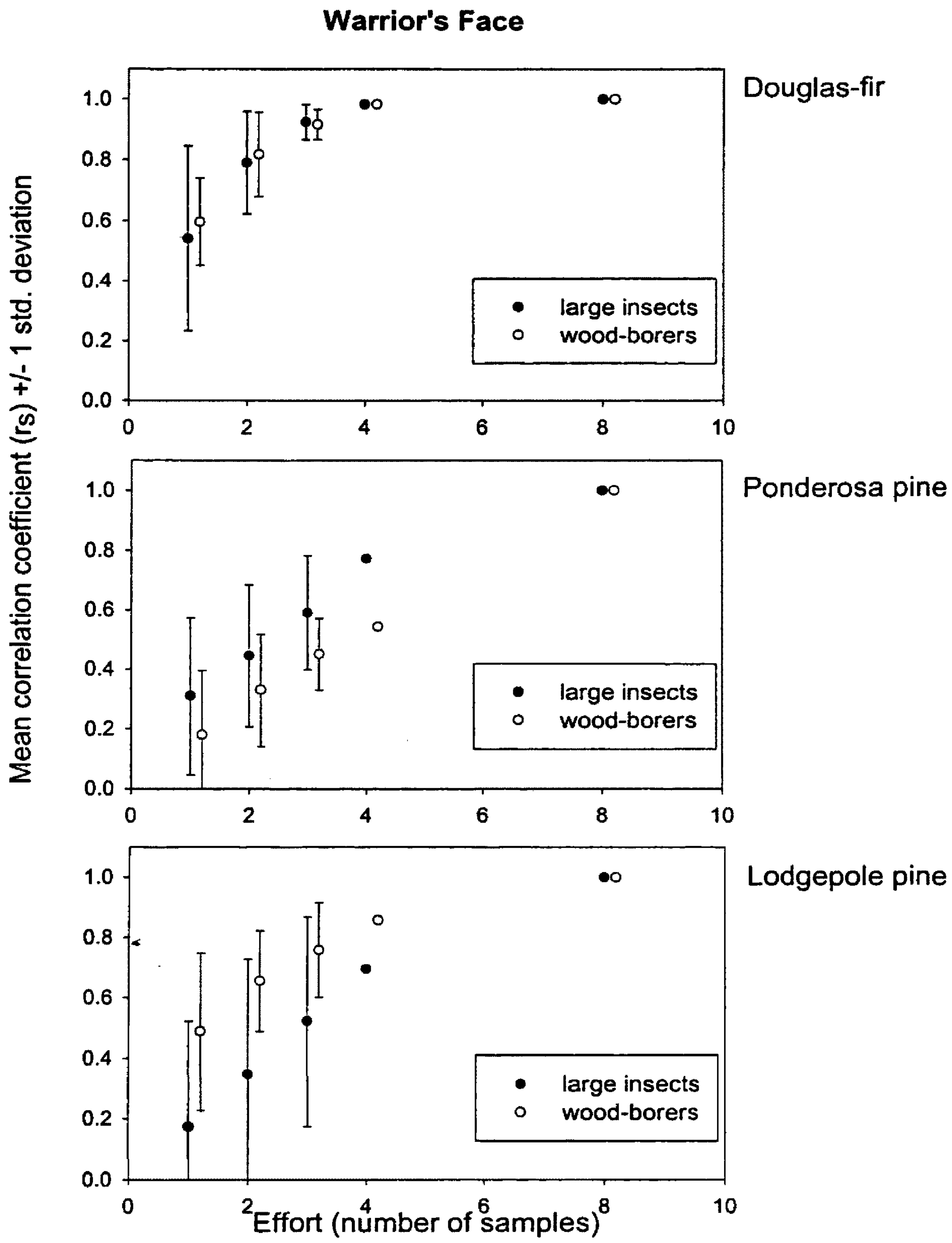

Figure 3. Mean correlation coefficients for all combinations of one, two, three, and four eye-level bark samples against the full sample, for two insect measures, for each tree species at Warrior's Face. In lodgepole pine, correlations were markedly stronger for wood-borers than large insects. Correlations were weak for ponderosa pine.

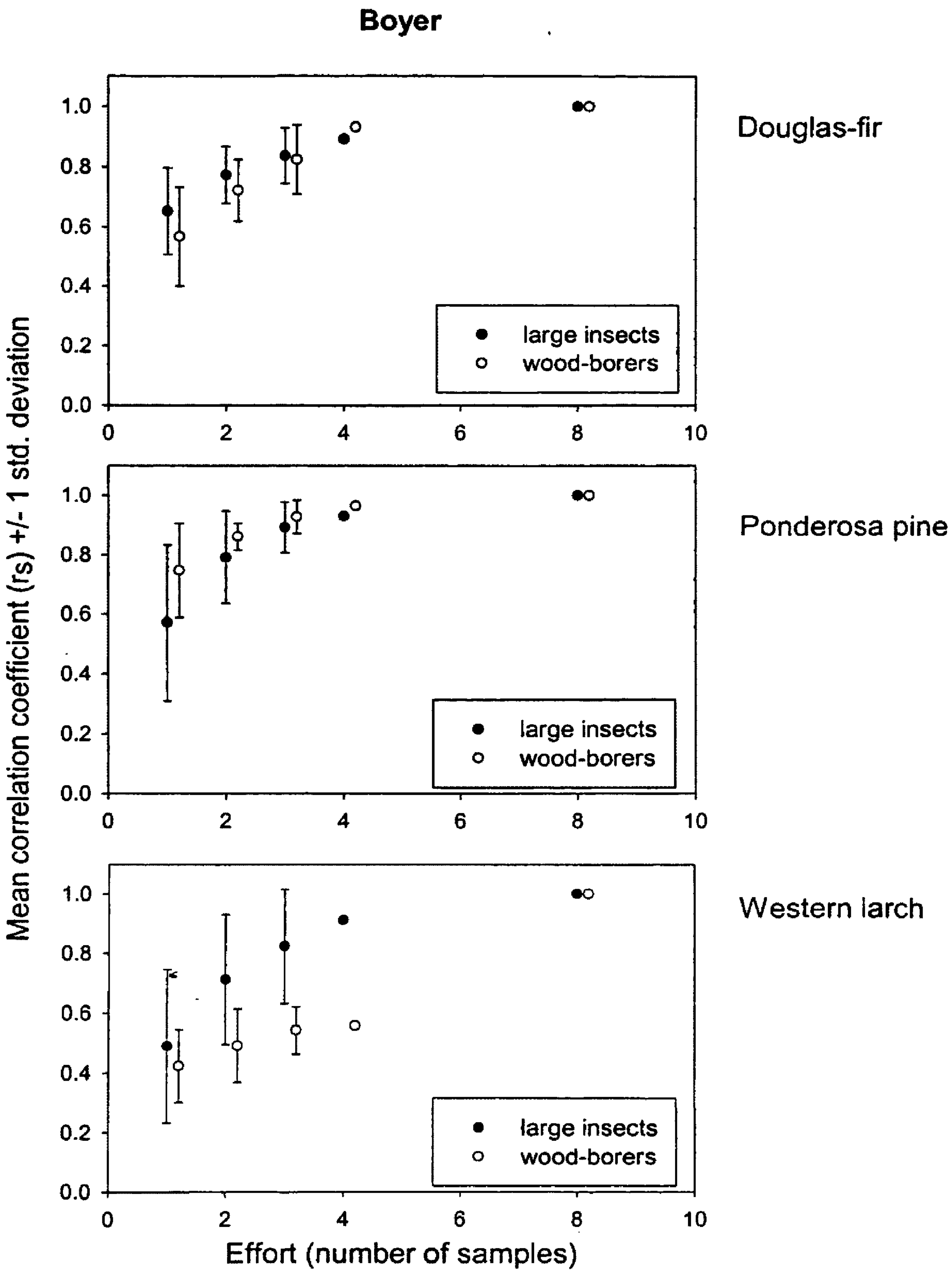

Figure 4. Mean correlation coefficients for all combinations of one, two, three, and four eye-level bark samples against the full sample, for two insect measures, for each tree species at Boyer. In western larch, correlations were markedly stronger for large insects than wood-borers.

fir, east+south for ponderosa pine, and north+south for western larch at Boyer (Figure 5). For all tree species except ponderosa pine at Warrior's Face, several other two-sample combinations yielded correlations of similar strength, indicating the possibility of a standard-sample combination that would provide good results across tree species.

For a level of effort of one sample per tree, the best-correlated tree sides were west for Douglas-fir, east for ponderosa pine, and north for lodgepole pine at Warrior's Face; the best-correlated tree side was south for all tree species at Boyer (Figure 5).

Effects of side and height. At Warrior's Face, there was no significant effect of tree side on number of wood-borers for any tree species (Figure 6). At Boyer, however, tree side was highly significant at both sampling heights (Friedman's test: 1.7 m, $\chi^2 = 15.9$, df = 3, $p = 0.001$; 6 m, $\chi^2 = 22.0$, df = 3, $p < 0.001$; Figure 7). South and west sides generally contained more large insects than north and east sides (Figure 7).

At Warrior's Face, sampling height had a significant effect on number of wood-borers in Douglas-fir (Wilcoxon's signed-ranks: $Z = -2.762$, $p = 0.006$) and ponderosa pine (Wilcoxon's signed-ranks: $Z = -2.456$, $p = 0.014$) (Figure 6). Interestingly, ponderosa pine contained more insects at 6 m than at 1.7 m, which was opposite the trends observed in other species. At Boyer, there was no significant difference in insect numbers between sampling heights for any tree species (Figure 7).

DISCUSSION

Usefulness of a ground-based, two-sample method. This is the first study that has attempted to estimate the accuracy of wood-borer abundance estimates taken from a small number of bark samples. However, similar analyses have been used routinely in bark beetle studies. Pulley et al. (1977) tested the precision and variance of estimates

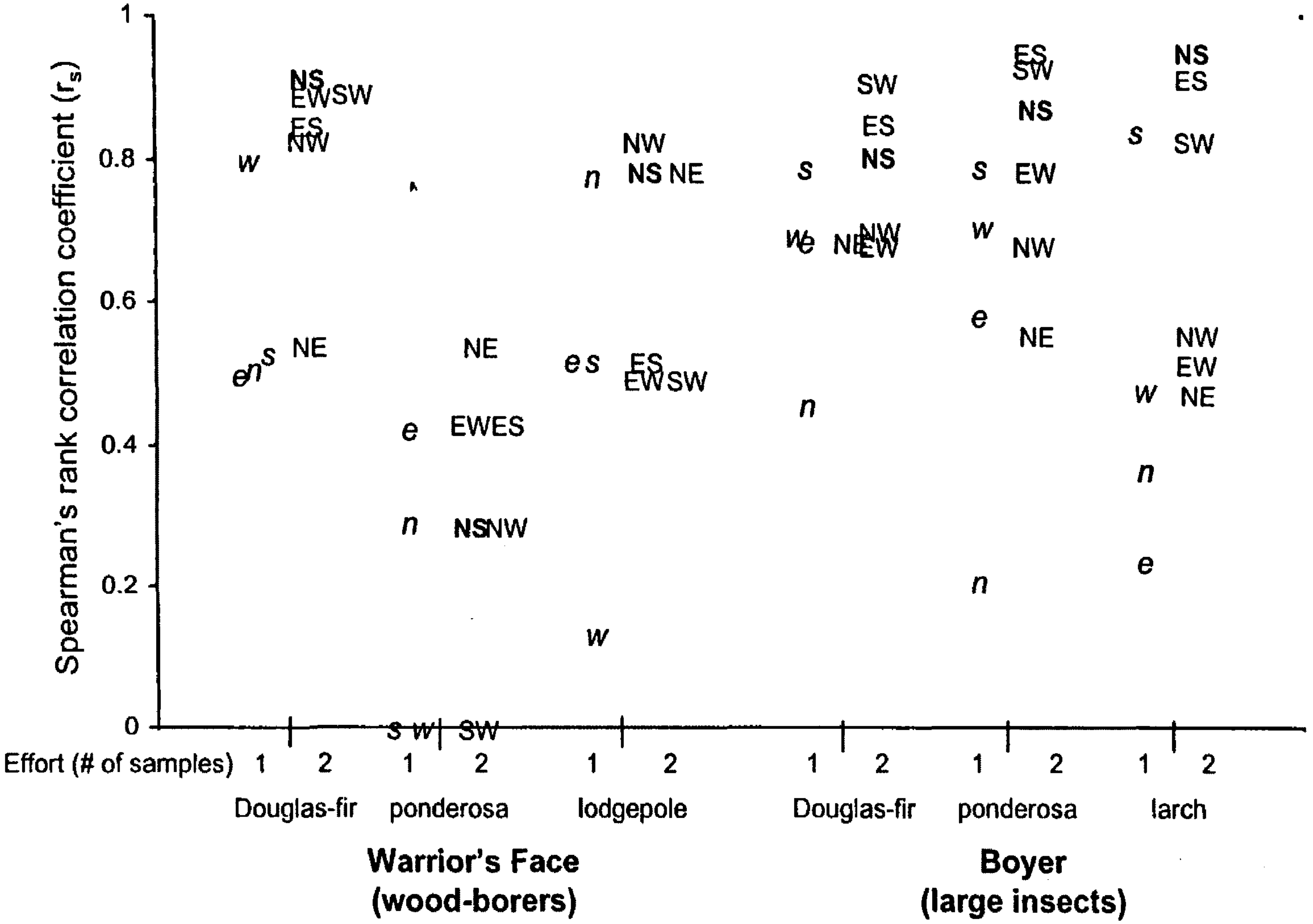

Figure 5. Correlations for individual bark samples (n,s,e,w) and two-sample combinations (NS,EW,SW,ES,NW,NE) against the full eight samples per tree. The standard sample (NS) was strongly correlated with the full sample for all tree species except ponderosa pine at Warrior's Face. At Boyer, the south side alone provided an estimate of wood-borer abundance nearly as accurate as the best combination of two samples.

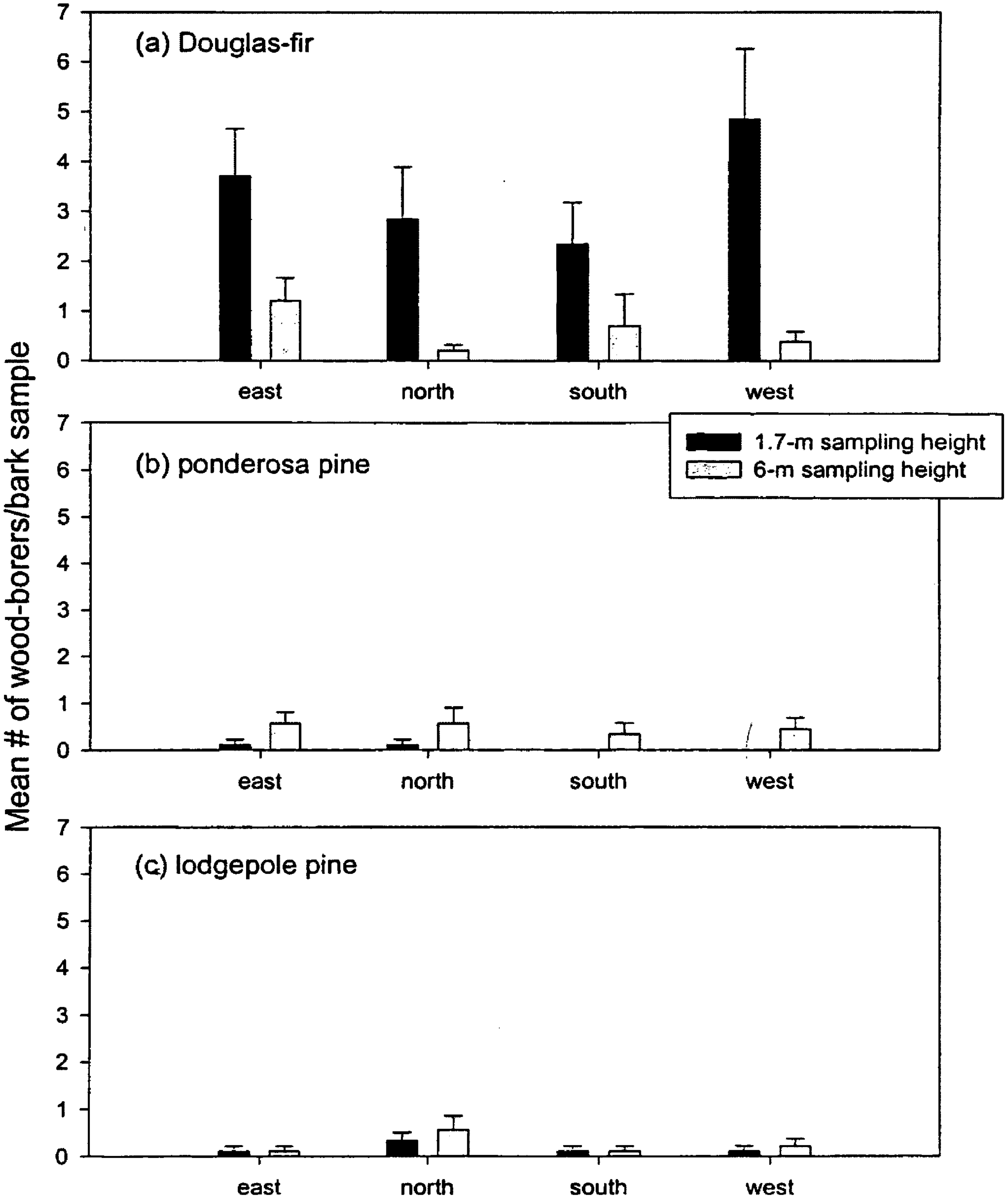

Figure 6. Mean number of wood-borers per bark sample, for each combination of tree side, sampling height, and tree species. Data are from Warrior's Face.

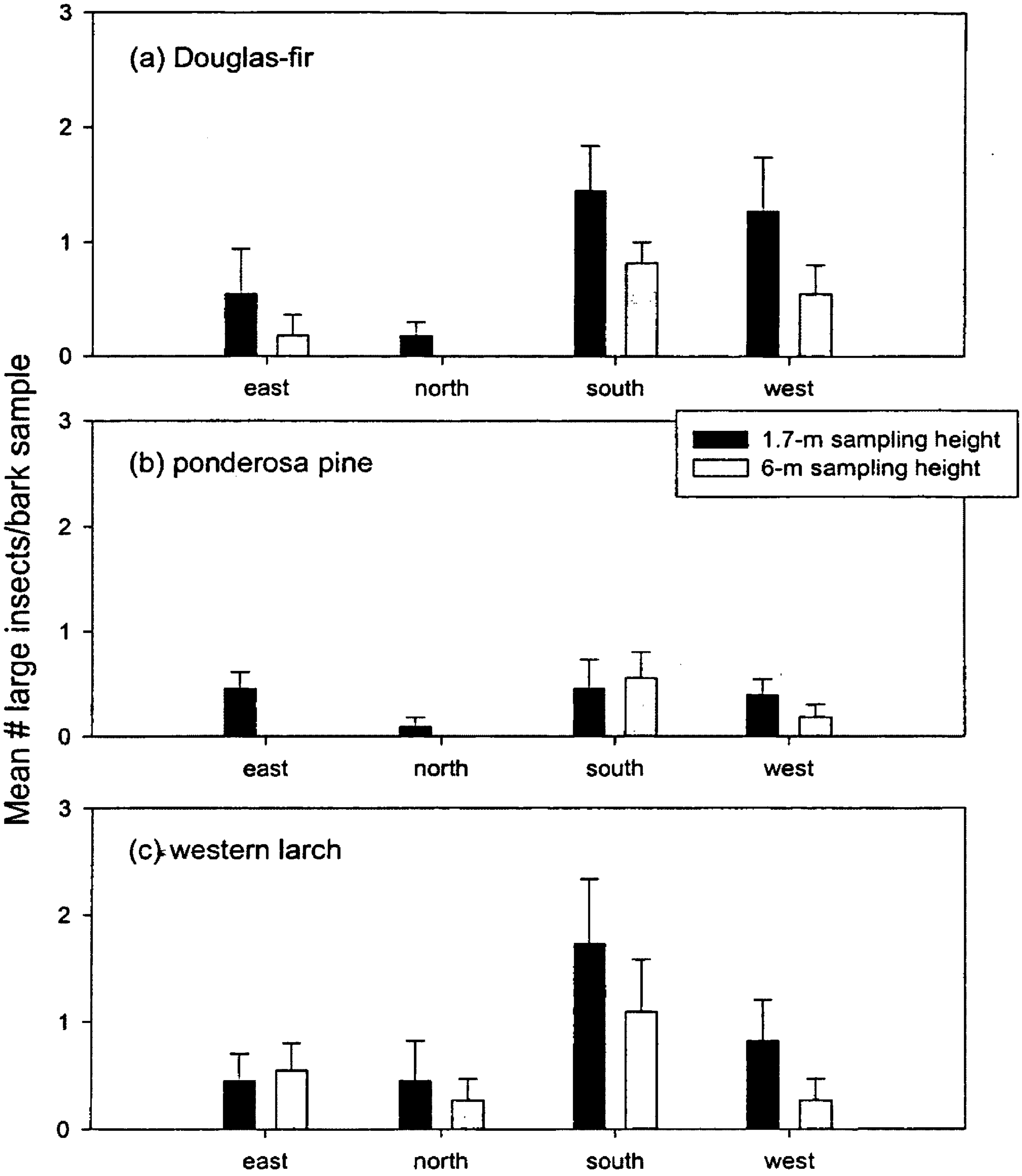

Figure 7. Mean number of large insects per bark sample, for each combination of tree side, sampling height, and tree species. Data are from Boyer.

calculated from subsamples of a large dataset (consisting of 28 bark samples per tree, for 44 trees). Precision of estimates using a single sampling height increased with up to 4 bark samples, as in this study. However, their comparison indicated a strong effect of sampling height, and that small-sample estimates were most reliable when they were taken from the middle of the infested bole (Pulley et al. 1977). By contrast, wood-borers in this study tended to be more abundant at eye-level than at the 6-m sampling height, meaning that samples taken from lower on the tree contained more information about the wood-borer abundance in the tree as a whole.

Continuing the search for a quick assessment of bark beetle population size, Schowalter et al. (1982) tested 'no-data' estimates against estimates from a dataset similar to that of Pulley et al. (1977). They found that simply measuring a tree's diameter and multiplying by the height of the infested bole gave an index that was highly correlated with the density of larvae (r = 0.784), pupae (r = 0.672), and emerging adults (r = 0.590) (Schowalter et al. 1982). Correlation strengths declined with ensuing life stages, presumably because of mortality factors (e.g., predation, parasitism, competition for phloem) that were unrelated to the simple tree characteristics (tree diameter and infested bole height) that made up the index (Schowalter et al. 1982).

Considerably less work has been conducted on colonization patterns of wood-borers in dead trees, but one study has determined a relationship between wood-borer abundance at breast height (1.45 m) and total wood-borer abundance in the tree. Zhang et al. (1993) reported patterns of colonization of the cerambycid *Monochamus sutor* in burned *Larix* and *Pinus* in China. Members of the genus *Monochamus* are common in dead (including fire-killed) conifers (Wickman 1964, Hughes and Hughes 1982, Edmonds and Eglitis 1989) and have been reported as prey of the Black-backed Woodpecker (Wickman 1965, Villard and Beninger 1993). Using counts of emergence holes, Zhang et al. (1993) developed linear regression equations for species of *Larix* and *Pinus* that predicted total emergence from a 0.1 m^2 sample at breast height. While emergence-hole data may not accurately estimate within-tree beetle populations (Pulley et al. 1977), Zhang et al.'s study suggests that it is possible to estimate wood-borer populations from a small sample taken near the ground.

The above studies benefit from having exhaustive sampling data (i.e. 'the truth') against which to test their small-sample estimates, but their aim was for considerably more precision than in this study. This study's objective was to rank overall insect abundance (as estimated by a larger bark sample) among trees using bark samples taken from ground level. Spearman's rank correlation coefficient proved to be a useful test for this objective. Its non-parametric approach measured the similarity between subsamples and the full sample by transforming the data to ranks, which is exactly the level of precision desired in the study. The high correlations that I found suggest that a relatively small sample of bark can provide as accurate a ranking of insect abundance as would a larger sample.

Optimum sampling design. In general, correlations with the full sample improved as more bark samples were included. Considering the tradeoff between effort and accuracy, it appeared that increasing effort from one to two bark samples greatly improved the likelihood of achieving a correlation greater than the 0.600 cutoff (see Figure 2). However, there was considerable variance in the correlations, probably because of the effect of tree side on insect numbers. The high variance at low levels of effort points out the importance of carefully choosing the tree sides used in small-sample estimates.

For a level of effort of two bark samples per tree, the standard sample design (north+south) was consistently highly correlated across trees species and sites, with the exception of ponderosa pine at Warrior's Face, where no combination of two bark samples exceeded the 0.600 correlation level (Figure 5). At Boyer, east+south and south+west had correlation strengths similar to the standard sample.

While taking two samples per tree proved to be a manageable level of effort, there was evidence that reliable results might be obtained using only one sample per tree. Each tree species at Warrior's Face had a single tree side whose correlation with the full sample was comparable to correlations using two bark samples (Figure 5). These correlations were above 0.600 for Douglas-fir (west side, $r_s = 0.812$) and lodgepole pine (north side, $r_s = 0.781$), but a particular tree side was not consistently strongly correlated across tree species, obviating the possibility of a sampling scheme standardized across tree species for this site. However, at Boyer, the correlation for the south side alone against the full sample was consistently high (Douglas-fir, $r_s = 0.797$; ponderosa pine, $r_s = 0.806$; western larch, $r_s = 0.842$; Figure 5), suggesting that effort could have been reduced to a single sample per tree with negligible effects on the accuracy of tree rankings.

Differences between insect measures. Although subsamples were highly correlated with the full sample at each site, these high correlations were for different measures of insects. Why were large insects less reliably predicted at Warrior's Face, and wood-borers less so at Boyer? It is possible, but not testable, that the differences resulted from environmental conditions peculiar to each site. Alternatively, burn age might have affected distribution of large insects within trees. Large insects at Warrior's Face, which was one year older than Boyer, might have been more mobile or had more time to move within the tree; hence, they could have migrated to the more moderate microclimates of the east and west sides of the tree. This hypothesis predicts that correlation between east-west sides and north-south sides for large wood-borers should be low, but the same correlation for small and medium wood-borers should be strong. This prediction is supported: north-south to east-west correlations are low for large wood-borers ($r_s = 0.389$), but high for small and medium wood-borers combined ($r_s = 0.668$).

Another alternative is that large wood-borers could have left the phloem and entered the xylem, where they would have been undetected by my method. In this case, there should be substantially fewer large wood-borers recorded than xylem entry holes. (In my observations, wood-borers less than 10 mm long rarely constructed xylem galleries.) This was not the case for Douglas-fir, lodgepole pine, and western larch, but was possible for ponderosa pine at Warrior's Face (Table 2). Ponderosa pine at Warrior's Face contained more than five times as many xylem entry holes as large wood-borers, while these figures were nearly equal at Boyer (Table 2).

This difference probably reflects the difference in burn age between the two sites. For *Monochamus scutellatus* in Ontario, larvae do not begin to tunnel into the wood until they reach the third instar, which generally happens in September of their first season (Rose 1957). If wood-borers at Boyer (in July of their first season) followed a similar schedule, most would have been too young to initiate xylem holes, accounting for

Table 2. Number of large wood-borers compared to number of wood-borer xylem holes found in bark samples of each of three tree species at two sites. Note that ponderosa pine bark contained fewer large wood-borers than xylem entry holes, suggesting that large wood-borers may spend more time in xylem in ponderosa pines than in xylem of other tree species.

Site	Tree species	Number of large wood-borers	Number of xylem entry holes
Warrior's Face	Douglas-fir	57	68
	Lodgepole pine	3	4
	Ponderosa pine	11	63
Boyer	Douglas-fir	48	1
	Ponderosa pine	18	25
	Western larch	62	32

the much lower incidence of holes compared to Warrior's Face (July of their second season; Table 2). Therefore, estimates of large insects in ponderosa pine at Warrior's Face may have been consistently low, but were probably reliable at Boyer. These data, although very limited, invite speculation that Douglas-fir phloem may be more abundant or more nutritious to wood-borers than ponderosa pine phloem, resulting in a longer period of foraging by wood-borers in Douglas-fir phloem.

Limitations of the sampling method: Although this method can reliably rank wood-borer abundance among trees, care should be taken to document the foraging behavior of the species under study before this method is assumed to indicate food availability (Wolda 1990). Woodpeckers that use surface-foraging, ground-foraging, or flycatching techniques (i.e. Red-cockaded Woodpecker [*Picoides borealis*] Northern Flicker [*Colaptes auratus*], or Lewis' Woodpecker [*Melanerpes lewis*], respectively) may forage for guilds of insects that would be overlooked by this method. In addition, woodpeckers that have been observed foraging consistently below the bark may switch tactics in different habitats or seasons (Conner 1979). This method may prove useful for estimating wood-borer availability in downed logs as well as standing dead trees, but I did not test this.

Ponderosa pines appeared to have different colonization patterns than other trees in this study. They were the only tree species where insect density at 6 m tended to be greater than at ground level, and this pattern was significant at Warrior's Face. Also, large wood-borers may reside in the xylem of ponderosa pines more frequently than they do in other tree species (at least in burns greater than one year old, where xylem galleries already exist). Therefore, if study animals forage heavily in ponderosa pine, this method should be used with caution, and sampling at heights higher than eye level should be considered.

Summary. Numbers of wood-boring beetle larvae in bark samples taken from the north and south sides of a tree at ground level were used to rank overall insect abundance among trees. Usefulness of the method was evaluated by comparing the results to rankings determined from the contents of a larger bark sample.

The standard, two-sample, eye-level method provided a reliable way to compare the relative abundance of wood-borers among trees with a minimum of sampling effort. However, wood-borer abundance and distribution can vary markedly across sites and tree species. At Boyer, accurate rankings of wood-borer abundance could have been calculated from just one eye-level sample (the south side), whereas two samples from each tree were necessary at Warrior's Face. By first testing small-sample tree-ranking designs against larger samples of bark, as in this study, researchers can identify both the level of effort and the particular tree sides needed to provide accurate rankings of wood-borer abundance.

At Warrior's Face, the standard sample did not reliably indicate insect abundance in ponderosa pine. Wood-borers may colonize ponderosa pine in a pattern different than other conifers, and caution should be used with this species. However, errors from ranking ponderosa pine using the standard sample did not alter rankings of ponderosa pine relative to other tree species.

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CHAPTER II

USING PREY DENSITY TO UNDERSTAND HABITAT USE BY THE BLACK-BACKED WOODPECKER IN TWO POST-FIRE FORESTS OF THE NORTHERN ROCKY MOUNTAINS

INTRODUCTION

Field studies of an animal's behavior can identify habitat components it finds valuable, an important goal in studies of environmentally sensitive or threatened species. A common approach for studying habitat use, stemming from the idea that vegetation structure affects habitat occupancy (MacArthur et al. 1962), is to develop a gestalt of a species' habitat using multivariate statistics on vegetation measurements (Cody 1981). Habitat components that appear more often in occupied than random sampling plots should contain items that the study animal requires or 'prefers'. While this approach describes vegetative associations that a study animal finds useful, it does not illuminate the underlying mechanisms.

Animals probably closely track a certain resource only when it is in short supply (MacArthur 1961, Wiens 1977). Central place foragers, in particular, settle in their habitats primarily in relation to the distribution of the most limited resource (Orians and Wittenberger 1991). Accordingly, habitat use might be better understood by measuring the availability of specific resources that are suspected to limit population size, such as (for birds) nest sites or food (Lack 1954).

I used this approach to investigate the foraging behavior of the Black-backed Woodpecker (*Picoides arcticus*) in two stand-replacement-burned (hereafter, simply post-fire) forests of the northern Rocky Mountains. The Black-backed Woodpecker is a rare habitat specialist that in the West is nearly restricted to early post-fire forests (Hutto 1995, Murphy and Lehnhausen 1998). Because of the rarity of fires and the frequency of salvage logging, the Black-backed Woodpecker may now exist at population levels much lower than in historic times (Hutto 1995). Conservation of the Black-backed Woodpecker depends in part upon identifying important resources for retention when habitat is to be logged. In the case of post-fire forests, this is critical because of the strong economic incentive to harvest burned trees.

Post-fire forests are unique because they consist almost entirely of standing dead trees (snags). Starting immediately after the fire, these snags are colonized by wood-boring beetles (Coeloptera: Buprestidae and Cerambycidae) and, perhaps to a lesser extent, bark beetles (Coleoptera: Scolytidae) (Parmelee 1941, Furniss 1965). Studies of woodpeckers in insect outbreaks have suggested that woodpeckers are not able to curb insect populations during outbreaks, implying that food availability is not limiting at such times (Otvos 1965, 1979; Crockett and Hansley 1978). Similarly, food availability may be very high in wood-borer and bark beetle attacked snags during the early years post-fire.

The Black-backed Woodpecker possesses strong excavator morphology compared to other *Picoides* species (Spring 1965), and frequently excavates nests in hard, intact-topped snags with little decay (Bent 1939, Short 1974, Saab and Dudley 1998, Hejl pers. comm.). Such snags are numerous in post-fire forests, implying that nest site availability may be very high. Therefore, at least during the period that insect food is abundant in post-fire forests, resources may not limit woodpecker populations (Murphy and Lehnhausen 1998). If this is so, it may be dispersal to the newly created habitat that limits population sizes (e.g. Hubbell 1998).

However, food limitation usually is not an all-or-none phenomenon, because food availability varies continuously throughout most habitats (Raphael and Maurer 1990). If some degree of food limitation exists, within-burn variation in food availability should result in disproportionate use of food-rich parts of the habitat. Higher degrees of food limitation could cause individuals to settle in patches with relatively more food than surrounding parts of the same habitat, cause within-species competition for high-quality sites, or even cap the number of individuals that occupy the habitat. In the extreme case, animals simply do not persist in areas where food is too scarce for survival. Thus, identifying levels of food limitation within a site may help understand habitat use at several levels. If food is distributed in such a way that Black-backed Woodpeckers must track prey-rich habitat components, this information would be important for conservation planning.

Alternatively, it is possible that food is abundant enough in burned forests that Black-backed Woodpeckers forage indiscriminately, or in response to some other variable, such as ease in removing insects or distance to nest sites. A third alternative is that Black-backed Woodpecker foraging is constrained by either a dietary preference or a stereotyped foraging style.

At two post-fire sites, I tested the hypothesis that within burns, Black-backed Woodpeckers settle and forage in prey-rich areas. I suspected that woodpeckers might use prey-rich areas at one of three levels: 1) individually prey-rich trees; 2) a tree species consistently higher in prey than other tree species; or 3) prey rich areas within a burned forest. I measured prey density at these levels and compared use to availability at each. The different insect and tree assemblages of the two sites allowed me to assess diet and tree use independently. To be sure that insect measurements accurately represented available insects, I measured the diet of Black-backed Woodpeckers at each study location. I also recorded foraging tactics and habitat associations at foraging sites.

I compare my habitat-use data with published reports of Black-backed Woodpeckers foraging in a range of habitats. Published reports generally agree that Black-backed Woodpeckers are habitat specialists, but habitat components upon which this species is specialized have not been clearly identified. I discuss two hypotheses for the criteria that govern their habitat selection: a) that Black-backed Woodpeckers are dietary specialists on wood-boring beetles; or b) that they occupy habitat where dead trees provide rich food resources, but within such habitats they are dietary generalists. Finally, because little is known about insect colonization of burned forests, and because insects are extremely important to the insectivorous birds that occupy post-fire forests, I summarize what is known about factors affecting insect populations in burned forests.

METHODS

STUDY AREAS

In 1998, I studied the two-year-old Warrior's Face burn in Salmon Co., Idaho (45° 43′ N, 114° 38′ W). Situated in the Selway-Bitterroot Wilderness, the site had never been logged and was dominated by, in order of abundance, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*). The portion of the site I studied had burned severely and continuously, killing virtually all trees and leaving very few green patches. The stand-replacement-burned area constituted approximately 191 ha, of which I surveyed about 150 ha. The study area supported 9 pairs of Black-backed Woodpeckers.

In 1999, I studied the one-year-old Boyer Creek burn near Plains, Mineral Co., Montana (47° 27′ N, 114° 46′ W). The forest was dominated by, in order of abundance, Douglas-fir, ponderosa pine, western larch (*Larix occidentalis*), and grand fir (*Abies grandis*). It had been extensively logged in the 1930s, and regenerating trees were selectively logged in the 1960s (T. O'Connor, pers. comm.). The burn was severe but patchy, perhaps partly because the many logging roads and post-logging seral stages served as fire breaks. The site was not logged after it burned. After surveying the entire stand-replacement-burned area early in the season, I concentrated my research in approximately 230 ha of the site, which contained 5 pairs of Black-backed Woodpeckers.

DIET

I identified prey by recording food brought to nestlings and by examining bark from sites where birds had foraged successfully. Because I did not examine stomach contents or collect nestling food, taxa included in the Black-backed Woodpeckers' diet are best estimates. My goal was to determine whether diet at these study sites is similar to reports in the literature. I considered it particularly important to distinguish between wood-borers and bark beetles as the predominant prey, since these two guilds are reported to be common prey items but differ greatly in size, abundance, and distribution in burned forests (Beal 1911, Lester 1980, Goggans et al. 1988, Murphy and Lehnhausen 1998).

Videotaping nests. I used a Canon 2500 Hi-8 videocamera equipped with a 22-x optical zoom and Fuji Hi-8 MP videotape to record food brought to nestlings. I positioned the camera at roughly the level of the nest entrance and at right angles to the cavity orientation so that I obtained profiles of adults as they visited the nest (Franzreb and Hanula 1995). At the end of the field season, I watched tapes using an RCA Hi-8 video editor and measured prey lengths and exposed culmen simultaneously on stilled images.

I estimated actual prey length by calculating the ratio of prey length to exposed culmen measured from videotape and then multiplying by a mean exposed culmen length calculated for male (n = 6) and female (n = 7) adult Black-backed Woodpeckers banded and measured at Warrior's Face. I also calculated 95% confidence intervals for the mean culmen lengths. Using these confidence intervals, I estimated that prey length estimates for 95% of birds would be inaccurate by no more than 5.6% (for males) and 3.4% (for females) of the actual prey length, or about 1 mm for a 20-mm prey item.

Videotape measurements gave me a size distribution for prey insects, but in most cases taxon was not identifiable. For larger insects (> 10 mm long), taxon could be inferred as wood-borers from size distributions of available insects (see Results). The method of observing prey at nests is vulnerable to bias toward large prey for three reasons: smaller prey can be hidden in the beak; many small prey carried in the beak can be recorded as one large insect; and adults may save larger prey for returning to the nests, eating smaller items as they forage (Pechacek and Kristin 1996). I minimized these biases by 1) recording at least one prey item brought for all feeding visits, even if the beak appeared empty (prey length recorded as zero); 2) recording the number of prey apparently fed to nestlings (when parents fed at the lip of the cavity), assuming that only one prey item was delivered per feeding motion; and 3) using an independent method of identifying prey: examining galleries and xylem entry holes in bark samples taken immediately following an observed prey capture.

I normally videotaped nests for two hours each day; on two occasions at Boyer, I recorded for four hours per day. For each day of videotape, I calculated two mean prey lengths: a conservative mean that included feeding visits with prey of length zero; and a maximum mean calculated from lengths of visible prey only. I assumed that these two means bracketed the true mean prey length delivered to nestlings. I then averaged each daily mean for each nest and calculated overall mean prey lengths from nest means.

Successful foraging sites. I also identified prey by sampling bark after observing successful foraging by adult Black-backed Woodpeckers. I climbed trees using Ben Meadows™ tree-climbing spurs and belt. I removed a 5 x 5 cm square of bark centered on the point I saw the bird obtain prey. I then removed the surrounding bark to make a 15 x 15 cm sample for comparison to standard bark samples (see below). In most cases, I could identify the prey type from the galleries it had made in the bark. I identified prey as wood-borers if the bark sample met one of three criteria:

1. The 5 x 5-cm sample was empty of insects and there was a wood-borer entry hole in the xylem.
2. Both 5 x 5-cm and 15 x 15-cm samples were empty, wood-borer holes were absent, but wood-borer galleries were present in the xylem.
3. The 5 x 5-cm sample was empty and the 15 x 15-cm sample contained nothing other than wood-borers.

All other prey items were classified as non-wood-borer. Bark beetles (constituting a few prey items) were identifiable among non-wood-borer prey because of their distinctive phloem galleries.

It is possible that I was more likely to see larger prey extracted from the bark than smaller prey, and that this might bias my observations toward larger taxa. I countered this bias by observing from close distances (usually < 20 m) with 10-x binoculars. Black-backed Woodpeckers have stereotyped behaviors when eating: turning head sideways to extract insects, holding prey in beak for delivery to nest or snapping beak shut several times and extending tongue, making it apparent when prey was obtained (pers. obs.).

HABITAT USE

Vegetation. Available tree species were determined by systematically sampling trees in 11.3-m radius (0.04 ha) plots at 200-m intervals across the Warrior's Face site (40 plots) and 160-m intervals across the Boyer site (63 plots). I recorded diameter at breast height (dbh), burn severity, and tree species for all trees > 8 cm dbh. Relative frequencies of tree species were calculated for each sample point and then averaged for each site. The 8-cm-dbh cutoff prevented dense stands of saplings from biasing distributions of larger trees that were of greater importance to woodpeckers. The smallest tree recorded in a foraging observation was 13 cm dbh.

Foraging observations. I recorded foraging observations of adult Black-backed Woodpeckers from May through July 1998 and 1999. For each observation, I recorded key variables including tree species, top condition (intact, broken, or forked), diameter at breast height (dbh), estimated foraging height, relative foraging height (lower, middle, or upper third of tree), position in the tree (trunk vs. branch), and foraging technique used (glean, flake, drill, or a combination of flaking and drilling). *Gleaning* was defined as obtaining prey from the bark surface; *drilling* as pecking forcefully, perpendicular to the tree trunk; and *flaking* as removing bark using pecks directed obliquely (e.g., Conner et al. 1979). Combination flake/drilling was recorded when woodpeckers used a rapid succession of these two techniques. I also recorded the number of snags over 30 cm dbh within 11.3 m of the foraging observation, to compare to previous findings indicating that Black-backed Woodpeckers occupy sites with high snag densities relative to surrounding areas (Saab and Dudley 1998, Hejl pers. comm.).

Because of the relatively small populations of Black-backed Woodpeckers at both sites, I attempted to keep my foraging observations as independent of each other as possible. I recorded only one foraging observation per individual per 15 minutes (Hejl et al. 1990), and in practice I recorded only a few total foraging observations each day. In each case I recorded the first foraging attempt I saw 1 min after first observing the bird, to offset a bias from differential detectability of birds on different substrates. Although most foraging occurred on snags, I recorded foraging on other substrates (i.e. logs, ground) when they met the above criteria. For data analysis, I treated all observations as statistically independent.

Spatial use of burn. At Warrior's Face, I systematically surveyed Black-backed Woodpecker use of the study area by walking gridded transects each morning between 0600 and 1100 MST. At other times during the day, I recorded foraging observations opportunistically. I recorded the compass bearing and distance from each foraging observation to the nearest gridpoint and marked each fed-upon tree with a numbered, aluminum tree tag. I plotted systematic and opportunistic observations of foraging birds on a USGS 7.5' quadrangle enlarged to 1" = 100 m, yielding a map of areas of the site used for foraging (Figure 8).

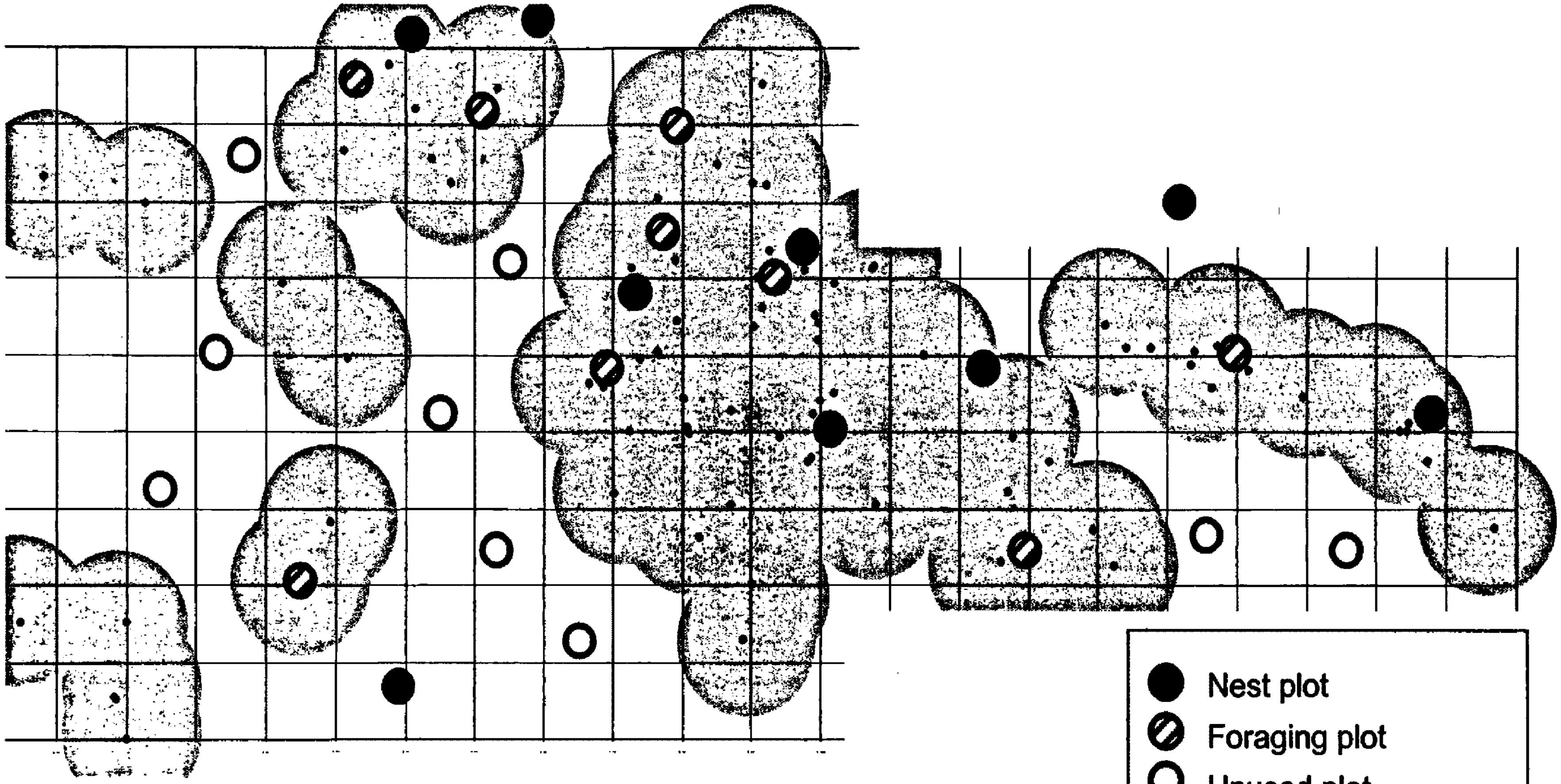

Figure 8. Schematic map of the Warrior's Face study area, showing locations of plots used to estimate insect densities in three patch types. The foraged area of the site (gray) was defined as all areas within 100 m of a foraging observation. Unused sampling plots were distributed systematically within the remaining area (white). Distance between grid intersections = 100 m.

Standard samples. I compared insect abundance among trees using an index of insect density obtained from two bark samples (one 15 x 15-cm bark square, taken at a height of 1.7 m, from each of the north and south sides) in each tree. Phloem and bark were broken apart and all insects > 1 mm in length were counted and identified to family (when possible). Each insect was categorized by length (small: < 5 mm; medium: 5 – 10 mm; large: 10 – 20 mm; extra large: > 20 mm) and width (A: < 1 mm; B: 1 – 2 mm; C > 2 mm). I developed this method from standard bark-beetle sampling methods (e.g. Pulley et al. 1977).

Expanded samples. My method for comparing insect abundance among trees was streamlined so that I could complete the necessary sampling within a field season. Estimates of insect abundance came from only two samples taken at eye level (1.7 m). To check that this standard sample represented numbers of insects in the tree as a whole, I performed more intensive sampling for a subset of trees (Warrior's Face: 14 Douglas-firs, 9 ponderosa pines, 9 lodgepole pines; Boyer: 11 each of Douglas-fir, ponderosa pine, and western larch). I sampled north, south, east and west sides at heights of 1.7 m and 6 m, yielding a total of eight bark samples per tree. I then calculated correlations between the standard bark sample and the full eight samples per tree (see Chapter 1 for details of the analysis). With one exception, the samples were highly correlated (see Chapter 1), giving me confidence that trees with many insects in the standard sample contained a high overall insect density, while trees lacking insects in the standard sample contained fewer insects. My goal was not to estimate total numbers of insects in trees, but rather gauge each tree's insect load accurately enough to rank insect abundance among trees.

The goal of the expanded sample was to determine if insect measures in the standard sample represented overall insect abundance in the tree. To be useful, this insect measure must be directed at the subset of insects that Black-backed Woodpeckers used as prey. Two potential prey measures were number of wood-borers and number of large (i.e. > 10 mm long; includes extra-large category) insects, which consisted mostly of wood-borers. Because many wood-borers were less than 10 mm long, however, measurements of wood-borers in bark samples were higher than measurements of large insects.

Random trees. I paired samples of fed-upon trees with randomly chosen trees sampled the same day or no more than three days after the foraging observation. I selected random trees by choosing points at a random bearing and distance from a randomly selected grid point. At these points I sampled the closest tree of each species present, plus (at Warrior's Face) one tree of the same species and similar dbh as the fed-upon tree with which it was paired.

Patch samples. At the end of the nesting season (late July-early August) at Warrior's Face, I compared average insect densities in foraging, unused, and nest patches. I designated all parts of the study area within 100 m of a foraging observation as potential foraging area, and all parts > 100 m from any foraging observation as unused (see Figure 8). Nest plots were centered on each of the nine nest trees used that season. I then selected nine foraging patches from parts of the burn that contained the greatest concentrations of systematic foraging observations. I systematically distributed nine unused patch plots by choosing points equally spaced across a map of the unused portion of the site. I then measured the distance and direction from the map point to the nearest grid point to locate sampling points on the ground. At each of these 27 plots I sampled insects in up to 8 Douglas-firs and 2 trees of each other species within a 25-m radius of the point center. I recorded tree species, dbh, and burn severity for all trees within the 25-m radius. Sampling was weighted toward Douglas-fir because nearly all foraging observations at this site were on Douglas-firs (see Results).

DATA ANALYSIS

Raw counts in bark samples were combined to give an index of prey density for each tree. These data contain many zero values and approximate the negative binomial distribution (Fowler and Cohen 1990, White and Bennetts 1996). Therefore, non-parametric tests (Mann-Whitney U, Kruskal-Wallis) were used when comparing densities among single-tree samples. I also conducted *t*-tests for pairwise comparisons of foraging vs. random trees matched by date and, for Warrior's Face, by tree size, to control for prey-density differences owing to time of season and tree size.

Reliability of the standard sampling technique was assessed by calculating Spearman's rank correlation coefficient between the number of insects in the standard sample and the expanded sample (see Chapter 1).

For the comparison of foraging, nesting, and unused patches, mean insect density was calculated for each plot and compared using two-way ANOVA (n= 9 points/patch type) with patch type (foraging vs. unused vs. nesting) and tree species as fixed factors.

RESULTS

DIET

Videotaping nests. I recorded 103 prey items brought to 4 nests at Warrior's Face, and 289 prey items brought to 3 nests at Boyer (Table 3). The rate of nestling

Table 3. Summary of prey-size estimates and prey-delivery rates for seven Black-backed Woodpecker nests at two sites in the northern Rocky Mountains.

	Conservative estimate					**Maximum estimate**					
Nest ID	Mean length (mm)	SE	No. of prey	n	Prey/min	Mean length (mm)	SE	No. of prey	n	Prey/min	Total min of video
CY I10.5	13.7		10	1[a]	0.08	22.9		6	1[a]	0.05	123
SC F8.5	21.5		3	1[a]	0.03	21.5		3	1[a]	0.03	109
SC A3	4.2		6	1[a]	0.05	12.5		2	1[a]	0.02	123
SC Z5	11.2	2.5	84	10[a]	0.05	15.6	2.2	66	10[a]	0.04	1475
Warrior's Face Mean	**12.7**	**3.6**	**103**	**4[b]**	**0.05**	**18.1**	**2.5**	**77**	**4[b]**	**0.04**	**1830**
Ours	6.7	1.1	73	3[a]	0.2	10.2	1.1	47	3[a]	0.13	366
FKN	14.9	1.2	39	4[a]	0.1	19.9	2.5	31	4[a]	0.01	385
Polly's	11.3	1.8	176	11[a]	0.13	15.1	1.6	132	11[a]	0.09	1278
Boyer Mean	**11**	**2.4**	**288**	**3[b]**	**0.14**	**15.1**	**2.8**	**210**	**3[b]**	**0.09**	**2029**
Overall Mean	**11.9**	**2.1**	**391**	**7[b]**	**0.09**	**16.8**	**1.8**	**287**	**7[b]**	**0.06**	**3859**

[a] for nest means, n = number of days of videotaping [b] for group means, n = number of nests

provisioning at Boyer was twice the Warrior's Face rate (0.10 prey/min at Boyer vs. 0.05 prey/min at Warrior's Face). Mean prey length estimates at Warrior's Face were12.7 mm (conservative) and 18.1 mm (maximum); for Boyer, mean prey length estimates were 11.0 mm (conservative) and 15.1 mm (maximum).

These two estimates indicate that between 54% and 78% of prey were greater than 10 mm long (Figure 9a). By comparing the distributions of prey lengths to the distributions of available insects (Figure 9b), it is apparent that Black-backed Woodpeckers used large (and extra-large) insects far in excess of their availability.

The probable identity of these large prey items can be ascertained by examining the distribution of large and extra-large insects among different insect groups (Figure 10). At Warrior's Face, wood-borers comprised 78% of all large and extra large insects in random-tree samples; at Boyer, 94% of large and extra large insects were wood-borers (Figure 10). Given this distribution, and the fact that at least some prey items < 10 mm long were probably also wood-borers, it seems likely that the incidence of wood-borers in Black-backed Woodpecker diets in these study areas was similar to that published elsewhere (60 – 75%; Beal 1911, Murphy and Lehnhausen 1998).

Successful foraging sites. Bark samples taken after watching Black-backed Woodpeckers forage also suggest that wood-borers were the main prey item. I classified 22 of 28 (79%) of the Warrior's Face observations and 24 of 38 (63%) of the Boyer observations as wood-borers using criteria based on contents of bark samples, phloem galleries and wood-borer xylem holes.

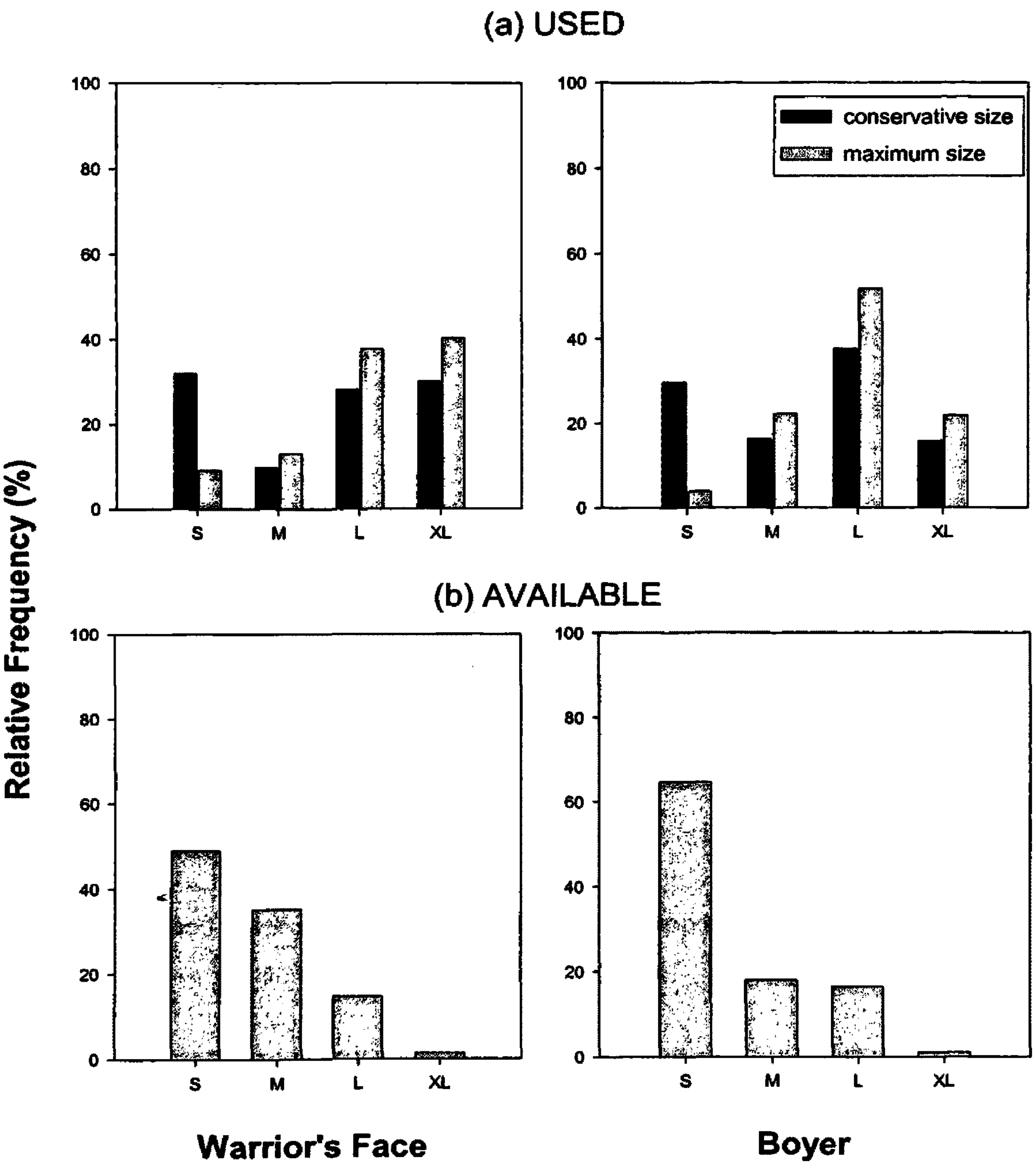

Figure 9. Size distributions of (a) nestling prey and (b) insects in random bark samples, for two sites. Letters denote length categories: S = < 5 mm, M = 5-10 mm, L = 10-20 mm, XL = > 20 mm.

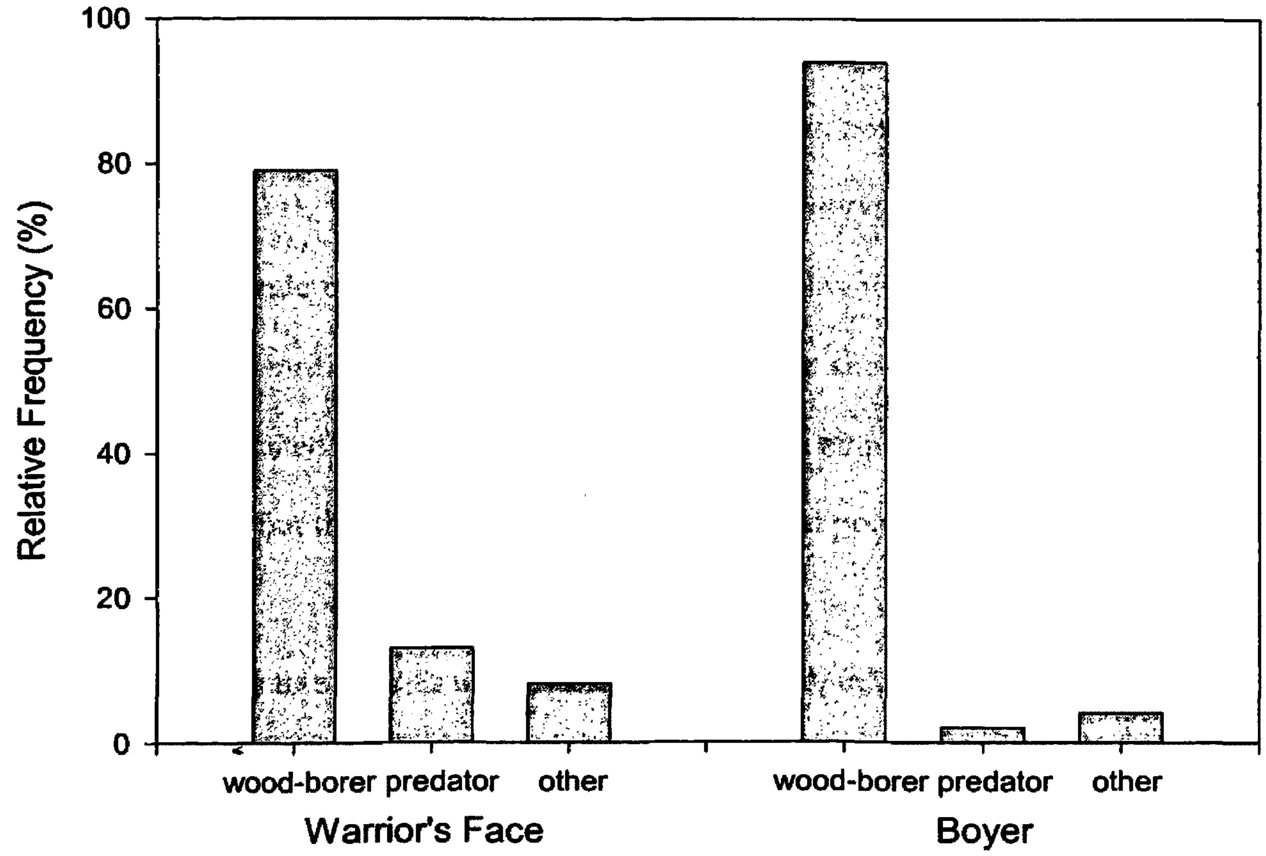

Figure 10. Predominance of wood-borers among insects > 10 mm in length. Data are from random trees at each of the two sites.

HABITAT USE

Vegetation. The Warrior's Face site consisted primarily of Douglas-fir, lodgepole pine, and ponderosa pine; other species, including subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), and grand fir, were rare. Boyer was dominated by Douglas-fir, with smaller amounts of ponderosa pine, grand fir, western larch, lodgepole pine, and western redcedar (*Thuja occidentalis*) (Figure 11b).

Foraging behavior. At Warrior's Face, 91% of 98 foraging observations were on Douglas-fir; the remaining few were on lodgepole pine, ponderosa pine, and Engelmann spruce (Figure 11a). At Boyer, 53% of 76 foraging observations were on western larch, 33% were on ponderosa pine, and 11% were on Douglas-fir. The remaining 4% were in grand fir or unidentified downed logs. Comparing tree species use to tree species availability indicated that Black-backed Woodpeckers emphasized Douglas-fir at Warrior's Face, but they emphasized western larch and ponderosa pine at Boyer (Figure 12).

Apart from tree species use, Black-backed Woodpeckers generally foraged similarly at the two sites (Table 4). Mean tree size was much greater for fed-upon trees than for trees in systematic vegetation plots. The difference in mean size of fed-upon trees at the two study sites (Table 4) probably reflects differing distributions of large trees as a result of the logging histories of the two sites. Foraging birds were nearly always found on trunks of intact snags. Black-backed Woodpeckers foraged on lower or middle thirds of snags (mean foraging height around 9 m; Table 4), using a combination of flaking and drilling techniques.

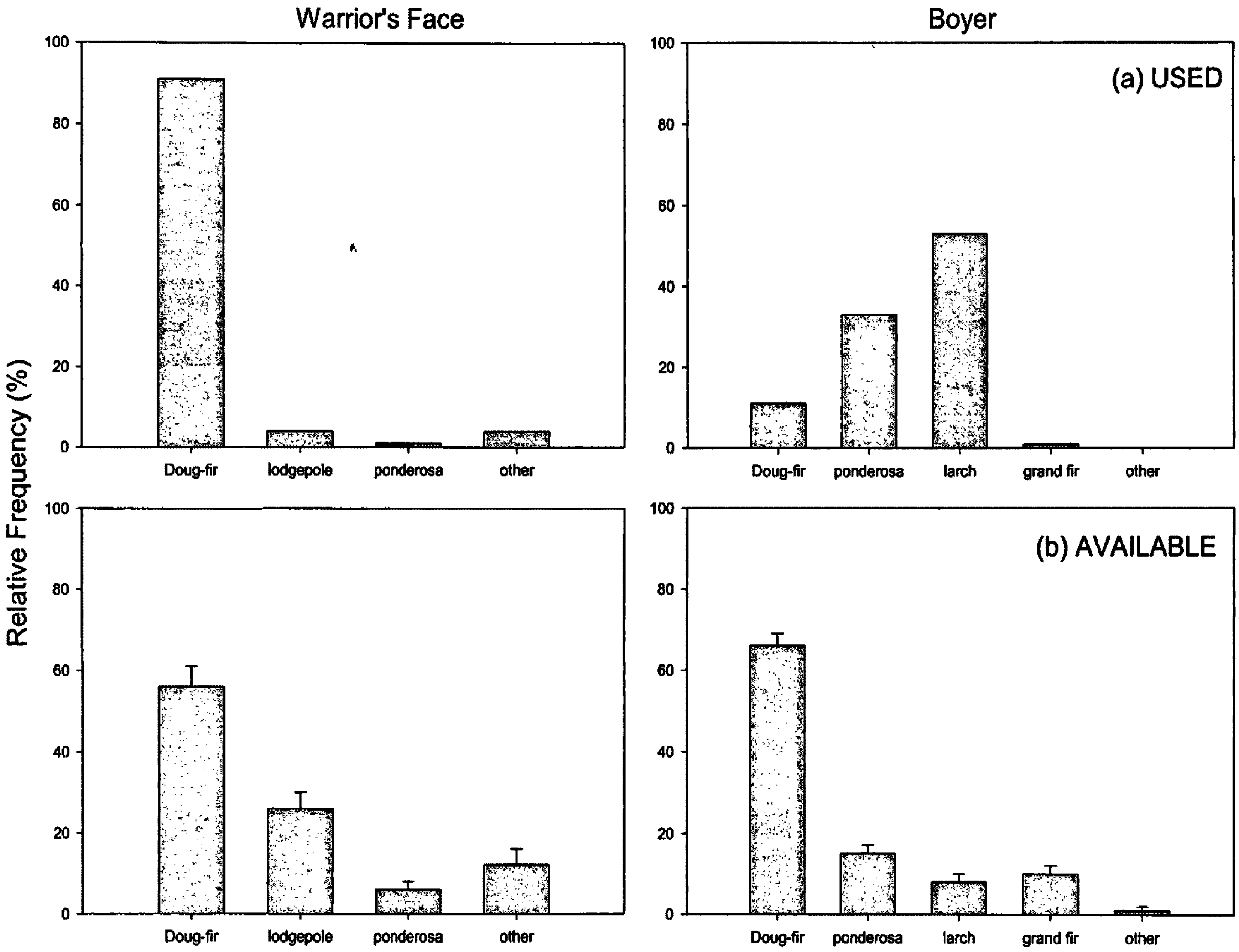

Figure 11. Relative frequencies of (a) used and (b) available tree species, for each of the two sites. Tree use was nonrandom, but the emphasized tree species differed between sites.

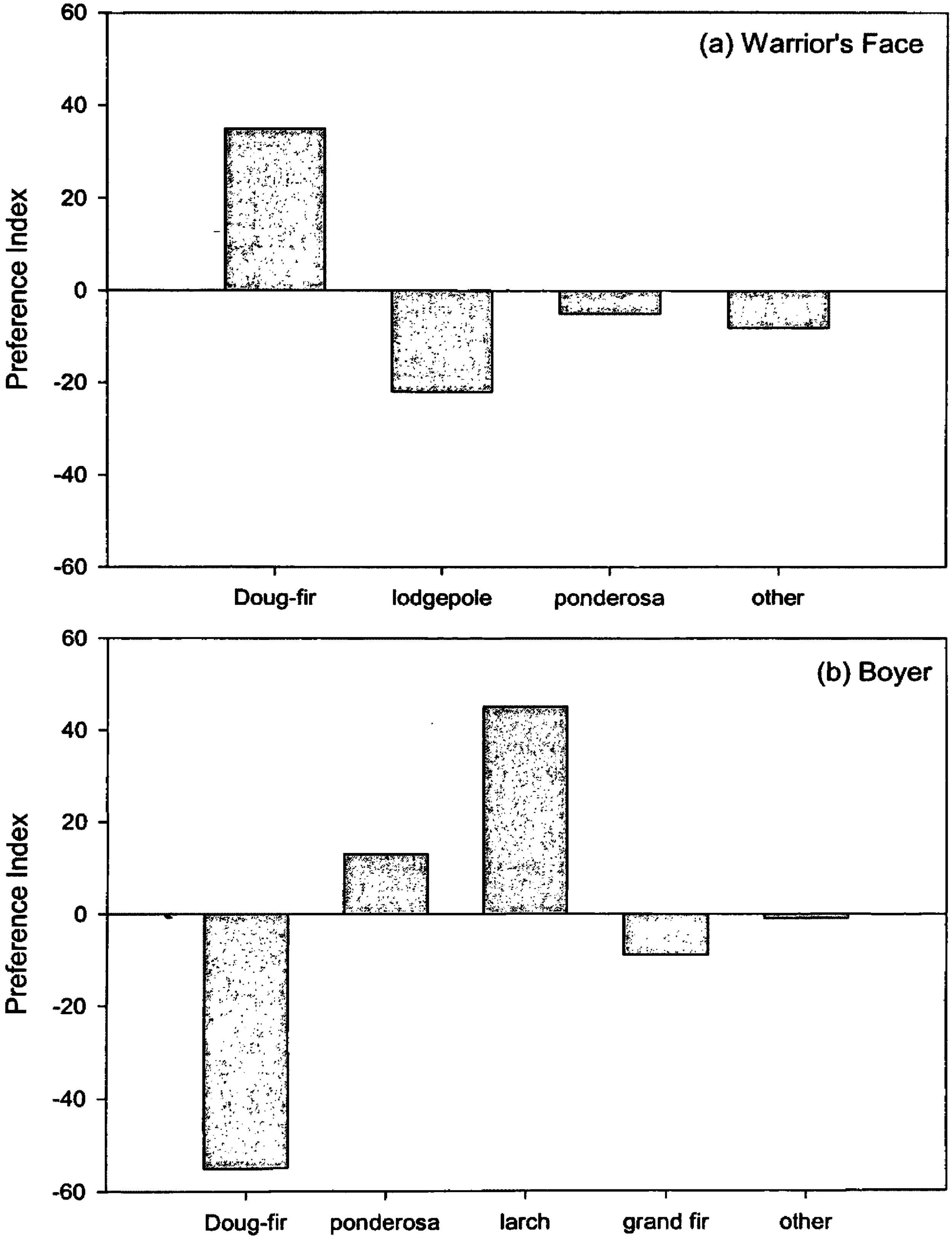

Figure 12. Preference indices (use minus availability) for tree species at (a) Warrior's Face and (b) Boyer. Tree species differ between x-axes, reflecting different tree compositions at the two sites.

Table 4. Summaries for data from 183 observations of foraging Black-backed Woodpeckers in two post-fire forests. Values in parentheses are standard errors.

		Warrior's Face	**Boyer**
Number of observations		98	85
Emphasized tree species		Douglas-fir	western larch, ponderosa pine
Mean dbh (SE)	used	44.4 (1.66) cm	30.9 (1.68) cm
	available	21.9 (0.91) cm	20.8 (0.6154) cm
Mean foraging height (SE)		10.1 (.46) m	8.1 (.79) m
Relative height on tree	lower 1/3	27%	59%
	mid 1/3	54%	29%
	upper 1/3	19%	12%
Position in tree		97% trunk	100% trunk
Substrate type		98% snags	97% snags
Tree top condition		98% intact	98% intact
Foraging method	flake	18%	26%
	drill	55%	16%
	flake/drill	20%	56%
	glean	7%	2%
Mean number of trees > 30 cm dbh/ 0.04 ha (SE)			
	used	6.1 (.28)	3.1 (.23)
	available	3.8 (.38)	4.4 (.36)

Observations from previous studies (Saab 1998; Hejl and McFadzen, unpubl. data) of Black-backed Woodpeckers occupying burn patches with higher-than-average densities of large snags (> 30 cm dbh) were not clearly supported in my observations. Foraging sites at Warrior's Face contained more large snags than systematic vegetation plots of the same size. However, this apparent preference for areas containing large snags was reversed at Boyer; foraging sites contained fewer large snags than systematic vegetation plots of the same size. Differences between foraging and random sites at both study areas were significant at $p = 0.01$ (Warrior's Face: $n = 125$, $U = 875.5$, $Z = -4.4$; Boyer: $n = 139$, $U = 1776$, $Z = -2.6$).

INSECT DENSITY

Insect assemblage. At each site, wood-borers constituted 35% of the total number of insects collected in random tree samples (Figure 13). Bark beetles were much more abundant at Boyer than at Warrior's Face, as expected for a one-year-old burn vs. a two-year-old burn. At Warrior's Face, fly larvae (most < 5 mm long) were the most numerous group, but most of these were aggregated in large ponderosa pines. Because wood-boring beetles often are much larger than either bark beetles or fly larvae, it is safe to conclude that the majority of insect biomass in the bark samples was composed of wood-boring beetles. Furthermore, bark beetles and fly larvae occurred primarily in clumped distributions of tens or hundreds in a few individual trees, while wood-borers were much more diffusely distributed throughout trees, making them more generally available as prey.

Expanded samples. The best-correlated prey measure between the standard and expanded samples differed for the two sites (see Chapter I). For Warrior's Face,

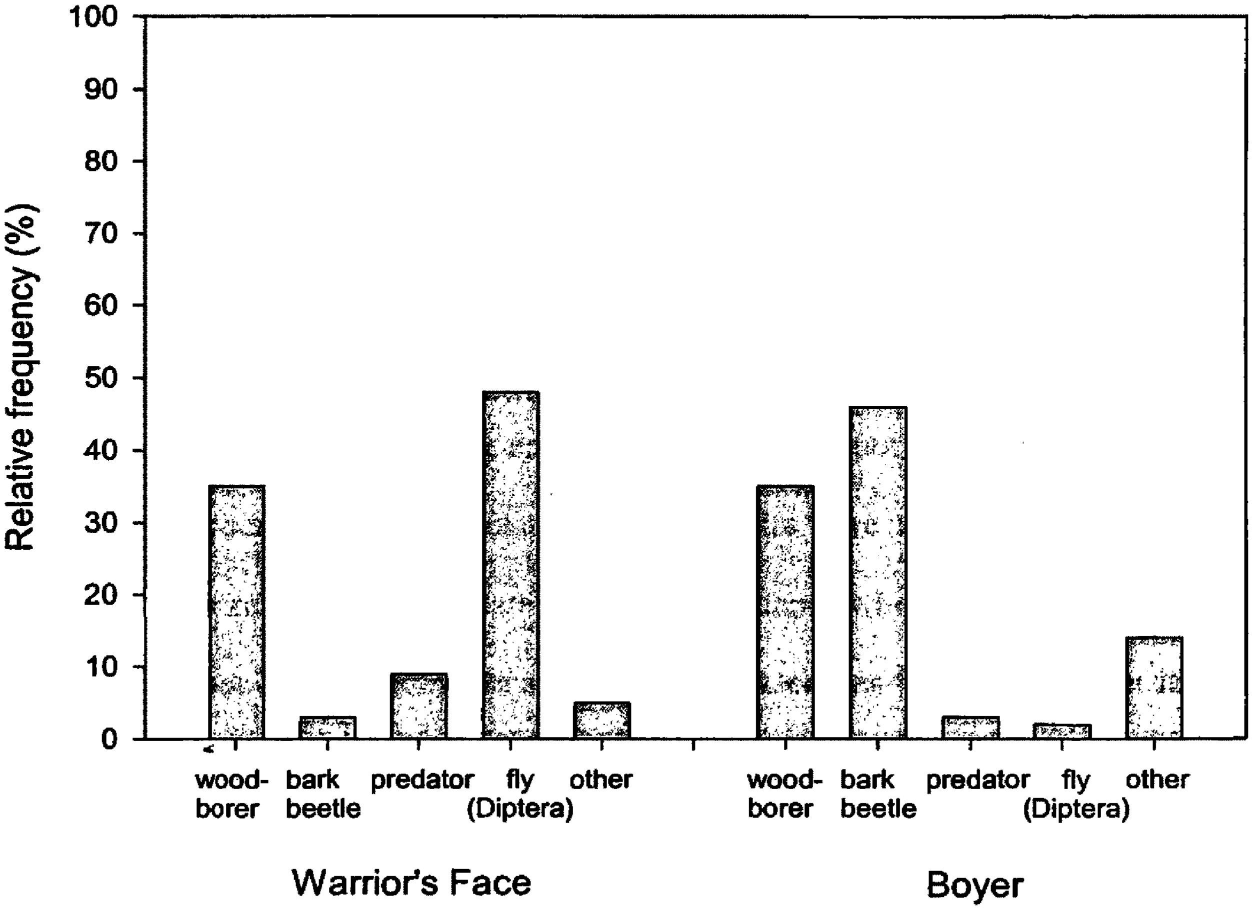

Figure 13. Relative frequencies of five insect guilds in bark samples from random trees. Note the high frequency of bark beetles at Boyer, but not at Warrior's Face. Large ponderosa pines at Warrior's Face accounted for most of the dipteran larvae.

comparing all wood-borers between the two samples gave the strongest correlation, but correlations for ponderosa pine were weak (Table 5). For Boyer, counting all large insects (94% of which were wood-borers) in the standard sample best represented the expanded sample (Table 5). Because large insects constituted 54% to 74% of Black-backed Woodpecker prey at Boyer (see Figure 9), I assumed this was an appropriate measure to use for prey density. When discussing results for each site, I use that site's best-correlated insect measure (i.e. wood-borers for Warrior's Face, all large insects for Boyer).

Random trees: among species. At Warrior's Face, I sampled bark from 76 randomly selected trees: 20 Douglas-firs, 16 lodgepole pines, 12 ponderosa pines, 4 subalpine firs, and 24 "similar-dbh" Douglas-firs selected to match the diameters of specific fed-upon trees. Other tree species at the site were not sampled due to their low frequency of occurrence. The similar-dbh Douglas-firs were used to control for the effects of tree size and sampling date on insect abundance when comparing fed-upon to random trees (see below). Random and similar-dbh Douglas-firs did not differ in wood-borer abundance ($U = 215.5$, $Z = -0.582$, $p = 0.561$), so I pooled them to yield a sample size of 44 random Douglas-firs to test for differences in wood-borer abundance among tree species. Douglas-firs contained significantly more wood-borers than any other tree species (Kruskal-Wallis test; $\chi^2 = 28.2$, $df = 3$, $p < 0.001$; Figure 14a). At Boyer, I sampled bark from 63 Douglas-firs, 58 ponderosa pines, 42 western larches, and 17 grand firs (Figure 14b). Unlike at Warrior's Face, potential prey insects were numerous in several tree species. A Kruskal-Wallis test detected a significant effect of tree species on numbers of all large insects ($\chi^2 = 14.3$, $df = 5$, $p = 0.014$), but when the test was restricted

Table 5. Spearman's rank correlation coefficients (r_s) for standard samples compared to the full sample, for each tree species at each site. The best-correlated insect metric differed between the two study sites. Large insects includes all insects > 10 mm in length.

		Wood-borers		**Large insects**	
	n	**r_s**	**p**	**r_s**	**p**
Warrior's Face					
ouglas-fir	14	**0.918**	**< 0.001**	0.518	0.058
erosa pine	9	**0.287**	**0.011**	0.192	0.038
epole pine	9	**0.793**	**0.453**	0.694	0.621
Boyer					
ouglas-fir	11	0.786	0.004	**0.807**	**0.003**
erosa pine	11	0.822	0.002	**0.877**	**< 0.001**
stern larch	11	0.557	0.075	**0.953**	**< 0.001**

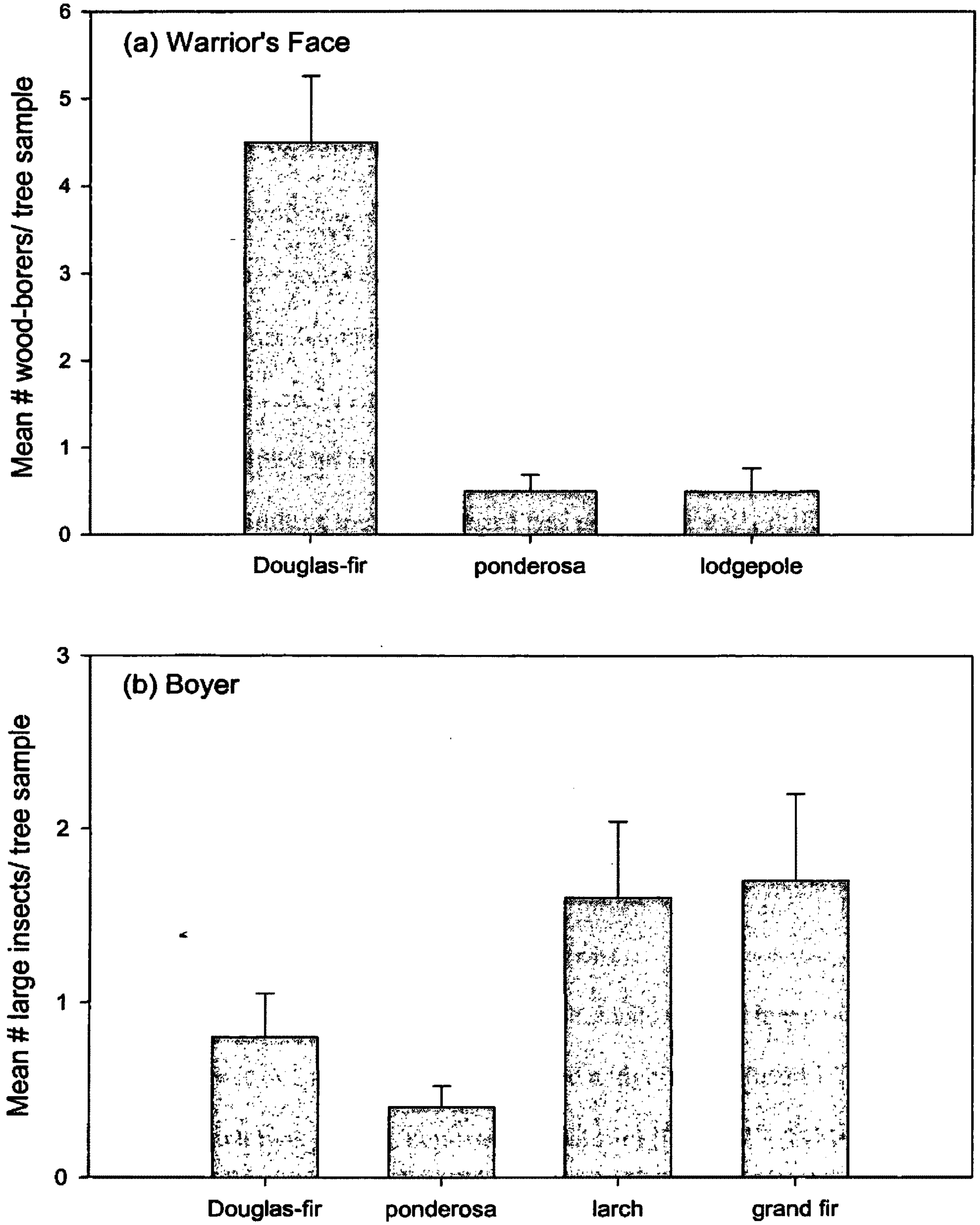

Figure 14. Mean insect density in bark samples of random trees, for common tree species. (a) Warrior's Face; (b) Boyer. Note that different insect metrics are used for the two sites. Error bars indicate one standard error.

to the three most heavily used tree species (western larch, ponderosa pine, and Douglas-fir) there was no significant difference ($\chi^2 = 4.03$, df = 2, p = 0.13).

Fed-upon trees vs. random trees. At Warrior's Face there was no significant difference in numbers of wood-borers found in fed-upon and random trees of the same species or of the same species and similar dbh (Figure 15). To test for the possibility that insect densities between fed-upon and random trees were confounded by differences in sampling date or tree size, I paired each fed-upon tree with a random tree of the same species and size, sampled no more than three days later, and conducted a *t*-test for paired comparisons. The resulting mean difference was not significantly different from zero ($t = -0.675$, df = 23, p = 0.51).

At Boyer, however, fed-upon trees were more prey-rich than randomly selected trees of the same species (U = 3283.5, Z = -4.6, $p < 0.001$; Figure 15). This difference was also significant when date was controlled using paired comparisons ($t = 2.13$, df = 52, p = 0.038). When comparing tree species individually using Mann-Whitney U-tests (Figure 16), fed-upon trees were significantly more prey rich than random trees (at $\alpha = 0.05$) for all species except ponderosa pine (p = 0.08)

Patch samples. For each 25-m-radius patch, I calculated a mean number of insects for each tree species. A 2-way ANOVA indicated a highly significant effect of tree species but not patch type (use vs. non-use vs. nest site) (Figure 17, Table 6). The interaction term was not significant (Table 6).

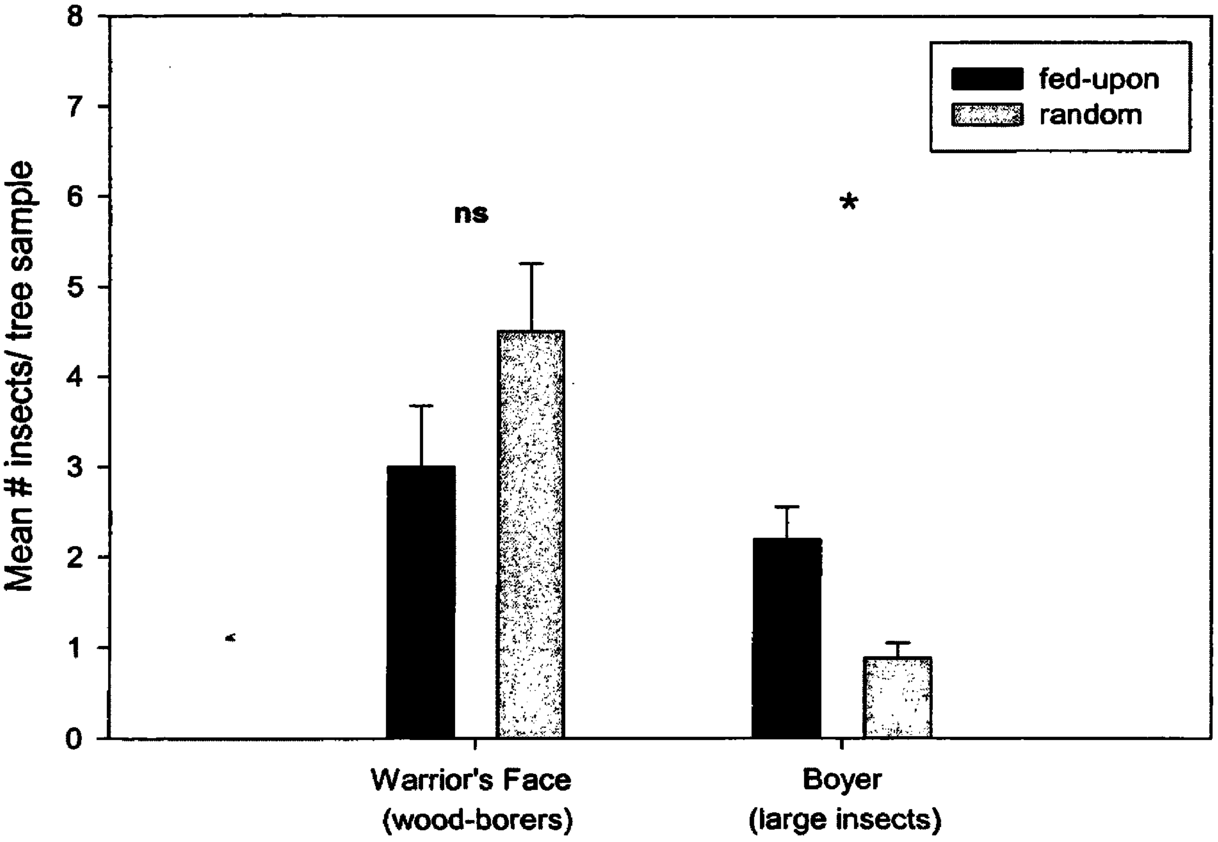

Figure 15. Mean insect densities, with standard errors, for fed-upon vs. random tree samples at Warrior's Face and Boyer. Trees used for foraging contained more insects than random trees at Boyer, but not at Warrior's Face. At Warrior's Face, all bark-sampled, fed-upon trees were Douglas-firs. The insect metric differs between the two sites. Error bars indicate one standard error. * $U = 3283.5$, $Z = -4.6$, $p < 0.001$.

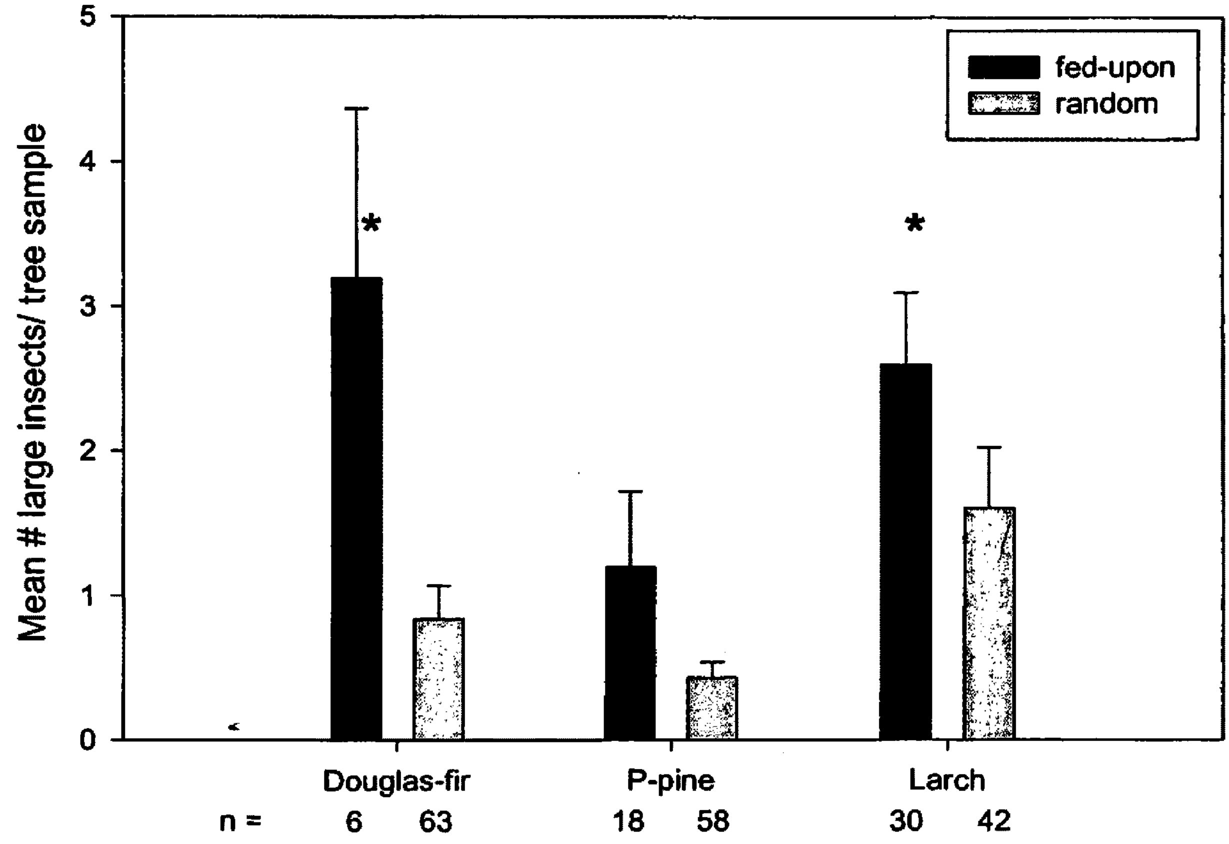

Figure 16. Mean insect densities in fed-upon and random trees at Boyer, by tree species. Error bars indicate one standard error. * Mann-Whitney U-tests, $p < 0.02$

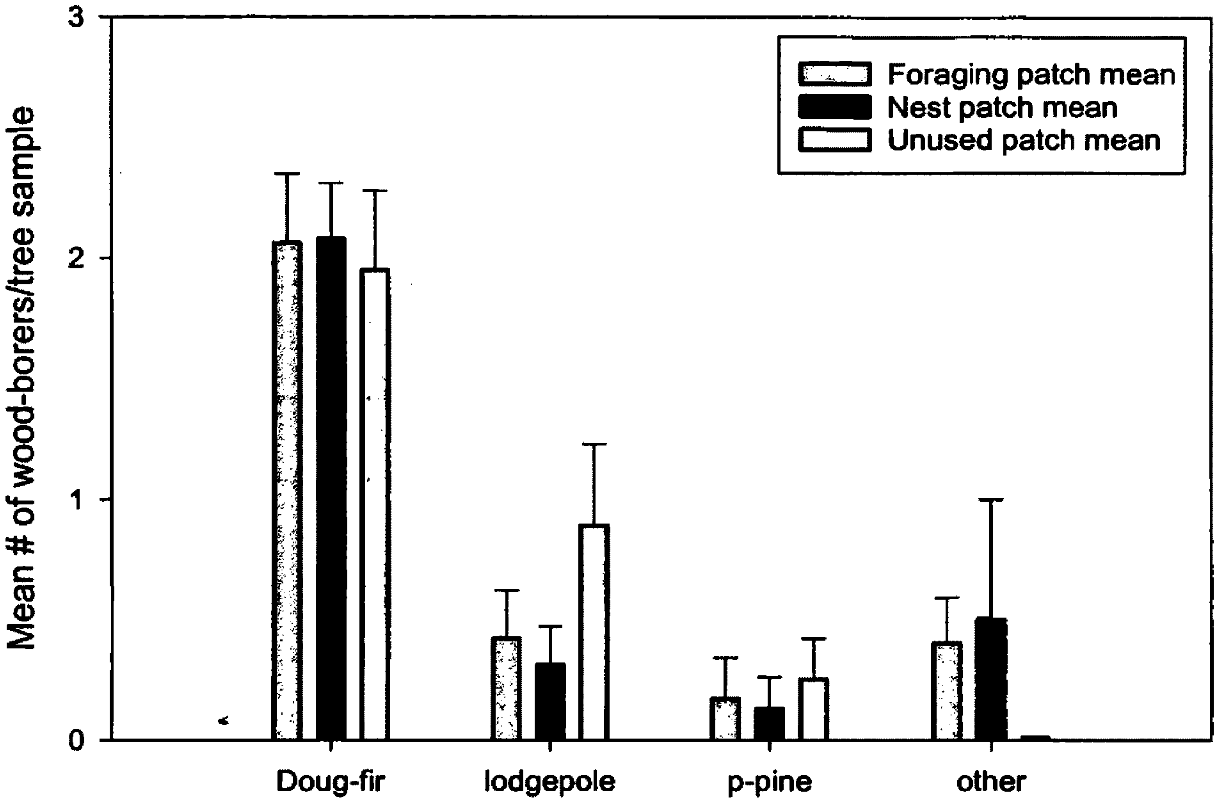

Figure 17. Mean insect densities in foraging, nesting, and unused patches, for four tree species. Patches were defined as 25-m radius plots, and up to 8 Douglas-firs and 2 trees of each other species were sampled per plot. Data are from Warrior's Face. Error bars indicate one standard error.

Table 6. Effects of patch type (nesting, foraging, unused) and tree species on mean number of wood-borers per patch at Warrior's Face.

Source	df	F	Significance
Patch type[a]	2	0.36	0.696
Tree species[a]	5	19.31	0.000
Trtmt X Tree spp.	9	0.80	0.616
Error	59		
Total	75		

[a]fixed effects

DISCUSSION

MEASURING FOOD AVAILABILITY

Hutto (1990) noted three problems with using a simple measure of prey density to represent food availability in field studies: 1) imperfect knowledge of a bird's feeding constraints means that not all insects measured by a sampling method are potential prey, while other potential prey items may go unmeasured; 2) the scale of measurement researchers use to assess prey may differ from the scale at which a bird seeks prey; and 3) sampling techniques estimate food crops at one point in time, ignoring the possibility that prey are replenished at different rates. This study was designed to reduce biases from these three common pitfalls, as discussed below.

Feeding constraints. A simple measurement of the numbers of insects in the places a bird visits when foraging can inaccurately represent potential prey if certain prey are less palatable, harder to capture, or harder to handle than others. Avoiding this problem for woodpeckers requires careful consideration of the kinds of trees used for foraging, as well as differential accessibility of insects because of their position in the tree or because of differences owing to physical characteristics of particular tree types.

In this study, Black-backed Woodpeckers foraged primarily on large, wood-boring beetle larvae within the trunks of dead trees. By counting these insects in bark samples, my methods would incorrectly estimate prey availability only if wood-borers were deeper within some trees than others (i.e. in the xylem rather than the phloem, Figure 18), or if certain trees were more difficult to penetrate than others (i.e., because of differences in bark type or thickness).

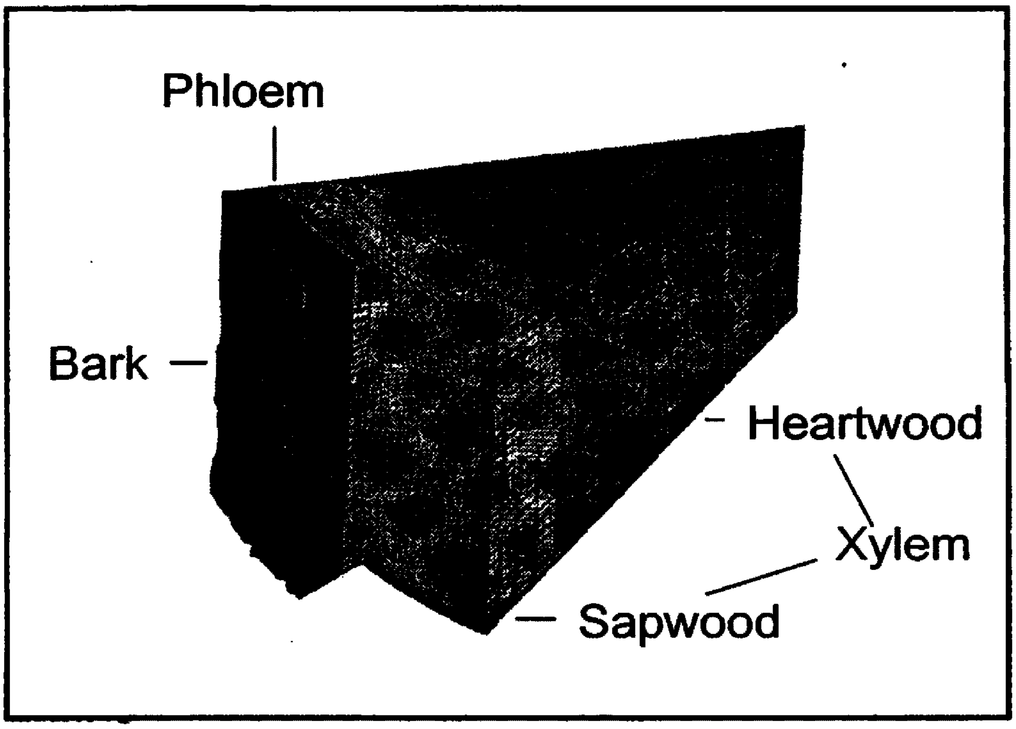

Figure 18. Cross-section of tree trunk, indicating bark, phloem, xylem, sapwood, and heartwood. From Bull et al. (1997).

To test the first possibility, I compared the number of xylem entrance holes at each bark sample among tree species. This number represents the maximum number of wood-borers per bark sample that could have gone uncounted (if all holes had contained hiding wood-borers). If trees with prey-poor bark actually contained more wood-borers than trees with prey-rich bark, then the trend in number of xylem holes by tree species should be the reverse of the trend in bark insects. However, trends in xylem-hole densities matched trends for prey found in bark, meaning that tree species with prey-poor bark did not support higher densities of wood-borers than tree species with prey-rich bark.

Considering the second possibility, if bark morphology greatly affected the energy needed to extract prey from a tree, then simple counts of prey insects would inaccurately represent the relative food values of tree species with different bark types. In fact, some authors have suggested that the flaky bark of trees such as western larch, ponderosa pine, or lodgepole pine is more easily removed than the thicker bark of Douglas-fir or grand fir, and that this difference makes the flaky-barked trees more favorable foraging sites (i.e. Douglas-fir, grand fir) (Bull et al. 1986, Goggans et al. 1988, Marshall 1992).

While bark type probably affects a Black-backed Woodpecker's net energy intake per tree, the effect may be small, for four reasons. First, smaller trees (such as those predominating on second-growth sites like Boyer) have fairly uniformly thin bark regardless of the tree species. Second, bark thickness declines with height on an individual tree, so even trees with thick bark at the base have thinner bark at heights of foraging woodpeckers. Third, large, thick-barked trees can be strongly ridged, and

Black-backed Woodpeckers flake off the ridges, exposing thinner bark below (pers. obs.). Fourth, during the nestling stage, foraging adult Black-backed Woodpeckers usually extract only one prey from each bout of flaking, so flakier bark may not dramatically increase prey capture rate (pers. obs.).

Scale of measurement. Conclusions about prey density are valid only if prey density is measured at the same spatial scale to which Black-backed Woodpeckers respond. For instance, if woodpeckers foraged in regions of consistently prey-rich trees, then measurements of individual trees within those regions might not detect a difference between used and unused trees. While it is difficult to know exactly which spatial scale is important to woodpeckers, it clearly is important to measure prey density at several spatial scales (Hutto 1990).

At Warrior's Face, I measured prey densities at two different spatial scales: patch and individual tree. Black-backed Woodpeckers did not consistently occupy prey-rich patches within the burn. Therefore it appeared that measuring prey density at the individual-tree level was appropriate. The individual-tree scale would be inappropriate if these woodpeckers foraged in prey-rich bark patches independent of the tree's overall insect level, or if they assessed prey density of patches at a scale different from my 25-m radius definition.

Standing crop. This study examined habitat use over the course of a single breeding season on each site. If insects in certain patches or trees were replaced at a faster rate than others, then measuring each tree only once might be misleading. However, wood-borer populations under bark are typically regenerated only during flights of emerging adults at the beginning and end of the summer; flights in midsummer are rare (Linsley 1961). Pairing foraging and random samples by date did not change interpretations of the data.

At least with respect to Hutto's (1990) list of the three most common flaws in food availability measurements, this study measures potential prey insects in a way that provides a fairly unbiased estimate of food availability among a variety of tree species and burn patches. With such an estimate in hand, I can now assess the effects of differing prey availabilities on Black-backed Woodpecker foraging behavior.

THE INFLUENCE OF PREY DENSITY ON HABITAT USE

This is the first study to interpret foraging behavior of Black-backed Woodpeckers by measuring prey density. The results suggest that prey density is useful for identifying foraging trees for Black-backed Woodpeckers in burned forests, but it is not the only variable that accounts for tree use. Looking at the results from the two sites together strengthens this conclusion. The two sites differed markedly in tree species availability, relative insect abundance among tree species (prey availability), and woodpecker use of tree species. These site differences allow me to look among several possible explanations for the one that consistently explains tree use at the two sites. Neither use of a 'favorite' tree species nor use of the most abundant tree species was consistent between sites, but trees used for foraging were consistently higher in prey density than trees selected at random.

Interestingly, Black-backed Woodpeckers appeared to track prey density at different levels at the two sites. At Warrior's Face, woodpeckers used, almost exclusively, the one tree species at the site that was consistently prey-rich, while at Boyer (where tree species presented a range of prey richness) they selected individual trees that contained significantly more insects than random trees.

At Boyer, both western larch and grand fir appeared to contain more prey than other tree species, yet of these two species only western larch was frequently used. A number of factors could explain the non-use of grand firs at Boyer despite its high measures of prey density. First, grand fir had a localized distribution on the site (abundant along small drainages, absent elsewhere) so they may not have been as available as more widely distributed species. Second, woodpeckers may not have distinguished grand fir from Douglas-fir, which has very similar bark when burned, was much more abundant, and contained fewer insects. Third, grand fir's close-adhering bark may have deterred foraging given the abundance of insects in western larch. Fourth, something about grand fir's resin may have made insects in grand fir unpalatable ('sour sap', as Furniss [1965] noted for Douglas-firs at an Idaho burn).

Prey density at two spatial scales. Black-backed Woodpeckers appeared to choose high-prey foraging locations at an individual-tree level, but not at a larger scale (e.g. patch). When prey densities were estimated for each tree species in twenty-seven 25-m-radius plots (Warrior's Face only), there was no difference in mean prey density among three patch types (treatments): nest sites, foraging sites, and unused patches. Variation among patch means ranged over a factor of 4, but not consistently by treatment. This suggests that Black-backed Woodpeckers could have used prey density as the primary reason to occupy an area, but they instead occupied burn areas for a different reason. However, within-patch variation was also high, and a one-way ANOVA did not detect a patch effect on mean insect density (see Table 6). Within-patch variance could be better estimated by sampling more trees per patch, but this would require considerable effort. Furthermore, I measured mean prey density per patch at only one site, where prey density may have been at a peak. Prey density at the scale of patches within a burn might be a more important territory quality in years of lower overall insect density.

Early post-fire forests are thought to contain abundant food resources for woodpeckers (e.g. Bent 1939, Apfelbaum and Haney 1981, Harris 1982, Villard and Beninger 1993, Murphy and Lehnhausen 1998). Despite this abundance, prey availability may not be completely unlimited for Black-backed Woodpeckers in burned forests, as suggested by their non-random use of prey-rich trees. However, their apparent indifference to relatively prey-rich areas at Warrior's Face suggests that food limitation was low there, and that some other factor is more important in determining territory placement.

BLACK-BACKED WOODPECKER FORAGING BEHAVIOR

No other published studies have measured prey density for Black-backed Woodpeckers; however, numerous studies contain data on their use of various habitat components. With the underlying prey distributions that likely affect foraging behavior unknown, the range of habitat associations found in these studies is difficult to interpret as a whole. While Black-backed Woodpeckers show substantial variation in use of certain habitat components, such as tree species used for foraging, other aspects of their foraging behavior are consistent among studies. The following section summarizes literature concerning Black-backed Woodpecker foraging behavior, and then reinterprets these observations, considering the effect of prey availability on habitat use.

Literature review. Bent (1939) compiled many anecdotes of Black-backed Woodpecker occurrence and behavior from more than 100 years ago. More recent studies of foraging woodpeckers typically have recorded habitat characteristics around foraging observations and then compared these to data from random points. Investigators have interpreted differences between variables measured at foraging and random sites as preference (e.g. Raphael and White 1984). Preference in this sense means non-random use of habitat variables, and does not imply a bird's choice given equal availability of alternatives.

Studies measuring Black-backed Woodpecker foraging behavior have been conducted in a range of forest types and disturbances. A few studies are from recently burned forests (Harris 1982, Villard and Beninger 1993, Murphy and Lehnhausen 1998, Kreisel 1999). Raphael and White (1984) studied burned forests that were more than six years old. Other studies are from bark beetle outbreaks (Bull et al. 1986, Goggans et al. 1988) or unburned forests (Spring 1965, Short 1974, Villard 1994). Some studies of burned-forest communities include Black-backed Woodpeckers, but do not report foraging variables by bird species (Bock and Lynch 1970, Hutto 1995, Hitchcox 1996, Caton 1996). A few papers summarize many studies or observations of Black-backed Woodpeckers (Bent 1939, Bock and Bock 1974, Yunick 1985, Marshall 1992). Some studies of nesting Black-backed Woodpeckers do not report new foraging data, but cite earlier findings (Lester 1980, Hoffman 1997, Weinhagen 1998).

Prey. Prey in stomachs of collected birds has been identified from a windthrown area (Wickman 1965), an early post-fire forest in Alaska (Murphy and Lehnhausen 1998), and from unknown habitats (Beal 1911). In each case, the primary food item was wood-boring beetle larvae. Others infer from observed outbreaks that prey are bark beetles (Lester 1980, Goggans et al. 1988). Using similar logic, Villard and Beninger (1993) deduced that primary prey in Canada was a wood-borer (Cerambycidae: *Monochamus scutellatus*). Some papers that do not directly determine prey species lump bark and wood-boring beetles together as the preferred prey (Marshall 1992, Hoffman 1997, Weinhagen 1998). My results suggest that, at least in burned forests, wood-borers are the primary prey, and that it may be wrong to consider bark and wood-boring beetles together as prey.

Tree species use. Individual studies often find non-random use of a particular tree species, but the range of tree species used across studies indicates that tree species use in the Black-backed Woodpecker is not narrowly restricted. Hutto (1995), Hitchcox (1996), Caton (1996), and Kreisel (1998, 1999) reported that western larch was used disproportionately often for foraging by many woodpecker species in burned forests of the Intermountain West. Other reports from the same area mentioned Douglas-fir was used (Bent 1939, Kreisel 1999). Both these tree species were used by Black-backed Woodpeckers in the present study, although Douglas-fir was emphasized at only one of the study sites. Goggans et al. (1989) and Bull et al. (1986) reported Black-backed Woodpeckers using bark-beetle-killed lodgepole pines in most foraging observations. In Canada and Alaska, they used spruce (*Picea* spp.) (Villard 1994, Murphy and Lehnhausen 1998) or white pine (*Pinus strobus*) (Villard and Beninger 1993) most frequently. In California, red fir (*Abies magnifica*) was the tree species most frequently used (Raphael and White 1984).

Tree characteristics. Most foraging observations were on dead trees, but some studies reported use of live trees (Raphael and White 1984—61%, Bull et al. 1986—50%, Goggans et al. 1988—32% of observations were on live trees). Standing dead trees were used more than fallen logs in all cases, but in an unburned forest in Canada, logs were used in 41% of observations (Villard 1994); and in older burns (> 6 years old) in California, logs were used in 18% of observations (Raphael and White 1984). In all studies, including the present one, Black-backed Woodpeckers virtually always foraged on trunks of trees or logs.

Some authors have noted that Black-backed Woodpeckers tend to forage on relatively large-diameter trees, and this was evident at both sites in this study. At Warrior's Face, 50% of trees used for foraging exceeded 44 cm dbh, but only 5% of trees in random vegetation measurement plots exceeded this size. At Boyer, median size of fed-upon trees was 26 cm dbh, and only 20% of trees in random vegetation measurement plots were larger than this. One explanation for non-random use of larger trees by woodpeckers (e.g. Goggans et al. 1988) is that phloem thickness, and as a result wood-borer density, increase with tree diameter (Zhang et al. 1993). Interestingly, this pattern was not evident at either site when mean insect density was plotted as a function of tree size (Figure 19). At Boyer, there was a trend for greatest insect density in trees around 25 cm dbh, which closely matches the median tree size used for foraging (26 cm dbh).

There is some evidence that, in burned forests, Black-backed Woodpeckers place nest sites in patches of greater-than-average density of large snags (Saab and Dudley 1998, Hejl and McFadzen, unpubl. data). This tendency was observed for foraging sites at Warrior's Face, but was not evident at Boyer (see Table 4). This result is difficult to interpret: large snags should be rarer (and probably more patchily distributed) at a logged site (i.e. Boyer) than at a non-logged site (i.e. Warrior's Face). Therefore, if woodpeckers indeed preferred to forage in patches containing many large snags, we would expect this preference to be most pronounced at Boyer, the logged site. Instead, the reverse was observed. Possibly, there was reduced incentive to use areas containing large snags at Boyer because of the trend for prey-richness in smaller (around 25 cm dbh) trees (Figure 19). Another explanation is that density of large snags is important only when choosing nest sites, and the patterns observed for foraging woodpeckers at the two sites are the result of chance.

Foraging technique. Published reports define foraging techniques differently, but usually include three or four stereotyped behaviors: gleaning, pecking, flaking, and excavating (Conner 1979, Raphael and White 1984, Bull et al. 1986, Harris 1982, Goggans et al. 1988, Murphy and Lehnhausen 1998). Definitions of foraging techniques for these studies are similar to those used in my study, with pecking substituting for drilling, and excavating defined as removing material to penetrate the cambium or sapwood (depending on the observer's definition). In most reports, gleaning is rare (but see Raphael and White [1984] where Black-backed Woodpeckers often foraged on live trees).

Estimations of time spent using different foraging techniques vary from mostly scaling or flaking (Bull et al. 1986, Harris 1982, this study) to mostly excavating (Murphy and Lehnhausen 1998). Differences in these estimates probably result from differences in observer's definitions of the techniques. In practice, foraging modes used by Black-backed Woodpeckers appear to fall into only two functionally distinct

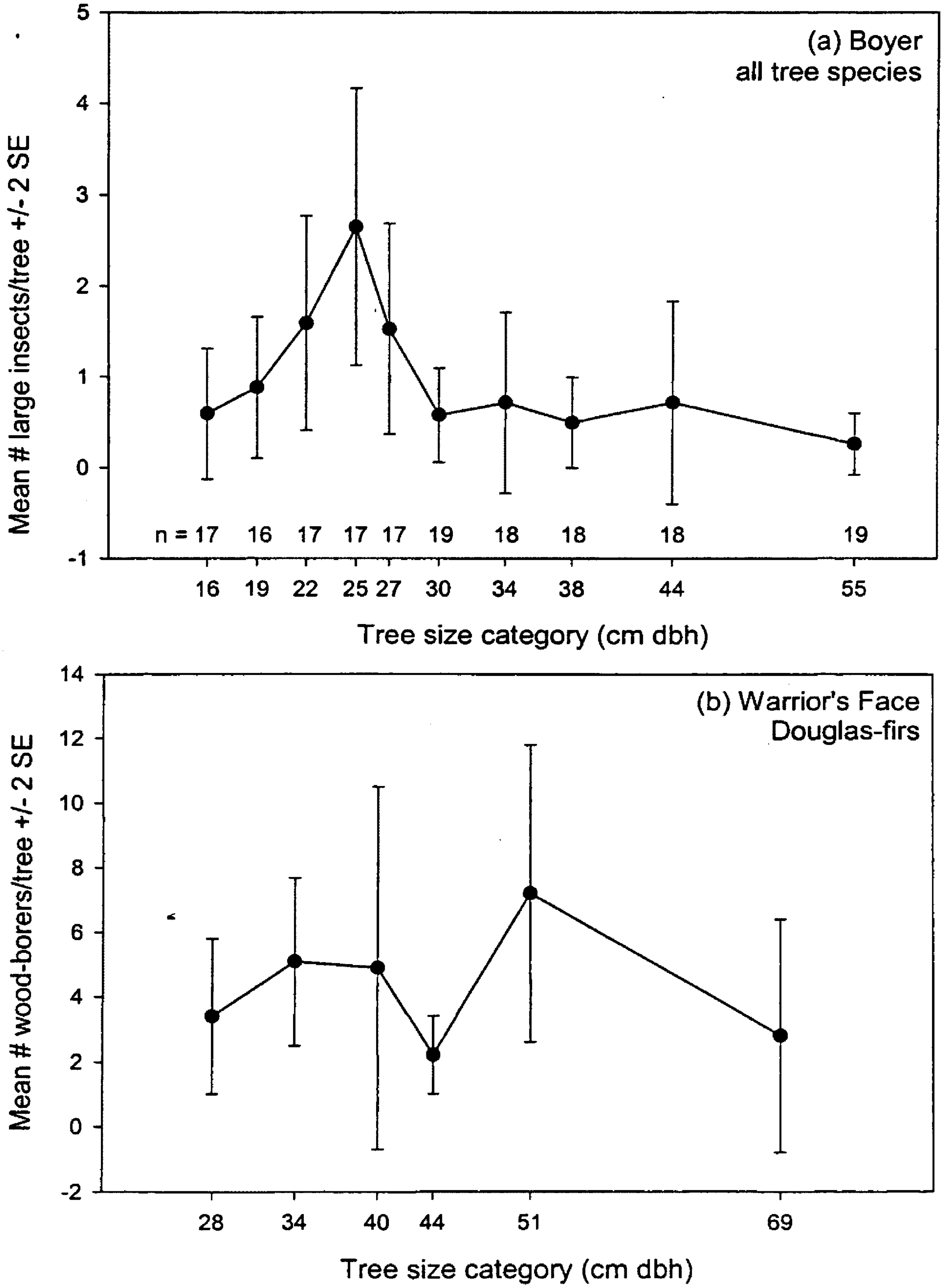

Figure 19. (a) At Boyer, trees around 25 cm dbh contained more prey than either larger or smaller trees. This trend contradicts the generalization that larger diameters support greater insect densities (e.g. Zhang et al. 1993). (b) Neither trend was apparent at Warrior's Face. Size categories were chosen to keep sample sizes similar within categories for each site; x-axes indicate median diameters of each category. Error bars indicate two standard errors.

categories: cambial-layer foraging and sapwood foraging. Both modes require pecking, flaking, and excavating to make holes through the outer bark.

Synthesis. Across studies, Black-backed Woodpeckers consistently foraged below the bark, low on trunks of relatively large snags or logs, but otherwise their foraging behavior was variable (see also Yunick 1985). Generalizations about Black-backed Woodpecker foraging behavior are elusive, in part because of the range of disturbance types in which studies have been conducted and the lack of accompanying data on prey availability. Different disturbance agents occurring in stands of different ages and tree species compositions are likely to present dissimilar foraging conditions, particularly with respect to the availability of dead wood and, as a result, availability of potential prey insects. Thus, the variation in habitat use recorded in previous studies may have been the result of woodpeckers foraging consistently with respect to prey density. Previous studies may have overemphasized the frequency of two behaviors in particular: woodpeckers' association with flaky-barked trees and the use of bark beetles in their diet. My results suggest that Black-backed Woodpeckers are not restricted to using flaky-barked trees, and that it may be incorrect to lump bark beetles with wood-borers as preferred prey items (see also Murphy and Lehnhausen 1998).

Reevaluation of the importance of flaky bark. Support for the idea that Black-backed Woodpeckers are strongly associated with flaky-barked trees stems from an early study of woodpecker morphology (Spring 1965). Spring compared Black-backed Woodpecker morphology to a 'traditional' (four-toed) *Picoides* (Hairy Woodpecker, *P. villosus*). He found that Black-backed Woodpecker posture, as a result of foot structure, permits harder hammering but requires a more ungainly movement up the tree. He further noticed that this tradeoff matched interspecific differences in movement during foraging, where Black-backed Woodpeckers spent long periods on a single tree, while Hairy Woodpeckers moved rapidly among trees. Some authors cite this work as evidence that the Black-backed Woodpecker is energetically constrained to using trees with flaky bark (Goggans et al. 1988, Marshall 1992).

If Black-backed Woodpeckers can deliver especially hard blows to wood, then why should they be constrained to foraging on trees where the bark is easy to remove? A possible answer is that they eat wood-boring beetle larvae; wood-borers spend most of their time deep within the tree, where woodpeckers must excavate sapwood to reach them (Goggans et al 1989). However, wood-borers feed in a tree's phloem as long as it persists, and in my study wood-boring beetle larvae up to 30 mm long were often found in the phloem. Furthermore, wood-borer xylem galleries often terminate less than 5 cm into the sapwood (Mitchell and Martin 1980) and woodpeckers extract the larvae through their galleries (removing insect frass instead of sapwood) rather than by excavating new holes (pers. obs.) This requires patience, but not immense excavating power. I suspect that the benefit of greater excavating power lies in allowing the Black-backed Woodpecker to excavate nest holes in harder (i.e. safer, or more common) trees than poorer excavators can use.

My results suggest that instead of being specialized to use a particular type of bark, Black-backed Woodpeckers can use a variety of bark types when they contain prey. At Warrior's Face, woodpeckers used a thick-barked tree almost exclusively, despite a high incidence of flaky-barked species (ca. 32% of trees were lodgepole and ponderosa pines). Observations collected over two days at a Black-backed Woodpecker nest in an unburned site also suggest that they change foraging sites to track food resources. In the absence of snags, these birds foraged exclusively on downed logs and cut stumps, where they ate ant pupae and bark beetle larvae, as well as a few wood-borer larvae (unpubl. data).

I suggest that prey density and prey accessibility (determined by bark type) interact to affect tree species use by Black-backed Woodpeckers (Figure 20). When prey density differences are large, prey density overrides prey accessibility in substrate choice. When prey density is high across tree species, prey accessibility is a deciding factor. At Warrior's Face, Black-backed Woodpeckers foraging in flaky-barked trees were faced with meager food availability, but thick-barked trees provided sufficient food. At Boyer, they used a relatively prey-rich, flaky-barked tree (western larch) over thick-barked trees of similar prey richness (grand fir).

Reevaluation of diet composition. Black-backed Woodpeckers in this study ate primarily wood-boring beetles, matching results from earlier studies of stomach contents (Beal 1911, Wickman 1965, Murphy and Lehnhausen 1998). Even though bark beetles were present at both sites, they were used only rarely. At Boyer, bark beetles were numerically the most common sub-bark insect group, but their clumped distribution on trees probably reduced their availability to Black-backed Woodpeckers. Wood-borers constituted the majority of sub-bark insect biomass in both years, so specialization on wood-borers would be predicted on the basis of optimal foraging theory (e.g. Stephens and Krebs 1986). Thus, the general conclusion that Black-backed Woodpeckers are dietary specialists on wood-borers is not warranted.

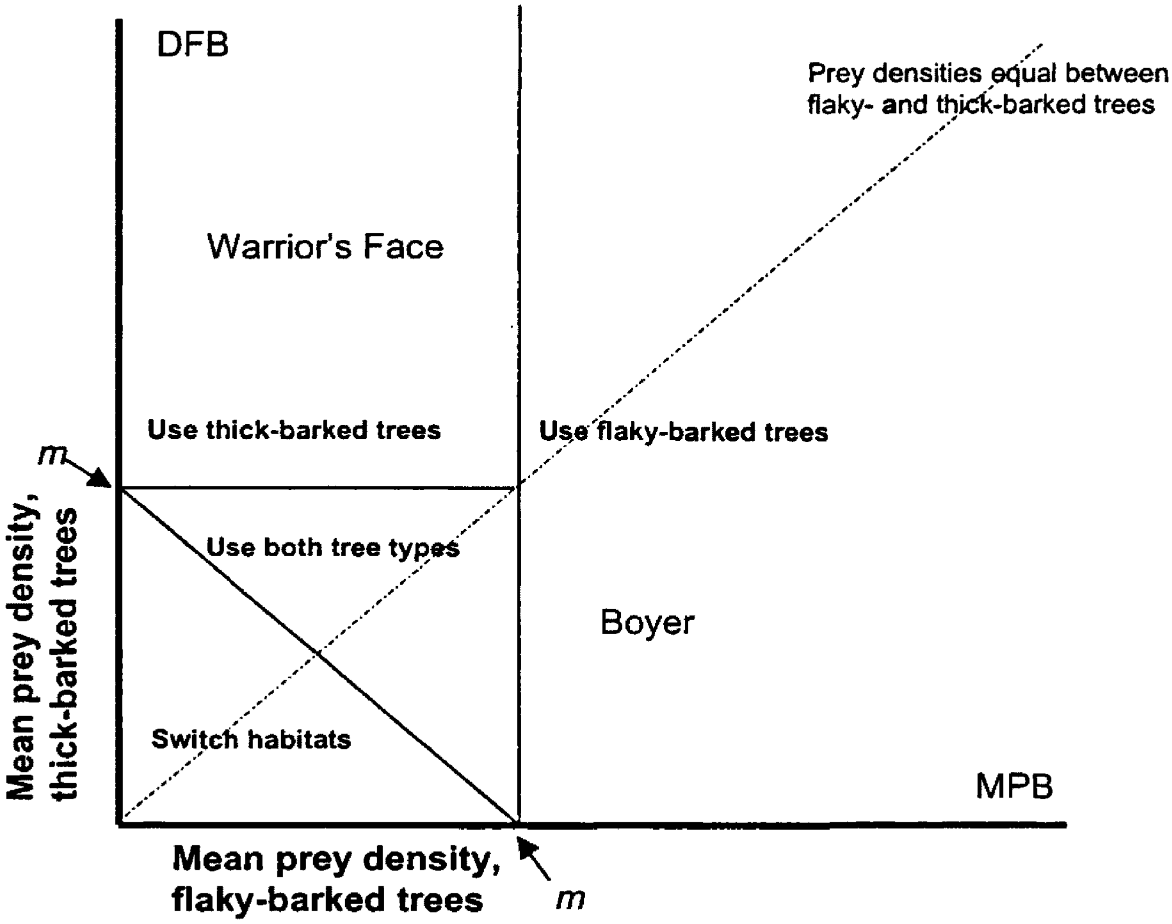

Figure 20. Conceptual model of the effect of bark type on habitat use by Black-backed Woodpeckers, given relative prey densities among trees with flaky and thick bark. The model assumes that flaky-barked trees are easier to forage in than thick-barked trees, and that tree availability is equal between the two types. Approximate prey conditions for Warrior's Face, Boyer, a mountain pine beetle outbreak (MPB), and a Douglas-fir beetle outbreak (DFB) are plotted on the graph as examples. When prey density is low in all trees, Black-backeds should either switch habitats or use both tree types to meet food requirements. Woodpeckers should forage in flaky-barked trees when prey density is above a minimum (*m*), resulting in the commonly observed pattern of Black-backeds foraging on flaky-barked trees. If prey density is above *m* in thick-barked trees but below it in flaky-barked trees, thick-barked trees should be used exclusively, as in Warrior's Face. This point is well illustrated in the case of bark beetle outbreaks, where all trees containing prey are of one bark type. Black-backeds in mountain-pine-beetle-infested ponderosa or lodgepole pine (MPB) should forage in these flaky-barked trees, as Goggans et al. (1988) observed. In Douglas-fir beetle outbreaks (DFB) they should use thick-barked trees.

The question of diet breadth in this species remains important, because bark beetles may differ from wood-borers in both their profitability as prey and their abundance in different disturbance types. As a result, foraging opportunities of particular disturbance types may depend on the diet breadth of Black-backed Woodpeckers. To explain this idea further, it is necessary to review some key differences between bark beetles and wood-borers.

DIFFERENCES BETWEEN BARK BEETLES AND WOOD-BORERS

When discussing woodpecker diets, some authors refer collectively to bark beetles and wood-borers (e.g. Bent 1939, Goggans et al. 1988, Marshall 1992). This is done, probably out of convenience, for two reasons. First, life histories of the two beetle groups are similar: both bark beetles and wood-borers spend most of their lives inside dead or dying trees, emerging as adults for only a brief period. Second, bark beetles are well studied and their life histories are well understood (Mitton and Sturgeon 1982). Comparatively, there are very few detailed studies of wood-borers, making it tempting to use results from bark beetle studies to fill the gaps. Certain generalizations about the two groups are valid: bark beetles and wood-borers both attack recently dead trees; both benefit from thick, moist phloem; competition is fierce for better phloem sites; and larger species inhabit lower portions of the trunk (Wood 1982, Linsley 1961). However, some differences between wood-borers and bark beetles could be crucial to their value as woodpecker prey. These differences are their body sizes, size and spatial distribution of populations, generation times, and dependence on dead wood.

Bark beetles are small (< 6 mm in length) but very numerous, and densely aggregated in the phloem. They do not enter the xylem, and they remain in the bark for less than a year before emerging as adults. Certain species, including many in the genus *Dendroctonus,* are able to kill living trees, so are not dependent on disturbances to provide dead wood (Wood 1982, Mitton and Sturgeon 1982). If they attack burned trees, it is primarily in the first year after tree death, before phloem conditions deteriorate. *Dendroctonus ponderosae* and *D. brevicomis*, two aggressive species that attack lodgepole and ponderosa pines, show little attraction to burned wood (Wood 1982, Amman and Ryan 1991). However, *Dendroctonus pseudotsugae* commonly attacks burned Douglas-fir (Furniss 1965, Amman and Ryan 1991).

By contrast, wood-borer larvae can be much larger (to 50 mm) but less numerous and less clumped than bark beetles. They can occur in either the phloem or the xylem, and they can remain as larvae in dead wood for one to three years (Linsley 1961). Most wood-borers are unable to attack living trees, but some species are very common in fire-killed wood (Zhang et al. 1993, Muona and Rutanen 1994, Dajoz 1998). Some genera find burning or recently burned habitat by sensing smoke (e.g. the cerambycid *Monochamus*) or heat (e.g. the buprestid *Melanophila*) (Parmelee 1941, Wickman 1964, Evans 1966, Hart 1998).

To a foraging woodpecker deciding between the two prey types, bark beetles have two potential benefits as a prey item: their larvae are densely aggregated (though this is a disadvantage until the woodpecker finds the aggregation), and they are never deeper than the tree's cambial layer. In bark beetle outbreaks, finding aggregations of bark beetles is probably easy, and specialization on bark beetles might be profitable, as has been suggested for the Three-toed Woodpecker (Murphy and Lehnhausen 1998, Fayt 1999).

Wood-borers are advantageous prey because they can be much larger than bark beetles (by nearly one order of magnitude in length, or nearly three orders of magnitude in mass!), their distribution on a burned tree is more uniform, and they persist in burned wood longer than bark beetles. However, they spend some of their time within the xylem, at which point they are less accessible than bark beetles.

POSSIBLE MECHANISMS OF HABITAT SELECTION

Black-backed Woodpeckers are thought to select habitats containing concentrations of standing dead trees (Bent 1939, Bock and Bock 1974). Some authors stress, specifically, the species' association with post-fire forests (Beal 1939, Hutto 1995, Murphy and Lehnhausen 1998), while others suggest that bark beetle outbreaks or mature forests are particularly important (Bull et al. 1986, Goggans et al. 1989). Despite these suggestions, very few data exist concerning the relative importance of different habitat types to Black-backed Woodpecker populations. I suggest that foraging habitat selection in the Black-backed Woodpecker might be better understood by learning more about their diet breadth. Then, by comparing the range of acceptable prey types to the relative abundance of those insects within and among potential habitats, we might better understand patterns in their habitat selection.

Within the post-fire forests I studied, Black-backed Woodpeckers ate the largest, most abundant prey type (wood-borers) found beneath the bark, and they foraged on trees that were rich in those insects compared to nearby trees. This is consistent with the suggestion that Black-backed Woodpeckers specialize on wood-boring beetle larvae (Goggans et al. 1988, Murphy and Lehnhausen 1998), and that this constrains their habitat use. However, it does not falsify the alternative hypothesis that habitat selection constrains their diet. These two explanations are more than trivially different. If Black-backed Woodpeckers specialize on wood-borers and occupy only habitats where those are abundant, they should use a narrower range of habitats than if they simply specialize on habitats with abundant prey. For example, bark beetle outbreaks may contain fewer wood-borers than burned forests (reasons discussed below) even though they contain immense numbers of bark beetles. Should we consider outbreaks and post-fire forests equal in value to foraging Black-backed Woodpeckers?

Bark beetle outbreaks could equal burned forests in foraging opportunities if a) wood-borers are as abundant in bark beetle outbreaks as they are in burned forests, and Black-backed Woodpeckers eat wood-borers in bark beetle outbreaks (this would support the wood-borer-specialist hypothesis); or b) in bark beetle outbreaks, Black-backed Woodpeckers eat bark beetles (this would support the habitat-specialist hypothesis).

Bark-beetle-killed forests probably support lower wood-borer abundance than burned forests, even though they consist of many snags. Wood-borers may occur at lower densities in beetle-killed forests than in early post-fire forests for three reasons: (1) trees in beetle outbreaks are killed over many years (e.g. > 15 in Goggans' study), so many snags are in advanced (less favorable for wood-borers) stages of decay; (2) in bark-beetle-killed trees, much of the nutrient-rich phloem is consumed by bark beetles, and later-arriving wood-borers are faced with strong competition for high-quality food (Coulson et al. 1979); and (3) bark beetles are highly host-tree-specific (Wood 1982), so outbreaks in mixed-species forests never kill all the trees, meaning that total snag density is less than in a burned forest of similar tree species composition.

Studies of Black-backed Woodpeckers are typically conducted in only one disturbance type, complicating the problem of comparing their abundance across habitats. They are reported from bark beetle outbreaks in Oregon and northwestern Montana (Bull et al. 1986, Lester 1980, Goggans et al. 1988), but density estimates are substantially lower than in post-fire forests. For instance, Goggans et al. (1989) estimated home range size at over 400 ha for a Black-backed Woodpecker pair, compared to 9 pairs holding territories in 200 ha of post-fire forest (23 ha/pair) (Hejl and McFadzen, unpubl. data). Furthermore, in summer 1999, I spent 7 days surveying 550 ha of mountain-pine-beetle-infested lodgepole pine forest at 4 different sites in Montana. The search failed to produce any Black-backed Woodpecker sightings while turning up 7 Three-toed and 6 Hairy woodpeckers (unpubl. data).

Although these data are limited, the lower abundance of Black-backed Woodpeckers in bark beetle outbreaks may indicate that outbreaks are not equal to burned forests in foraging value. An alternative hypothesis is that Black-backed Woodpeckers' habitat selection mechanism overlooks beetle outbreaks. If further work were to find lower wood-borer abundance in bark beetle outbreaks than burned forests, this would support the idea that Black-backed Woodpeckers are wood-borer specialists.

CAUSES OF VARIATION IN INSECT POPULATIONS IN BURNED TREES

Insect assemblages are undoubtedly an important part of a habitat's suitability for Black-backed Woodpeckers. It is expedient to think about the effects of a disturbance type, such as fire, on insect diversity and abundance by drawing generalizations. We know that burns cause increases in wood-borer, bark beetle, and some other insect populations, but the magnitude and direction of changes in insect assemblages both among and within burned forests can be extremely variable (McCullough et al. 1998). This variation means that individual post-fire forests can present very different foraging opportunities to woodpeckers. By understanding the effects of a few specific factors on wood-borer and bark beetle populations, and integrating this knowledge with site conditions, we can make more detailed predictions than simply that insect numbers will increase. Several studies of bark beetles (e.g. Amman and Ryan 1991, Rasmussen et al. 1996, Ryan and Amman 1996) and wood-borers (Zhang et al. 1993, Muona and Rutanen 1994, Ehnstrom et al. 1995, Dajoz 1998, Werner *in press*) have identified some factors that commonly affect insect populations in burned forest, discussed below.

Studies that attempt to isolate variables at a single locality may be limited by one very influential cause of variation: source populations of insects in surrounding areas. If insect colonizers are absent from surrounding forest, insect levels may be low regardless of site conditions. Therefore, low numbers of an insect in a single study might not indicate that proximate factors under study (e.g. burn severity, tree species) were unsuitable for the insect (Peterson and Arbaugh 1989, Muona and Rutanen 1994).

Conditions affecting insect populations operate at various temporal and spatial scales, including among and within years, among tree species, among trees, and within a tree. Among years, insect populations change primarily according to burn age, overall burn severity, and presence of nearby source populations. Within a year, recent weather and levels of predators and parasites affect survival of developing insects (Wood 1982). Within a particular patch of a burn the important variables are aspect, slope, and local burn severity (which affect tree microclimates), stand age, and tree species composition. Among trees, bark and phloem thickness and phloem moisture content affect survival and fecundity of the brood (Haack et al. 1987). Within a tree, insect numbers vary with microclimatic differences on different sides of the tree and at different heights. Tree species and size are strong predictors of phloem thickness (Amman and Ryan 1991), so they are useful variables to measure.

Tree size. Larger trees typically contain thicker phloem, which supports more and larger insects (Linsley 1961, Mitton and Sturgeon 1982, Zhang et al. 1998). In a study of wood-borers in burned, 80 to 150 year-old trees in China, Zhang et al. (1993) found a significant positive correlation between the number of wood-borer emergence holes and both tree diameter and bark thickness. This pattern is not evident in my data. Averaging wood-borer density for trees grouped by size showed no relationship for Warrior's Face, while the most insect-rich trees at Boyer were intermediate in size (around 25 cm dbh; see Figure 19). The discrepancy between the two studies may result from the methods used to count wood-borers. I measured numbers of larvae; Zhang et al. (1993) counted emergence holes of adult insects. Also, Zhang et al. (1993) calculated data from successive 2-m sections of the entire tree trunk, so their trend may also include an effect of height on emergence density.

Burn severity. Fires occur at a range of severities and cause a range of injury to trees, ranging from scorching the lower trunk, to burning parts of the crown, to killing the entire tree, to burning the tree so severely that all the needles are consumed. These levels are easily observed and can provide clues to other effects of the fire on the tree, such as the degree of injury (or dehydration) of the phloem, a particularly important characteristic affecting bark beetle and wood-borer colonization.

In studies of bark beetles, colonization increases with burn severity up to the point of complete defoliation (Amman and Ryan 1991, Rasmussen et al. 1996), whereupon colonization drops off dramatically (Furniss 1965, Amman and Ryan 1991). The effect on insect populations of slight differences in burn severity after the point of tree death is unknown.

In Alaska, Murphy and Lehnhausen (1998) noted bark beetles occurred only under uncharred bark, primarily of spruces. I found bark beetles mainly under charred bark of Douglas-firs and ponderosa pines. This was true even on single trees where some of the bole was charred and the rest unburned, as Furniss (1965) also noted. Murphy and Lehnhausen (1998) suggested that wood-borers did not attack highly burned trees and therefore avoided the burn interior. On my study sites, most trees that were 'totally burnt' (as defined by Murphy and Lehnhausen [1998]) retained considerable moisture in the phloem. These trees contained many wood-borers and were the sites of most of my foraging observations.

Burn interiors and completely blackened trees in my study were not poorer foraging sites than edges or less severely burned trees, but in Alaska they were (Murphy and Lehnhausen 1998). If the Alaska site trees had thinner bark than those at my study sites, then a similar fire intensity could have produced poorer conditions in those trees than at my sites.

Insect populations across years. Insect density is related to age since fire, and has been offered by many authors as an explanation for changes in woodpecker density (Bent 1939, Harris 1982, Goggans et al. 1988, Murphy and Lehnhausen 1998). Overall, insect densities are said to peak shortly after the fire and then decline abruptly with wood-borer emergence 4 to 5 years later (e.g. Harris 1982). Unfortunately, long-term studies of insect density in burns do not exist, so no specific relationship of insect density with time has been identified. Murphy and Lehnhausen (1998) suggested that wood-borer abundance may decline sharply as soon as three years post-fire. To investigate this idea, I calculated monthly averages in wood-borer density for Warrior's Face (two years post-fire) and Boyer (one year post-fire), and compared these with data I collected in August 1999 at Warrior's Face (three years post-fire) (Figure 21).

Although a direct comparison of wood-borer densities between the two sites is not valid, it is interesting to note the direction of change in wood-borer densities within each post-fire year. At Boyer, during the first year post-fire, insect densities increased in all tree species measured; at Warrior's Face, during the second year post-fire (1998), insect densities did not change or declined slightly. At Warrior's Face, at the end of the third post-fire breeding season (1999), Douglas-firs contained fewer wood-borers than in either month of the previous Warrior's Face dataset. The data concerning insect trends during each of the years post-fire come from only one site, so there is no power to make strong conclusions; however, they support the possibility that declines in wood-borer populations may be as rapid as three years (Murphy and Lehnhausen 1998).

SUMMARY

At Warrior's Face, I found Black-backed Woodpeckers foraging almost exclusively in Douglas-firs. Douglas-firs also contained significantly more prey than any other tree species. This result raised two possibilities: either Black-backed Woodpeckers at this study site used Douglas-firs for foraging as a result of some preference or constraint, or they tracked their prey and used rich prey-sources. Previous work on

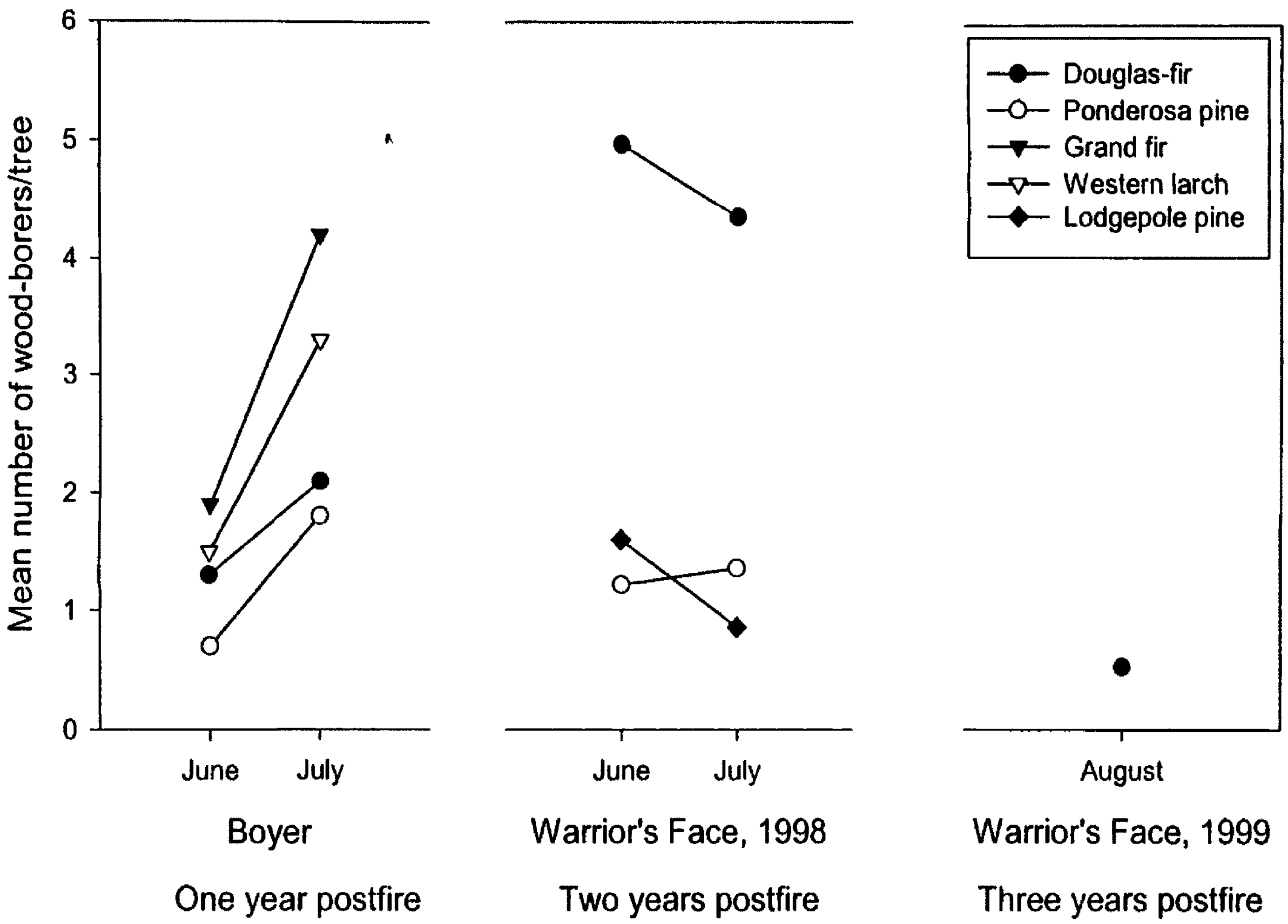

Figure 21. Observed trends in wood-borer densities in three years post-fire. These limited data support Murphy and Lehnhausen's (1998) idea that woodborer abundance can peak and decline by as early as the third year postfire.

Black-backed Woodpeckers suggests that they have favorite foraging tree species, but these studies also suggest that the most-used trees have flaky bark, unlike Douglas-fir. I tested the two alternatives by studying foraging behavior and prey density at another site (Boyer), where tree species composition and insect colonization were different. At this second location, Black-backed Woodpeckers foraged primarily in western larch, which contained more prey than the much more abundant Douglas-firs. This comparison suggests that Black-backed Woodpeckers track prey density when deciding where to forage. Interestingly, Black-backed Woodpeckers did not use grand fir, despite the fact that this species had similar estimates of prey density and tree availability as western larch. Non-use of grand fir indicates that prey density is not the only factor affecting tree use by Black-backed Woodpeckers.

The important conclusion that Black-backed Woodpeckers track prey density could not have been made had this study included data from only one site. By measuring foraging behavior, tree species availability, and insect availability at two different sites, I was able to rule out alternative explanations for foraging behavior, such as consistent use of a 'favorite' tree species or use of tree species in proportion to their availability.

Food availability. Food availability appears to influence Black-backed Woodpecker foraging behavior. They used relatively prey-rich trees (even within a prey-rich habitat) and they used larger insects much more frequently than expected based on their availability. However, Black-backed Woodpecker use of patches at Warrior's Face was not related to prey density, so another factor may have been more limiting than food availability. It may be that no site-specific factors (i.e. food or nest-site availability, predation, or interspecific competition) limit Black-backed Woodpecker populations in burned forests; instead, population size may be determined by the number of Black-backed Woodpeckers that disperse into each burn.

Diet breadth. Black-backed woodpeckers ate primarily wood-borers in this study. Wood-borers were the biggest prey items found under the bark. Although bark beetles were present at both sites, Black-backed Woodpeckers were rarely observed eating them. Studies of woodpeckers in bark-beetle outbreaks have assumed that bark beetles were the main prey item, but these studies did not measure diet to conclude that wood-borers were not eaten (Lester 1980, Goggans et al. 1988). Further work in different habitats is necessary to decide if bark beetles are indeed a preferred prey type.

Conservation implications. Wildlife habitat management aims to conserve areas that are valuable for particular species or groups of species. Often, valuable areas are identified by studying use vs. nonuse of potential habitat. However, this approach may not yield generalizable results when habitat variables substitute for underlying requirements (such as food density) that are unpredictable across sites. In this case it may be more instructive to study the next lower trophic level to understand why certain habitat variables are selected (Saab 1998). As this study shows for Black-backed Woodpeckers, food availability is important; and, at least in burned forests, wood-borers are an important food resource. For these woodpeckers, the most valuable habitat component may be wood-borers rather than a particular tree species, because no single tree species is consistently prey-rich. Therefore, the focus should be on conserving the prey-rich tree species at a site rather than conserving a tree species that was shown to be important in previous studies.

In burned areas slated for salvage logging, conservation for fire-associated species is important because these species may not be common elsewhere (Hutto 1995). Authors acknowledge the importance of conserving foraging habitat as well as saving potential nest trees (Goggans et al. 1988, Caton 1996, Hitchcox 1996, Murphy and Lehnhausen 1998). While my results suggest that, within a burn, one tree species may be a more profitable foraging site than another, this is not a recommendation for selectively removing prey-poor trees throughout a burn. Studies of cavity-nesting birds in salvage-logged, burned forests indicate that species such as Black-backed and Three-toed woodpeckers and Brown Creeper (*Certhia americana*) occupy salvage-logged areas at much lower densities than unlogged, burned forests (Hitchcox 1996, Saab and Dudley 1998, Hejl pers. comm.). Because even partial logging of post-fire stands effectively eliminates habitat for species such as these, I suggest that areas designed to conserve Black-backed Woodpecker habitat should focus on large patches of predominately prey-rich trees. If parts of burned forests are to be logged, sale planners should target areas with a majority of prey-poor trees. If prey density varies consistently by tree species this should be fairly easy to accomplish. Because insect colonization can vary at each site, this will require determining which trees at each site or year contain the most prey.

Future Work. Many questions about insect distribution, prey choice, and foraging behavior remain. The approach I used to study Black-backed Woodpecker foraging behavior could be used in the future, even on relatively small-scale studies (i.e. a field crew of two). The interesting question of *Picoides* woodpecker coexistence in burned forests (Murphy and Lehnhausen 1998) could be investigated by studying diet and prey density in Black-backed, Three-toed, and Hairy woodpeckers simultaneously.

Other questions related to Black-backed Woodpecker habitat selection remain unanswered. The relative values as foraging habitat of mature/overmature forests, bark-beetle outbreaks, and burned forests (Goggans et al. 1988, Hutto 1995) could be estimated by measuring prey choice and prey availability in each of these habitat types. Measuring Black-backed Woodpecker diet with different combinations of available prey types would help understand whether this species is a wood-borer specialist or a prey-rich-habitat specialist. This problem could be tackled using an experimental approach in the field. By placing sections of snags containing various insect types near Black-backed Woodpecker nests, prey choice given different insect availabilities could be determined. An approach for precisely manipulating woodpecker prey is described in a study of optimal foraging in Downy Woodpeckers (Lima 1983, 1984).

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