SPACING BEHAVIOR OF THE MIDDLE SPOTTED WOODPECKER IN CENTRAL EUROPE

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Abstract: Knowledge of the ranging behavior and spatial requirements of a species is fundamental for establishing meaningful conservation strategies. Such information is lacking for the middle spotted woodpecker (*Dendrocopos medius*), a species endangered throughout its westpalearctic range. By radiotracking, we studied spacing behavior of this habitat specialist in a lowland oak forest of northeastern Switzerland from 1992–1996. Home range and core area size decreased from winter to late spring, with males and females having home ranges of similar size. Overlap of male home ranges was highest in winter (up to 40%) and lowest in late spring, whereas core area overlap remained low. For both home ranges and core areas, overlapping parts were used randomly in winter but more often than expected in early spring. Overlap of female ranges and of core areas did not change from early to late spring, and the shared parts of these home ranges were used as expected in both seasons. Aggressive interactions were most common in March and April and occurred mainly between individuals of the same sex. Our results suggest that the middle spotted woodpecker is not territorial in winter but defends nearly exclusive territories during spring, with both sexes participating to similar degrees in territorial defense. Based on this seasonal territoriality, we propose consideration of core areas in early spring (Mar and Apr) as a reliable estimate of the area requirements of the species to be used in management plans.

Key words: core area, *Dendrocopos medius*, home range, middle spotted woodpecker, oak forest, *Piciformes*, radiotelemetry, social behavior, space use, Switzerland, territoriality.

The study of space use by animals has received increasing attention during the past 2 decades. Knowing more about spacing behavior of endangered species is important to develop conservation strategies (Wegge and Rolstad 1986, Storch 1995, Jenny 1996, Caro 1999). For instance, Eadie et al. (1998) have shown that differences in territorial behavior and female reproductive tactics in cavity-nesting waterfowl can have dramatic consequences for the success of management projects. Moreover, determining size and composition of an area that fulfills critical life history requirements of endangered species is an important initial step for successfully establishing conservation reserves. Bingham and Noon (1997) argued that specific areas within the breeding home range that are most intensively used should be identified and given priority in conservation plans. Such intensively used areas—commonly referred to as core areas (Ford 1983, Samuel et al. 1985) within a home range—are assumed to provide

critical habitat elements for survival and reproduction, although the veracity of this assumption has not been assessed. The appropriateness of the core area concept is likely to differ between species in accordance to their spacing behavior. In some long-lived species, for example, territories are maintained for many years and their sizes are adapted to long-term average resource conditions (Southern 1970, MacLean and Seastedt 1979, Patterson 1980). Area requirements of such species are expected to vary less among seasons than those of species with seasonal territoriality, which adjust their territory sizes in response to actual resource levels. In the latter species, the core area concept might lead to the protection of an area too small to support viable populations, for example due to differing habitat requirements outside the territorial phase (i.e., during the nonreproductive period).

Here, we report results of the first major radiotracking study of the endangered middle spotted woodpecker to examine its spacing behavior. Specifically, our objectives are to (1) document patterns of range use, range overlap, and social interactions from winter to late spring; (2) identify the season most appropriate to establish area requirements; and (3) apply knowledge of spacing behavior to determine size of areas relevant

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to species management. The nonmigratory middle spotted woodpecker inhabits mature deciduous forests rich in oaks (*Quercus* spp.; Winkler et al. 1995). This habitat preference appears to be linked to the foraging ecology of this bird. The outstanding importance of oaks as foraging trees is well documented (Pettersson 1983, Pasinelli and Hegelbach 1997) and is based on the arthropod richness of oaks (Southwood 1961, Nicolai 1986). The middle spotted woodpecker feeds on arthropods of the tree surface during the year (Glutz von Blotzheim and Bauer 1980, Cramp 1985). Furthermore, both old oaks and potential cavity trees are key habitat structures influencing the size of middle spotted woodpecker home ranges (Pasinelli 2000*a*). Due to severe habitat loss, middle spotted woodpecker numbers have declined in large parts of its westpalearctic range, and it is now considered an endangered species (Mikusinski and Angelstam 1997).

STUDY AREA

We conducted our study in the northeastern part of the Swiss lowlands. Our study area (47°37′N, 8°37′E; 120 ha, 380 m above sea level) was in the Niderholz, an 800-ha forest 35 km north of Zürich near the Rhine River. Our study area consisted of an old oak–hornbeam forest managed for centuries as coppice-with-standards (Mittelwald)—a forestry practice that promotes large trees (e.g., oaks) forming a loose canopy and small trees (e.g., hornbeams [*Carpinus betulus*]) below the canopy. Hornbeam and oak were the dominant tree species, while scots pine (*Pinus sylvestris*), spruce (*Picea abies*), lime (*Tilia* spp.), and Norway maple (*Acer platanoides*) were found in low numbers. Our study area was surrounded by deciduous and coniferous forest of varying tree species composition and age classes, with some further oak–hornbeam forest stands inhabited by the middle spotted woodpecker. The Niderholz is 1 of the most important breeding areas of the middle spotted woodpecker in Switzerland, hosting up to 60 breeding pairs.

METHODS

Trapping and Radiotracking

Twenty-four middle spotted woodpeckers were trapped in January through April with mist nets at feeders (1 per 12 ha, not refilled after trapping), 4 in March through April by attracting the birds with a playback tape and a stuffed woodpecker dummy placed underneath a mist net 10 m above ground,

3 at their breeding cavity with a mist net placed in the flight path to the entrance, and 1 in the morning at the roosting cavity with a trap door and a bag net. Each bird was banded with 1 aluminum and 3 color rings and then fitted with a 1.5–2.0-g radiotransmitter (~3.5% of the bird's body weight), glued onto the base of the 2 central tail feathers using a cyanoacrylate glue (Stabiloplast No. 448, Firma Renfert, Germany). At no time did we observe the woodpeckers pulling on the transmitter, which did not hamper the birds when entering their cavities (Rolstad and Rolstad 1995). Transmitters worked an average of 56 days (range 13–123) and fell off during moult in summer.

We collected data during 1992–1996 from January to June. A bird was located with the method of homing-in (White and Garrott 1990) at most 5 times/day, with 81.7% of the 2,497 locations at least 1 hr apart. We also included locations 15–60 min apart, which previously have been shown to be spatiotemporally independent as well (Pasinelli 2000*a*).

Home Range and Core Area

We defined home range as the area including all activities of an individual during a specific time period (Newton 1979). Home range analyses were carried out with RANGES V software (Kenward and Hodder 1995) on a seasonal basis, defining January and February as winter, March to the start of incubation in early May as early spring, and incubation to fledging of the young in June as late spring. Home range size was estimated with the minimum convex polygon method (100% polygons). Based on incremental area plots—which show changes in range size as successive locations are added (Kenward and Hodder 1995)—an average of 27 locations was needed to obtain stable home range sizes. Therefore, ranges with fewer than 27 locations were discarded.

Core areas were identified with a procedure similiar to the 1 proposed by Wray et al. (1992). First, the home range and its range center were calculated based on all locations of an individual in a given season. Second, peeled polygons (Kenward and Hodder 1995) were computed excluding locations farthest from the range center at 5% steps. As range center, we used the arithmetic mean of the locations recalculated after each exclusion. Third, plots of % locations versus % polygon area (utilization plots) were produced for each individual. Based on these plots, the core area was then defined as the polygon separated from the next polygon by the greatest increase in area. Finally, an average of 23 locations

(range 8–39) was needed for core areas to reach asymptotic sizes, which was met by all core areas.

To examine between-season site fidelity of home ranges and core areas, respectively, we first calculated for each individual the distance the arithmetic range center moved from winter to early spring. If this distance was ≤ the mean distance of all winter locations of the same individual to its winter range center (H_0), the early spring range was considered to exhibit site fidelity. The same procedure was applied to investigate shifts in the position of early and late spring home ranges and core areas. As a second approach, we calculated the area overlap of early spring by winter home ranges (core areas) in percent using RANGES V. The same approach was used for the area overlap of late by early spring home ranges (core areas).

Range Overlap

A territory was defined as the space defended against conspecifics. Three approaches were used to assess territoriality. First, seasonal changes in area overlap of home ranges were examined, expressing overlap as the percentage of a woodpecker's home range shared with the ranges of all neighboring woodpeckers. Ranges of tagged birds that did not overlap were included as 0% overlap in the analyses if they could be considered neighbors. These were defined either as ranges not separated through unsuitable habitat (e.g., clearcuts) or, retrospectively defined from late spring, as ranges with no breeding pair in between them. The same analyses were conducted with core areas. Second, we checked whether the woodpeckers used the shared areas proportional to the unshared areas. For each season, observed use was quantified as the number of locations of a given bird within the shared portions of its range. Then, we compared it to the expected use, which was calculated by multiplying the number of locations of the same bird with the proportion of the shared area. We expected the birds to use the shared areas randomly in the absence of territorial behavior. These analyses were done both for home ranges and core areas. Third, the distribution of aggressive interactions from winter to late spring was examined to identify the beginning of territoriality. For this purpose, we assigned each location to a behavioral category (aggressive/not aggressive) depending on whether fights between individuals had been observed or not. Detailed descriptions of fights are given in Glutz von Blotzheim and Bauer (1980) and Cramp (1985).

To examine space use of pair-partners, area overlap was quantified as the percentage of an individual's home range or core area shared with that of its mate. Intensity of overlap was expressed as percentage of the locations of an individual within the shared area.

Statistics

Only data from resident birds were used in all analyses. A woodpecker was considered resident if it bred in the study area in the same year. Home range size and core area were log-transformed to achieve normality (Kolmogorov-Smirnov test: $P > 0.1$ in both cases) and thereafter used as the dependent variables in separate general linear models (procedure GLM in Systat [1996]) with year, season, and sex as independent variables. To control for the influence of multiple home range estimates of the same woodpecker, the individual bird was included as a factor. For the analysis of range overlap, data of the same individuals from different years were considered as independent if the overlapping neighbors had changed. Nonparametric tests were used for proportions and percentages. All tests are 2-sided, unless otherwise noted.

RESULTS

Home Ranges and Core Areas

Home range size (100% polygons) differed between seasons (Table 1). During winter, home ranges were an average 1.7× larger than in early spring (Tukey's HSD: $P < 0.005$) and 2.4× larger than in late spring ($P < 0.001$; Table 2). Ranges in early spring tended to be larger than those in late spring ($P = 0.099$). There was also a trend of an annual effect on range size (Table 1); however, pairwise comparisons did not reveal any significant difference between years. No other variable that we measured significantly influenced home range size, and males and females had similar range sizes during all seasons.

Core areas comprised 70–100% of a woodpecker's locations (median = 95% in each season), resulting in core areas of 35.6–100% of the home ranges (medians: winter = 67.8%, early spring = 75.3%, late spring = 71.3%). Core area size differed between seasons (Table 1). Core areas in winter were 1.7× larger than in early spring (Tukey's HSD: $P < 0.002$) and 2.6× larger than in late spring ($P < 0.001$; Table 2). Additionally, core areas in early spring were 1.6× larger than those in late spring ($P < 0.006$). No other variable significantly influenced core area size, and the core

Table 1. Factors affecting home range and core area size of the middle spotted woodpecker in northeastern Switzerland, showing general linear models with home range or core area size as dependent variable, year (1992–1996), season (winter, early spring, late spring), sex (male, female) and individual (1–27) as independent variables (*n* = 60).

Source of variation	Home range					Core area				
	SS	df	MS	F	P	SS	df	MS	F	P
Constant	8.55	1	8.55	88.53	<0.001	5.58	1	5.58	69.49	<0.001
Year	0.85	4	0.21	2.19	0.097	0.51	4	0.13	1.60	0.203
Season	2.51	2	1.26	13.00	<0.001	3.42	2	1.71	21.28	<0.001
Sex	0.01	1	0.05	0.08	0.933	0.01	1	0.01	0.01	0.995
Individual	2.83	23	0.12	1.27	0.271	2.88	23	0.13	1.56	0.134
Sex*Season	0.01	2	0.01	0.05	0.955	0.08	2	0.04	0.52	0.600
Model	10.55	32	0.33	3.42	<0.001	10.77	32	0.34	4.19	<0.001
Error	2.61	27	0.10			2.17	27	0.08		

areas of males and females were similar in size during all seasons.

Not included in the above analyses were 3 unpaired females that in early spring had home ranges of 46.6 ha (*n* = 44 locations), 79.1 ha (*n* = 28), and 146.9 ha (*n* = 22). Their core areas were 12.3 ha (95% of all locations), 37.6 ha (70%), and 45.3 ha (85%), respectively. Home ranges of these floaters were superimposed on those of the resident woodpeckers in prime oak habitat, but also covered large parts of suboptimal non-oak forest (Fig. 1).

The arithmetic range centers of 6 male home ranges tracked continuously from winter to late spring moved an average 68.7 ± 30.2 m ($\bar{x}$ ± SD) between winter and early spring, while the mean distance of the winter locations from the winter range centers was 149.9 ± 21.4 m. We rejected the hypothesis that the range centers moved beyond the average distance of the winter locations to the centers (1-sided paired *t*-test: t_5 = −6.89, *P* = 0.99). Similarly, range centers showed no significant shift from early to late spring (47.3 ± 32.5 m vs. 127.1 ± 30.2 m, t_5 = −4.62, *P* = 0.99). The position of the arithmetic

centers of core areas also remained stable between consecutive seasons, both from winter to early spring (78.4 ± 43.5 m vs. 135.5 ± 31.6 m, t_5 = −3.99, *P* = 0.99) and from early to late spring (60.2 ± 50.9 m vs. 113.7 ± 19.9 m, t_5 = −2.41, *P* = 0.97).

Median overlap of early spring by winter home ranges of the 6 males was 89.3%, and overlap of late spring by early spring ranges was 87.9%. Median overlap of early spring by winter core areas was 87.2%, and overlap of late spring by early spring core areas averaged 78.3%. To summarize, all analyses relating either to the distance

Table 2. Variation in home range and core area size of resident middle spotted woodpeckers from winter to late spring. *n* = number of ranges; data from 15 males and 12 females.

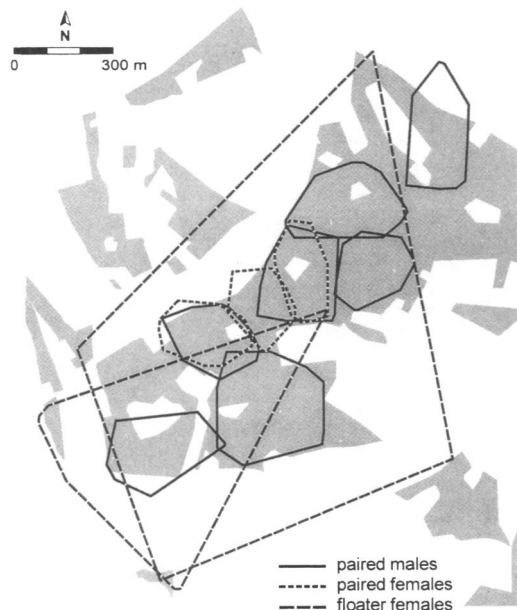| Sex	Winter			Early spring			Late spring		
	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Home range									
Males	17.5	7.7	9	10.6	3.7	15	7.4	3.6	12
Females	15.6	5.8	2	10.2	5.1	12	7.0	2.6	10
Core area									
Males	12.3	4.4	9	7.3	3.0	15	4.6	1.3	12
Females	9.4	2.9	2	7.0	3.2	12	4.6	1.3	10

Fig. 1. Location of home ranges of territorial and floating middle spotted woodpeckers in early spring 1994. Shaded: mature forest with oak as dominating tree species; white: non-oak forest.
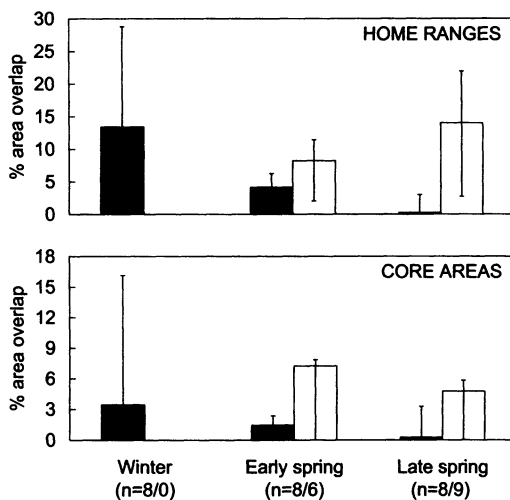
Fig. 2. Mean intrasexual home range and core area overlap in %. Black bars: males; open bars: females. n = number of male/female ranges; data from 16 birds. Shown are medians ± interquartile ranges.

moved by the range centers or to between-season area overlap of the same individuals indicate strong site fidelity for male home ranges and core areas from winter to late spring.

Range Overlap

Within the Sexes.—Area overlap between adjacent home ranges of males decreased from winter to late spring (Kruskal-Wallis test: $H_2 = 7.41$, $P = 0.025$; Fig. 2). Overlap was highest during winter with values up to 40%, but low both in early and late spring. In females, area overlap seemed to be smaller in early spring than in late spring, but the difference of 5.8% was not significant (Mann-Whitney U test: $U = 38.0$, $P = 0.195$; Fig. 2). However, over-

lap between female home ranges was larger than between male ranges in late spring ($U = 62.0$, $P = 0.011$), but not in early spring ($U = 34.0$, $P = 0.196$).

Area overlap between core areas of males did not significantly change from winter to late spring (Kruskal-Wallis test: $H_2 = 1.62$, $P = 0.445$; Fig. 2). Similarly, female core areas showed no change in area overlap between early and late spring (Mann-Whitney U test: $U = 22.5$, $P = 0.596$). Finally, overlap between female and male core areas differed neither in early ($U = 39.0$, $P = 0.052$) nor in late spring ($U = 51.0$, $P = 0.144$).

In winter, overlapping parts of male home ranges were used as expected from their size (Wilcoxon test: $z = -1.52$, $P = 0.128$, $n = 7$), whereas in early spring, the shared areas were used 1.8× more frequently than expected ($z = -2.52$, $P = 0.012$, $n = 8$). No test was possible for the male late spring ranges because only 4 of 8 overlapped. Females used the area shared with other females both in early ($z = -1.15$, $P = 0.249$, $n = 6$) and in late spring ($z = 0.14$, $P = 0.889$, $n = 8$) as expected.

The overlapping parts of the winter core areas of males were used as expected from their size (Wilcoxon test: $z = -1.36$, $P = 0.173$, $n = 6$), while the shared areas were used 2.8× more often than expected in early spring ($z = -2.20$, $P = 0.028$, $n = 6$). Again, no test was possible for late spring core areas due to the few overlaps in that season. Similarly, early spring core areas of females could not be tested, but seemed to be used as expected from their size. In late spring, females used the shared parts of core areas as expected ($z = -0.42$, $P = 0.674$, $n = 8$).

Between Pair-Partners.—Home ranges and core areas of males were overlapped by their mates equally in early and in late spring (home ranges: $U = 8.0$, $P = 0.624$, core areas: $U = 5.0$, $P = 0.221$; Table 3). However, the shared area was used less

Table 3. Area and intensity of overlap between males (M) and females (F) within pairs. Area overlap: % of an individual's range overlapped by the range of its mate; intensity: % of an individual's locations within the shared area. Shown are medians (Med) and interquartile ranges (IQR) of n = 4 pairs in early spring and n = 5 pairs in late spring.

Overlap	Area overlap				Overlap intensity			
	Early spring		Late spring		Early spring		Late spring	
	Med	IQR	Med	IQR	Med	IQR	Med	IQR
Home range								
M by F	75.3	66.9–81.1	74.8	60.7–77.2	81.8	74.3–82.6	61.1	54.5–66.5
F by M	92.5	87.6–97.6	69.6	43.7–71.3	86.2	79.7–93.1	68.4	63.6–69.9
Core area								
M by F	77.7	69.6–83.3	68.0	44.7–72.0	72.7	60.1–76.5	58.3	43.8–58.7
F by M	95.1	91.1–95.6	68.5	60.3–74.1	83.1	78.4–88.6	63.6	50.0–64.0

intensively by males in late than in early spring (home ranges: $U = 2.0$, $P = 0.05$, core areas: $U = 3.0$, $P = 0.086$), with intensity of overlap measured as percentage of an individual's locations within the shared area. Home ranges and core areas of females were overlapped by their mates to a larger extent in early than in late spring (both home ranges and core areas: $U = 1.0$, $P = 0.027$), and the use of the shared area by the females significantly decreased as well (home ranges: $U = 1.0$, $P = 0.027$, core areas: $U = 0.0$, $P = 0.014$).

Aggressive Interactions

From 1994–1996, 125 aggressive interactions were observed. First interactions were recorded in February, with an increasing frequency toward the end of the month. Most conflicts were observed in March and April, while their numbers decreased rapidly after egg laying at the beginning of May. Considering only tagged individuals and when accounting for their numbers, both sexes participated equally in territorial defense ($\chi_1^2 = 1.45$, $P = 0.228$): males were the active sex in 68.1% and females in 31.9% of the 91 interactions (Fig. 3). During February, males seemed to interact more often than females, but there was no significant difference after accounting for the number of tagged birds (19.8% vs. 1.1%; $\chi_1^2 = 1.29$, $P = 0.256$). However, in March, males were involved in more territorial conflicts than females (37.4% vs. 8.8%; $\chi_1^2 = 5.95$, $P = 0.015$), whereas females did so in April (7.7% vs. 22.0%; $\chi_1^2 = 4.91$, $P = 0.027$).

Of the 52 interactions where both parties could be identified, 22 occurred between males and 18 between females. These 40 sex-specific conflicts were significantly more than the 26 expected by chance ($\chi_1^2 = 8.13$, $P = 0.004$). Conflicts between residents and intruders of the opposite sex (2), between neighboring pairs (6), or between pairs and floaters (4) were rarely observed. In the latter 2 cases, both partners simultaneously participated in the defense.

DISCUSSION

Spatial Organization

Although woodpeckers are generally supposed to be territorial throughout the year (Short 1982), few studies have quantified the spatial organization of noncommunally structured woodpecker populations. Defining a territory as the defended area (Nice 1941)—which leads to more or less exclusive use—our results suggest that the middle spotted woodpecker is not terri-
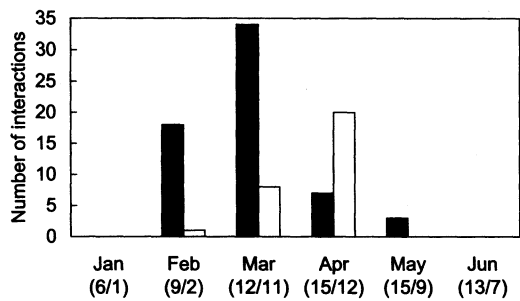

Fig. 3. Distribution of aggressive interactions between middle spotted woodpeckers from January to June in 1994–1996 ($n = 91$). Black bars: males; open bars: females. In parentheses = numbers of tagged males/females per month.

torial during winter but defends territories in early and late spring. Aggressive interactions were not observed in January, and their frequency increased only toward the end of February. Moreover, during these months, individual male home ranges overlapped most (up to 40%), and the shared parts of both home ranges and core areas were regularly used. During March and April, territorial conflicts culminated and the overlapping home range area was smaller, but used more intensively than expected, which is probably due to control and defense of the range boundary. Thus, male middle spotted woodpeckers seem to become territorial at the end of winter (~ Feb in our study area) and thereafter defend almost exclusive territories. In females, both the distribution of aggressive interactions over time and the seasonal pattern of home range overlap imply that their territorial phase is most pronounced in early spring. In late spring, neither sex engaged in aggressive interactions, but home ranges overlapped considerably more in females than in males. Hence, the degree of territoriality seems to change from early to late spring in females but not in males, which might be related to different roles of the sexes in territory defense (see below). Nevertheless, the position of home range and core areas of middle spotted woodpeckers remained remarkably stable from winter to late spring. This indicates that despite their greater space use in winter, the birds are already associated with a specific part of their range, which later becomes the breeding territory. Whether this site fidelity is associated with increased resource holding potential, conferring advantages in territory defense and/or reproductive success, remains to be studied.

Pair-partners showed a more pronounced use of the shared parts of home ranges and core areas in early rather than in late spring, which suggests a horizontal separation of their common territory during the latter period (i.e., the breeding period). Differences in foraging behavior of male and female middle spotted woodpeckers have been found to be smaller in the breeding than in the prebreeding period (Pasinelli 2000*b*). Therefore, the segregation of male and female home ranges and core areas in late spring may be a mechanism to reduce food competition between the sexes, whereas in the prebreeding period this seems to be achieved by sex-specific foraging behavior. Alternatively, the greater overlap in early spring might reflect mate-guarding behavior. In this case, pair-partners should have been regularly observed together, which, however, could not be confirmed.

Territory Defense

Overall, both sexes participated to similar degrees in territorial defense. However, in March, males were observed fighting more often than females, whereas females were involved in more conflicts than males in April. This pattern likely results from different roles of the sexes in the prebreeding period and may also indicate different functions of territorial behavior between the sexes. Males establish their territories in early March and defend them against other males, resulting in a great amount of territorial activity. Simultaneously, pair formation occurs and is usually completed within the first 2 weeks of March (G. Pasinelli, unpublished data). In April, the breeding cavity is excavated—primarily by males—and, once completed, has to be guarded against usurpers such as great spotted woodpeckers (*Dendrocopos major*) or starlings (*Sturnus vulgaris*; Pettersson 1984, Michalek 1998). Thus, territoriality in male middle spotted woodpeckers seems to focus mainly on resources such as food, nesting sites, and mates. In females, on the other hand, the peak of territorial interactions in April reflects an increased effort of floater females to displace established birds, which has been witnessed to occur in 1 case. Hence, females might primarily defend their position as paired females as well as their mates rather than the territory as an area itself because range overlap after egg laying (i.e., in late spring) was greater in females than in males.

Our results suggest that territory defense is carried out by the territory holder corresponding in

sex to the intruder. Similar results have been found in other woodpecker species (Winkler et al. 1995) as well as in some passerines (e.g., the nuthatch *Sitta europaea*; Matthysen 1986). Such intrasexual aggression promotes monogamy (Arcese 1989), while strong female–female competition prevents conspecific brood parasitism (Eadie et al. 1998), explaining perhaps the absence of extra-pair young in the middle spotted woodpecker (Michalek 1998). Moreover, the certainty of paternity and maternity, respectively, assures parental care of both partners, which is crucial for rearing a successful brood in noncommunally breeding woodpeckers with long nestling periods (Short 1982, Ligon 1993, but see Wiktander 1998).

Home Range, Core Area, and Spacing Behavior

For resident middle spotted woodpeckers, we found a seasonal decrease in home range size from averages of 17.1 ha in winter to 10.4 ha in early spring and 7.2 ha in late spring. Comparable data using radiotracked individuals of this species are scarce; the sizes of 3 male home ranges in a floodplain forest in the Upper Rhine Valley (Germany) were 7.2 ha in late winter, 3.9 ha in late spring, and 5.1 ha in the post-fledging period (Spitznagel 2001), whereas Villard (1991) reported an average breeding territory size of 3.5 ha ($n = 2$) and a post-fledging home range of 8.5 ha, respectively, in a French oak forest. In Sweden, Pettersson (1984) estimated an average territory size of 25 ha based on observations of unmarked individuals during late spring. Thus, the size of areas used by the middle spotted woodpecker in spring seems to differ largely between study sites, which likely reflects differences in methodology and habitat quality. Pasinelli (2000*a*) has shown that the availability of both large oaks and potential cavity trees (i.e., trees with either polyporous fungi, limb holes, or old cavities) affects home range size of this species. This relation between space use and habitat quality, also suggested by other studies of this woodpecker (Müller 1982, Bühlmann and Pasinelli 1996), makes it difficult to determine area requirements of general validity. Additionally, a major problem in determining area requirements of animals lies in the distinction of needed and not needed parts within the home range of the individuals, which none of the cited studies addressed. The concept of core area has been widely applied in wildlife management to identi-

fy specific areas within the home range that are most intensively used (Samuel et al. 1985, Wauters and Dhondt 1992, White et al. 1996). The core area is assumed to provide all critical habitat resources needed for survival and reproduction. Considering the seasonal territoriality of the middle spotted woodpecker revealed by our study, we suggest early spring to be the appropriate season to determine size of core areas (and hence area requirements), because territoriality is assumed to limit the number of reproducing pairs in an area (Newton 1998). Alternatively, core areas in late spring (the breeding period) might be proposed as being more adequate (Bingham and Noon 1997). However, average core area size decreased from early (7.2 ha) to late spring (4.6 ha), and the larger core area in early spring might be important for females to acquire sufficient energy for producing the clutch. Furthermore, core areas in early spring encompassed those of late spring, as shown by their stable position between the seasons, so that using early spring core areas is a meaningful approach to estimate area requirements and is more likely to include all critical resources for this habitat specialist.

It has been argued that protecting or managing areas based on breeding time needs could be inappropriate for securing survival outside that period due to differing area and/or habitat requirements (Buchanan et al. 1998). Based on our understanding of the middle spotted woodpecker's biology, there is no evidence for winter core area to be more appropriate than early spring core area as an estimate of required area. First, the middle spotted woodpecker is not territorial in winter, so at that time the birds can use a wider area than in spring, which is reflected by their larger average core areas (11.8 ha) and their more overlapping home ranges in winter than in spring. Second, mature oak forest is the critical habitat in northeastern Switzerland from winter to late spring (Pasinelli 2000a), which is supported by foraging behavior studies (Jenni 1983, Pettersson 1983, Pasinelli and Hegelbach 1997); obviously, the species does not depend on other habitat types in winter than in spring.

MANAGEMENT IMPLICATIONS

We have examined spacing behavior of resident middle spotted woodpeckers in 1 study area, which we recognize to be no more than an initial—though important—step for a comprehensive conservation strategy of this species. Given the relation between habitat composition and space use, comparisons of the ranging behavior of the species in different habitats and at different geographical locations are urgent.

Given the costs that territoriality incurs for territory owners, the strong territorial behavior of middle spotted woodpeckers implies that core areas in early spring should represent required area. All studied, resident individuals attempted to breed, and 75% of the pairs were successful, indicating that the territories provided all necessary resources. The failures were due mainly to weather and in a few cases to predators (Pasinelli 2001). Conner (1979) suggested providing habitat in the range of a species' mean ± 1 SD for critical habitat factors or types, both to maintain genetic variability of the species and to minimize detrimental effects of human or natural habitat alterations. Based on this, we estimate required area of a breeding pair in early spring to range from 4.2 to 10.2 ha (7.2 ± 3.0 ha). Thus, a breeding population of 50 pairs may need 210 to 510 ha of continuous old oak forest. Considering that our study was conducted in a high-quality habitat, the latter measure will be more realistic in most other cases. Additionally, the high-quality habitat in our study forest affects estimated mean and standard deviation so that a population of 50 pairs in less optimal habitat will need even more than 510 ha of oak forest (Pettersson 1985), because space use of individuals is inversely related to the availability of old oaks and potential cavity trees (Pasinelli 2000a). Thus, size of a forest reserve suitable for the middle spotted woodpecker will depend both on the target population size and on the composition of an oak forest. The basis of any management plan for this species is therefore a forest inventory determining the availability of old oaks and potential cavity trees.

The ongoing trend to harvest old oak forests and the lack of middle-aged oak stands in many parts of central Europe (Bühlmann 1993, Lehnemann 1993) will soon lead to an increased threat for this species. To counteract this problem, protection of the remaining oak forests is of crucial importance for the conservation of the middle spotted woodpecker. Timber harvesting in these forests should be conducted only to improve conditions for the middle spotted woodpecker—for example, by selectively removing non-oaks to provide sunny oak crowns, which are preferred by this species (Pasinelli and Hegelbach 1997). A promising approach to enforce such forestry methods involves payments to compensate for the financial loss incurred by forest owners who do not harvest old oaks (Pasinelli et al. 1998).

Furthermore, nonbreeding individuals during the reproductive season (floaters) are common in many bird species (Zack and Stutchbury 1992, Newton 1998) and have been reported for the middle spotted woodpecker as well. Although such individuals play an important role in population demography (Rohner 1996), they would not be considered in a conservation strategy based on core areas of reproducing individuals. Future studies should address floater behavior to extend conservation measures to suboptimal habitats. This could help us understand the value of habitat corridors with suboptimal habitat for dispersing middle spotted woodpeckers.

ACKNOWLEDGMENTS

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