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TERRITORIES AND CACHING-RELATED BEHAVIOR OF RED-HEADED WOODPECKERS WINTERING IN A BEECH GROVE

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ABSTRACT.—We describe caching and related behavior of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) wintering in a beech grove during a mast year and relate territorial behavior and territory size to territory-specific mast abundance. We found no difference between territories of adults and juveniles in either territory size or abundance of mast. Rates of caching and social interaction decreased over the course of the winter. *Received Oct. 1995, accepted 8 Mar. 1996.*

Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are larder hoarders during the fall and winter (Bent 1939, Kilham 1983). In autumn, these birds aggregate and establish singular winter territories at sites of high mast production (Smith and Scarlett 1987). Each territorial bird sequesters mast in one or a few larder trees which are then defended both inter- and intraspecifically. Red-headed Woodpeckers are known to store mainly acorns and beechnuts and an occasional insect (Hay 1887, Agersborg in Beal 1911, Kilham 1983). While acorn storing has been described for Red-headed Woodpeckers in Maryland, Louisiana, and Florida by Kilham (1983), MacRoberts (1975), and Moskovits (1978), respectively, no quantitative data exist on the storage of beech mast by this species. The present study describes caching and related behavioral patterns of Red-headed Woodpeckers wintering in a beech grove during a mast year and relates territorial behavior and territory size to territory specific mast abundance. We also searched for differences in behavior and territories between juvenile and adult woodpeckers.

METHODS

From 1 Nov. 1992 to 19 Mar. 1993 we observed 14 Red-headed Woodpeckers (6 juveniles and 8 adults) for a total of 160 h in a woodlot located in Morrow County, Ohio. The woodlot was dominated by mature American beeches (*Fagus grandifolia*), red maples (*Acer rubrum*), and sugar maples (*A. saccharum*). Other tree species at this site were white oak (*Quercus alba*), red oak (*Q. rubra*), ash (*Fraxinus* sp.), ironwood (*Carpinus* sp.), and hickory (*Carya* sp.). Beech was the only tree species experiencing a "mast year." We used focal bird techniques to gather behavior data. We watched each focal bird for 10-min periods. For the first 240 sec of this period, we noted which category of activity the bird was engaged in every 10 sec (N = 25). The five mutually exclusive categories were (1) lookout–the bird was perched and alert, (2) flight—the bird was in flight, (3) bipedal locomotion—the bird

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was moving over a tree, (4) peck—the bird was actively pecking, and (5) preen—the bird was preening. In addition to these five categories, we also recorded whether the bird was actively caching or engaged in any type of visual and/or auditory signaling or locomotory interaction. If the bird was caching, we noted whether the bird was on a trunk, limb, branch, or a twig, each of the last three substrate categories being an offshoot of the previous one. Visual displays consisted of an agonistic pose (Kilham 1983) or head bobbing. The display vocalization we witnessed has been described as "quirr" by Kilham (1958b). A chase was defined as one bird flying after another.

Over 10-min periods, we recorded the number of caches a focal bird made and every (previously-numbered) tree it visited. Temperature (°C), wind velocity (m/sec, Velometer Jr., Alnor Instrument Company, Niles, Illinois), solar radiation (mW/cm^2; Solar Meter, Dodge Products, Houston, Texas), and any precipitation were recorded for each observation period.

Juveniles could be distinguished from adults by plumage. Although the birds were not individually marked, we were able to identify individuals by idiosyncratic plumage patterns and behavior, as did Kilham (1958a).

We estimated the size of the beech crop by sampling fallen mast as follows: over a two-day period in early December, we gathered mast and leaf litter from below each beech tree in every bird's territory. For each tree, we gathered all leaf litter and mast within a 1660-cm^2 circular area located half way between the trunk and the outer edge of the canopy in each of the four cardinal directions. The samples were bagged and later sorted to determine number of beechnuts. Infertile nuts were excluded from the count.

Using a compass and a range finder, we constructed a map of all the marked trees in the study area. Each territory was delineated as the minimum-area polygon that included all the trees visited by the same bird. We drew each polygon to connect the positions of trunks, not canopy boundaries, a procedure that underestimated territory sizes. The polygons were then digitized and territory areas calculated.

The individual bird was the primary sampling unit, and all observations of the same individual were averaged before being analyzed. The data met the requirements for parametric tests.

To increase degrees of freedom when general linear models were employed, the individual bird was included as a factor. General linear models were performed in a stepwise fashion with the individual bird, time of day, day of winter (1 Nov. = day 1), average temperature, average wind speed, and average solar radiation included as independent variables. Only the independent variables retained in the model are reported. All statistical calculations were performed using Minitab (Anonymous 1991) or Systat (Wilkinson 1992) software.

RESULTS

Probable mortality between November and March was low (7%). The only bird disappearing during the study was a juvenile, and its territory was not usurped or occupied by any other Red-headed Woodpecker.

We could find no differences in the wind speed, temperature, or solar radiation associated with adult and juvenile territories (Table 1). There was no significant difference in size between territories of juveniles and adults (Table 1; Fig. 1). Neither the number of beechnuts per territory nor beechnut density was significantly different between the two woodpecker age classes (Table 1). We could find no difference between adult and juvenile birds in either the number of beech trees or the total number of trees defended (Table 1). Power analyses of these tests demonstrated

TABLE 1

MEAN ± SD FOR VARIABLES ASSOCIATED WITH ALL RED-HEADED WOODPECKER, JUVENILE RED-HEADED WOODPECKER AND ADULT RED-HEADED WOODPECKER TERRITORIES[a]

Variable	Total (N = 14)	Juvenile (N = 6)	Adult (N = 8)	*P*	Sample sizes from power analysis
Wind speed (m/sec)	0.9 ± 0.2	0.9 ± 0.1	0.9 ± 0.3	0.75	23
Temperature (°C)	1.4 ± 2.2	0.5 ± 2.5	2.0 ± 2.1	0.27	938
Solar radiation (mW/cm^2)	4.1 ± 3.6	3.7 ± 1.6	4.3 ± 1.2	0.48	316
Territory size (ha)	0.04 ± 0.03	0.03 ± 0.03	0.05 ± 0.03	0.28	236
Number of beech trees	4.8 ± 2.7	4.2 ± 2.4	5.3 ± 2.9	0.47	127
Total trees	8.9 ± 3.8	8.3 ± 2.3	9.4 ± 4.8	0.49	75
Beechnuts/territory[b]	24.5 ± 13.4	19.3 ± 15.0	28.3 ± 11.6	0.23	127
Beechnuts/m^2	62.3 ± 26.4	62.6 ± 31.4	62.0 ± 24.8	0.97	75
Interspecific interactions/min	0.23 ± 0.13	0.21 ± 0.09	0.2 ± 0.2	0.73	137

[a] *P*-values are significance levels of t-tests between juveniles and adults. The listed sample sizes from power analysis are those that would be required to detect a difference between juvenile and adult territories at $\alpha = 0.05$ and $\beta = 0.05$ given a 25% detectibility threshold and the current coefficient of variation.

[b] In thousands.

that detecting a significant difference with $\alpha = 0.05$ and $\beta = 0.05$ would require sample sizes of 23 to 316 (Table 1). Thus, our non-significant differences were probably not due to small sample sizes alone. There was some tendency for juvenile territories to be on the edge of the woodlot (Fisher's exact test, $P = 0.09$).

Although Red-headed Woodpeckers sometimes collect mast from the ground (TCG, pers. obs.), all of the birds we watched cached beechnuts gathered only from trees. Often, newly-collected beechnuts were broken on an "anvil", any portion not eaten immediately was stored. Although harvested corn fields were nearby, we never saw corn being gleaned and cached. The birds usually cached beechnuts on a trunk (30.9%), limb (43.9%), or branch (24.3%) and seldom on a twig (1.2%). There was no difference between caching rates of juveniles and adults, but over the months, the caching rate did decline for all birds (Fig. 2). A general linear model with the individual bird as a factor to account for the variation among individuals, and with day of winter as a covariate, showed that day of winter had a significant negative association with caching rate ($t = -3.48$, df = 135, $P = 0.001$).

There was no statistical difference between activity budgets of adults and juveniles. The birds spent most of their time looking about (69.9 ± 9.6%), with the rest of their time being divided among pecking (15.6 ± 8.7%), flying (8.6 ± 2.9%), bipedal locomotion (5.8 ± 2.4%), and preen-

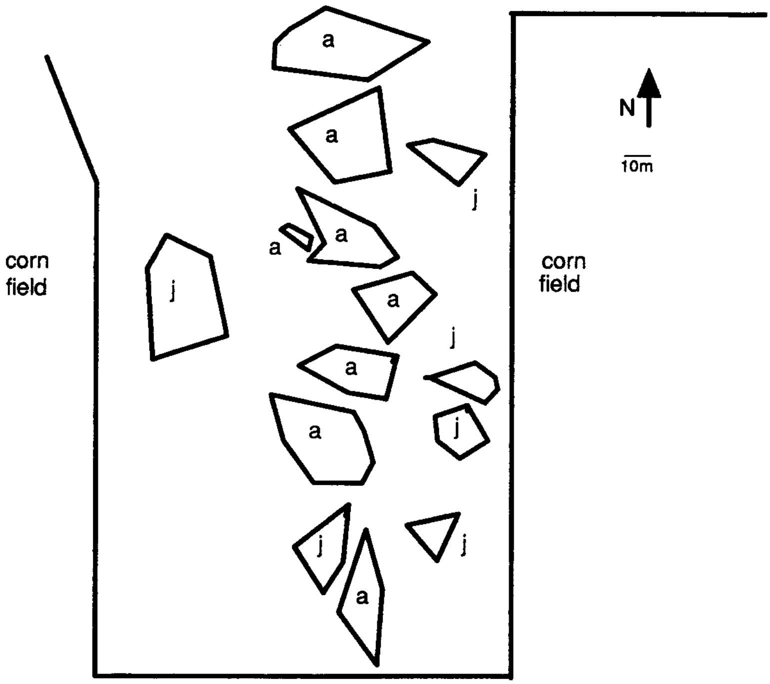

FIG. 1. Study area and Red-headed Woodpecker territories. A and J denote territories of adults and juveniles, respectively.

ing (0.2 ± 0.1%). A general linear model, with time spent looking about as the dependent variable, and day of winter and individual bird as factors showed that the percentage of time looking about increased as the winter progressed ($t = 4.13$, df = 135, $P < 0.000$).

The territories we observed were very small, about 0.05 ha (Table 1). Across the mosaic of territories, we witnessed 50 agonistic interactions involving Red-headed Woodpeckers. Nineteen of these were between Red-headed Woodpeckers, 13 were with Blue Jays (*Cyanocitta cristata*), 11 consisted of a Red-headed Woodpecker chasing mixed-species foraging flocks, six occurred with individual Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), white-breasted Nuthatches (*Sitta carolinensis*), or Downy Woodpeckers (*Picoides pubescens*), and once we witnessed a Red-headed Woodpecker chase off a fox squirrel (*Sciurus niger*). We could find no difference between juveniles and adults in the rate of interspecific interactions (Table 1). Although Red-bellied Woodpeckers (*Melanerpes carolinus*) resided in the woods just north of the study site, we rarely saw them and never witnessed them interacting with

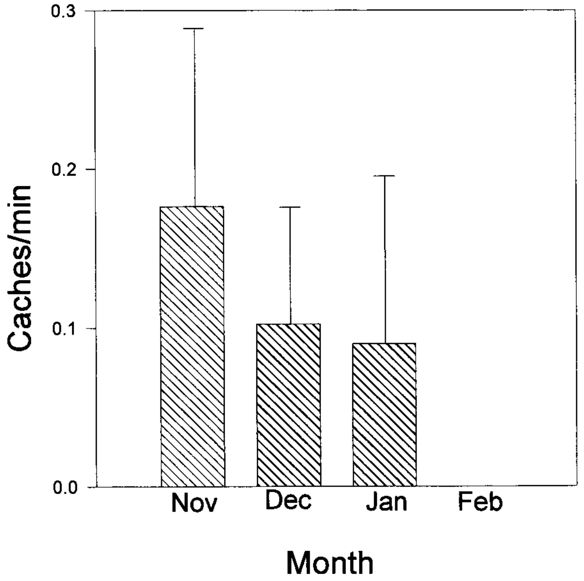

FIG. 2. Mean ± SD number of beechnuts cached per minute by Red-headed Woodpeckers wintering in a beech grove. N = 14.

M. erythrocephalus. Even though they are larger, Red-bellied Woodpeckers are socially subordinate to Red-headed Woodpeckers (e.g., Williams and Batzli 1979).

Behavior during agonistic interactions consisted of only a visual display (1.7%), vocalization with or without a visual display (72.1%), or chasing with or without a vocalization (26.2%). The frequency of interactions decreased over the course of the winter. A general linear model performed with percentage of 10-min recording periods lacking any social interaction as the dependent variable, individual bird as a factor, and day of winter as a covariate showed that the percentage of time devoid of social interaction increased with time (t = 3.10, df = 135, P = 0.002).

DISCUSSION

The average territory size of 0.04 ha was considerably smaller than that reported by Kilham (1958b, 0.1–0.2 ha), MacRoberts (1975, 0.8–1.2) or Moscovits (1978, 0.97 ha), although Moskovits did have a few territories as small as 0.04 ha. MacRoberts (1975) hypothesized that territory size is highly compressible and negatively correlated with mast production. This would seem to be so, but, unfortunately, other studies (including MacRoberts 1975) have no data on mast production (but see Smith and

Scarlett 1987). T.C.G. does have unpublished records pertaining to this point from two consecutive winters (1983–1985) when an index of beech mast was taken in the same woodlot with similar methods. During 1983, beech mast density was estimated at 231.1 nuts/m^2 and Red-headed Woodpecker density at 2.4 ± 0.2 birds/ha. The following year when beech mast was estimated at 57 ± 7.5 nuts/m^2, the woodpecker density was 3.6 ± 0.3 birds/ha. Such an increase in Red-headed Woodpecker density during a lower mast year contradicts both MacRoberts' (1975) assertion and Smith and Scarlett's (1987) data. Other potentially causal factors, such as differing mast levels in neighboring woods and/or differing woodpecker reproduction in previous summers could account for this disparity.

Although Kilham (1958a) thought that adults held smaller, more easily defended and "more desirable" areas, we could not support this assertion, nor could Moskovits (1978) find any difference between adult and juvenile territory sizes. There may have been some tendency for juvenile territories to be on the edge of the woodlot, a trend apparent in Kilham's (1958a) study area in Maryland where all juvenile territories bordered an old field (Kilham 1958a). Kilham (1958a) thought there were more dead trees for roosts and mast storage in the territories of adults. Such a disparity might account for the distribution of adult and juvenile territories in his study area, because the east side of his study area (where more of the adults were located) had many more dead locust trees. In our study area, there were few dead trees; the Red-headed Woodpeckers roosted in holes in dead limbs of living trees. We could find no difference in either the total number of trees or number of beech trees defended by juvenile and adult birds.

If, indeed, the territories of juveniles tend to be concentrated on the edge of woodlots, another possible explanation is that the winter microclimate on the edge of a wood is more severe than in the interior, with juveniles forced to take the lesser quality habitat. However, we could find no difference in the wind speed, temperature, or solar radiation associated with juvenile or adult territories that might support this idea.

Another way in which edge (juvenile) territories could be inferior relates to the number of intruders. Often, intruding birds were chased from territory to territory until they left the study area. Each successive woodpecker would be alerted by an intruder's interactions with other territory holders. The only Red-headed Woodpecker that would have no warning would be the initial bird, and so those occupying edge territories may have suffered more from the effects of intrusions. However, in compensation, owners of edge territories would benefit from fewer intraspecific interactions than owners of central territories. Since 19 of the 50 interactions we observed (38%) were intraspecific, such an advantage could accrue to individuals on the edge of the territorial mosaic.

Kilham's (1958a) and MacRoberts' (1975) reports on Red-headed Woodpeckers in Maryland and Louisiana suggest that the birds closely monitor the acorn crop when selecting winter habitat. Willson's (1970) and Reller's (1972) observations in Illinois found them less dependent on mast crops and acting more as generalists by also feeding on insects. The local distribution and activity budgets of the birds we studied suggested that they were almost totally dependent on the stored beech mast crop for winter food.

MacRoberts (1975) reported that Red-headed Woodpeckers retrieved acorns from the ground. Only twice did we see a Red-headed Woodpecker on the ground and never in conjunction with mast collection. Even at the end of our study period, there were still beechnuts in the canopy, so there appeared to be no need for the woodpeckers to descend to the ground for food.

In our study area, all of the nuts an individual bird cached were apparently taken from within its territory. MacRoberts (1975) had similar findings, but in Kilham's (1958a) and Moscovits' (1978) studies, nuts were brought from a distance, sometimes from communal gathering areas as far as 100 m away from an individual's territory. Perhaps, in their study areas the distributions of cache sites and cachable food did not overlap to the extent evident at our study site.

The Red-headed Woodpeckers spent most of the late fall and early winter caching nuts. Time spent looking about and the percentage of time with no interactions increased as the winter progressed. Also, the rate of caching decreased over the winter as the birds became more sedentary and focused their behavior at a favorite site, only leaving to intercept intruders. Thus, the birds appeared to spend less time caching and more time guarding their caches once their territories had been established and stocked with provisions. Even within their extremely small territories, the birds spent most of their time in a "core" area centered on their storage area, as reported by MacRoberts (1975).

The Red-headed Woodpecker is a very aggressive bird in the winter when it is defending its territories. We found it to dominate every interaction, as did Moskovits (1978). In MacRoberts' study (1975), the Red-headed Woodpeckers rarely trespassed, and territory boundaries were hard to delineate. Such was not the case in this study. Territory lines were readily defined. As soon as a bird ventured into another bird's territory, an interaction ensued.

Kilham (1958b) found that Red-headed Woodpeckers defended their entire winter home ranges both intra- and interspecifically, while Mac-

Roberts (1975) determined that the species defended only those areas immediately around cache sites. As in Kilham's study (1958a), the territories we observed were very small and more easily defended than those of MacRoberts' (1975) birds.

Kilham (1958a), Reller (1972), MacRoberts (1975) and Moskovits (1978) all commented on the prevalence of interactions with the Red-bellied Woodpecker. We did not find Red-bellied Woodpeckers to be major competitors.

Most of the interactions consisted of vocalizations. This was probably the most efficient means of communicating, since chasing was probably more expensive energetically and a visual display would probably have had a lower probability of being received. We did find the number of interactions decreased as the winter passed, as did Moskovits (1978).

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