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Down Logs as Habitat for Forest-dwelling Ants—the Primary Prey of Pileated Woodpeckers in Northeastern Oregon

Abstract

Logs on the forest floor in 240 sample plots in the Blue Mountains of northeastern Oregon were counted and their physical characteristics described in relation to ant colonization. The plots were located in 12 home ranges of pileated woodpecker (*Dryocopus pileatus* (L.)), a Management Indicator Species in USDA Forest Service management guidelines. One or more species of ants were found in 62% of 1,385 sectioned logs. Of 13 species of ants found, the most common were *Lasius alienus* (Foerster), *Formica neorufibarbis* Emery, and *Camponotus modoc* (Wheeler). Wood-dwelling ants that colonize down logs and snags are the primary prey for pileated woodpecker. Relationships between physical characteristics and species of down logs, their colonies of ants, and foraging pileated woodpeckers are discussed. Differential occurrences among genera and species of ants suggest a complex picture of species, sizes, and stages of decay of logs chosen for colonization. The relationships of logs and ants to management of pileated woodpecker and to western spruce budworm (*Choristoneura occidentalis* (Freeman)), a major forest-defoliating insect, are also explored.

Introduction

Down logs are an important colonizing substrate for forest-dwelling ants. Although these ants are a largely ignored component in mixed-conifer stands of the Pacific Northwest, they play important roles in ecosystem function. They are actively involved in decomposition of dead wood, nutrient cycling, plant pollination, seed dispersal, and predation upon insects. In addition, ants are the prey for other arthropods and wildlife species in the forest (Petal 1978, Youngs 1983, Holldobler and Wilson 1990, Way and Khoo 1992). Maser and Trappe (1984) and Hall and Thomas (1984) recognized the importance of ants in Pacific Northwest forests, but little work has been done to clarify ecological associations between ants and other forest-dwelling vertebrates and invertebrates. Notable exceptions are studies describing relationships between ants and the pileated woodpecker (*Dryocopus pileatus* (L.)) (Beckwith and Bull 1985, Bull et al. 1992), and between ants and the western spruce budworm (*Choristoneura occidentalis* (Freeman)) (Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984).

Bull et al. (1992) reported that *Camponotus* and *Formica* ants are the principal food for pileated woodpeckers in northeastern Oregon, where they comprised about 97% of the woodpecker's diet as represented in 330 scat samples gathered year-round. The pileated woodpecker is a large, tree-cavity excavator that is ecologically tied to old-growth mixed-conifer stands. This association is principally a result of the woodpecker's need for large dead trees for nesting, large hollow trees for roosting, and abundant standing and down dead wood for foraging (Bull and Holthausen 1993).

Because pileated woodpecker populations can be adversely affected by management activities that reduce the number of large trees (Bull and Meslow 1977), this bird was selected by the USDA Forest Service as a Management Indicator Species (U.S. Laws, Statutes, etc. 1976). Under this designation, National Forests in the Pacific Northwest Region must be managed to provide habitat to maintain viable populations of pileated woodpecker within its natural range.

Toward this goal, the USDA Forest Service has developed various sets of standards and guidelines in each of several National Forests to provide adequate nesting areas. Less attention, however, has been given to requirements for foraging habitat. Current guidelines provide for foraging areas of about 120 ha but do not address specifically the amounts, species, or size classes of down logs where 38% of foraging occurs (Bull and Holthausen 1993). No studies have addressed the arthropod community residing in snags where another 38% of foraging by the woodpecker occurs. This is possibly either because of the need to destructively sample the limited number of snags, or the risks involved in falling the snag, or in climbing and sampling.

In addition to being an important food source for pileated woodpecker, ants are predators of the western spruce budworm (Youngs and Campbell 1984, Torgersen et al. 1990). Populations of this important forest insect sporadically erupt into outbreaks in mixed-conifer stands throughout the West, where the larvae may defoliate trees (Brookes et al. 1987). Of the 13 species of ants that prey on the budworm, 12 species colonize standing or down dead wood (Smith 1979; R.D. Akre, Washington State University, Pullman, Wash., personal communication). Unfortunately, little is known about the frequency of occurrence of forest-ant colonies, or about the size, species, and physical characteristics of the logs in which they occur.

Because down wood plays an important role as habitat for these ants, whose numbers influence those of both the pileated woodpecker and western spruce budworm (Figure 1), we undertook this study. Our specific objectives were to (1) describe the number, size, species, and other physical characteristics of logs used by forest-dwelling ants in home ranges of pileated woodpeckers; and (2) identify and determine the relative frequency of the species of ants that used those logs.

Methods

Study Sites

We used 12 study areas, each delineated by the home range of a pair of pileated woodpeckers. These home ranges, which averaged 597 ha (range 200-1464 ha), were in the Blue Mountains of northeastern Oregon in Baker, Union, and Wallowa Counties (Bull and Holthausen 1993). Forested areas within the home ranges were predominantly uneven-aged mixed-conifer stands of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.)); Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco)); ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.); western larch (*Larix occidentalis* Nutt.); and lodgepole pine (*Pinus contorta* Dougl. ex Loud.)

Aerial photographs with sketched boundaries of each home range were used to define the study areas. Twenty sampling points per home range were systematically selected by using a grid overlaid on the aerial photos. Points falling in nonforested, grassy openings were relocated to the nearest grid-point in a forested area. When a

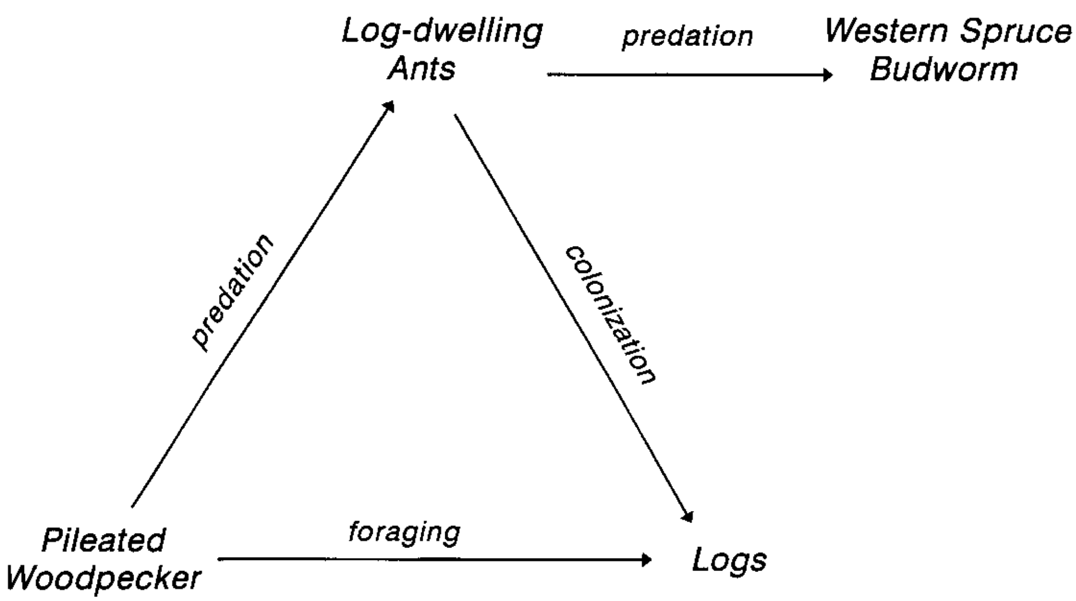


Figure 1. Diagram showing functional relationships between log-dwelling ants, logs, pileated woodpecker, and western spruce budworm in northeastern Oregon.

sample point shown on an aerial photo was located on the ground, that point became the SW corner of a 20- X 20-m plot laid out in cardinal directions.

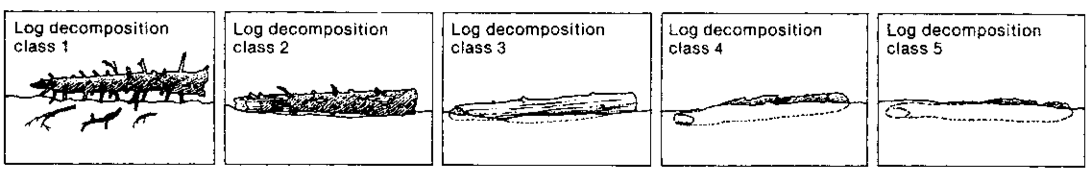
Sampling

Log sampling was done between 24 May and 25 June 1991. In each plot, all logs ≥ 15 cm in diameter at the large end and ≥ 2 m long were measured and described. A 15-cm large-end diameter of logs was chosen based on field observations by the junior author, who found few signs of pileated woodpecker foraging in logs below this minimum. The 2-m minimum length was based on our judgment that shorter logs did not provide suitable habitat for ants, and on constraints of available time and labor. Recorded log measurements included length within the plot, and large- and small-end diameters 10 cm from each end or where the log crossed the plot boundary. The large-end diameter of butt logs with some of the root wad present were measured just distad of the butt swell. Logs were classified by large-end diameter into four categories that approximate the classes for diameter at breast height (DBH) of standing trees used by the Forest Service (USDA Forest Service 1985). These classes are: 15-22 cm (6.0-8.9 in.) for poles; 23-37 cm (9-14.9 in.) for small logs, 38-50 cm (15.0-19.9 in.) for medium-sized logs; and ≥ 51 cm (≥ 20 in.) for large logs. Mean log diameter was obtained by averaging the large- and small-end diameters. Volume of logs was calculated by using the length of the log and its mean diameter to compute the volume of the log as a cylinder.

Species of each log was recorded. About 10% of the logs were devoid of bark or had decayed to the point that species could not be determined, so they were recorded as "unidentifiable." Douglas-fir and grand fir were especially difficult to separate reliably, so they were combined as "firs."

We chose separate classifications to describe external qualities of the entire log and internal qualities of the wood. To describe overall qualities of entire logs, we classified them according to five log-decomposition classes (Maser et al. 1979). These describe a range of logs from ones that retained some twigs ≤ 3 cm in diameter and intact bark to those in advanced stages of decomposition that had partly been incorporated into the forest floor (Figure 2).

To describe qualities of internal wood texture and degree of decomposition, we classified the wood condition as sound, moderately decayed, or in advanced decay. The significant distinction here is that "wood condition" refers to the physical properties of the wood at a sectioning cut. Specifically, it is the extent to which the wood has become soft, friable, spongy, or pitted as a result of attack by decay-causing organisms and channelizing by invertebrates. Our wood condi-



Log characteristics	Log decomposition class				
	1	2	3	4	5
Bark	intact	intact	trace	absent	absent
Twigs <3 cm (1.18 in)	present	absent	absent	absent	absent
Texture	intact	intact to partly soft	hard, large pieces	small, soft, blocky pieces	soft and powdery
Shape	round	round	round	round to oval	oval
Color of wood	original color	original color	original color to faded	light brown to faded brown or yellowish	faded to light yellow or gray
Portion of log on ground	log elevated on support points	log elevated on support points but sagging slightly	log is sagging near ground	all of log on ground	all of log on ground

Figure 2. Log decomposition classes (from Maser *et al.* 1979).

tion categories equate with the classes of "internal succession" of Maser et al. (1979).

Ant Collections

To determine the presence of ants within logs, we sectioned six logs per plot with a chainsaw. To assure representation of logs from throughout the plot, we attempted to obtain at least one log from each of the quadrants in the plot. Two logs in each of three diameter-size classes (15-25 cm, 26-40 cm, and >40 cm) were selected for sectioning. Logs were sequentially cut into 1-m lengths beginning 10 cm from the large end or from where the log crossed the boundary of the plot. At sectioning cuts where ants were encountered, we recorded wood condition and whether the log was in contact with the ground.

At each sectioning cut, about 20 specimens of the largest ants (i.e., major workers) were collected and placed into vials containing 70% ethyl alcohol. Each vial was labeled with information on the home range, plot, and log in which the ants were collected. Ants were later identified with the keys of Hansen and Akre (1985) and Wheeler and Wheeler (1986). To confirm identifications, we compared specimens with species verified by D.R. Smith, USDA, ARS, Systematic Entomology Laboratory, U.S. National Museum of Natural History, Washington, DC. Voucher collection is stored at the Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, La Grande, Oregon 97850.

Statistical Analyses

For analysis, species of *Camponotus* and *Formica* were each tallied as a separate group. Species in the genera *Lasius, Tapinoma, Leptothorax,* and *Aphaenogaster* were grouped and referred to as "Other". Thus, three groups are treated here - *Camponotus, Formica,* and Other. Except where noted, when an ant group was found more than once in a log, it was counted only once—i.e., as a single colony. Ants form large colonies that are aggressive toward other ants—even other ants of the same species. Thus, we assumed that ants of the same species that occurred in a single log belonged to the same colony.

Statistical analyses were based on the percentage occurrence of *Camponotus, Formica,* or Other ants in sampled logs of a given variable—e.g., log species, large-end diameter class, etc.—in the home range of each pair of pileated woodpeckers. Standard errors of percentage occurrences were based on 12 home ranges. One-way analysis of variance (ANOVA)(Snedecor and Cochran 1980) was used to determine if the classes of selected variables for sectioned logs were used equally by each ant group. When ANOVA showed that mean percentage occurrences were statistically different ($P \leq 0.05$), we used Tukey's multiple comparisons (Miller 1981) to determine which classes within a variable were statistically different. The variables compared were log species, large-end diameter, length, log-decomposition class, wood condition, and log-contact with the ground. Chi-square analysis was used to test whether the presence or absence of one ant group in a log influenced the presence or absence of another group. Chi-square analyses were also used to determine if the pattern of usage of a given variable differed among ant groups. Stepwise discriminant analysis was used to determine which were the significant predictor variables for each group (SAS 1988). Statistical significance throughout was set at $P \leq 0.05$.

Results

Characteristics of All Logs Sampled

There were 2,779 logs ($\overline{x}$ = 289.5 logs per ha) on the 9.6 ha within the 240 sample plots in the 12 pileated woodpecker pairs' home ranges. Douglas-fir and grand fir (combined as "firs") dominated among the logs (32.4%), but the most common single identifiable species was ponderosa pine (25.7%). Lodgepole pine was more common than larch (17.9% vs. 13.9%), but it also showed more variation in occurrence among the 12 home ranges (standard errors of 5.4% vs. 1.6%) (Table 1).

Nearly half (46.2%) of the logs were in the smallest of the four diameter classes (15-22 cm), representing only 11.9% of the volume (13.2 m^3). Conversely, 8.3% of the logs were in the largest diameter class (51-120 cm), but they represented 37.6% of the volume (41.6 m^3) (Table 2). The mean large-end diameter was greatest for larch (32.3 ± 0.8 cm) and smallest for lodgepole pine (22.7 ± 0.3 cm). The mean large-end diameter for all species of logs was 28.9 ± 0.3 cm. The mean length for all logs, calculated by using both entire logs and the portions of logs within the plots, was 6.4 ± 0.04 m; maximum length was 14 m.

TABLE 1. Number and proportional representation of species of logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991.

Species of log	n	Occurrence % ± SE[a]	Large-end Diameter $\bar{x}$ ± SE (cm)
Ponderosa pine	673	25.7 ± 6.2	30.3 ± 4.10
Firs[b]	841	32.4 ± 4.1	29.9 ± 4.30
Lodgepole pine	611	17.9 ± 5.4	22.7 ± 2.17
Larch	360	13.9 ± 1.6	32.3 ± 4.30
Other spp.[c]	16	0.5 ± 0.4	24.1 ± 1.93
Unidentifiable	278	9.6 ± 2.1	32.0 ± 4.19
Total	2779		

[a] Standard error based on 12 pileated woodpecker home ranges.

[b] Douglas-fir and grand fir were combined as "Firs" because of difficulties in identifying decayed logs of these species.

[c] Englemann spruce, *Picea engelmannii* Parry ex Engelm., and black cottonwood, *Populus trichocarpa* Torr. & Gray.

Occurrence of Ants

In all, 1,385 logs were cut into 3,221 sections. One or more ant groups were found in 855 (61.8%) of the logs. In these ant-inhabited logs, ants were encountered at 1,063 of the 1,988 sectioning cuts.

Thirteen species of ants were collected from sectioned logs. The most common species encountered were *Lasius alienus*, *Formica neorufibarbis,* and *Camponotus modoc*, which were found in 58% of the sampled logs and comprised 75% of 1,063 occurrences. Overall, the most common species was *Lasius alienus,* which represented 43% of all occurrences of ants. *Formica neorufibarbis* (18%) was only slightly more common than *C. modoc* (14%)(Table 3).

The *Camponotus* were least often associated with another group. The least common combination of groups was the occurrence of *Camponotus* and *Formica* in a single log (Table 4). Chi-square (X^2) analysis indicated that the presence of both *Camponotus* and *Formica* in a log occurred statistically less often than expected (X^2 = 8.12, 1 df; P = 0.0044). The occurrence of *Camponotus* had no significant influence on the likelihood that the Other group would be present in the same log (X^2 = 3.20, 1 df; P = 0.0736). On the contrary, the occurrence of *Formica* in a log was positively related to the occurrence of Other ants (X^2 = 8.97, 1 df; P = 0.0027) there.

Characteristics of Logs Preferred by Ants

Species. Species of logs were used in statistically different proportions only by the *Camponotus* (P = 0.0016). Specifically, *Camponotus* occurred in larch logs in significantly greater proportion than in lodgepole pine (Figure 3A). Chi-square analysis to test whether *Camponotus, Formica,* and Other ants occupied species of logs in the same proportions revealed no statistically significant differences in occupancy of logs by the three groups.

Large-end Diameter. Size class of logs used for colonization appeared to be important only to *Camponotus* (P ≤ 0.0001), which occurred more commonly in the largest diameter class (51-120 cm) than in the smallest class (15-22 cm) (Figure 3B). This pattern of occurrence of *Camponotus* was statistically different than occurrence of either *Formica* (X^2 = 16.32, 3 df; P = 0.0010) or Other ants (X^2 = 24.18, 3 df; P <0.0001), which occurred more uniformly among size classes of logs.

TABLE 2. Number and volume of logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991

Large-end diam. size class (cm)	Total no. of logs	Logs per ha $\bar{x}$ ± SE[a]	Volume per log (m³) $\bar{x}$ ± SE	Volume per ha (m³) $\bar{x}$ ± SE
15-22	1284	133.7 ± 17.8	0.0985 ± 0.0035	13.2 ± 0.5
23-37	920	95.9 ± 6.4	0.3044 ± 0.0064	29.2 ± 0.6
38-50	344	35.9 ± 2.5	0.7275 ± 0.0268	26.1 ± 1.0
51-120	231	24.0 ± 3.2	1.7317 ± 0.0912	41.6 ± 2.2
All size classes	2779	289.5 ± 22.6	0.3826 ± 0.0112	110.8 ± 3.2

[a] Standard error based on 12 home ranges.

TABLE 3. Frequency of ant species or groups occurring in sectioned logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991

Species of ants	Number of occurrences[a]	% logs ± SE[b]
Camponotus species		
C. modoc (Wheeler)	151	10.8 ± 1.1
C. vicinus Mayr	16	1.1 ± 0.7
C. laevigatus (F. Smith)	6	0.4 ± 0.2
Unknown	4	0.3 ± 0.1
Total[c]	177	12.5 ± 1.6
Formica species		
F. neorufibarbis Emery	195	14.0 ± 1.6
F. accreta Francoeur	72	5.2 ± 1.2
F. haemorrhoidalis Emery	6	0.4 ± 0.2
F. densiventris Viereck	5	0.4 ± 0.2
F. subnuda Emery	2	0.2 ± 0.1
F. lasioides Emery	1	0.1 ± 0.1
Unknown	10	0.7 ± 0.3
Total[c]	281	20.2 ± 2.2
Other species		
Lasius alienus (Foerster)	455	32.9 ± 2.6
Tapinoma sessile (Say)	71	5.2 ± 1.0
Leptothorax muscorum (Nylander)	45	3.3 ± 0.9
Aphaenogaster occidentalis (Emery)	24	1.7 ± 0.7
Total[c]	567	41.1 ± 3.0

[a] Each species or group counted only once per log.

[b] Based on 1,385 logs in 12 home ranges.

[c] "Total" categories are not simple sums of the tallies for individual species because occurrences of a genus or group are counted only once in a log.

Length. The length of logs influenced the presence of *Formica* and Other ants, both of which showed statistically significant differences in occurrence among the four log-length classes (P = 0.0155 and 0.0137, respectively). Both these groups favored logs ≥ 7 m long over logs that were 1-3 m. *Camponotus* used all the log-length classes about equally (P = 0.3904)(Figure 3C). Compared to each other, none of the groups used the log-length classes in statistically different ways (all $X^2 \leq 4.92$, 3 df; all P ≥ 0.1777).

TABLE 4. Frequencies of occurrence of ant groups alone or in combination with other groups in sectioned logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991.

		Formica		Other	
		Yes	No	Yes	No
Camponotus	Yes	21	152	60	113
	No	260	952	507	705
Other	Yes	93	188		
	No	474	630		

Results of Chi-square tests. 1 df – *Camponotus* vs. *Formica*, X^2 = 8.12, P = 0.0040; *Camponotus* vs. Other, X^2 = 3.20, P = 0.0736; *Formica* vs. Other, X^2 = 8.97, P = 0.0027.

Log-decomposition Class. Only *Formica* used the various decomposition classes in significantly different proportions (P<0.0001). In particular, *Formica* occurred significantly less commonly in log-decomposition class 5, the most decomposed logs, than in classes 1-4 (Figure 3D). Overall, the proportions in which *Formica* used logs among the decomposition classes differed from both *Camponotus* (X^2 = 11.55, 4 df; P = 0.0210) and Other ants (X^2 = 9.8, 4 df; P = 0.0439).

Ground Contact. Log contact with the ground at the site of occurrence of ants was not a significant factor for either *Camponotus* or *Formica* (Figure 3E), nor did these two groups differ from one another (X^2 = 0.6800, 1 df; P = 0.4096). However, *Formica* showed a tendency, though non-significant (P = 0.0700), to occur in log sections without ground contact. The Other ants showed a clear preference for log sections with ground contact (P = 0.0166) (Figure 3E) - opposite of the preference displayed by *Formica* (X^2 = 7.44, 1 df; P = 0.0064).

Wood Condition. Solid wood supported colonies of *Camponotus* significantly more commonly (P = 0.0038) than did wood with moderate or advanced decay (Figure 3F). Neither *Formica* nor the Other ants showed differential preference for a particular wood condition, and both groups differed significantly from *Camponotus* in this regard ($X^2 \geq 35.18$, 2 df; P<0.0001).

Discriminant Analysis

Stepwise discriminant analysis considered the following variables: large- and small-end diameters, log-length, tree species, length x species, log-decomposition class, and ground contact. The

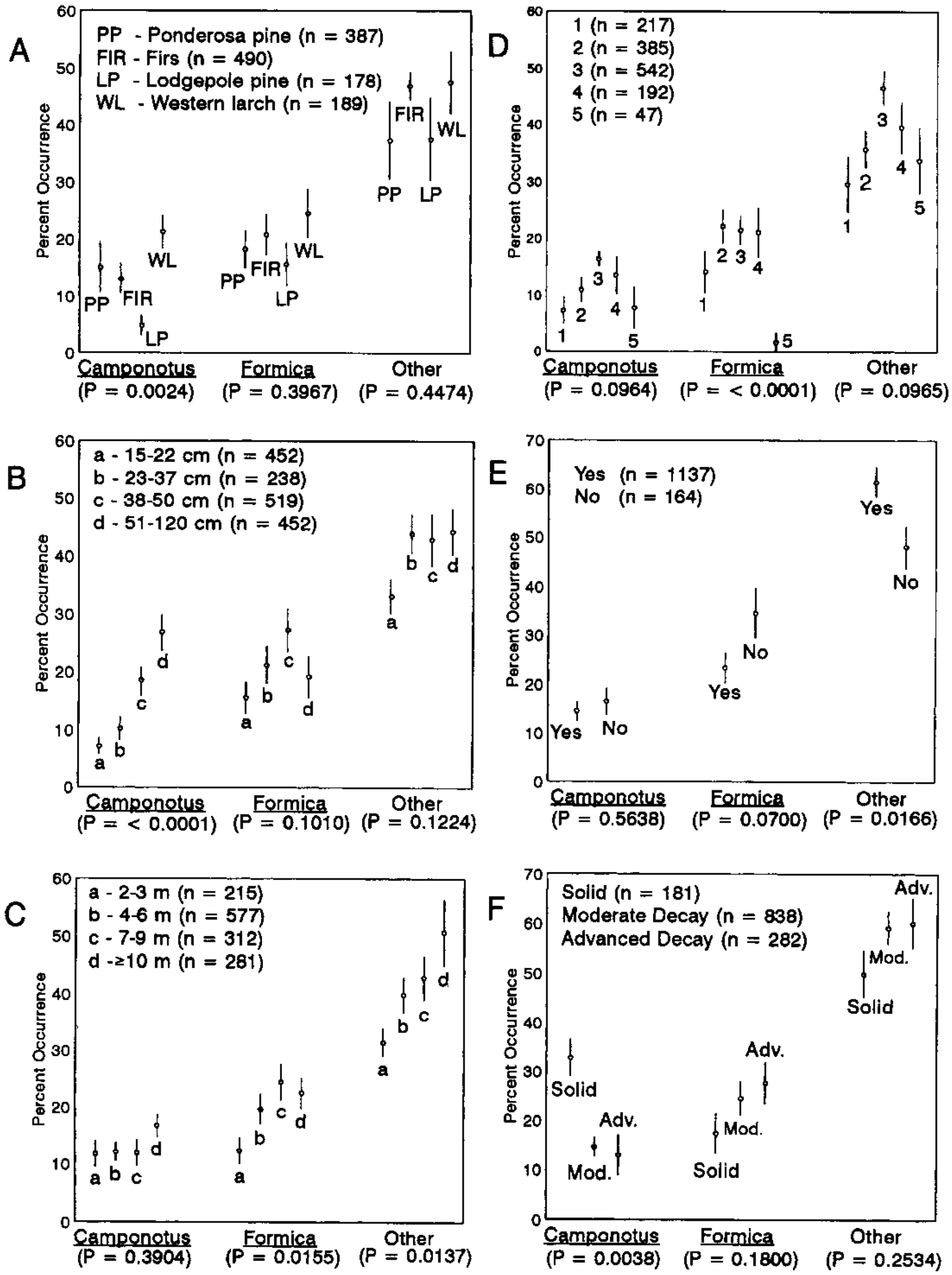


Figure 3. Percent occurrence of ants among logs classified by (A) tree species, (B) large-end diameter, (C) length, (D) log-decomposition, (E) ground contact, and (F) wood condition at sectioning cuts, in northeastern Oregon, May-July, 1991.

analysis indicated that the dominant variables for *Camponotus*, in the order entered, were large-end diameter (+), larch (+), log-decomposition class 3 (+), log-decomposition class 5 (-), and lodgepole pine (-). For *Formica* the dominant variables, in their order, were log-length (+), ground contact (-), log-decomposition class 5 (-), large-end diameter (+), and log-decomposition class 2 (+).

Discussion

Down wood is an important structural component for colonies of log-dwelling ants, as well as a foraging substrate for pileated woodpeckers looking for those ants. In addition, some of the ants are important because they are predators of larval western spruce budworm, a potentially damaging defoliating insect. The logs are the substrate that links these functional systems.

Logs of larch were the most significant colony substrate for the *Camponotus* ants, which showed an apparent aversion for lodgepole pine. Because larch logs averaged among the largest diameter logs, and lodgepole pine logs were the smallest, we were at first unsure whether species or diameter was the more significant variable. Discriminant analysis revealed that large-end diameter of logs was the dominant driving variable relating to occurrence of *Camponotus*. These ants used the largest diameter class of logs (51-120 cm) more than logs in the smallest diameter class (15-22 cm). The same analysis indicated that lodgepole pine logs were avoided even if they were of large diameter. The firs were used by *Camponotus* in about the same proportions (35.8%) in which they occurred among the sectioned logs (32.4%)(Table 1).

Significantly, Bull and Holthausen (1993), who sampled the same logs as used in this study, determined that pileated woodpeckers concentrated their foraging on larch and Douglas-fir and mostly avoided lodgepole pine. The birds also foraged more in logs with large-end diameters >37 cm—that is, in our two largest diameter classes (38-50 and 51-120 cm). Neither *Formica* nor the Other species showed significant differences in the proportions in which they occurred among species of logs or large-end diameter classes. Given that *Camponotus* is the preferred ant prey of pileated woodpecker (Bull et al. 1992), it is not surprising that the woodpeckers concentrated their foraging on logs that were most likely to yield *Camponotus* ants.

Discriminant analysis revealed that *Camponotus* favored logs that, outwardly, were in the middle log-decomposition class (class 3), and both *Camponotus* and *Formica* tended to avoid the most decomposed logs (class 5). Contact of the log with the ground was a significant negative variable for *Formica*, which is consistent with their apparent aversion for the most decayed logs (log-decomposition class 5). Wood condition (i.e., the log's internal consistency) at the site of the sectioning cuts influenced the occurrence of *Camponotus*, which distinctly preferred more solid wood (Figure 3F). *Camponotus* and *Formica* tended to avoid the most outwardly decomposed logs with advanced internal deterioration, where presumably they would be most vulnerable to predation by a large, powerful excavator such as the pileated woodpecker. Overall, *Camponotus* and *Formica* tended to favor less decayed, large-diameter logs of larch or fir where they are most secure from predation by pileated woodpecker.

Of the nine identifiable species of *Camponotus* and *Formica* found in the sectioned logs (Table 3), six are documented predators of western spruce budworm in the montane West—*C. modoc, C. vicinus, C. laevigatus, F. neorufibarbis, F. accreta,* and *F. lasioides* (Youngs and Campbell 1984). Another species, *F. subnuda*, is a suspected predator.[1] The three species of *Formica* that are not documented predators of the budworm—*F. haemorrhoidalis, F. densiventris,* and *F. subnuda*—represented only 2.8% of the occurrences of ants and occurred in only 1% of all the logs. *Camponotus modoc*, the most common of the *Camponotus* we found, may emerge as the target prey species for the woodpecker in northeastern Oregon. Bent (1964) cites a record of pileated woodpecker stomach contents containing *C. herculeanus modoc* (=*C. modoc*, Smith 1979) obtained from two specimens of *Ceophloeus pileatus picinus* Bangs (=*D. pileatus*) in Yosemite Park, Calif. Bull et al. (1992) were not able to identify the *Camponotus* species in scat samples because identifying characters on the ants had been obliterated by passage through the gut of the woodpeckers.

A single species, rarely two, of documented budworm-foraging ants were found in 31.8% of the sectioned logs. Assuming that each log represented a single colony of ants, there would be about 92 colonies of budworm-foraging ants among the 289.5 logs per ha. The volume of 110.8 $\pm$ 3.24 m^3 per ha of downed woody material in our plots (Table 2) falls within the range of volume estimates (115.9 $\pm$ 3.5 m^3 per ha) for the mixed-conifer vegetation types predicted by Maxwell and Ward (1980). The volumes calculated for our study plots did not include logs with large-end diameters <15 cm, whereas the comparable volumes from Maxwell and Ward (1980) included diameters down to 7.9 cm. Thus, even without the volume that would have been contributed by diameters between 7.9 and 14.9 cm, volumes in our pileated woodpecker home ranges were higher than the average of volumes observed by Maxwell and Ward (1980). This suggests that in mixed-conifer stands the upper levels of size classes 2, 3, and 4 of Maxwell and Ward (1980) approximate the tonnage of down wood needed to provide adequate foraging habitat in home ranges of pileated woodpecker.

The differential choice of down logs by each group of ants suggests a complex picture of the use of various species of logs of different sizes and in differing stages of decomposition. The possible temporal succession of particular groups of ants in different age classes of log decay may be a necessary function in the decomposition of down woody debris. This study and that of Bull and Holthausen (1993) together form a more complete picture of how the pileated woodpecker and its prey base are related to down woody debris in the mixed-conifer stands of northeastern Oregon. Logging or firewood cutting practices that leave inadequate or unsuitable down-wood substrates for log-dwelling ants could affect populations of pileated woodpeckers.

Practices that result in inadequate amounts and kinds of down wood could affect pileated woodpecker populations and the beneficial role that foliage-foraging ants have in maintaining forest health. The relationships among ants, pileated woodpecker, forest-defoliating insects, and down logs illustrate the complex of interconnecting life-systems that form a functional ecosystem. Resource managers need to consider this diversity in developing guidelines that prescribe size, species, and amounts of large woody debris in order to conserve functional processes that foster sustainable forest ecosystems.

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Literature Cited

Beckwith, R. C., and E. L. Bull. 1985. Scat analysis of the arthropod component of pileated woodpecker diet. The Murrelet 66:90-92.

Bent, A. C. 1964. Life histories of North American woodpeckers. Smithsonian Institution. US National Museum Bull. 174. *In* Life Histories of North American Woodpeckers. Dover Publications, New York. Pp. 181-184.

Brookes, M. H., R. W. Campbell, J. J. Colbert, R. G. Mitchell, and R. W. Stark. 1987. Western spruce budworm. USDA Forest Service—Coop. State Research Serv., Tech. Bull. 1694. Washington, DC. 198 p.

Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. J. Wildl. Manage. 57:335-345.

Bull, E. L., and C. Meslow. 1977. Habitat requirements of the pileated woodpeckers in northeastern Oregon. J. For. 75:335-337.

Bull, E. L., R. C. Beckwith, and R. S. Holthausen. 1992. Arthropod diet of pileated woodpeckers in northeastern Oregon. Northw. Nat. 73:42-45.

Campbell, R. W., and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. Environ. Entomol. 11:111-114.

Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous ants in the population dynamics of the western spruce budworm. For. Sci. 29:779-790.

Hall, F. C., and J. W. Thomas. 1984. Silvicultural options. *In* Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington. Pp. 128-147. J. W. Thomas ed. USDA For. Serv., Agr. Handb. 553. 512 p.

Hansen, L. D., and R. D. Akre. 1985. Biology of carpenter ants in Washington State (Hymenoptera:Formicidae: Camponotus). Melanderia 43:1-5.

Holldobler, B., and E. O. Wilson. 1990. The Ants. The Belknap Press of Harvard Univ. Press. Cambridge, Mass. 732 p.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. Williams, and R. E. Martin. 1979. Dead and down woody material. *In* Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington. Pp. 78-90. J. W. Thomas ed. USDA For. Serv., Agr. Handb. 553. 512 p.

Maser, C., and J. M. Trappe. 1984. The seen and unseen world of the fallen tree. USDA For. Serv.. Gen. Tech. Rep. PNW-164. 56 p.
Maxwell, W. G., and F. R. Ward. 1980. Photo series for quantifying natural forest residues in common vegetation types of the Pacific Northwest. USDA For. Serv., Gen. Tech. Rep. PNW 105. 229 p.
Miller. R. G. 1981. Simultaneous statistical inference. Springer-Verlag. Pp. 37-48.
Petal, J. 1978. The role of ants in ecosystems. Pp. 293-325. *In* Production ecology of ants and termites. M. C. Brain ed. Cambridge University Press, Cambridge. 408 p.
SAS. 1988. SAS/STAT User's guide. Release 6.03 edition. SAS Institute Inc., Carey. North Carolina. 1029 p.
Smith, D. R. 1979. Superfamily Formicoidea. *In* Catalog of hymenoptera in America north of Mexico. Vol. 2. Apocrita. eds. K. V. Krombein, P. D. Hurd, D. R. Smith. and B. D. Burks. Smithsonian Institution Press, Washington DC. Pp. 1323-1467.
Snedecor, G. W.. and W. G. Cochran. 1980. Statistical methods. 7th Ed. Iowa State Univ. Press, Ames.
Torgersen, T. R.. R. R. Mason, and R. W. Campbell. 1990. Predation by birds and ants on two forest insect pests in the Pacific Northwest. *In* Avian foraging: theory, methodology, and applications. eds. M. L. Morrison, C. J. Ralph. J. Verner. and J. R. Jehl, Jr. Studies in avian biology 13:14-19. Cooper Ornith. Soc., Allen Press, Lawrence. Kansas.
U.S. Laws, Statutes, etc. 1976. Public Law 94-588 {S. 3091}, Oct. 22, 1976 National Forest Management Act of 1976. *In* United States code congressional and administrative news. 94th Congress, 2nd Session, 1976. Vol. 2, Pp. 2949-2963. West Publ. Co., St. Paul, Minn. [1976.] [16 U.S.C. sec. 1600 1976].
USDA Forest Service. 1985. Field procedures. Stand examination. Pacific Northwest Region. 62 p., appendices A-O.
Way, M. J., and K. C. Khoo. 1992. Role of ants in pest management. Ann. Rev. Entomol. 37:479-503.
Wheeler, G. C., and J. N. Wheeler. 1986. The ants of Nevada. Natural History Museum of Los Angeles County. Allen Press, Lawrence, Kansas. 138 p.
Youngs, L. C. 1983. Predaceous ants in biological control of insect pests of North American Forests. Bull. Entomol. Soc. Amer. 29:47-50.
Youngs, L. C., and R. W. Campbell. 1984. Ants preying on pupae of western spruce budworm. *Choristoneura occidentalis* (Lepidoptera:Tortricidae), in eastern Oregon and western Montana. Can. Entomol. 116:1665-1669.

Note

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