Research Article

Foraging Ecology of Pileated Woodpeckers in Coastal Forests of Washington

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Abstract

*In the Pacific Northwest, providing adequate habitat for pileated woodpeckers (*Dryocopus pileatus*) has been a key component of federal forest management strategies for over 20 years. Although their nesting and roosting ecology has been well studied, information on their foraging ecology is limited. From 1990 to 1995, we studied food habits of pileated woodpeckers in coastal forests (with scat analysis); estimated the relative abundance of their primary prey, carpenter ants (*Camponotus *spp.), associated with logs and cut stumps; and investigated selection of forest structures and site characteristics used by pileated woodpeckers for foraging. Pileated woodpeckers primarily consumed carpenter ants (54% of diet), but round-headed beetle larvae (Coleoptera, Cerambycidae) and dampwood termites (Isoptera, Termopsidae) were important food items during the breeding season (Mar–Jun). Selection of foraging structures was related to wood characteristics and microsite conditions that influence the presence and abundance of arthropod prey. Pileated woodpeckers foraged almost exclusively (95%) on standing structures, selecting tall, large-diameter snags in early to moderate stages of decay. Contrary to previous studies, pileated woodpeckers rarely (2%) foraged on logs. Carpenter ants were scarce at logs in closed-canopy habitats, which suggested that in coastal forests logs are too cool and wet to support abundant populations of carpenter ants. Selection of foraging sites by pileated woodpeckers was influenced by the abundance of potential foraging structures; 0.4-ha plots with recent foraging activity had greater densities of large snags (>51 cm dbh and ≥7.5 m tall) than plots without recent foraging. The efficacy of management strategies designed to provide habitat for pileated woodpeckers would be enhanced if they included specific provisions for foraging habitat and accounted for regional differences in the types of structures that provide suitable conditions for wood-dwelling arthropods.* (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1266–1275; 2006)

Key words

carpenter ant, Dryocopus pileatus, *foraging, forest management, habitat selection, log, Pacific Northwest, pileated woodpecker, scat analysis, snag.*

The pileated woodpecker (*Dryocopus pileatus*) occupies large home ranges (>4 km^2) in forested landscapes and uses relatively large dead or live trees with heart-rot decay for nesting and roosting, as well as a wide variety of standing and downed structures for foraging (Bull and Jackson 1995, Aubry and Raley 2002*a*). We believe the pileated woodpecker is a keystone habitat modifier that provides unique ecological benefits in forested ecosystems, including the creation of breeding or resting sites for relatively large secondary cavity-users (e.g., small owls, cavity-nesting ducks, forest carnivores), many of which are of conservation concern (Aubry and Raley 2002*b*). For these reasons the pileated woodpecker is designated as a management indicator species in many National Forests throughout its range in North America. In the Pacific Northwest, managing for pileated woodpecker nest trees and preserving areas of late-successional forest to provide habitat for this species have been key components of federal forest management strategies for over 20 years (U.S. Forest Service 1984, 1986, U.S. Forest Service and U.S. Bureau of Land Management 1994).

The standing structures, site conditions, and forest types used by pileated woodpeckers for nesting and roosting have been well studied, both in the Pacific Northwest (Bull 1987, Harestad and Keisker 1989, Bull et al. 1992*b*, Mellen et al. 1992, McClelland and McClelland 1999, Aubry and Raley 2002*a*, Hartwig et al. 2004) and elsewhere in North America (Bull and Jackson 1995). Although the trees used by pileated woodpeckers for nesting and roosting in northwestern forests share many characteristics, recent studies indicate that selection of nest trees varies regionally. In wet coastal forests, dead trees (snags) and live trees with dead or broken tops (decadent trees) are commonly used for nesting by pileated woodpeckers (Aubry and Raley 2002*a*, Hartwig et al. 2004), whereas in drier inland forests, live trees are used much less frequently (Bull 1987, Bull et al. 1992*b*, McClelland and McClelland 1999). These patterns probably reflect regional differences in the decay characteristics and suitability of available nest trees.

Similarly, evidence suggests that the types of structures used for foraging by pileated woodpeckers may also vary regionally. In inland forests of northeastern Oregon, USA, pileated woodpeckers forage on downed wood (logs) more than a third of the time (Bull 1987, Bull and Holthausen 1993). However, during a previous study of the nesting and roosting ecology of pileated woodpeckers in coastal forests of Washington (Aubry and Raley 2002*a*), we rarely observed evidence of foraging on logs. Because carpenter ants (*Camponotus* spp.) are the primary prey of pileated woodpeckers in the Pacific Northwest (Beckwith and Bull 1985; Bull et al. 1992*a*; C. Raley and K. Aubry, United States Forest Service, unpublished data), we speculated that regional differences in the foraging ecology of pileated woodpeckers may result from the influence of contrasting

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moisture regimes on the distribution and abundance of carpenter ants (Aubry and Raley 2002*a*). In coastal forests, microhabitat conditions in logs may be too cold and wet to support carpenter ant colonies. Consequently, forest management strategies designed to provide foraging habitat for pileated woodpeckers may need to account for regional differences in their ecological relations.

Field studies of pileated woodpecker foraging ecology are restricted in number and geographic scope, although the literature contains a variety of anecdotal accounts of pileated woodpecker foraging sign or behavior (e.g., Tanner 1942, Hoyt 1950, 1957, Conner and Crawford 1974, Kilham 1976, McClelland 1979, Conner 1982, Mannan 1984) and descriptions of scat or stomach contents (e.g., Beal 1911, Bent 1939, Beckwith and Bull 1985, Bull et al. 1992*a*). Several small-scale ($\leq$110 independent observations) studies have been conducted on pileated woodpecker foraging behavior and habitat in mixed-hardwood forests in southwestern Virginia (Conner 1979, 1980, 1981) and eastern Texas, USA (Conner et al. 1994). Flemming et al. (1999) compared the characteristics of trees with old or recent pileated woodpecker foraging excavations ($n = 831$) to those of random trees ($n = 777$) in spruce (*Picea* spp.) and hardwood forests in southern New Brunswick, Canada.

The most comprehensive studies of pileated woodpecker foraging ecology were conducted in mixed-conifer forests in northeastern Oregon. Bull and Meslow (1977) collected data on 152 structures with old or recent pileated woodpecker foraging signs and compared their characteristics to available structures. Bull and her colleagues (Bull et al. 1986, Bull 1987) made 72 visual observations of foraging by pileated woodpeckers and compared results among seasons and between sexes. Lastly, Bull and Holthausen (1993) compared the characteristics of 2,509 foraging structures identified from visual observations on 25 radiomarked birds with those of 3,337 available structures. No information is available on the characteristics of structures used for foraging by pileated woodpeckers in any other forest type or region in the Pacific Northwest.

To understand the potential effects of different forest management strategies on pileated woodpecker populations in the Pacific Northwest, comprehensive information is needed on their foraging ecology in coastal forests. Our objectives were to 1) describe the food habits of pileated woodpeckers in coastal forests of Washington based on scat analyses, 2) estimate the relative abundance of carpenter ants associated with logs and cut stumps in different forest conditions, 3) identify the types, conditions, and sizes of structures selected by pileated woodpeckers for foraging, and 4) identify the vegetative and physiographic characteristics of sites selected by pileated woodpeckers for foraging.

Study Area

We conducted this study on the Olympic Peninsula in northwestern Washington, USA, about 20 km from the Pacific coast on the west slope of the Olympic Mountains. The study area comprised 9,350 ha of highly dissected, mountainous terrain ranging from 92 to 488 m in elevation with a mean annual precipitation of 305 cm (Henderson et al. 1989). Western hemlock (*Tsuga heterophylla*) was the predominant tree species, but Pacific silver fir (*Abies amabilis*) and western redcedar (*Thuja plicata*) were important codominants in many locations. About 47% of the study area was unmanaged late-successional forest >200 years old, 11% naturally regenerated 70-year-old stands, 20% second-growth forest <35 years old, 13% recent clearcuts, and 9% hardwoods or nonforested habitats. For additional information on the ecological and physiographic characteristics of our study area, see Aubry and Raley (2002*a*).

Methods

Collecting Pileated Woodpecker Scats for Diet Analysis

We used scat analysis (Rosenberg and Cooper 1990, Bull et al. 1992*a*) to describe the diet of pileated woodpeckers. From 1990 to 1995, we captured 31 adult pileated woodpeckers at nest and roost trees and outfitted them with backpack radio transmitters (Aubry and Raley 2002*a*). We followed radiomarked birds year-round and attempted to locate each individual 2–3 times per week spaced at least 1 day apart. To collect pileated woodpecker scats, we searched the area below the bird whenever we observed a radiomarked bird defecating. We also collected scats while capturing and handling birds at nest and roost trees. An entomologist experienced in pileated woodpecker scat analysis (R. Beckwith, United States Forest Service [retired], La Grande, Oreg.) identified and tallied all arthropod remains in the scats.

Estimating the Relative Abundance of Carpenter Ants

We used pitfall traps to estimate the relative abundance of carpenter ants associated with logs and cut stumps in different forest conditions. Pitfall captures provide a useful index of abundance for ants that are active on the ground surface if results are interpreted within the context of microsites sampled and the behavior of target species (Bestelmeyer et al. 2000, Southwood and Henderson 2000). Carpenter ants regularly travel from their galleries in dead wood to forage for arthropod prey in the understory and canopy vegetation (Hansen and Akre 1985, Tilles and Wood 1986). If carpenter ant colonies are present in logs and cut stumps, pitfall traps placed at these sites will intercept foragers as they leave or return to their galleries. One of the most common carpenter ant species in western Washington (*C. modoc*) exhibits similar foraging behavior (i.e., trail construction and activity levels) in nonforested habitats as in dense, closed-canopy forest (Hansen and Akre 1985). Thus, we were confident that pitfall traps would provide reliable indices for comparisons of carpenter ant abundance among different habitat conditions in coastal forests. We used plastic pitfall traps designed to capture arthropods (Carolina Biological Supply, Burlington, North Carolina) that consisted of a cup buried 12 cm deep with the

Table 1. Sampling design and effort for estimating the relative abundance of carpenter ants associated with logs and cut stumps in 3 habitat conditions in coastal forests of Washington, USA, 1994.

Structure	Forest condition		
	Precanopy, early-successional stands	Closed-canopy, second-growth stands	Closed-canopy, late-successional stands
Decay-class 2 logs[a]			
No. structures sampled	19[b]	none[c]	20
No. pitfall traps per structure	2		2[d]
No. trap-nights[e]	1,820		2,044
Decay-class 3 logs[f]			
No. structures sampled	20	20	20
No. pitfall traps per structure	2	2[d]	2[d]
No. trap-nights[e]	1,932	2,044	2,058
Cut stumps			
No. structures sampled	20	20	none[g]
No. pitfall traps per structure	2	2	
No. trap-nights[e]	1,904	1,946	

[a] Bark mostly intact, sapwood slightly decayed, heartwood mostly sound (Sollins 1982).

[b] We could not locate a decay-class 2 log at one sample point.

[c] Second-growth stands contained inadequate numbers of decay-class 2 logs to include in the study.

[d] One log had 4 pitfall traps.

[e] Number of trap-nights varied because some traps were destroyed by animals or covered by debris.

[f] Bark sloughing or absent, sapwood moderately decayed or deteriorated, heartwood mostly sound and supporting its own weight (Sollins 1982).

[g] Late-successional stands did not contain cut stumps.

rim at ground level, a removable inner cup 5 cm deep, and a funnel that prevented captured arthropods from escaping. We poured a small amount of propylene glycol (antifreeze; about 35 mL) in the inner cup to preserve captured arthropods until the end of each trapping period.

We conducted pitfall trapping for carpenter ants at 20 randomly located points (5 points × 4 stands) in each of 3 forest conditions: unmanaged late-successional stands, second-growth stands, and early-successional stands regenerating after clearcuts (Table 1). Although we sampled 20 random points in each forest condition, limitations on the availability of study sites resulted in some minor differences in the number of stands sampled in each condition (4–5) and the number of points sampled in each stand (2–6). At each random point, we sampled the nearest logs that were ≥20 cm at the large end, ≥2 m long, and defined as decay-class 2 or 3 (Table 1), as well as the nearest cut stump ≥20 cm in diameter at the cut. We placed 1 pitfall trap on each side of the log as close to the log–ground interface as possible for every 10 m that was in contact with the ground; for stumps, we placed 1 pitfall trap on opposite sides (2 traps per stump), as close to the stump–ground interface as possible. We restricted our sampling to logs in decay-classes 2 and 3 because moderate stages of decay appear to provide the most suitable habitat conditions for carpenter ants (Torgersen and Bull 1995).

In western Washington, carpenter ants actively forage from April to October (Hansen and Akre 1985). We conducted pitfall trapping for 7 weeks during the summer of 1994, including 3 2-week trapping sessions from mid-July through August and a 1-week trapping session in late September. We identified carpenter ants to species using keys presented in Creighton (1950) and Hansen and Akre (1985); voucher specimens were verified by an entomologist knowledgeable in the taxonomy of ants (J. Longino, The Evergreen State College, Olympia, Wash.).

Describing Structures and Sites Used for Foraging

Selection of foraging structures by pileated woodpeckers may be influenced by habitat conditions occurring at multiple spatial scales, especially the structure itself and the site in which it occurs. To test this hypothesis, we collected data on the structures (decadent trees, snags, cut stumps, and logs) and sites used by pileated woodpeckers for foraging in 2 types of habitat plots, each of which was a 0.4-ha (1-acre) circle: 1) 261 habitat plots located with randomization techniques along a series of parallel transects that encompassed the study area (Aubry and Raley 2002*a*), and 2) 209 plots centered on trees that were used for nesting or roosting by pileated woodpeckers during our study (24 nest trees, 45 cavity-start trees, and 140 roost trees). Of the 261 random habitat plots, 209 were in closed-canopy conditions (stands in which crown growth of conifers had formed an upper canopy) and 52 were in open conditions (grass-forb, shrub, or precanopy sapling-pole stands). Because our field observations indicated that pileated woodpeckers rarely foraged in open conditions (<3% of observations of radiomarked birds foraging; C. Raley and K. Aubry, unpublished data), we included only data from closed-canopy plots in analyses of resource selection. All cavity-tree plots were in closed-canopy stands and were well distributed. Closed-canopy stands included managed and unmanaged forests and typically had ≥70% canopy cover.

In each habitat plot, we searched all snags and decadent trees ≥20 cm diameter at breast height and ≥1 m tall for recent pileated woodpecker foraging excavations. We defined recent excavations as those that had foraging chips beneath them lying on top of the litter layer. The presence of foraging chips on top of the substrate indicated that foraging had occurred recently (i.e., <1 yr old). We did not search live trees with live tops for recent excavations because they were rarely used by pileated woodpeckers for foraging (9 of 412 structures used by radiomarked birds were live, intact trees; C. Raley and K. Aubry, unpublished data).

To collect data on the use of cut stumps and logs by pileated woodpeckers for foraging, we subsampled each habitat plot. We searched for recent foraging excavations on stumps ≥20 cm in diameter at the cut in a 0.1-ha circular plot centered in each habitat plot. For logs we used a random azimuth to establish a 71.4-m line transect through

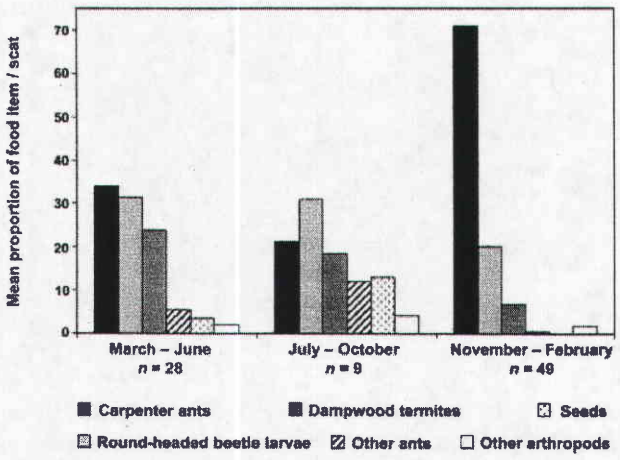

Figure 1. Frequency of occurrence of 5 arthropod and 1 vegetative food groups in pileated woodpecker scats during the mating and nesting period (Mar–Jun), the juvenile-rearing and dispersal period (Jul–Oct), and the nonbreeding period (Nov–Feb) in coastal forests of Washington, USA, 1991–1995.

the center of the plot, and we then searched for recent foraging on logs that intercepted the line and were ≥20 cm in diameter at the large end, ≥1 m in length, and either undecayed or in moderate stages of decay (decay classes 1 and 2–3, respectively; Sollins 1982).

In each plot, we collected data on all structures (with or without recent excavations) that met the size and decay-condition criteria described above. The variables we sampled included tree species, height or length, diameter at breast height for standing structures, diameter at cut for stumps, diameter at large end for logs, and several indicators of decay condition (percentage of bark remaining, number of dead limbs, and presence of small twigs and dead foliage). Additionally, in each plot we recorded slope, aspect, elevation, and dominant tree species in the upper canopy. To investigate selection of individual structures for foraging, we classified structures with recent pileated excavations as *used* and those with old excavations or no foraging sign as *not used*. Because the structures on which we observed radiomarked birds foraging were located opportunistically, it was not appropriate to include them in analyses of resource selection. To investigate selection of habitat conditions at foraging sites, we classified plots containing ≥1 structure (i.e., decadent tree, snag, cut stump, or log) with recent foraging excavations as *used* and those without recent excavations as *not used*. We included data from both random and cavity-tree plots in analyses of selection for individual foraging structures. However, because cavity-tree plots had been selected by pileated woodpeckers for nesting or roosting, we restricted analyses of selection for foraging sites to data obtained in random habitat plots.

Statistical Analyses

We used frequency of occurrence to describe the contents of pileated woodpecker scats. Because pileated woodpeckers may switch food resources if conditions change, we analyzed diet composition separately for 3 periods of the year with potentially different energetic demands for pileated woodpeckers: 1) the mating and nesting period (Mar–Jun), 2) the juvenile-rearing and dispersal period (Jul–Oct), and 3) the nonbreeding period (Nov–Feb). To estimate the relative abundance of carpenter ants, we calculated the number captured per trap-night at each log in decay-class 2 and 3 and each cut stump during the 4 trapping sessions. In our calculations of ants captured per trap-night at each type of structure, we accounted for minor differences in the number of pitfall traps placed along logs and traps that were destroyed by animals or covered with debris (Table 1). We derived an index of ant abundance at logs and cut stumps in each of the 3 forest conditions sampled by averaging the number of ants captured per trap-night for all sample points in each stand and then for all stands in each forest condition. To estimate the amount of wood in snags and decadent trees potentially available to wood-boring arthropods, we used a taper value of 0.12 cm/dm (Spies and Franklin 1991) to estimate the diameter at the top of the tree, and then we calculated volume using the formula for a cone section (Bell et al. 1984).

We used logistic regression (Keating and Cherry 2004) to test hypotheses that tree condition (snag vs. decadent tree), diameter at breast height, height, and measures of decay condition for trees with recent pileated woodpecker foraging excavations did not differ from such structures without recent foraging excavations (structure-level analysis). Because we sampled potential foraging structures within 0.4-ha plots, resulting data may be spatially autocorrelated. To ensure that resulting P values accounted for this potential bias, we used the GENMOD procedure in SAS for spatially clustered data (Allison 1991, SAS Institute 2002–2003). We also used logistic regression (GENMOD procedure for nonclustered data; SAS Institute 2002–2003) to identify habitat characteristics that distinguished plots with recent pileated woodpecker foraging activity from those with no recent foraging (site-level analysis). We used variable-selection and model-building strategies suggested by Hosmer and Lemeshow (2000). We used a stepwise approach and began each modeling process by evaluating descriptive statistics and univariate logistic regression coefficients and likelihood-ratio (LR) tests for each habitat parameter. These procedures enabled us to identify candidate variables that were biologically meaningful and potentially useful for distinguishing used from not-used structures or sites. To construct the final models, we entered candidate variables one at a time and evaluated interactions among variables, coefficients, and LR tests to determine the most parsimonious combination of variables that best explained the variation in our data.

Results

Scat Analysis

We collected 86 pileated woodpecker scat samples: 77 from 15 radiomarked birds (8 F and 7 M) and 9 from unknown individuals. Arthropod remains in pileated woodpecker scats consisted of small fragments of exoskeleton; consequently, it

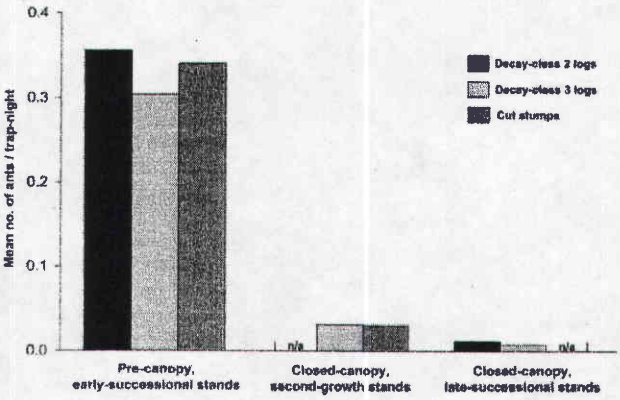

Figure 2. Relative abundance of carpenter ants captured at logs and cut stumps in 3 habitat conditions in coastal forests of Washington, USA, Jul–Sep 1994. Second-growth stands contained inadequate numbers of decay-class 2 logs to include in the study, and late-successional stands did not contain cut stumps. Captures at 1 decay-class 2 log in an early-successional stand during the first 2-week sampling period were unusually high (523 ants compared to typical capture rates ≤95 ants); we eliminated this outlier from calculations of relative abundance.

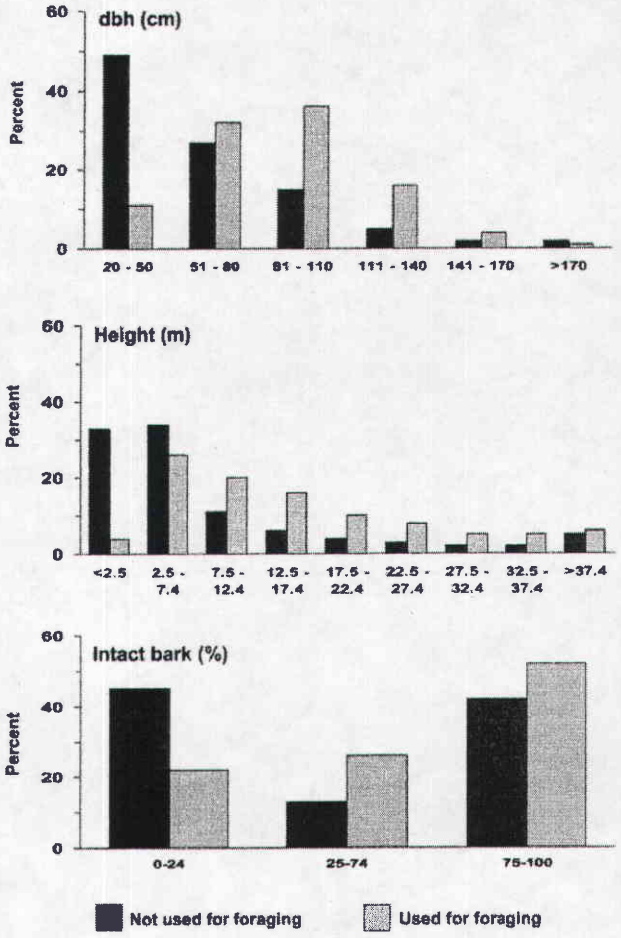

Figure 3. Frequency distributions comparing dbh, height, and bark condition of snags and decadent trees that contained recent pileated woodpecker foraging excavations (used, $n = 572$) with trees that did not (not used, $n = 9,187$) in closed-canopy coastal forests of Washington, USA, 1990–1995.

was often difficult for us to make species-level identifications with certainty. Carpenter ants were the primary prey (54% of food items) consumed by pileated woodpeckers, and it appeared that most of the remains we found in scats were of a single species, *C. modoc*. Pileated woodpeckers also consumed round-headed wood-boring beetle larvae (Coleoptera, Cerambycidae; 25% of food items) and dampwood termites (probably Pacific dampwood termites [*Zootermopsis angusticollis*]; 14% of food items). Only 3% of the food items we found in scats were non–carpenter ant species (*Formica* spp. and *Lasius* spp.). Other arthropods we found in pileated woodpecker scats included one or several individuals in the following orders: mites (Acari), spiders (Araneae), flies (Diptera), true bugs (Hemiptera), and adult beetles. Only 4 scat samples contained seeds; however, 2 of the samples had >200 seeds that were either salal (*Gaultheria shallon*) or red huckleberry (*Vaccinium parvifolium*; D. Thysall, U.S. Forest Service, personal communication).

During the mating and breeding period, the mean proportions of scat contents were 34% carpenter ants, 31% round-headed beetle larvae, and 24% dampwood termites (Fig. 1). Although our sample sizes were small for the juvenile-rearing and dispersal period, carpenter ants, round-headed beetle larvae, and dampwood termites comprised 70% of food items consumed by pileated woodpeckers during that period (Fig. 1). During the nonbreeding period, pileated woodpeckers consumed more carpenter ants (71%) than any other arthropods; however, round-headed beetle larvae were also important prey, accounting for 20% of food items consumed during that time of year (Fig. 1).

Table 2. Logistic regression model from structure-level analysis distinguishing snags and decadent trees that contained recent pileated woodpecker foraging excavations (used, $n = 572$) from those that did not (not used, $n = 9,187$) in closed-canopy coastal forests of Washington, USA, 1990–1995.

		Likelihood-ratio tests	
Parameter	β	Chi-square	*P*
Tree condition: dead	3.008	92.44	<0.001
Tree dbh	0.349	73.11	<0.001
Tree height	0.041	71.46	<0.001
% bark remaining on bole	0.148	7.39	0.007

Relative Abundance of Carpenter Ants

Most (98%) of the carpenter ants we captured from mid-July through September 1994 were *C. modoc*; 1% were *C. laevigatus*, and 1% *C. vicinus* or *Camponotus* spp. We captured large numbers of carpenter ants (2,306 individuals) along logs and near cut stumps in precanopy, early-successional stands. In contrast, we rarely captured carpenter ants along logs in late-successional stands (23 individuals) or along logs or near cut stumps in second-growth stands (115 individuals). The relative abundance of carpenter ants differed substantially between precanopy and closed-canopy habitat conditions; capture rates along logs and near cut stumps in precanopy stands were ≥10 times greater than

Table 3. Continuous physiographic and vegetative variables we measured in randomly located 0.4-ha plots with (used, $n = 86$) and without (not used, $n = 123$) recent pileated woodpecker foraging excavations on decadent trees, snags, cut stumps, and logs in closed-canopy coastal forests of Washington, USA, 1990–1995.

	Random habitat plots			
	Used		Not used	
Variable	$\bar{x}$	SD	$\bar{x}$	SD
Elevation (m)	261.8	93.4	249.9	95.1
Slope (degrees)	22.9	11.9	22.4	13.8
No. decadent trees per plot	0.4	0.9	0.4	0.7
No. snags and decadent trees per plot[a]	23.0	12.0	18.7	10.3
No. snags 20–51 cm dbh and <7.5 m tall per plot	8.7	7.3	8.0	5.8
No. snags 20–51 cm dbh and ≥7.5 m tall per plot	1.9	2.4	2.0	2.4
No. snags >51 cm dbh and <7.5 m tall per plot[a]	7.6	4.7	6.1	3.9
No. snags >51 cm dbh and ≥7.5 m tall per plot[a]	4.6	3.4	2.3	2.4
No. of all snags >51 cm dbh per plot[a]	12.1	6.6	8.3	5.3
No. snags with ≥75% intact bark per plot	7.6	5.5	6.5	5.5
No. snags with 26–74% intact bark per plot[a]	3.2	2.7	2.2	2.0
No. snags with ≤25% intact bark per plot[a]	11.9	7.8	9.6	5.9
No. Pacific silver fir snags and decadent trees per plot[b]	1.5	1.8	1.5	2.4
No. Pacific silver fir snags per plot[b]	1.5	1.8	1.5	2.4
No. snag and decadent tree species per plot	1.8	0.8	1.8	0.7
No. tree species composing the upper canopy	2.2	0.9	2.2	0.9
No. logs ≥20 cm diameter and ≥1 m long per hectare	270.9	170.6	255.4	235.3
Log volume (m^3/ha)	117.5	75.4	96.3	86.1

[a] Variables included in site-level stepwise logistic regression analysis (i.e., candidate variables).

[b] We considered data on Pacific silver fir trees separately because this species was selected by pileated woodpeckers for nesting in our study area (Aubry and Raley 2002*a*).

capture rates at the same microsites in closed-canopy stands (Fig. 2).

Selection of Foraging Structures and Sites

We identified 600 different structures with recent pileated woodpecker foraging excavations in 209 random and 209 cavity-tree plots occurring in closed-canopy conditions. Virtually all structures used by pileated woodpeckers for foraging were trees (93% snags and 2% decadent); 3% were cut stumps and 2% logs. Pileated woodpeckers did not appear to be selective in their use of tree species when foraging on snags and decadent trees; the proportions of western hemlock and Pacific silver fir trees used for foraging (78% and 20%, respectively) were similar to those that were not used (82% and 13%). However, results of logistic regression analysis showed that pileated woodpeckers selected relatively tall, large-diameter snags in early to moderate stages of decay for foraging (structure-level analysis; Table 2). Fifty-seven percent of trees with recent foraging excavations were ≥81 cm diameter at breast height (median = 85 cm), 70% were ≥7.5 m tall (median = 15 m), and 52% had ≥75% intact bark (median = 80%; Fig. 3). In contrast, trees without recent foraging excavations were smaller and more decayed; 76% were <81 cm diameter at breast height (median = 52 cm), 67% were <7.5 m tall (median = 5 m), and 58% had <75% intact bark (median = 40%; Fig. 3). Based on median values of diameter at breast height and height, the estimated volume of wood in trees used for foraging was 7 times greater than for trees that were not used.

Table 4. Categorical physiographic and vegetative variables we measured in randomly located 0.4-ha plots with (used, $n = 86$) and without (not used, $n = 123$) recent pileated woodpecker foraging excavations on decadent trees, snags, cut stumps, and logs in closed-canopy coastal forests of Washington, USA, 1990–1995.

	% of random habitat plots	
Variable	Used	Not used
Plot aspect		
Cool (N, NE, E)	38	40
Moderate (NW, SE)	26	19
Warm (W, SW, S)	36	41
Pacific silver fir snags[a,b]		
Absent on plot	42	54
Present on plot	58	46
Western redcedar snags[b]		
Absent on plot	96	98
Present on plot	4	2
Cut stumps		
Absent on plot	80	75
Present on plot	20	25

[a] Variables included in site-level stepwise logistic regression analysis (i.e., candidate variables).

[b] We considered data on Pacific silver fir and western redcedar trees separately because in our study area, these species were selected for nesting and roosting, respectively (Aubry and Raley 2002*a*).

Forty-one percent (86/209) of random habitat plots had ≥1 structure (i.e., decadent tree, snag, cut stump, or log) with recent pileated woodpecker foraging excavations. Among the 22 habitat variables we evaluated to analyze selection of foraging sites by pileated woodpeckers, we identified 7 candidate variables (6 continuous [Table 3] and 1 categorical [Table 4]) for inclusion in the stepwise modeling process. However, the final model contained only one variable that was important for distinguishing used from not-used plots (site-level analysis); pileated woodpeckers selected sites for foraging that had greater densities of large (>51 cm dbh and ≥7.5 m tall) snags ($\beta_{\text{large snags}} = 0.272$, LR = 29.38, $P < 0.001$). Most (70%) plots with recent pileated woodpecker foraging activity had ≥3 large snags (median = 4). In contrast, plots with no recent foraging activity typically had <3 large snags (63%; median = 2).

Discussion

Arthropod Diet of Pileated Woodpeckers

Pileated woodpeckers consumed a variety of wood-dwelling arthropods year-round; however the proportions of carpen-

ter ants, round-headed beetle larvae, and dampwood termites in their diet varied seasonally. Only 2 previous studies have been conducted that provide quantitative data on the diet of pileated woodpeckers in a particular region and forest type. In mixed-conifer forests of northeastern Oregon, ants (primarily carpenter ants) comprised >90% of pileated woodpecker diets ($n = 48$ scats; Beckwith and Bull 1985). In a larger study area in northeastern Oregon, carpenter ants and thatching ants (*Formica* spp.) represented 68% and 29% of pileated woodpecker diets, respectively ($n =$ 330 scats; Bull et al. 1992*a*). We speculate that the more diverse diet of pileated woodpeckers in coastal forests compared to northeastern Oregon reflects differences in the presence and abundance of available prey. Furniss and Carolin (1977) reported that carpenter ants are common in western forests, except in very shady, wet locations. Thus, carpenter ants may be less abundant in wet coastal forests than in the drier forest conditions of northeastern Oregon. In contrast, the Pacific dampwood termite is most abundant in northern California, USA, and western Oregon and Washington, especially in coastal forests where it colonizes both standing dead and downed structures (Furniss and Carolin 1977). Additional information is needed on the species of round-headed beetle larvae that pileated woodpeckers are consuming to determine if their distribution or abundance differs among regions or forest types.

Similar to findings in northeastern Oregon (Bull et al. 1992*a*), pileated woodpeckers in coastal forests consumed a much higher proportion of carpenter ants during the nonbreeding season than any other food type. Bull et al. (1992*a*) speculated that pileated woodpeckers foraged primarily for carpenter ants in standing structures during the winter because snow covered the ground and logs where thatching ants (their predominant prey during summer) occurred. However, there is no evidence of seasonal differences in the availability or accessibility of potential prey for pileated woodpeckers in coastal forests. Because snowfall rarely occurs in coastal forests, both downed and standing structures are accessible to pileated woodpeckers year-round. Furthermore, all 3 primary prey groups are perennial; carpenter ant and termite colonies persist over the winter (Ebeling 1968, Hansen and Akre 1985), and round-headed beetle larvae typically take several years to develop (Furniss and Carolin 1977). We believe that carpenter ants are the mainstay of pileated woodpecker diets in coastal forests but that during the breeding season, when energetic demands are presumably greatest (i.e., adults are laying eggs and feeding young), they expand the breadth of their diet to include higher energy foods. Pacific dampwood termites are relatively large (9–25 mm long), soft-bodied insects (Ebeling 1968) that may provide a higher energy food source for pileated woodpeckers than carpenter ants. Similarly, many of the round-headed beetle larvae are large (20–70 mm) and fleshy, potentially providing energy-rich and easily digestible food for pileated woodpecker nestlings. However, additional work is needed on the biomass and caloric content of these arthropods to determine their potential food value to pileated woodpeckers.

Selection of Foraging Structures

In coastal forests of Washington, pileated woodpeckers selected relatively large, hard snags for foraging but were not selective of tree species. In northeastern Oregon, pileated woodpeckers selected Douglas fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) for foraging, selected against ponderosa pine (*Pinus ponderosa*), and used grand fir (*Abies grandis*) and lodgepole pine (*Pinus contorta*) in proportion to availability (Bull and Meslow 1977). In a subsequent study conducted in a larger study area in northeastern Oregon, pileated woodpeckers selected ponderosa pine, Douglas fir, and western larch when foraging on snags, but selected Douglas fir and western larch, and avoided lodgepole pine when foraging on logs (Bull and Holthausen 1993). We believe the lack of concordance in these studies indicates that selection of foraging structures by pileated woodpeckers is not related to the characteristics of individual tree species, but rather to wood characteristics and microsite conditions that influence the presence and abundance of arthropod prey.

Several studies conducted in western coniferous forests found that pileated woodpeckers commonly foraged on logs (Bull and Meslow 1977, McClelland 1979, Mannan 1984, Bull 1987, Bull and Holthausen 1993). In mixed-conifer forests in northeastern Oregon, where there was an average of 290 logs/ha (>15 cm at the base and >2 m long), 38% of pileated woodpecker foraging observations were on logs (Bull and Holthausen 1993). Destructive sampling of logs in that area showed that 13% contained carpenter ant colonies (Torgersen and Bull 1995). Despite the abundance of logs in coastal forests (Table 3), pileated woodpeckers rarely foraged on them. In addition, although carpenter ants (primarily *C. modoc*) were relatively abundant at decay-class 2 and 3 logs in precanopy habitat conditions, they were scarce at the same microsites in closed-canopy forests. In the Coast Range of Oregon, >50% canopy cover greatly reduced the likelihood that *C. modoc* could successfully establish and maintain their nests (Nielsen 1986). This species was only found in forest clearings where there was enough solar radiation to warm the forest floor and associated coarse woody debris. Our results provide additional evidence that logs in coastal forests are too cool and wet to support abundant populations of carpenter ants.

We hypothesize that in wet coastal forests of Washington, standing structures provide the most suitable habitat for carpenter ants because they contain drier and warmer microhabitat conditions than logs; consequently, they provide the best foraging opportunities for pileated woodpeckers. In the Coast Range of Oregon, Nielsen (1986) found more *C. modoc* nests in standing dead wood than in logs and hypothesized that standing structures provided superior nest sites because their greater vertical surface intercepted more solar radiation, creating warmer conditions for brood maturation. Similar habitat limitations may also exist for round-headed beetle larvae, but additional work is

needed to determine the species on which pileated woodpeckers are preying. Although Pacific dampwood termites occur in moist decaying wood (Ebeling 1968, Rosengaus et al. 2003), perhaps very cool, wet conditions in logs also limit their ability to successfully establish reproductive colonies.

Snags used by pileated woodpeckers for foraging were larger in diameter and height and less decayed than those that were not used. Carpenter ant colonies are often large (Hansen and Antonelli 2005) and need correspondingly large structures to accommodate colony growth. Round-headed beetle larvae feed on dead wood, and many species require several years to develop (Furniss and Carolin 1977). Additionally, dampwood termite colonies nest and feed entirely within the host structure (Rosengaus et al. 2003). Thus, relatively large snags would provide greater volumes of wood and better habitat conditions for these arthropods over a longer period of time than small snags. In closed-canopy coastal forests, the coolest and dampest environmental conditions are near ground level. Snags that are taller than the understory vegetation will receive greater solar radiation and more drying action from wind than those near the ground, creating more suitable temperature and moisture regimes for wood-dwelling arthropods. However, snags in the late stages of decay may not have the structural integrity needed by carpenter ants for constructing their extensive galleries. Furthermore, because round-headed beetle larvae and dampwood termites feed on cellulose, advanced sapwood and heartwood decay may provide unsuitable conditions for their growth and development.

Selection of Foraging Sites

Our results support our hypothesis that selection of foraging sites by pileated woodpeckers is influenced by the abundance of potential foraging structures. Pileated woodpeckers probably expend considerable energy searching for suitable foraging structures and excavating in wood to obtain arthropod prey. Because snags tend to be patchy in distribution (Bull et al. 1997), pileated woodpeckers may maximize energetic returns by foraging in areas that have high densities of potential foraging structures. Additionally, wood-dwelling arthropods may be more abundant in areas with high volumes of dead wood. Large carpenter ant colonies often establish satellite colonies in other structures near the parent colony (Sanders 1964, Hansen and Akre 1985). Thus, sites with high densities of large snags may provide optimal habitat for carpenter ant colonies to grow and persist. Although little is known about the ecology of round-headed beetles, adults typically lay their eggs in or on the bark of dead trees (Furniss and Carolin 1977). Therefore, adult round-headed beetles may be attracted to sites with high densities of dead trees, where they are more likely to find suitable egg-laying sites. Dampwood termites produce winged reproductives that disperse to new substrates and establish new colonies (Ebeling 1968). When reproductives leave the colony they are especially vulnerable to predation by birds, reptiles, and other arthropods (Snyder 1948); thus, higher densities of suitable structures would decrease dispersal distances and exposure to predation and increase the likelihood that reproductives would be able to establish new colonies.

Despite the presence of potential foraging structures and large numbers of carpenter ants in open precanopy habitat conditions, they were rarely used by pileated woodpeckers for foraging. Three radiomarked pileated woodpeckers were killed by northern goshawks (*Accipiter gentilis*), and several others appeared to have been killed by raptors (based on evidence at kill sites and on carcasses). Pileated woodpeckers are not fast fliers and typically evade predators by flying in erratic, undulating patterns through the forest (C. Raley, personal observation). Consequently, open habitats in coastal forests may provide inadequate escape cover for pileated woodpeckers.

Management Implications

Current standards and guidelines for maintaining populations of cavity-nesting birds on federal lands in western Washington and Oregon focus on providing snags for nesting habitat (U.S. Forest Service and U.S. Bureau of Land Management 1994, Neitro et al. 1985); there are no specific provisions for either foraging or roosting habitat. Furthermore, pileated woodpecker foraging habitat in western Washington and Oregon is reported to include both snags and logs (Brown 1985). Our results indicate that maintaining populations of pileated woodpeckers in coastal forests may require a more comprehensive management strategy that also includes provisions for foraging (this study) and roosting (Aubry and Raley 2002*a*) habitat. Management strategies addressing foraging habitat would be most effective if they accounted for regional differences in the types of structures that provide suitable habitat conditions for arthropod prey, especially carpenter ants and round-headed beetle larvae. To maintain or improve foraging habitat for pileated woodpeckers, we suggest that managers emphasize the retention of large (>51 cm dbh and ≥7.5 m tall), relatively hard snags. Additionally, we suggest that retaining patches of large snags (rather than dispersed structures) in closed-canopy habitat conditions would provide optimal foraging habitat for pileated woodpeckers. Prescriptions in the Northwest Forest Plan (U.S. Forest Service and U.S. Bureau of Land Management 1994) for retaining the largest hard snags in harvest units within 0.2–1.0 ha (or larger) patches of green trees provide managers with opportunities to improve foraging habitat for pileated woodpeckers in coastal forests managed for timber production without the need to modify current standards and guidelines.

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