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FOREST CHARACTERISTICS RELATED TO PILEATED WOODPECKER TERRITORY SIZE IN MISSOURI[1]

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Abstract. To determine which forest structure characteristics were related to and possibly affected Pileated Woodpecker (*Dryocopus pileatus*) territory size in Missouri, we followed radio-marked Pileated Woodpeckers, sampled habitat within territories, and examined the statistical relationships between territory size and habitat characteristics. Pileated Woodpecker territory size ranged from 53–160 ha. Percent forest overstory canopy cover, percent saw timber cover, and log and stump volume within territories were negatively related to territory size. In light of the structural cues hypothesis (Smith and Shugart 1987), we suggest forest log and stump volume, and percent overstory canopy cover may be structural cues used by Pileated Woodpeckers to ascertain food availability within a forest and Pileated Woodpeckers may adjust territory size in response to these structural cues. We recommend forest managers leave thinning and logging slash on site after management operations so debris can serve as foraging substrates for woodpeckers.

Key words: Dryocopus pileatus; *forest habitat; Pileated Woodpecker; territories; structural cues hypothesis.*

INTRODUCTION

Pileated Woodpeckers (*Dryocopus pileatus*) are primary cavity excavators (Evans and Conner 1979) and year-round residents of mature, dense forests of the United States (Bock and Lepthien 1975). To meet their life requirements, Pileated Woodpeckers actively defend (Kilham 1959, 1973; pers. observ.) large type A (Nice 1941) territories. Their territories range in size from 43 ha (Tanner 1942) to 70 ha (Kilham 1976) in southern deciduous-coniferous forests, to as much as 450 ha in northwestern coniferous forests (Mellen 1987). Territories encompass older, mature timber in a forest (Mannan 1984, Mellen 1987) and within territories, Pileated Woodpeckers typically use large dead trees or dead portions of live trees as nest sites (Conner et al. 1975, Bull and Meslow 1977, McClelland 1979, Brawn et al. 1984, Bull 1987, Mellen 1987).

Dead trees, logs, and tree stumps are predominant Pileated Woodpecker foraging sites throughout the year (e.g., Hoyt 1957, Conner and Crawford 1974, Kilham 1976, Conner 1980, Bull 1987), but are most important during winter when Pileated Woodpeckers more frequently excavate into wood for insects because fewer invertebrates are available on the outside of dead or living trees (Conner 1981). Seventy-eight percent of the Pileated Woodpecker diet consists of invertebrates (Beal 1911). Pileated Woodpeckers eat a variety of wood-boring insect adults and pupae, including termites (Isoptera) and carpenter ants (*Camponotus* spp.) (Hoyt 1957, Conner and Crawford 1974, Kilham 1976, McClelland 1979, Conner 1981, Conner 1982, Beckwith and Bull 1985).

In general, animals establish territories around limited resources when those resources are defensible in time and space (Brown 1964). Food abundance or food density may be an ultimate cause determining where birds establish territories, but vegetation physiognomy seems to be the proximate cue birds use to determine where to live (Hilden 1965). Several workers have observed an inverse relationship between bird territory size and food density (Stenger 1958, Gill and Wolf 1975). Others have observed that habitat structure or vegetation physiognomy is related to territory size (Wiens 1973) and food density or availability (Stenger and Falls 1959, Morse 1976, Cody 1978, Seastedt and MacLean 1979, Smith and Shugart 1987). Food density and vegetation physiognomy may appear to be unrelated, but Smith and Shugart (1987) recently presented evidence to support a hypothesis that

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uses both factors to explain observed variations in intraspecific territory size. This structural cues hypothesis is one of several hypotheses proposed to explain the observed negative relationship between bird territory size and food abundance (Hooper et al. 1982, Smith and Shugart 1987). The hypothesis proposes that birds establish a territory not by directly monitoring their food supply, but by using habitat structural features that are indicative of the potential food supply as cues to determine how large an area they need to defend. It has been suggested that birds cue on structural features instead of directly monitoring food abundance because on some occasions bird territory size has been positively related to food abundance (Seastedt and MacLean 1979). Structural features are better proximate cues than food density because structural cues remain relatively constant over time, whereas actual food abundance may vary greatly from year to year (Smith and Shugart 1987).

With the structural cues hypothesis in mind, we examined the relationships between Pileated Woodpecker territory size and forest habitat characteristics in central Missouri. Our objectives were to determine Pileated Woodpecker territory size under a range of habitat conditions and to determine which habitat features were correlated with Pileated Woodpecker territory size. Because we did not sample the potential food base of Pileated Woodpeckers, we will not be able to support or dispute the structural cues hypothesis.

STUDY AREAS AND METHODS

This study was conducted on the University of Missouri's Thomas S. Baskett Wildlife Research and Education Center (BWRC) in 1985–1987 and on a U.S. Forest Service management compartment, Mark Twain National Forest, Cedar Creek (CC) district, in 1987. The 900-ha BWRC primarily consisted of mature and regeneration oak-hickory forest (74%), and old fields (26%). The forest principally occupied intermittent stream drainages, with some forest occupying slopes and ridges between drainages. The CC study area was 667 ha in size. The forest cover on this study area generally formed a narrow band along intermittent streams and comprised 55% of the study area. Pasture and old fields occupied the remainder of the area. The dominant tree species on both study sites were white oak (*Quercus alba*), black oak (*Q. velutina*), red oak (*Q. rubra*), and shagbark hickory (*Carya ovata*).

Pileated Woodpecker nests were located during March–May of each year. Woodpeckers were caught at nest cavities with mist-net covered dip nets on extended poles (Renken, unpubl.) or with mist-net covered dip nets on rat traps (Bull and Pedersen 1978). Captured adults were fitted with 8- to 9-g backpack style radio transmitters. Bird locations were determined by triangulation from three or four positions along the roads bisecting or surrounding the study areas. Only error polygons of ≤3 ha were accepted as woodpecker locations. Birds were located one to six times daily and we collected data from 15 min before sunrise to 15 min after sunset. Radiotelemetry continued until late July or August of each year.

Nest fate also was noted. Adult woodpeckers were considered successful nesters if young were observed in the nest.

The minimum convex polygon (MCP) home range estimator (Hayne 1949) was used to calculate Pileated Woodpecker territory size. Territory sizes also were estimated using the 95% harmonic mean (HM) (Dixon and Chapman 1980) estimator. However, only the MCP estimator could give correctly scaled territory boundaries on maps for use in later analyses. The microcomputer home range computation program (Samuel et al. 1985) was used to calculate both the MCP and HM territory size estimates. For four birds, the number of locations used for calculating MCP and HM territory sizes differed. We chose to use fewer locations for MCP estimates for these territories because we believed some locations were outliers even though the HM estimation technique did not classify them as outliers. Hence, we were more conservative in use of the MCP estimates than the HM estimates.

Forest vegetation structure was sampled within the territory of each bird. Samples were collected in a random sampling design stratified by timber stand type, size (saw timber, pole timber, sapling), and density (16–39%, 40–69%, and ≥70% stocked). Territories were sampled at an intensity of one plot for every 1.4 ha of forest cover within the territory. Within the 0.04-ha sample plots, we measured the diameter at breast height (dbh) and identified to species all trees with a dbh ≥10 cm. The dbh of all snags (standing dead trees >1.4 m in height; ≥10 cm dbh) also was measured. Overstory canopy cover was estimated with a densiometer and overstory can-

TABLE 1. Habitat variables used in Pearson's simple and Spearman's rank correlations with minimum convex polygon (MCP) territory sizes.

Tree density—trees ≥10 cm dbh/ha (TD)
Snag density—dead trees ≥10 cm dbh/ha (SD)
Density of trees ≥30 cm dbh—trees/ha (T30D)
Density of snags ≥30 cm dbh—dead trees/ha (S30D)
Density of snags ≥54 cm dbh—dead trees/ha (S54D)
Tree basal area—m^2/ha (TBA)
Density of sycamores—sycamore trees ≥10 cm dbh/ha (SYCD)
Average tree dbh—cm (ATDBH)
Average snag dbh—cm (ASDBH)
Log and stump volume—m^3/ha (LSVOL)
Log and stump density—logs and stumps/ha (DENSL)
Overstory canopy cover—% (CANOPY)
Overstory canopy height—m (CANHT)
Percent of territory composed of forest cover (PCFOR)
Percent of territory composed of saw timber (PCSAW)
Percent of territory composed of pole timber (PCPOLE)
Percent of territory composed of floodplain timber (PCFLDP)

opy height was estimated using a Haga altimeter. Greatest diameter and length/height of logs (fallen dead trees or branches) and stumps having a diameter ≥10 cm and a length or height ≥30 cm also were measured.

Vegetation samples were used to estimate tree density (TD), snag density (SD), large tree density (T30D, trees with a dbh ≥30 cm), large snag density (S30D, snags with a dbh ≥30 cm), and huge snag density (S54D, snags with a dbh ≥54 cm) per ha within forested portions of territories (Table 1). We selected dbh values of 30 cm and 54 cm for the variables large tree/snag density and huge snag density because of the minimum nest tree/snag and average nest tree/snag dbh values recorded at nest sites. The smallest nest tree/snag used by Pileated Woodpeckers was 30 cm dbh and the mean nest tree/snag dbh was 52 cm. Because Brawn et al. (1984) observed an average nest tree/snag dbh of 56 cm for Pileated Woodpecker nests in central Missouri, we chose the midpoint between 52 cm and 56 cm for the dbh value of huge snag density. Sycamore (*Platanus occidentalis*) density per ha (SYCD) also was estimated from vegetation samples because analysis suggested Pileated Woodpecker densities were correlated with sycamore density (Renken 1988). Average tree dbh (ATDBH), average snag dbh (ASDBH), tree basal area (TBA), log and stump density (DENSL), and log and stump volume (LSVOL) were calculated from sample data. Percentages of the territory covered by forest, saw timber (stands of trees with an average dbh ≥30 cm), pole timber (stands of trees with an average dbh ≥15 cm and <30 cm), and floodplain timber also were estimated for each territory. Percentage forest cover included the stand types of oak-hickory, pine (*Pinus* spp.), and oak-pine, and stand sizes of saw timber, pole timber, and small tree. Old fields, cedar (*Juniperus virginiana*) stands, pastures, and regeneration cuts were not included in the estimate of percent forest cover. Sycamore, Ohio buckeye (*Aesculus glabra*), and pawpaw (*Asimina triloba*) were used as indicators of floodplain forest cover. Areas of floodplain timber cover also had ≤2% slope. Areas of all cover types were digitized from topographic maps of the study areas.

We examined relationships among habitat characteristics and territory size in Pearson's simple and Spearman's rank correlation analyses. We also examined plots of habitat characteristics vs. territory size to determine if curvilinear relationships existed among variables. Variables that demonstrated a significant relationship with territory size were used as independent variables in a regression model of territory size. The Statistical Analysis System computer package (SAS Institute 1985) was used for correlation and regression analyses.

RESULTS

Thirteen adult Pileated Woodpeckers were caught and fitted with radio transmitters. We captured an adult at 12 nest sites, and in 1985 we caught both adults at one nest site. Eleven birds provided enough (≥25) observations to use in territory size computation methods. The criterion of ≥25 locations for calculating territory size follows techniques of Jaremovic and Croft (1987).

Woodpeckers were followed for 11–43 days (Table 2). Five adults nested successfully and five others were unsuccessful. The nest fate of bird F could not be determined because no young were observed in the nest, yet the adults continued to enter the cavity even after the assumed egg-hatching date. Territories of successful and unsuccessful nesters did not differ in size (Randomization test, two-tailed, $T = 1.33$, $P = 0.25$). Changes in territory size between first and second halves of tracking periods did not follow a con-

TABLE 2. Minimum convex polygon (MCP) and harmonic mean (HM) estimates of Pileated Woodpecker territories in Missouri. Nest fate and tracking periods for individuals are also noted.

Bird	Study area	MCP (ha)	HM (ha)	Tracking period
A (U[a])	BWRC	58.3 (54[b])	109.2 (54[b])	10 Jun–16 Aug 1985 (24[c])
B (S)	BWRC	72.8 (47)	90.9 (47)	23 Jun–8 Aug 1985 (22)
C (S)	BWRC	96.1 (94)	101.8 (94)	9 May–28 Jun 1986 (32)
D (U)	BWRC	90.4 (104)	123.0 (104)	6 May–28 Jun 1986 (36)
E (S)	BWRC	68.1 (90)	88.3 (90)	4 May–20 Jun 1986 (35)
F (?)	BWRC	52.9 (97)	101.0 (99)	1 May–28 Jun 1986 (38)
G (U)	BWRC	129.0 (122)	197.5 (122)	5 May–20 Jun 1987 (39)
H (S)	BWRC	77.8 (125)	117.0 (125)	2 May–20 Jun 1987 (41)
I (U)	CC	160.1 (140)	199.3 (142)	16 Apr–19 Jun 1987 (43)
J (S)	CC	76.9 (66)	113.1 (67)	16 Apr–7 May 1987 (18)
K (U)	CC	79.5 (33)	70.2 (34)	24 Apr–6 May 1987 (11)

[a] U = unsuccessful nester; S = successful nester; ? = nest fate unknown, see text.
[b] No. of telemetry locations used for territory size estimation.
[c] No. of days birds were followed during the tracking period.

sistent pattern among birds or among successful and unsuccessful nesters (Renken 1988).

Pileated Woodpecker territories ranged from 52.9 to 160.1 ha using the MCP estimator, and from 70.2 to 199.3 ha using the 95% HM estimator (Table 2). There were no differences in MCP territory size estimates between sexes (Randomization test, two-tailed, $T = -0.97$, $P = 0.352$) or study areas (Randomization test, two-tailed, $T = 1.18$, $P = 0.255$). There were also no differences in MCP territory size estimates between 1985 vs. 1986 (Randomization test, two-tailed, $T = -0.72$, $P = 0.523$), or 1986 vs. 1987 (Randomization test, two-tailed, $T = -1.31$, $P = 0.286$); 1985 and 1987 territories were different (Randomization test, two-tailed, $T = -1.36$, $P < 0.001$). We suspect habitat differences between territories in 1985 and 1987 probably caused this difference. In 1985, radio-marked birds occupied mature forest habitat on BWRC, whereas two of five 1987 birds occupied less mature forest habitat on BWRC and the other 1987 birds occupied stream corridor forest habitat on CC. For further analyses, we assumed that sex of the bird, study area, and year of capture did not affect territory size.

Several habitat characteristics within Pileated Woodpecker territories were intercorrelated (Table 3). In general, average tree (ATDBH) and snag (ASDBH) dbh were positively related to large tree (T30D) and large snag (S30D) density. Canopy height (CANHT) was positively related to average tree dbh (ATDBH). Also, log and stump volume (LSVOL) and log and stump density (DENSL) were negatively related to percent pole timber cover (PCPOLE).

Transformations of means of habitat variables were necessary for some variables so they could be used in Pearson's correlation analysis (Table 4). Percent floodplain timber cover (PCFLDP) was transformed with a log transformation (LPCFLDP). Variables not transformed into a normal distribution were also used in Spearman's rank correlation so we would not overlook a relationship between those variables and MCP estimates.

Four habitat characteristics (canopy cover, percent saw timber cover, percent forest cover, percent floodplain timber cover) were negatively correlated with MCP territory size estimates in either Pearson's correlation or Spearman's rank correlation (Table 5). Canopy cover was not correlated with percent saw timber cover (Pearson's correlation $r = 0.43$, $P = 0.19$; Spearman's correlation $r = 0.37$, $P = 0.26$), percent forest cover (Pearson's correlation $r = 0.22$, $P = 0.51$; Spearman's correlation $r = 0.21$, $P = 0.54$), or percent floodplain timber cover (Pearson's correlation $r = 0.24$, $P = 0.47$; Spearman's correlation $r = -0.02$, $P = 0.96$). However, percent saw timber cover, percent forest cover, and percent floodplain timber cover were intercorrelated (Table 6). Because percent saw timber cover is correlated with percent floodplain timber cover and percent forest cover, it appears that percent saw timber cover describes the same forest features as percent floodplain timber cover and percent forest cover, therefore we did not use percent floodplain timber cover and percent forest cover in the next analysis. No variables appeared to be curvilinearly related to territory size (Renken 1988). We included the Pearson's simple and

TABLE 3. Pearson's correlation values of relationships among habitat characteristics within Pileated Woodpecker territories. Probability values are listed below the correlation values. Only correlations with a probability value ≤0.15 are listed (n = 11).

	Habitat characteristics						
	PCSAW	LPCFLDP	PCFOR	PCPOLE	TD	SD	T30D
PCSAW	–						
LPCFLDP	0.70 (0.02)	–					
PCFOR	0.82 (0.002)	–	–				
PCPOLE	–	–	0.52 (0.10)	–			
TD	−0.52 (0.10)	–	−0.63 (0.04)	–	–		
SD	−0.62 (0.04)	−0.58 (0.06)	−0.54 (0.09)	–	0.79 (0.004)	–	
T30D	–	–	–	–	–	–	–
S30D	–	–	–	–	–	–	0.50 (0.11)
S54D	–	0.46 (0.15)	–	–	–	–	–
ATDBH	–	–	–	–	−0.64 (0.03)	−0.55 (0.08)	0.51 (0.11)
ASDBH	–	–	–	–	–	–	0.47 (0.14)
CANHT	–	–	–	–	−0.62 (0.04)	–	–
SYCD	–	–	−0.49 (0.12)	−0.50 (0.12)	–	–	–
CANOPY	–	–	–	–	–	–	–
LSVOL	–	–	–	−0.60 (0.05)	–	0.50 (0.12)	–
DENSL	–	–	–	−0.55 (0.08)	–	–	–

Spearman's rank correlation values for MCP and log and stump volume (Table 5) because we noted that overall, log and stump volume was correlated with MCP in scatter diagrams (Fig. 1), even though the statistical correlation was not significant because of the undue influence of bird I. Bird I occupied the northern portion of CC which was characterized by a narrow band of forest along four intermittent stream tributaries. Therefore, the MCP territory size estimate for this bird included more pasture (66.3%) than the amount of pasture or open habitat incorporated into the 10 other MCP estimates (average = 19.0%). The inclusion of pasture area in this MCP estimate makes it unusual and we omitted this territory from the next correlation analysis to remove this territory's bias.

Without bird I, there was a negative relationship between territory size and log and stump volume (Table 7) and the correlation supports the linear relationship observed in the scatter plot. The correlation between territory size and canopy cover increased and the correlation between percent saw timber cover and territory size decreased when bird I was omitted. Without bird I, canopy cover was not correlated with percent saw timber cover (Pearson's correlation $r = 0.41$, $P = 0.23$; Spearman's correlation $r = 0.28$, $P = 0.43$). Canopy cover was correlated with log and stump volume in Pearson's simple correlation ($r = 0.64$, $P = 0.04$), but not in Spearman's rank correlation ($r = 0.15$, $P = 0.68$). Percent saw timber cover was correlated with log and stump volume (Pearson's correlation $r = 0.69$, $P = 0.03$; Spearman's correlation $r = 0.78$, $P = 0.008$).

The correlation between log and stump volume and percent saw timber cover suggests log and stump volume is greater in saw timber stands

TABLE 3. Extended.

Habitat characteristics								
S30D	S54D	ATDBH	ASDBH	CANHT	SYCD	CANOPY	LSVOL	DENSL
—								
—	—							
0.57 (0.07)	—	—						
0.89 (0.0003)	—	0.52 (0.10)	—					
—	—	0.62 (0.04)	—	—				
—	—	—	—	—	—			
—	—	—	—	−0.66 (0.03)	—	—		
—	—	—	0.59 (0.06)	—	0.52 (0.10)	0.48 (0.14)	—	
—	—	—	—	−0.81 (0.002)	—	0.64 (0.03)	0.83 (0.002)	—

than in pole timber and small tree stands. We tested this relationship and observed that log and stump volume tends to be greater in saw timber than in pole timber and small tree stands (Mann-Whitney *U*-test, two-tailed, $U = 85$, $0.05 \leq P \leq 0.10$).

Our results to this point indicated that Pileated Woodpecker territory size was related to three habitat characteristics (canopy cover, log and stump volume, percent saw timber cover). We used multiple regression analysis to further examine the relationship between territory size and the three variables, with the ultimate objective of producing a regression equation to describe territory size. Bird I was omitted from the regression analysis.

A regression equation with all three characteristics was adequate in explaining much of the variation in territory size (Table 8). However, a regression equation with only canopy cover and log/stump volume better describes Pileated Woodpecker territory size (Table 8). (An arcsine transformation of overstory canopy cover was used in the regression analysis because the transformed variable produced a better fitting equation.) The inclusion of percent saw timber cover into the regression appeared to weaken the power of the equation because none of the parameter estimates (B_xs) differed significantly from zero. The correlation between log and stump volume and percent saw timber cover may make this regression equation less stable. The final regression with canopy cover and log and stump volume was a more powerful equation with parameter estimates that were different from zero. We believe the final regression equation of territory size on canopy cover, and log and stump volume is a more stable, powerful, and meaningful equa-

TABLE 4. The mean and range of means for habitat characteristics within Pileated Woodpecker territories in Missouri ($n = 11$). Refer to Renken (1988) for means and standard deviations of habitat characteristics within each territory.

Habitat characteristic	Mean	Range
Tree density (no./ha)	486.9	414.3–635.0
Snag density (no./ha)	65.3	43.3–92.1
Density of trees ≥30 cm (no./ha)	88.2	60.0–100.7
Density of snags ≥30 cm (no./ha)	7.6	6.1–10.0
Density of snags ≥54 cm (no./ha)	0.6	0.0–1.4
Sycamore density (no./ha)	5.3	0.0–22.1
Mean tree dbh (cm)	20.9	19.9–21.8
Mean snag dbh (cm)	17.1	15.7–19.8
Tree basal area (m^2/ha)	22.3	19.0–33.0
Log and stump density (no./ha)	228.7	73.0–278.6
Log and stump volume (m^3/ha)	32.3	10.6–48.1
Canopy cover (%)	89.1	74.7–96.0
Canopy height (m)	18.0	16.2–22.2
Forest cover (%)	73.4	33.7–95.9
Saw timber cover (%)	57.5	30.0–90.6
Pole timber cover (%)	13.0	0.0–29.2
Floodplain timber cover (%)	6.7	0.0–29.9

tion in describing the relationship between Pileated Woodpecker territory size and vegetation structural cues.

DISCUSSION

Pileated Woodpeckers spend much foraging time pecking and excavating insect adults and pupae from logs and stumps. Kilham (1976) observed Pileated Woodpeckers foraging on logs and stumps in 76% of his foraging observations. In Oregon, Bull and Meslow (1977) reported that 42% and 14% of the observed Pileated Woodpecker foraging sites were on logs and stumps, respectively. Mannan (1984) reported 96% of foraging observations were of birds using dead wood, and logs served as substrates 36% of the time. Mannan also reported Pileated Woodpeckers foraged on log and stump debris in 70- to 100-year-old timber that had undergone a selective cut. Bull (1987) observed 36% of the foraging substrates used by Pileated Woodpeckers were dead and down trees, and in total, 65% of Pileated Woodpecker foraging observations were of birds on dead wood, either snags or logs (Bull 1987). Eighty-two percent of the log-foraging observations were of birds excavating into logs >25 cm in diameter (Bull 1987). Bull speculated that larger dead wood had higher densities of wood-boring insects because of its greater surface area and greater moisture retention characteristics.

Logs and stumps provide substrates for many wood-boring and channelizing invertebrates. Several workers have noted the prevalence and abundance of insects in dead and down woody material. Fager (1968) reported that in an oak-ash-sycamore woodland, logs at least 7.5 cm in diameter and 70 cm long contained as many as 1,715 individuals/log and 62 species of invertebrates. Swift et al. (1984) detected signs of invertebrate activity in 60% of approximately 1,000 logs in an oak-beech woodland. Pine stumps about 15 cm tall and 10–35 cm in diameter contained 939–5,678 invertebrates (Wallace 1953). Ausmus (1977) reported densities of colonizing or channelizing invertebrates of 10 to 136 individuals/cm^3 in logs of a Tennessee hardwood forest. Swift et al. (1984) speculated larger branches showed more signs of invertebrate activity than smaller branches not only because they were bigger, but also because they decayed slower and probably remained on the forest floor longer than smaller branches.

Our results show Pileated Woodpecker territory size was inversely related to log and stump volume, and canopy cover within territories. We believe log and stump volume is a good indicator

TABLE 5. Pearson's simple and Spearman's rank correlation values of Pileated Woodpecker territory size (MCP) with habitat variables ($n = 11$).

Comparisons	Pearson's correlation	Spearman's correlation
MCP, CANOPY	r = −0.60 ($P = 0.05$)	r = −0.42 ($P = 0.20$)
MCP, PCSAW	r = −0.66 ($P = 0.03$)	r = −0.75 ($P = 0.007$)
MCP, PCFOR	r = −0.55 ($P = 0.08$)	r = −0.55 ($P = 0.08$)
MCP, LPCFLDP	r = −0.47 ($P = 0.15$)	r = −0.53 ($P = 0.09$)
MCP, LSVOL	r = −0.05 ($P = 0.89$)	r = −0.40 ($P = 0.22$)

TABLE 6. Pearson's simple and Spearman's rank correlation values of percent saw timber (PCSAW), forest (PCFOR), and floodplain timber (LPCFLDP) cover ($n = 11$).

Comparisons	Pearson's correlation	Spearman's correlation
PCSAW, LPCFLDP	r = 0.70 ($P = 0.02$)	r = 0.64 ($P = 0.03$)
PCSAW, PCFOR	r = 0.82 ($P = 0.002$)	r = 0.85 ($P = 0.0008$)
PCFOR, LPCFLDP	r = 0.38 ($P = 0.25$)	r = 0.48 ($P = 0.14$)

of the amount of dead wood within a forest because a stand of trees with few logs and stumps on the forest floor will likely have little standing dead wood (snags) or little dead wood on live trees. With little dead wood on the forest floor or on live trees, there will be few foraging substrates for Pileated Woodpeckers. To obtain sufficient food, birds will have to forage over more area and this will result in an increase in the size of the territory to incorporate enough foraging substrates.

The mature saw timber stands within territories have larger volumes of dead, woody material than less mature pole timber or sapling stands. Pileated Woodpecker territories decline in size as the percent of saw timber within the territory increases. Thus, as the percent of mature timber increases within woodpecker territories, the volume of dead, woody material increases also, and Pileated Woodpecker territories decline in size as the volume of foraging substrates increases.

Percent overstory canopy cover was not related to percent saw timber cover, yet typically mature timber has a greater canopy cover than younger timber stands. A closed canopy cover is characteristic of mature timber (Smith and Shugart 1987). We kept percent canopy cover in the regression to suggest that mature forest cover is important in Pileated Woodpecker territories. A large volume of logs and stumps, as in a clearcut, is not sufficient to support Pileated Woodpeckers. Pileated Woodpecker territories include not only dead and down woody material, but also mature forest with large trees that serve as foraging substrates and future snags.

Also, within stands of growing trees, canopy cover increases and there is greater competition among trees for limited resources (light, food, water) (Franklin et al. 1987). Trees that are outcompeted for these resources die (Peet and Christensen 1987) and form snags, logs, and stumps. Hence, as canopy cover increases, the volume of dead woody material should also increase, thus providing more foraging substrates for Pileated Woodpeckers.

Our hypothesis that Pileated Woodpecker territory size is inversely related to log and stump volume and canopy cover is supported by other studies. Bull and Meslow (1977) reported preferred Pileated Woodpecker foraging areas had high densities of logs and snags, and dense canopies. McClelland (1979) also reported Pileated Woodpeckers used logs and stumps as foraging substrates, and that feeding territories that were >200 ha included clearcuts, agricultural lands, or developed areas. McClelland stated that Pileated Woodpeckers probably had to include more area within their territories to include necessary feeding areas, and he also suggested minimum territory size was probably influenced by the productivity and abundance of carpenter ants and wood-boring insects. Although Hooper et al.

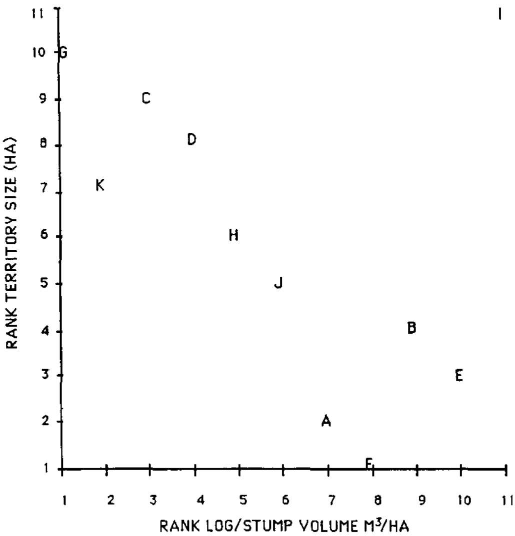

FIGURE 1. Scatter diagram of Spearman's rank correlation between ranks of Pileated Woodpecker territory size and log/stump volume. Letters represent individual birds.

TABLE 7. Pearson's simple and Spearman's rank correlation values of Pileated Woodpecker territory size (MCP) and log/stump volume (LSVOL), overstory canopy cover (CANOPY), and percent saw timber cover (PCSAW) ($n = 11$). Territory I omitted, see text for explanation.

Comparisons	Pearson's correlation	Spearman's correlation
MCP, LSVOL	$r = -0.79$ ($P = 0.006$)	$r = -0.87$ ($P = 0.001$)
MCP, CANOPY	$r = -0.76$ ($P = 0.01$)	$r = -0.37$ ($P = 0.29$)
MCP, PCSAW	$r = -0.53$ ($P = 0.11$)	$r = -0.67$ ($P = 0.03$)

(1982) did not believe habitat structure influenced territory size for the colonial Red-cockaded Woodpecker (*Picoides borealis*), the researchers observed a positive relationship between habitat structural features and territory size when a measure of population density was included. Thus Hooper et al. (1982) could not eliminate the possibility that habitat quality influenced territory size.

Although Pileated Woodpeckers will use immature forest habitat (Mellen 1987), they more frequently use older, mature, dense-canopied forest (Conner et al. 1975, McClelland 1979, Conner 1980, Mannan 1984, Bull 1987, Mellen 1987, and this study). We encourage forest managers to leave slash and debris from logging and thinning operations within saw timber and pole timber stands. This dead and down material is an important foraging substrate for Pileated Woodpeckers and the volume of this material also influences the amount of area a Pileated Woodpecker uses and defends. Holders of smaller territories may expend less energy moving from one foraging site to another, and this energy saving may be expressed in greater adult survival, reduced risk of predation, and greater nesting success.

Because we did not sample the wood-boring or channelizing invertebrate populations on logs or stumps, or within the territories with their various percentages of overstory canopy cover, we could not determine the validity of the structural cues hypothesis. Instead, we used the hypothesis to determine what forest structural features influenced Pileated Woodpecker territory size. Log and stump volume, and overstory canopy cover were negatively related to Pileated Woodpecker territory size. These habitat features may be proximate cues to Pileated Woodpeckers and may indicate the potential food base available in the area. Removal of thinning slash or logging debris from mature and immature forest stands reduces the indicators of habitat quality and also reduces habitat quality for Pileated Woodpeckers by removing potential foraging substrates.

TABLE 8. Regression equations with Pileated Woodpecker territory size (MCP) as the dependent variable and (a) overstory canopy cover (ACANOPY), log/stump volume (LSVOL), and percent saw timber cover (PCSAW) as independent variables, and (b) overstory canopy cover (ACANOPY) and log/stump volume (LSVOL) as independent variables ($n = 10$).

Dependent variable regression equation	R^2	F	$P > F$
(a) MCP = 193.0 − 64.8 ACANOPY − 1.3 LSVOL + 0.02 PCSAW	0.73	5.5	0.04
Test of Ho: $B_x = 0$			
$B_1 = 193.0$, T for Ho = 4.8, prob >T = 0.003			
$B_2 = -64.8$, T for Ho = −1.6, prob >T = 0.17			
$B_3 = -1.3$, T for Ho = −1.7, prob >T = 0.13			
$B_4 = 0.02$, T for Ho = 0.05, prob >T = 0.9			

Dependent variable regression equation	R^2	F	$P > F$
(b) MCP = 193.0 − 64.9 ACANOPY − 1.3 LSVOL	0.73	9.6	0.01
Test of Ho: $B_x = 0$			
$B_1 = 193.0$, T for Ho = 5.3, prob >T = 0.001			
$B_2 = -64.9$, T for Ho = −1.7, prob >T = 0.13			
$B_3 = -1.3$, T for Ho = −2.4, prob >T = 0.05			

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LITERATURE CITED

AUSMUS, B. 1977. Regulation of wood decomposition rates by arthropod and annelid populations, p. 180–192. *In* U. Lohm and T. Persson [eds.], Soil organisms as components of ecosystem. Ecol. Bull. 25. Swedish National Science Research Council, Stockholm.

BEAL, F.E.L. 1911. Food of woodpeckers of the United States. U.S. Dep. Agric. Biol. Surv. Bull. 37:1–64.

BECKWITH, R. C., AND E. L. BULL. 1985. Scat analysis of the arthropod component of Pileated Woodpecker diet. Murrelet 66:90–92.

BOCK, C., AND L. LEPTHIEN. 1975. A Christmas count analysis of woodpecker abundance in the United States. Wilson Bull. 87:355–366.

BRAWN, J. D., B. TANNENBAUM, AND K. E. EVANS. 1984. Nest site characteristics of cavity nesting birds in central Missouri. Res. Note NC-314, U.S. Dep. Agric., U.S. Forest Serv.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

BULL, E. L. 1987. Ecology of the pileated woodpecker in northeastern Oregon. J. Wildl. Manage. 51:472–481.

BULL, E. L., AND E. C. MESLOW. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. J. For. 75:335–337.

BULL, E. L., AND R. J. PEDERSEN. 1978. Two methods of trapping adult Pileated Woodpeckers at their nest cavities. N. Am. Bird Bander 3:95–99.

CODY, M. L. 1978. Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. Ecol. Monogr. 48:351–396.

CONNER, R. N. 1980. Foraging habitats of woodpeckers in southwestern Virginia. J. Field Ornithol. 51:119–127.

CONNER, R. N. 1981. Seasonal changes in woodpecker foraging patterns. Auk 98:562–570.

CONNER, R. N. 1982. Pileated Woodpecker feeds on horned passalus colony. Bull. Texas Ornithol. Soc. 15:15–16.

CONNER, R. N., AND H. S. CRAWFORD. 1974. Woodpecker foraging in Appalachian clearcuts. J. For. 72:564–566.

CONNER, R. N., R. G. HOOPER, H. S. CRAWFORD, AND H. S. MOSBY. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144–150.

DIXON, K. R., AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

EVANS, K. E., AND R. N. CONNER. 1979. Snag management, p. 214–225. *In* Proceedings of the workshop, management of north central and northeastern forests for nongame birds. U.S.D.A., U.S. Forest Serv. Gen. Tech. Rep. NC-51.

FAGER, E. W. 1968. The community of invertebrates in decaying oak wood. J. Anim. Ecol. 37:121–142.

FRANKLIN, J. F., H. H. SHUGART, AND M. E. HARMON. 1987. Tree death as an ecological process. Bioscience 37:550–556.

GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333–345.

HAYNE, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1–18.

HILDEN, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53–75.

HOOPER, R. G., L. J. NILES, R. F. HARLOW, AND G. W. WOOD. 1982. Home ranges of Red-cockaded Woodpeckers in coastal South Carolina. Auk 99: 675–682.

HOYT, S. F. 1957. The ecology of the Pileated Woodpecker. Ecology 38:246–256.

JAREMOVIC, R. V., AND D. B. CROFT. 1987. Comparison of techniques to determine eastern grey kangaroo home range. J. Wildl. Manage. 51:921–930.

KILHAM, L. 1959. Behavior and methods of communication of Pileated Woodpeckers. Condor 61: 377–387.

KILHAM, L. 1973. Unusual attack of intruding male on a nesting pair of Pileated Woodpeckers. Condor 75:349–350.

KILHAM, L. 1976. Winter foraging and associated behavior of Pileated Woodpeckers in Georgia and Florida. Auk 93:15–24.

MANNAN, R. W. 1984. Summer area requirements of pileated woodpeckers in western Oregon. Wildl. Soc. Bull. 12:265–268.

MCCLELLAND, B. R. 1979. The Pileated Woodpecker in forests of the northern Rocky Mountains, p. 283–299. *In* J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll [eds.], The role of insectivorous birds in forest ecosystems. Academic Press, New York.

MELLEN, T. K. 1987. Home range and habitat use of Pileated Woodpeckers, western Oregon. M.Sc.thesis, Oregon State Univ., Corvallis.

MORSE, D. H. 1976. Variables affecting the density and territory size of breeding Spruce-woods Warblers. Ecology 57:290–301.

NICE, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26:441–487.

PEET, R. K., AND N. L. CHRISTENSEN. 1987. Competition and tree death. Bioscience 37:586–595.

RENKEN, R. B. 1988. Habitat characteristics related to pileated woodpecker densities and territory size in Missouri. Ph.D.diss. Univ. of Missouri, Columbia.

Samuel, M. D., D. J. Pierce, E. O. Garton, L. J. Nelson, and K. R. Dixon. 1985. User's manual for program home range. Forest, wildlife, and range experiment station, Univ. of Idaho, Moscow.

SAS Institute. 1985. SAS user's guide. Statistics, 1985 edition. SAS Institute, Cary, NC.

Seastedt, T. R., and S. F. MacLean. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. Auk 96:131–142.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695–704.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory. Auk 75:335–346.

Stenger, J., and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

Swift, M. J., L. Boddy, and I. N. Healey. 1984. Wood decomposition in an abandoned beech and oak coppiced woodland in southeastern England. II. The standing crop of wood on the forest floor with particular reference to its invasion by *Tipula flavolineata* and other animals. Holarct. Ecol. 7: 218–228.

Tanner, J. T. 1942. The Ivory-billed Woodpecker. Natl. Audubon Soc. Res. Rep. 1.

Wallace, H. R. 1953. The ecology of the insect fauna of pine stumps. J. Anim. Ecol. 22:154–171.

Wiens, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah sparrows. Ecology 54:877–884.