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# SPATIAL ORGANIZATION OF THE YELLOW-NECKED MOUSE: EFFECTS OF DENSITY AND RESOURCE AVAILABILITY

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Space use in mammals may vary between the sexes. This may reflect demographic or reproductive differences between the sexes as well as different responses to changes in resource availability. We present the results of a 2-year study on the spatial organization of the yellow-necked mouse (*Apodemus flavicollis*) in a beech woodland in the eastern Italian Alps. We used radiotelemetry to monitor the movements of 64 mice during the breeding season (i.e., from July to October) in 2005 (high population density) and 2006 (low population density). In both years, home ranges of males were significantly larger than those of females and overlapped with the areas occupied by several individuals of both sexes. Females monopolized core areas and never shared burrows with other females—suggesting intrasexual territoriality—although their home ranges overlapped those of several males. Space use changed seasonally and among years, suggesting a relationship with resource abundance and distribution. Females exhibited reduced spatial exclusivity and larger home ranges during lower food availability; males varied their spatial distribution accordingly by also expanding their home ranges. After a decrease in habitat quality, we observed substantial and abrupt adult dispersal by both sexes. In sum, females varied their spatial and social relationships in response to environmental conditions, whereas males appeared to vary patterns of space use in response to females.

Key words: *Apodemus flavicollis*, dispersal, home-range overlap, mast, resource availability, territoriality

Observations of the spatial behavior of individuals can provide valuable information on the processes that determine population structure in small mammals. The resources available within an individual's home range (e.g., food and shelter) promote survival and reproduction, thus enhancing fitness. Spatial relationships also may be critical to population regulation through their effects on aggression (Watts 1969) and breeding status (Montgomery et al. 1997). Because resource use and demographic patterns often vary between males and females, it seems logical to expect sex-related variation in space use (Gaulin and Fitzgerald 1988; Lambin and Krebs 1991; Madison 1980; Tew and Macdonald 1994; Wolff 1985).

The spatial organization of females is expected to be closely related to the abundance, distribution, and renewal rates of resources, because of the relatively high costs of reproduction by members of this sex (Davies 1991; Trivers 1972). In particular, resources that are sparse, patchy in distribution, and have slow rates of renewal are expected to favor intrasexual territoriality (Ostfeld 1985, 1990; Wolff 1993). Changes in resource distributions should lead to changes in space use by females, with the result that members of a population may display variable spatial relationships over time (Maher and Lott 2000; Reiss 1988). In contrast, spatial organization of males is heavily influenced by access to mates and so is likely to be driven by the distribution of females rather than the acquisition of energy (Emlen and Oring 1977; Ostfeld 1990; Ribble and Millar 1996). Thus, changes in the spatial distributions of females should lead to associated changes in patterns of space use by males.

In mammal species with short life spans and high reproductive rates, survival is often strongly tied to food availability and changes in food abundance can generate fluctuations in population density (Krebs and Davies 1978; Ostfeld et al. 1996; Wolff 1996) that may influence space use and sexual interactions. For this reason, rodents frequently provide ideal opportunities to investigate the dependence of spatial and social relationships on habitat quality, resource availability, and demographic parameters. *Peromyscus* species

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have been particularly well studied in this respect (e.g., Taitt 1981; Vessey 1987; Vessey and Vessey 2007; Wolff 1985). Previous research on these animals has demonstrated that space use varies with resources, with home ranges typically being smaller when food was abundant and population density was high (Falls et al. 2007; Merritt et al. 2001). The same studies also revealed that although females defend territories, males are much more mobile and do not defend a specific portion of the habitat.

We examined space use in a population of the yellow-necked mouse (*Apodemus flavicollis*) in relation to sex, population density, and differences in resource availability. Ecologically, *Apodemus* is similar to *Peromyscus* (Tew and Macdonald 1994). *A. flavicollis* is found throughout Europe (Mitchell-Jones et al. 1999), typically in mature deciduous woodland with a high diversity of plant species (Angelstam et al. 1987). It is granivorous and often sympatric with the common wood mouse (*A. sylvaticus*), particularly in western Europe (Bergstedt 1965; Montgomery 1980). Most studies of the spatial behavior of *Apodemus* have focused on *A. sylvaticus*, and hence relatively little is known of the spatial organization or movements of *A. flavicollis* (but see Kotzageorgis and Mason 1996; Schwartzenberger and Klingel 1995). Based on these analyses as well as studies of *Peromyscus* (e.g., Ribble and Millar 1996; Vessey 1987), we predicted that home ranges of females would display limited spatial overlap with one another but would be overlapped by the home ranges of several males. Across years, we expected changes in resource abundance to affect space use, particularly among females. Finally, we predicted that dispersal should be related to resource availability but should not differ between the sexes. Our findings yield new insights into the importance of temporal variation in resource abundance in shaping patterns of space use among small mammals.

## Materials and Methods

*Study area and seed production*.—Fieldwork was carried out in Valle dei Laghi, Trentino (45°58′50″N, 10°57′47″E; elevation 750–800 m), in the northeastern Italian Alps. The study area consisted of an isolated calcareous ridge covered by broad-leaved woodland dominated by mature beech (*Fagus sylvatica*), with a sparse understory and only limited canopy cover. Other common species in this altitudinal range (e.g., hazel [*Corylus avellana*] and manna ash [*Fraxinus ornus*]) were present at low abundance. This study area was selected because, due to limited plant species diversity, it was considered representative but suboptimal habitat for *A. flavicollis*, which was the predominant rodent species we have encountered during 4 years of trapping in this region.

To quantify resource abundance at the study site, we collected data on beech seed production. From 2004 to 2006, 140 cone-shaped litter traps (diameter = 0.80 m) were maintained within the trapping grid established on the site (see below). On alternate weeks from the end of July to the middle of November, we counted the number of beech seeds per trap; we targeted this portion of each year because it corresponded to the annual period of beech seed production.

*Trapping and marking of animals*.—The study was based on capture–mark–recapture and radiotracking techniques. We set up an 18 × 18 trapping grid (total area = 6.7 ha), with 15 m between traps. Because some terrain features (e.g., hills and large rocks) caused small shifts in trap alignment, the locations of all traps were recorded with a global positioning system (GeoExplorer3 Trimble; Crisel, Roma, Italy) using postprocessed differential correction (accuracy approximately 1 m). From May to November 2005 and April to November 2006, we trapped members of the study population every 4 weeks for 5 consecutive nights. This represented a total of 9,976 and 12,960 trap-nights for 2005 and 2006, respectively. We used multiple-capture live traps (Special Mouse 2; Ugglan, Grahnab, Sweden) baited with sunflower seeds and pieces of potato. Traps were set in the evening and checked the following morning. On initial capture, each individual was permanently marked by injecting an implantable subcutaneous passive induced transponder tag (Trovan ID 100; Ghislandi and Ghislandi, Covo, Bergamo, Italy) beneath the skin at the nape of the neck. For each individual captured, we recorded sex, pelage color as an indication of the age class, breeding condition (e.g., testes scrotal for males and lactating for females), and body mass.

To minimize the inclusion of transient mice in our data set, we radiocollared individuals only if they were trapped a minimum of 3 times over more than one 5-day trapping session (Rajska-Jurgiel 2001). In July–October of both years, all nontransient adults (i.e., with brown pelage—Flowerdew 1984) weighing at least 29 g were fitted with a very-high-frequency radiotransmitter (BD-2C; Holohil Systems Ltd., Carp, Ontario, Canada) mounted on a nylon cable-tie collar. The weight of the complete transmitter package was <2 g and therefore <8% of minimum adult body mass (as recommended by Wolton and Trowbridge [1985]). Before attaching collars, we injected mice with 140 mg/kg of anesthetic Zoletil (Virbac, Milano, Italy). All collared animals were released at the point of capture. Transmitter batteries had an average life span of 53 days; whenever possible, collared animals were retrapped and the existing radiocollar was replaced before the battery expired. In 2005 we radiocollared a total of 20 males and 12 females; in 2006 we collared 19 males and 13 females. Generally, we marked a similar number of males and females during each 5-day trapping session, although this was not possible in October 2005 (Table 1).

All animal handling procedures were carried out in accordance with the protocols approved by the Scientific Committee of the Research Fund of the Autonomous Province of Trento and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

*Radiotracking*.—From July to October of both years, we completed four 21-day radiotracking sessions in the period between successive trapping sessions. Radiotracking was performed using ATS receivers (model R2000; Advanced Telemetry Systems, Isanti, Minnesota) in conjunction with a

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**Table 1.**—Numbers of adult and juvenile *Apodemus flavicollis* captured near Valle dei Laghi, Italy, in 2005 and 2006. Population size ($\hat{N}$) and density ($\hat{D}$) were estimated using capture–mark–recapture analyses of animals resident on an 18 × 18 station grid (15 m between traps). The number of adults monitored via radiotelemetry is indicated; the proportions of radiocollared individuals used to estimate home-range sizes are given in parentheses.

| Year | Month | Captured individuals | | $\hat{N} \pm SE$ (estimate for adults only) | $\hat{D} \pm SE$ (adult individuals/ha) | Radiotracked individuals | |
|---|---|---|---|---|---|---|---|
| | | Juveniles | Adults | | | Males | Females |
| 2005 | May | 111 | 89 | 93 ± 3 | 10.38 ± 2.50 | — | — |
| | July | 19 | 112 | 129 ± 12 | 13.62 ± 3.45 | 5 (4) | 11 (8) |
| | August | 5 | 122 | 125 ± 2 | 12.71 ± 2.91 | 7 (6) | 14 (13) |
| | September | 4 | 76 | 80 ± 3 | 6.79 ± 3.09 | 8 (4) | 18 (10) |
| | October | 4 | 36 | 37 ± 2 | 2.64 ± 4.20 | 3 (0) | 10 (4) |
| | November | 3 | 31 | 31 ± 0 | 2.31 ± 3.36 | — | — |
| 2006 | May | 0 | 6 | 8 ± 5 | 0.60 ± 0.68 | — | — |
| | June | 0 | 15 | 16 ± 1 | 1.66 ± 0.35 | — | — |
| | July | 0 | 22 | 22 ± 1 | 2.29 ± 0.43 | 9 (4) | 18 (8) |
| | August | 0 | 28 | 30 ± 4 | 2.44 ± 0.30 | 10 (7) | 22 (14) |
| | September | 0 | 14 | 14 ± 1 | 0.99 ± 0.27 | 9 (7) | 16 (13) |
| | October | 0 | 9 | 10 ± 15 | 0.85 ± 0.43 | 4 (3) | 9 (6) |
| | November | 9 | 4 | 4 ± 0 | 0.41 ± 2.19 | — | — |

4-element flexible yagi antenna (Biotrack Ltd., Dorset, United Kingdom). The locations of radiocollared mice were determined relative to a 3.5 × 3.5-m grid. Radiofixes falling outside the grid were mapped by global positioning system. We recorded animal movements from dusk to dawn, with intervals of ≥50 min between successive fixes; this interval was considered sufficiently short to follow movements of each mouse (Wolton 1985), but long enough to avoid autocorrelation of the data (Otis and White 1999; Rooney et al. 1998; Swihart and Slade 1985). We also recorded 1 fix per animal per day in daylight hours to locate burrows. For each fix, we recorded the date, time, meteorological conditions, status of the individual (i.e., active or inactive, according to the signal), and, if the individual could be observed, the behavior in which it was engaged at the time of the fix.

Some radiocollared individuals disappeared from the study population (and were presumed killed) before we could collect a sufficient number of radiofixes. We analyzed home ranges only for animals that showed an asymptotic curve in a plot of the cumulative number of fixes versus home-range size (Harris et al. 1990). In 2005, this was the case for 21 mice (14 males and 7 females); in 2006, data from 21 mice (11 males and 10 females) were appropriate for analysis. Plots for both sexes reached asymptotes when >50 fixes per individual were recorded.

*Density estimation*.—Population density was estimated for adults only. The assumption that the adult population was closed to immigration or emigration was tested following the procedure of White and Shenk (2001). We estimated population size ($\hat{N}$) for each trapping session using Program MARK version 5.0 (Cooch and White 2008), according to the model averaging procedure for a closed population (Stanley and Burnham 1999). Density estimates (individuals/ha, $\hat{D}$) were derived by dividing ($\hat{N}$) by the effective trapping area; the effective trapping area consisted of the trapping grid area plus a boundary strip, to account for the edge effect (e.g., Bondrup-Nielsen 1983). We estimated width of the boundary strip as the mean maximum distance moved between successive captures of the same animal, as from experimental comparison of density estimates calculated with different boundary strip values (Tioli et al. 2009).

*Data analysis*.—We tested all response variables for normality using the Shapiro–Wilk test and for homogeneity of variance using the Bartlett test (Crawley 2002). For data that were not normally distributed, we determined the actual distribution of errors by comparing the actual values of the response variable to the theoretical distribution of that parameter. We examined the relationships between response and predictor variables using the appropriate model distribution for each response variables (e.g., generalized linear or generalized linear mixed models—Crawley 2002). Where appropriate, response variables were log or arcsine transformed. We then applied an all-subset model selection procedure based on the Akaike information criterion (AIC), as corrected for small sample size ($AIC_c$—see Burnham and Anderson 2002). For each dependent variable we set an a priori full model based on the explanatory variables that we considered biologically meaningful (Burnham and Anderson 2002). We calculated AIC for all possible additive models starting from the a priori full model, and ranked the models according to $AIC_c$ values. From the differences in $AIC_c$ values ($\Delta AIC_c$), we calculated $AIC_c$ weights ($\omega$) and relative evidence ratios (Burnham and Anderson 2002; see Appendix I). When $\Delta AIC_c < 2$ (indicating approximately equal parsimony of models), we ranked all variables considered in the full model according to their importance (predictor weights, $\omega_+(j)$—Burnham and Anderson 2002). Parameter estimates were evaluated for the best model or, in cases of equal parsimony for multiple models, by model averaging, which consisted of weighting estimates from all possible models according to their $AIC_c$ value. When combining data from both years to produce a

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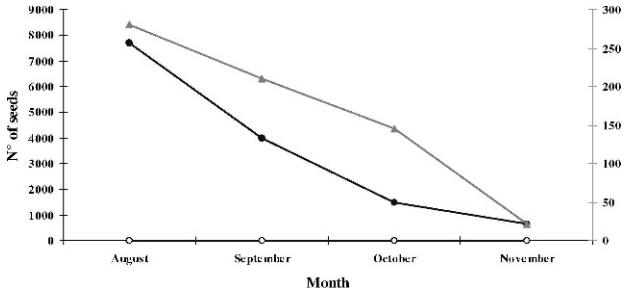



**FIG. 1.**—Monthly beech seed production in summer–autumn 2005 and 2006 near Valle dei Laghi, Italy. Vertical axes refer to data from 2004 (left) and 2006 (right), respectively; no beech seed production was detected in 2005. Closed circles = 2004; open circles = 2005; and triangles = 2006.

single best-fit model, we included in the full model any variables that were selected for the best model from either year as well as their biologically meaningful interactions. Statistical analysis was carried out using R version 2.3.1 (R Development Core Team 2006). All spatial analyses except home-range contours were carried out with ArcGIS 9.0 (ESRI, Redlands, California).

*Home-range size*.—For each radiotracking session, we determined the mean number of burrows used by an individual and the occurrence of burrow sharing by adult females. To compare space use by males and females and to evaluate seasonal and annual variation in spatial organization, we estimated home-range size, core-area size, and daily distances moved. Home-range size was determined using the 95% fixed kernel method, applying least-squares cross-validation to select the smoothing parameter (Kernohan et al. 2001). To calculate core-area size, we applied the kernel function at a 50% level (Harris et al. 1990). Kernel probability distributions and their relative 95% and 50% probability surfaces were calculated using R version 2.3.1 (R Development Core Team 2006) and the R package Adehabitat version 1.5-1.

We used mixed linear models to examine relationships between the response variables home-range size and core-area size and the predictor variables sex, month, and body weight in each year of the study; individual was treated as a random effect to account for pseudoreplication (Crawley 2002). The same approach was used to explore relationships between home-range size, core-area size, and the variables year, sex, and month when data from 2005 and 2006 were pooled.

*Home-range overlap*.—To compare patterns of spatial overlap between the sexes and to evaluate seasonal and annual variation in home-range overlap, we used Bhattacharyya's affinity (BA) to characterize how home ranges of males and females were arranged relative to each other. BA, which provides an index of overlap, is a function of the product of the probability surfaces of overlapping animals (Fieberg and Kochanny 2005). This index quantifies the degree of similarity among probability surface estimates on a scale from 0 (no range overlap) to 1 (complete overlap). We applied the BA index to all possible pairs of individuals resident on the study grid during the same radiotracking session to determine the degree of home-range overlap within and between the sexes. In addition, for those pairs of animals with overlapping home ranges, we estimated the probability of animal j being located in the home range of animal i and vice versa in each radiotracking session. This procedure is directional, such that 2 values describe the overlap of a pair ($PHR_{i,j}$ and $PHR_{j,i}$). We transformed these values into 2 binary variables, PHR50 and PHR95, that defined the presence (PHR = 1) or absence (PHR = 0) of overlap at 50% and 95% probability contours, respectively.

For each year of the study, we compared the number of females overlapping with individual males and vice versa using Mann–Whitney *U*-tests. We investigated the effects of pair composition (e.g., male–female) and month on BA using generalized linear models with gamma error. The same procedure was used to examine the effects of year and sex on BA when data for both years were combined. We used general linear models with binomial error to examine the effects of pair composition on PHR50 and PHR95 in each year.

*Patterns of movement*.—We plotted the frequency distribution of the daily distances moved (DM) by all individuals and grouped these distances into 2 classes according to whether they fell above or below the 75th percentile for the distribution (i.e., median DM + 1 quartile). We treated DM as a binary variable, with DM = 0 for values below the 75th percentile and DM = 1 for values above this cutoff. Thus, DM = 1 should have included excursions and dispersal events, allowing us to test whether the probabilities of these types of movements varied with time or sex. Resident individuals were considered to have dispersed when, after an excursion, they were radiotracked permanently outside of the study grid.

For both 2005 and 2006, we examined whether DM varied with sex or month using generalized linear mixed models with binomial error; individual was treated as a random effect in these analyses. We could not statistically model the proportion of dispersers by year and sex because of the small sample size.

## RESULTS

*Seed production*.—A total of 13,810 and 657 beech seeds were collected in 2004 and 2006, respectively. In each of these years, monthly production of beech seeds declined from August to November (Fig. 1). In contrast, no seed production was recorded for beech trees in 2005, meaning that no seeds were collected in our traps. In terms of seed availability to animals, that is, presence of seeds on the ground, the mast seed production in autumn 2004 may have assured presence of seeds on the ground throughout winter 2004–2005 and spring 2005. After depletion, no seeds would have been available on the ground until autumn 2006.

*Density estimation*.—In 2005, capture probabilities for *A. flavicollis* ranged from 0.39 to 0.64 per trapping session; in 2006, capture probabilities ranged from 0.20 to 0.51 per trapping session. The assumption that the population was demographically closed was met in all but the September 2005 trapping session (closure test: $z = -1.65$, $P = 0.048$; all other $P > 0.05$). In both years, population density was greatest during July–August and began to decrease in September. In

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2005, population density was moderate to high relative to previous studies of *A. flavicollis* in similar habitats (e.g., Mazurkiewicz and Rajska-Jurgiel 1998; Montgomery 1980; Rajska-Jurgiel 1992); densities in 2005 were consistently greater than those recorded in 2006 (Table 1). In 2005, juveniles were captured in all months of the study, with the largest number trapped in May 2005. In contrast, in 2006, the few juveniles captured were trapped in November (for number of radio-tracked individuals: Table 1).

*Home-range sizes.*—In 2005, the mean number of radio-tracking fixes per animal per trapping session was 12.4 ± 0.8 *SE* and 65.7 ± 2.2 for diurnal and nocturnal fixes, respectively. In 2006, these values were 11.4 ± 0.7 and 48.9 ± 2.6 (Table 1). In 2005, the mean number of burrows used per individual per tracking session was 3.57 ± 0.31 *SE* for males and 4.91 ± 0.39 for females; in 2006, these values were 3.47 ± 0.31 for males and 4.33 ± 0.46 for females (Table 1). In 2005, the 2 principal predictors of home-range size were sex and month (predictor weights: sex = 0.83, month = 0.58); these variables were included in the 2 equally parsimonious models that were averaged to produce the full model for home-range size (Table 2a). Home ranges of males were larger than those of females, as indicated by the positive model-averaged coefficients for this variable. Home-range size increased throughout the study period (Fig. 2a; Table 2a). In 2006, sex was the only explanatory variable in the best model for home-range size. Again, ranges were larger for males than for females although home-range size did not vary over the course of the season (Fig. 2b; Table 2b). When data from both years were pooled, home-range size was influenced by year and sex, with these effects being greater in 2006 (Table 2c). Home-range size was not influenced by body weight in either year (Tables 2a and 2b).

Analyses of the factors affecting core-area size produced generally similar results. In 2005, the full model revealed that core-area size was influenced by sex and month (predictor weights: sex = 0.93, month = 0.35). Parameter estimates (averaged across 7 models) revealed that core areas were larger for males and that core-area size increased throughout the season (Fig. 2c; Table 2a). As with analyses of home-range size, sex was the only significant predictor of core-area size in 2006 (predictor weight: sex = 0.63), with core areas being larger for males (Fig. 2d; Table 2b). When data from both years were pooled, year and sex were significant predictors of core-area size, which was greater in 2006 (Table 2c). As with home-range size, body weight had no significant effect on core-area size in either year.

*Home-range overlap.*—No adult females shared the same burrow. In general, overlap between the home ranges of neighboring females (FF) was less than that between male–female (MF) or male–male (MM) pairs of neighbors (BA in 2005, FF: 0.02 ± 0.01 *SE*; MM: 0.1 ± 0.02; MF: 0.1 ± 0.02; BA in 2006, FF: 0.04 ± 0.01, MM: 0.09 ± 0.03, MF: 0.1 ± 0.02). The number of females with home ranges that overlapped at least 1 home range of a male was significantly greater in 2006 than in 2005 (2005: 1.43 ± 0.32, 2006: 3.73 ± 0.71; $W = 126$, $P = 0.003$). In contrast, the number of males with home ranges that overlapped with at least 1 home range of a female did not differ between years (2005: 2.85 ± 0.34, 2006: 4.10 ± 0.72; $W = 47.5$, $P = 0.10$). In 2005, the BA index of degree of overlap was influenced primarily by sex (predictor weight: sex = 0.62; Table 2a). In 2006, the best-fit model for BA did not include any fixed effect (Table 2b). When all data were pooled, sex and year were the main predictors of BA (predictor weights: sex = 0.70, year = 0.52), occurring in the 2 equally most parsimonious models examined. Based on parameter estimates averaged across these models, the degree of overlap among animals was greater in 2006 than in 2005 (Table 2c).

The probability that an animal would be located within both the 50% (PHR50) and 95% (PHR95) contours of a neighbor's home range was influenced by sex. Sex-related variation in PHR95 was observed in 2005 (predictor weight: sex = 0.50), with the probability of overlap among male–male and male–female pairs being greater than that among female–female pairs (Table 2a; Fig. 3a). In 2006, however, the best model for PHR95 did not include any fixed effect (Table 2b; Fig. 3b). In 2005, overlap of core areas (50% contours) was rare and was completely absent among females (Fig. 3c). The best-fit model for PHR50 included sex as a fixed effect, although, because no overlap occurred between females, model coefficients could not be properly estimated (Table 2a). In 2006, PHR50 was affected by sex (predictor weight: sex = 0.62), with male–male and male–female pairs overlapping more frequently than female–female pairs (Table 2b; Fig. 3d). See patterns of home-range overlap in Figure 4.

*Animal movements.*—Based on actual distances moved by individuals in the study population, 75th percentile values were established as 60 m in 2005 and 95 m in 2006; from these, the proportion of individuals exhibiting large daily movement (DM = 1) was determined. In 2005, the main predictors of large daily movement were sex and month: the proportion of animals for which DM = 1 increased in October and was greater for males (Table 2a). In 2006, DM was affected only by sex, with more males having DM = 1 (Table 2b). When data from both sexes were pooled, the daily distance traveled was generally greater in 2006 (2005: 69.86 m ± 9.78 *SE*, $n = 469$; 2006: 82.45 ± 4.39, $n = 632$).

Dispersal by males and females was detected in each year of the study. In 2005, 7 of 13 radiocollared mice (4 males and 3 females) permanently moved away from the trapping grid between the end of September and early October. These dispersal events were abrupt and, for most individuals, occurred during a single night. Among the 7 individuals that dispersed, the mean total distance traveled during the dispersal event was 1,540 m ± 322.8 *SE* for males and 1,476 ± 356.7 m for females. In 2006, 3 of 16 collared mice (1 male and 2 females) dispersed during the same period; the mean distance traveled during these dispersal events was 1,104.5 ± 231.6 m.

## Discussion

We investigated the spatial organization of *A. flavicollis*, a granivorous rodent that relies on clumped and temporally

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**TABLE 2.**—Parameter estimates describing the spatial behavior of *Apodemus flavicollis*. Estimates were obtained from generalized linear or generalized linear mixed models. The best model is reported if model selection resulted in $\Delta AIC_c > 2$; otherwise, the full model is reported, with parameters estimated by model averaging. Data are from a) 2005, b) 2006, and c) both years combined.

| Best model (§) or full model (§§) | No. averaged models | Coefficients | Estimate $\bar{X} \pm SE$ |
|---|---|---|---|
| a) 2005 | | | |
| (§§) HR[a] ~ W[b] + M[c] +S[d] + (1/I)[e] | 7 | Intercept | 3.66 ± 0.08 |
| | | S (M) | 0.22 ± 0.05 |
| | | M (2) | 0.13 ± 0.03 |
| | | M (3) | 0.22 ± 0.04 |
| | | M (4) | 0.45 ± 0.06 |
| (§§) CA[f] ~ W + M + S + (1/I) | 7 | Intercept | 3.07 ± 0.07 |
| | | S (M) | 0.26 ± 0.07 |
| | | M (2) | 0.14 ± 0.02 |
| | | M (3) | 0.22 ± 0.03 |
| | | M (4) | 0.45 ± 0.04 |
| (§) DM[g] ~ S + M + (1/I) | — | Intercept | −2.70 ± 0.38 |
| | | S (M) | 1.08 ± 0.27 |
| | | M (2) | 0.74 ± 0.38 |
| | | M (3) | 0.85 ± 0.38 |
| | | M (4) | 1.47 ± 0.45 |
| (§§) BA[h] ~ M + S + M × S | 4 | Intercept | 14.92 ± 8.86 |
| | | S (MF) | 15.569 ± 4.34 |
| | | S (MM) | 15.357 ± 4.37 |
| (§) PHR50[i] ~ S | — | Intercept | −21.97 ± 6,891.14 |
| | | S (MF) | 20.39 ± 6,891.14 |
| | | S (MM) | 19.82 ± 6,891.14 |
| (§§) PHR95[j] ~ S | 2 | Intercept | −1.19 ± 0.68 |
| | | S (MF) | 1.25 ± 0.30 |
| | | S (MM) | 1.33 ± 0.19 |
| b) 2006 | | | |
| (§) HR ~ S + (1/I) | — | Intercept | 4.23 ± 0.06 |
| | | S (M) | 0.31 ± 0.08 |
| (§§) CA ~ W + M + S + (1/I) | 7 | Intercept | 3.68 ± 0.09 |
| | | S (M) | 0.28 ± 0.06 |
| (§) DM ~ S + (1/I) | — | Intercept | −1.71 ± 0.16 |
| | | S (M) | 1.04 ± 0.20 |
| (§) BA ~ 1 | — | Intercept | 5.07 ± 0.49 |
| (§§) PHR50 ~ S | 2 | Intercept | −2.07 ± 0.66 |
| | | S (MF) | 1.23 ± 0.35 |
| | | S (MM) | 1.31 ± 0.25 |
| (§) PHR95 ~ 1 | — | Intercept | 0.13 ± 0.14 |
| c) 2005 and 2006 | | | |
| (§) HR ~Y[k] + S + (1/I) | — | Intercept | 0.96 ± 0.29 |
| | | Y | 0.55 ± 0.05 |
| | | S (M) | 0.29 ± 0.05 |
| (§) CA ~Y + S + (1/I) | — | Intercept | 0.46 ± 0.32 |
| | | Y | 0.53 ± 0.06 |
| | | S (M) | 0.28 ± 0.06 |
| (§§) BA ~ S + Y + S × Y | 4 | Intercept | 14.27 ± 10.69 |
| | | S (MF) | 10.82 ± 9.14 |
| | | S (MM) | 10.56 ± 9.43 |
| | | Y | 2.10 ± 1.57 |
| | | S (MF) × Y | 13.09 ± 0.39 |
| | | S (MM) × Y | 13.55 ± 0.40 |

[a] HR: home-range size calculated by kernel 95%.
[b] W: body weight.
[c] M: month; (2) = August; (3) = September; (4) = October; reference level is July.
[d] S: sex; (M) = male; (MF) = male–female; (MM) = male–male. Reference levels are (F) = female or (FF) = female–female.
[e] 1/I: individual as random effect.
[f] CA: core-area size calculated by kernel 50%.
[g] DM: daily distance moved.
[h] BA: Bhattacharyya's affinity overlap index.
[i] PHR50: presence–absence of overlap at 50% probability contour of animal pairs, where S is sex (male–male, female–female, and male–female).
[j] PHR95: presence–absence of overlap at 95% probability contour of animal pairs, where S is sex (male–male, female–female, and male–female).
[k] Y: year; reference level is 2005.

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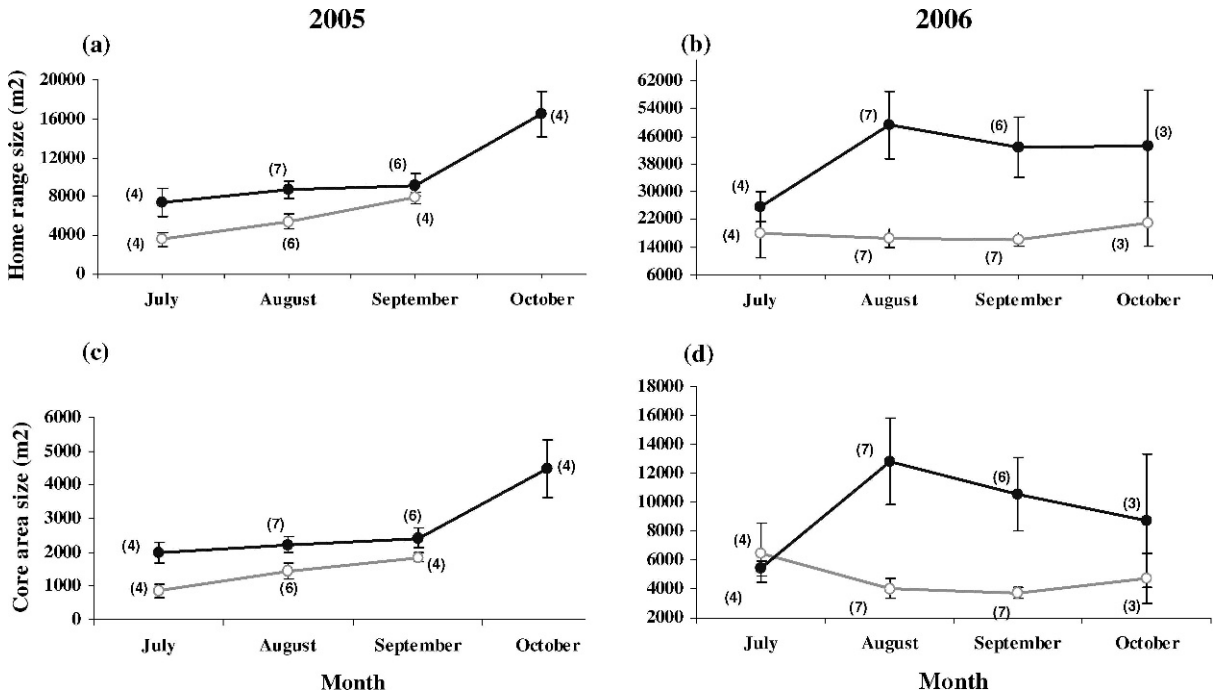



**Fig. 2.**—Mean (± *SE*) home-range and core-area sizes for *Apodemus flavicollis* near Valle dei Laghi, Italy, in a, c) 2005 and b, d) 2006. Home-range sizes were calculated using the 95% kernel method; core-area sizes were determined from 50% kernel analyses. Sample sizes are given in parentheses. Closed circles = males; open circles = females.

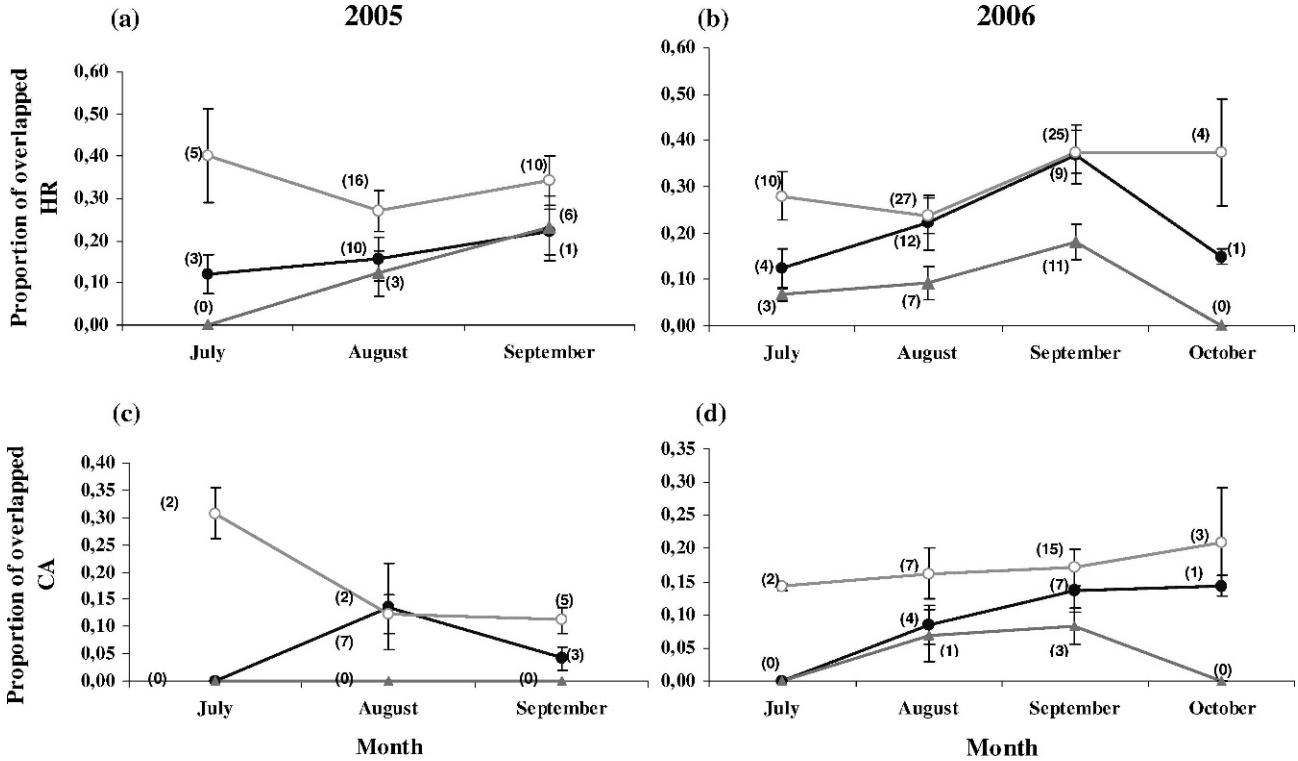



**Fig. 3.**—The mean (± *SE*) proportion of home ranges and core areas of *Apodemus flavicollis* that overlapped with at least 1 conspecific during summer and autumn in a, c) 2005 and b, d) 2006. Sample sizes are given in parentheses. Open circles = male–female pairs; closed circles = male–male pairs; closed triangles = female–female pairs.

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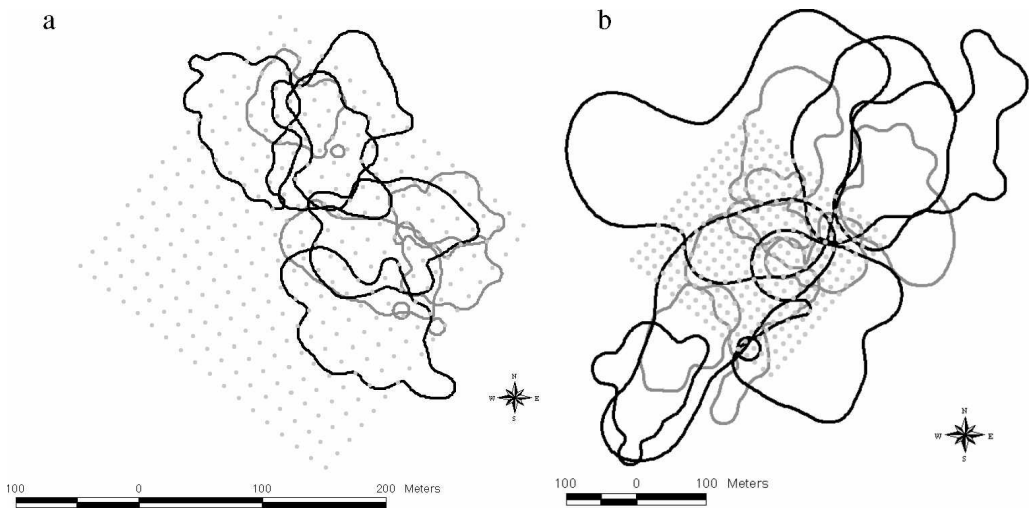



**FIG. 4.**—The spatial distribution of home ranges of *Apodemus flavicollis* near Valle dei Laghi, Italy. Data for a) 2005 are for 5 males (black lines) and 4 females (gray lines); data for b) 2006 are for 5 males and 5 females. Contours shown were generated using 95% kernel analyses. In both panels, gray dots depict the trapping grid on the study site. The spatial scale for each panel is indicated.

unstable food (i.e., seeds undergoing mast cycles—Pucek et al. 1993), changes in which may produce marked fluctuations in population size (Jensen 1982; Mazurkiewicz and Rajska-Jurgiel 1998; Ostfeld et al. 1996). Consistent with our expectations, home ranges of males were larger than those of females. Also consistent with our expectations, we observed relatively exclusive space use by females, with greater home-range overlap between the sexes and among males. Space use by both sexes may have been influenced by changes in food availability and population density. When resource availability decreased, the population size dropped, whereas ranging movements (including dispersal) and home-range overlap increased (i.e., between spring and autumn 2005 and between 2005 and 2006). These findings suggest that patterns of space use in *A. flavicollis* are responsive to annual changes in environmental and demographic conditions.

*Intersexual differences in space use*.—Our results provide several indications that space use differed between males and females in the study population. Males consistently occupied larger home-range and core areas than females, moved large daily distances with a higher probability, and displayed a greater degree of overlap with individuals of both sexes. Spatial overlap among females was rare, especially for core areas. These findings are consistent with data from *A. sylvaticus* (Montgomery et al. 1997; Tew and Macdonald 1994), in which females also exhibit more exclusive space use than males. Females of small-bodied species of mammals that rely on clumped and annually variable food resources may benefit from defending those resources, whereas males may not (Ostfeld 1990; Tew and Macdonald 1994; Wolff and Cicirello 1990). A potential outcome of such conditions is a promiscuous mating system, in which home ranges of males overlap with those of multiple females and vice versa (Ostfeld 1985; Ribble and Millar 1996). Our data are consistent with this pattern, thereby providing potential insights into the mating system of *A. flavicollis*. Genetic studies of parentage and reproductive success in this population would yield more definitive evidence regarding the mating system of these animals.

*Response to changes in resources and density*.—Our results suggest that variation in resource availability can have a profound and rapid effect on space use by *A. flavicollis*, with both sexes responding to these changes, but in somewhat different ways. For example, within and between years, both males and females displayed larger home ranges and greater daily travel distances when food availability was lower (i.e., autumn 2005 with respect to spring 2005 and 2006 with respect to 2005), perhaps as a result of the need to search for limited food resources. Consistently, examination of our field data suggests that dispersal also was affected by resource availability, with permanent movement away from the study grid being more frequent when seed production was low (e.g., autumn 2005 versus autumn 2006). Home ranges overlapped more when food availability was lower, even though overall population density was reduced (again, autumn 2005 as compared to spring 2005 and 2006 as compared to 2005). More specifically, females reduced the exclusivity of their home ranges (but not their core areas), whereas males increased the number of home ranges of females with which they overlapped. These observations are consistent with the hypothesis that space use by females is driven largely by food availability (Ostfeld 1990), whereas the distribution of males is related primarily to mating opportunities (Madison 1980).

Similar to our findings, Wilson et al. (1993) reported an inverse relationship between population density and home-range sizes in *A. sylvaticus*. Vessey (1987) observed that although male *Peromyscus leucopus* had flexible home ranges that became compressed at high population density, females maintained a small area of spatial exclusivity regardless of population density. In our study, when population density decreased from high to relatively low values (i.e., within 2005), home-range size increased. We suggest that this temporal variation was related primarily to resource availabil-

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ity as has been described for other rodent species (e.g., Ims 1987; Juškaitis 2002; Mazurkiewicz and Rajska-Jurgiel 1998; Taitt 1981; Wolff 1985, 1996) and that this variation affected the breeding status of females. In support of this hypothesis, juveniles showed a peak in abundance during spring 2005, after the mast year (2004), decreased to 0 during 2005, and then reappeared in autumn 2006, when seed production was again detected.

*Implications for the social and population biology of Apodemus*.—In our study population, patterns of space use appeared to vary in response to seasonal and annual variations in food resources and population density. This apparent plasticity in the response of *A. flavicollis* to ecological conditions has potentially important implications for other aspects of biology, such as the mating system of the study population. Future studies should investigate the mechanisms by which resources and density affect other aspects of behavior and demography, such as the inhibition of breeding (Montgomery et al. 1997). Manipulation of food availability would allow experimental evaluation of the effects of food resources on spatial structure and demographic trends (e.g., Akbar and Gorman 1993; Ims 1987; Watts 1970). Investigation of the genetic structure of the population would assess whether the observed pattern of intersexual space use corresponds to a promiscuous mating system (e.g., Ribble and Millar 1996). It also would be useful to determine whether the relationships observed in the present study can be generalized to other populations of *A. flavicollis* inhabiting environments where the spatiotemporal availability of resources differs substantially from that observed in the Alpine forest ecosystem described here.

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## APPENDIX I

Statistical analysis of variables describing the spatial behavior of *Apodemus flavicollis*. Data are from radiotelemetry studies of a population of this species located near Valle dei Laghi, Italy. Multivariate models were used to examine the effects of month, sex, and body weight on home-range size, core-area size, daily distance moved, Bhattacharyya's affinity (BA) statistic of home-range overlap, and the probability that an animal would occur within a

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neighboring animal's 50% and 95% home-range contours. Data are from a) 2005, b) 2006, and c) both years combined. Model selection was based on the Akaike information criterion (AIC) corrected for small sample sizes ($AIC_c$), beginning from an a priori full model involving the variables listed above. $\Delta AIC_c$ = difference in $AIC_c$ between the best and the actual model; $\omega_i$ = Akaike weight; evidence ratios = ratio of the Akaike weights of the best and the actual model. Only the highest ranked models for each analysis are shown.

| Full model | Model structure | *K* | $AIC_c$ | $\Delta AIC_c$ | $\omega_i$ | Evidence ratios |
|---|---|---|---|---|---|---|
| a) 2005 | | | | | | |
| HR[a] ~ W[b] + M[c] + S[d] + (1/I)[e] | M + S + (1/I) | 7 | −4.83 | 0.00 | $4.38 \times 10^{-1}$ | 1.00 |
| | S + (1/I) | 4 | −4.60 | 0.22 | $3.92 \times 10^{-1}$ | 1.12 |
| | M + (1/I) | 6 | −2.60 | 2.22 | $1.44 \times 10^{-1}$ | 3.04 |
| | 1 + (1/I) | 3 | 1.29 | 6.12 | $2.05 \times 10^{-2}$ | 21.34 |
| CA[f] ~ W + M + S + (1/I) | S + (1/I) | 4 | −0.99 | 0.00 | $6.37 \times 10^{-1}$ | 1.00 |
| | M + S + (1/I) | 7 | 0.59 | 1.58 | $2.90 \times 10^{-1}$ | 2.20 |
| | M + (1/I) | 6 | 3.89 | 4.88 | $5.56 \times 10^{-2}$ | 11.46 |
| DM[g] ~ S + M + (1/I) | S + M + (1/I) | 6 | 473.88 | 0.00 | $9.26 \times 10^{-1}$ | 1.00 |
| | S + (1/I) | 3 | 479.35 | 5.47 | $6.00 \times 10^{-2}$ | 15.41 |
| | M + (1/I) | 5 | 482.23 | 8.35 | $1.43 \times 10^{-2}$ | 64.97 |
| BA[h] ~ M + S + M × S | S | 4 | −1,165.73 | 0.00 | $5.77 \times 10^{-1}$ | 1.00 |
| | 1 | 2 | −1,164.82 | 0.91 | $3.65 \times 10^{-1}$ | 1.58 |
| | M + S | 7 | −1,160.24 | 5.50 | $3.69 \times 10^{-2}$ | 15.61 |
| PHR50[i] ~ S | S | 3 | 28.99 | 0.00 | $7.80 \times 10^{-1}$ | 1.00 |
| | 1 | 2 | 31.52 | 2.53 | $2.20 \times 10^{-1}$ | 3.55 |
| PHR95[j] ~ S | 1 | 2 | 43.99 | 0.00 | $5.00 \times 10^{-1}$ | 1.00 |
| | S | 3 | 44.03 | 0.03 | $5.00 \times 10^{-1}$ | 1.02 |
| b) 2006 | | | | | | |
| HR ~ W + M + S + (1/I) | S + (1/I) | 4 | 7.06 | 0.00 | $9.10 \times 10^{-1}$ | 1.00 |
| | 1 + (1/I) | 3 | 11.83 | 4.77 | $8.40 \times 10^{-2}$ | 10.84 |
| | W + S + (1/I) | 5 | 17.57 | 10.52 | $4.74 \times 10^{-3}$ | 192.02 |
| CA ~ W + M + S + (1/I) | S + (1/I) | 4 | 29.12 | 0.00 | $6.22 \times 10^{-1}$ | 1.00 |
| | 1 + (1/I) | 3 | 30.16 | 1.04 | $3.70 \times 10^{-1}$ | 1.68 |
| | W + S + (1/I) | 5 | 39.33 | 10.21 | $3.77 \times 10^{-3}$ | 165.11 |
| DM ~ S + (1/I) | S + (1/I) | 3 | 678.04 | 0.00 | $9.13 \times 10^{-1}$ | 1.00 |
| | S + M + (1/I) | 6 | 682.73 | 4.70 | $8.72 \times 10^{-2}$ | 10.47 |
| | M + (1/I) | 5 | 700.80 | 22.76 | $1.04 \times 10^{-5}$ | $8.75 \times 10^{4}$ |
| BA ~ M + S + M × S | 1 | 2 | −2,534.54 | 0.00 | $7.52 \times 10^{-1}$ | 1.00 |
| | S | 4 | −2,530.81 | 3.74 | $1.16 \times 10^{-1}$ | 6.47 |
| | M | 5 | −2,530.71 | 3.83 | $1.11 \times 10^{-1}$ | 6.80 |
| PHR50 ~ S | S | 3 | 51.00 | 0.00 | $6.20 \times 10^{-1}$ | 1.00 |
| | 1 | 2 | 51.98 | 0.98 | $3.80 \times 10^{-1}$ | 1.63 |
| PHR95 ~ S | 1 | 2 | 46.97 | 0.00 | $8.05 \times 10^{-1}$ | 1.00 |
| | S | 3 | 49.81 | 2.84 | $1.95 \times 10^{-1}$ | 4.14 |
| c) 2005 and 2006 | | | | | | |
| HR ~ S + M + Y[k] + S × Y+M × Y + (1/I) | S + Y + (1/I) | 5 | −5.62 | 0.00 | $9.14 \times 10^{-1}$ | 1.00 |
| | S + Y + S × Y + (1/I) | 6 | −0.86 | 4.76 | $8.50 \times 10^{-2}$ | 10.80 |
| CA ~ S + M + Y + S × Y + M × Y + (1/I) | S + Y + (1/I) | 5 | 24.11 | 0.00 | $9.15 \times 10^{-1}$ | 1.00 |
| | S + Y + S × Y + (1/I) | 6 | 28.95 | 4.84 | $8.10 \times 10^{-2}$ | 11.25 |
| BA ~ S + Y + S × Y | S | 4 | −3,690.9 | 0.00 | $4.80 \times 10^{-1}$ | 1.00 |
| | Y | 3 | −3,689.9 | 0.96 | $3.00 \times 10^{-1}$ | 1.61 |
| | S + Y | 5 | −3,688.8 | 2.06 | $1.70 \times 10^{-1}$ | 2.80 |
| | S + Y + S × Y | 7 | −3,686.7 | 4.20 | $6.00 \times 10^{-2}$ | 8.17 |

[a] HR: home-range size calculated by kernel 95%.
[b] W: body weight.
[c] M: month; (2) = August; (3) = September; (4) = October; reference level is July.
[d] S: sex; (M) = male; (MF) = male–female; (MM) = male–male. Reference levels are (F) = female or (FF) = female–female.
[e] 1/I: individual as random effect.
[f] CA: core-area size calculated by kernel 50%.
[g] DM: daily distance moved.
[h] BA: Bhattacharyya's affinity overlap index.
[i] PHR50: presence–absence of overlap at 50% probability contour of animal pairs, where S is sex (male–male, female–female, and male–female).
[j] PHR95: presence–absence of overlap at 95% probability contour of animal pairs, where S is sex (male–male, female–female, and male–female).
[k] Y: year; reference level is 2005.

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