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Where to sleep in a rural landscape? A comparative study of resting sites pattern in two syntopic *Martes* species

Jeremy Larroque, Sandrine Ruetten, Jean-Michel Vandell and Sébastien Devillard

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The niche-complementarity hypothesis predicts that two sympatric species must differ in their requirements for one of the three main ecological dimensions (i.e. habitat use, diet, and activity time) to coexist. European pine marten *Martes martes* and stone marten *M. foina* are syntopic medium-sized mustelids with very similar morphology and ecology for which resting sites are a key resource. To better understand how these species coexist, we investigated whether key features of their resting site pattern (number of resting sites, area over which they are distributed, main habitat type used for resting) differed. We used diurnal telemetry to identify resident individuals (e.g. spatially stable individuals over time) and to locate them during resting periods in a fragmented forested area in France. Stone marten used fewer resting sites distributed over a smaller surface area than pine marten. Most stone marten resting sites were located in open habitat (83%) in the proximity of human habitations, whereas pine martens rested almost exclusively in forest (98%). Sex, age, and season explained some variability in both the number of resting sites and the probability of resting within forested habitat for stone marten but not pine marten. The area covered by resting sites was larger in males than in females, but age modulated this difference in an opposite way for the two species. Such a pattern was expected given the intra-sexual territoriality and the reproductive phenology of these species. Overall, stone marten showed higher inter-individual variability in resting site pattern than pine marten. The particular pattern observed in subadult male stone martens during summer (increase in resting site surface area and in the probability to rest in forest) may reflect an attempt to settle in forests, and we discuss these implications in the context of interspecific competition.

Interspecific competitive relationships are a significant driver of species coexistence and community structure (Schoener 1982) which can be well described by the relative utilization of habitat, food resources, and activity time of the component species (Schoener 1974). Within a community, coexistence depends on how species uses resources to secure a sufficient part of their ‘fundamental niche’ (Hutchinson 1957) allowing survival and reproduction. According to the niche-complementarity hypothesis (Schoener 1974), two syntopic species (i.e. two related species which occupy the same macrohabitat) may coexist if they differ in their requirements for one of the three main ecological dimensions (i.e. habitat use, diet, and activity time). Mechanisms that allow for syntopy in terrestrial mammals are complex and varied. Difference in size and physiological needs can allow carnivore species to coexist (Rosenzweig 1966), and, for example, small to medium-sized mustelids have played a large role in the literature on morphological divergence and the analysis of inter- and intraspecific competition/coexistence (Powell and Zielinski 1983, Dayan et al. 1989, Dayan and Simberloff 1994, McDonald 2002, Meiri and Dayan 2003, Loy et al. 2004). When no obvious between-species differences in size, morphology, or physiology are reported,

various behavioural strategies might facilitate coexistence (i.e. predator avoidance, habitat-use partitioning, and prey-partitioning; Kitchen et al. 1999). Among mesocarnivores, differential habitat selection is a widely observed phenomenon facilitating coexistence (Schoener 1974, Jaksic et al. 1981) in canids (jackals *Canis mesomelas* and *C. adustus*, in Zimbabwe, Loveridge and Macdonald 2003; wolf *C. lupus*, and coyote *C. latrans* in US, Arjo and Pletscher 2004) and in mustelids (long-tailed weasel *Mustela frenata* and stoat *Mustela erminea* in Canada, St-Pierre et al. 2006; American marten *Martes americana* and fisher *Martes pennanti* in a mountain landscape in Canada, Fisher et al. 2013; Eurasian otter *Lutra lutra* and American mink *Mustela vison* in the UK, Bonesi and Macdonald 2004). In this last taxonomic group, the genera *Martes* and *Mustela* are those for which interspecific competitive relationships are more likely to drive coexistence (Powell and Zielinski 1983).

The European pine marten *Martes martes* (PM) and the stone marten *M. foina* (SM) are the most similar sympatric carnivores in Europe taking into account phylogenetic relationships (Koepfli et al. 2008), morphology, foraging behaviour (Sidorovich et al. 2005, Lanszki et al. 2007, Posluszny et al. 2007, Zalewski 2007, Remonti et al.

2012; but see Marchesi 1989, Posluszny et al. 2007 for contrasting results), and activity pattern (Kalpers 1984, Marchesi 1989, Lopez-Martin et al. 1992, Clevenger 1993, Herr et al. 2010). Both species weigh 1–2 kg and have a body length of 40–55 cm (Bright 1999, Broekhuizen 1999). They reach sexual maturity between 1 and 1½ yr of age. Both species occur at low density and present the typical mustelid pattern of socio-spatial organization, whereby same-sex individuals defend territories against one another while male territories overlap those of several females (Powell 1979). Their distribution overlaps across a large part of continental Europe, with PM being more northerly distributed (Mitchell-Jones et al. 1999). SM is found in a wide variety of habitats over its distribution area. For example, SM uses exclusively oak forest, resting in tree cavities in its northeastern area (Russia; Novikov 1962) while in Spain, Italy, and Portugal, the species uses forests (e.g. dense cork oak woodland), orchards, pasturelands, and rocky areas (Delibes 1978, 1983, Sacchi and Meriggi 1995, Rondinini and Boitani 2002) resting in dense vegetation, trees, underground burrows or brushwood piles (Genovesi and Boitani 1997, Santos and Santos-Reis 2010). Throughout its range, SM is considered to be a habitat generalist due to its ability to exploit human-dominated areas, from rural areas where buildings, especially barns, are frequently exploited (Lachat Feller 1993, Michelat et al. 2001), to big cities (Herr et al. 2009, Toth et al. 2009, Duduś et al. 2014), where it can rest in attics and roof spaces of inhabited buildings (Herr et al. 2010, Duduś et al. 2014), and in green areas (Toth et al. 2009). In contrast, PM is usually described as a forest specialist (coniferous, deciduous, or mixed forests; Brainerd 1990, Storch et al. 1990, Clevenger 1993, Brainerd and Rolstad 2002, Zalewski and Jedrzejewski 2006) using arboreal structures such as cavities or squirrel nests for resting (Storch 1988, Marchesi 1989, Brainerd et al. 1995, Zalewski 1997a, b). However, PM has now been well documented in landscapes where forests are not the dominant habitat type (Stier 2000, Pereboom et al. 2008, Balestrieri et al. 2010, Mergéy et al. 2011, Caryl et al. 2012) and when PM face landscapes with low forested cover or limited rock cavities, buildings or other man-made structures could also be used for resting to compensate for the scarcity of arboreal cavities (Birks et al. 2005). Both species co-exist over a large area, and, when syntopic both species seem to exhibit different habitat use and selection, with SM more frequently associated with rural and suburban areas while PM occupies forested areas (Freckop 1959, Waechter 1975, Delibes 1983, Herrmann 1994, Remonti et al. 2012).

Interspecific competitive relationships have been proposed to explain this pattern and some authors have argued that PM has forced SM to restrict itself to rocky places or human dwellings, and their immediate surroundings (Delibes 1983, Powell and Zielinski 1983, Herrmann 1994, Remonti et al. 2012). Remonti et al. (2012) even suggested that Italian SM could have been displaced from some agricultural areas as a consequence of the recent expansion of PM in Italy. Hence, differential habitat use appears to be the main driver underlying PM and SM coexistence.

To our knowledge, no fine-scale studies of habitat use (i.e. at the individual level) have been conducted on both species in the same place, but such efforts are needed to

better understand mechanisms underlying coexistence of PM and SM. We focus here on a particular resource which is of prime importance to both species, the resting site. Indeed, mustelids may compete strongly for resting sites, as described in two species of badger in China (Zhang et al. 2009) and suggested for *Martes* spp. (Brainerd et al. 1995, Ruggiero et al. 1998). Resting sites are a key resource for mustelids (Gough and Rushton 2000) to such an extent that the lack of resting sites has been suggested by numerous authors as a constraint on the distribution and abundance of *Martes* spp. (Thompson 1991, Brainerd et al. 1995, Halliwell and Macdonald 1996, Ruggiero et al. 1998). Three features are hypothesized to determine resting site selection by mustelids: thermal insulation, predator avoidance, and proximity to preferred feeding patches (Weber 1989, Lachat Feller 1993, Brainerd et al. 1995, Lindstrom et al. 1995, Yamaguchi et al. 2003, Zabala et al. 2007, Herr et al. 2010). Mustelid species require thermal insulation because they carry limited fat reserves (Buskirk and Harlow 1989), their long and thin body shape implies high energetic costs for thermoregulation (Brown and Lasiewski 1972, Harlow 1994), and their fur is not highly insulative (Scholander et al. 1950). Thermoregulatory constraints on resting site selection have been shown in both species in both wild and captive settings (Storch 1988, Lachat Feller 1993, Brainerd et al. 1995, Zalewski 1997a, Herr et al. 2010). In addition, PM and SM are likely to suffer from intraguild predation (on both adults and young) to the point that, although without clear evidence, predation by the red fox *Vulpes vulpes* may negatively influence marten population density (Storch et al. 1990, Brainerd et al. 1995, Lindstrom et al. 1995, Webster 2001). Thus, choosing safe resting sites has been proposed as an antipredator behaviour (Brainerd et al. 1995, Zalewski 1997a, Herr et al. 2010). Finally, resting sites could be selected based on their proximity to preferred food patches (Weber 1989, Yamaguchi et al. 2003, Zabala et al. 2007) to minimize travelling between resting and foraging areas (Kruuk 1978, Davison et al. 2008).

We investigate the spatial pattern of resting sites in both species using diurnal telemetry locations of 24 PM and 21 SM resident individuals in a fragmented rural area in France. In this area, resting site availability might be limited as both forest cover and human building cover (including isolated farms) are low (about 21 and 1%, respectively, Mergéy et al. 2012, Supplementary material Appendix 1, Table A1). Since PM is more of a forest specialist than SM, the former is likely to rest within the forest. Therefore, our particular objective is to investigate how SM gain access to the forest, and if they do not, how they use the open habitat for resting. To this end we assess whether 1) PM use more resting sites than SM as expected from studies on each of these species individually (Brainerd et al. 1995, Zalewski 1997a, Herr et al. 2010); 2) the PM resting sites are more widely distributed than those of SM as a result of a greater PM home range size (Krüger 1990, Herr et al. 2009, Mergéy et al. 2011); and 3) these species differ in the habitat elements selected for in resting sites. Investigating the number and distribution of resting sites might help us interpret the between-species difference of the resting pattern in terms of spatial distribution of food resources since spatial distribution of resting sites might be interpreted as a proxy of home range.

Methods

Study area and animal capture

The study was conducted in Bresse, a rural region (44 inhabitants km⁻²) in eastern France (5°13'E, 46°27'N). This area covers 911 km² (Fig. 1) and is highly fragmented with 21% forest coverage; forested areas and copses are linked by a heterogeneous hedgerow network (Mergey et al. 2012, Supplementary material Appendix 1, Table A1). The Bresse region is an open-air chicken farming area, where PM and SM are legally trapped and killed due to their predation on poultry (Stahl et al. 2002). Forty-four PM and 38 SM were live-captured in baited-box traps between December 2003 and 2007. Animals were anaesthetized by intramuscular injection of Domitor® (10 mg kg⁻¹) and revived with Antisédan® to ensure a quick reversal of sedation. During examination, we took several biometric measurements (body mass, body length, tail length, neck circumference, posterior foot length, and baculum length for males) and sexed visually each individual. We marked each individual with a transponder (Allflex®, Vitré, France) and radio-collared them before their release at their site of capture. Collars weighed 32 g and represented < 5% of the body mass for each individual (PM: 1328 ± 230 g [970–1750]; SM: 1289 ± 244 g [850–1850]). Collars were TXH-2 from Televilt® (Stockholm, Sweden) or TW-5 with a biothane collar from Biotrack® (Wareham, Dorset, UK) and had a mortality sensor that sends a specific signal after 2 h without any movement.

Age determination was made using data recorded from animals recovered dead from road-kills and trapping/hunting in the study area during the study period. From each marten recovered dead (n = 92 PM, 33 females and 59 males; n = 267 SM, 127 females and 140 males), we recorded the same biometric variables as on live animals and we extracted a premolar tooth (PM4) for ageing. The age in years was determined from the number of annual growth lines visible in the tooth cementum using a standardized cementum aging model for each species (Matson laboratories, Milltown, MT, USA). This data set on known-age individuals allowed us to derive sex- and species-specific discriminant functions based on biometric variables to assign a posteriori live-trapped animals to three age-classes (Ruelle et al. unpubl., Supplementary material Appendix 1). We defined three age classes based on the biology of the species (Canivenc et al. 1981); animals between [3–6] months old were classified as juveniles, those between [7–18] months old were classified as subadults, and > 18 months old ones were classified as adults.

Radiotelemetry

Radiotracking was carried out between December 2003 and March 2009. Animals were located at least twice a week when they were resting during the day (i.e. when they were inactive more than 30 min). Animals were all located by triangulation using a receiver with an attached antenna

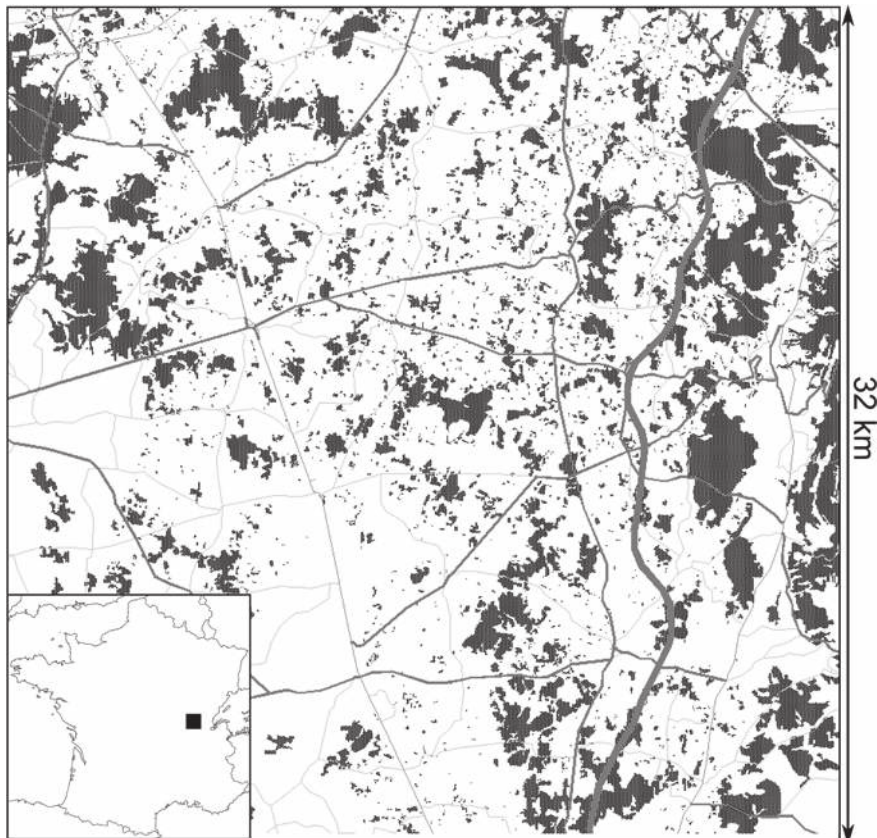


Figure 1. Study area located in Bresse region with forest in dark grey and main roads in light-gray.

(Yaesu®, Cypress, USA) on an equipped vehicle. Whenever possible, and depending on their experience of homing telemetry, fieldworkers came close to animals using a foldable antenna and located precisely the resting site (e.g. in a tree or wood heap) for 92/4528 locations (2%). Field workers were able to locate the resting site within a 10 m or a 50 m diameter circle in 1767 and 1816 out of 4528 locations (39 and 40%, respectively). Triangulation was only used for 853/4528 locations (19%) with an expected precision of about 100 m (i.e. the resting site was within a 100 m diameter circle). We excluded individuals with < 30 d of monitoring (10 PM, 7 SM), and 1 SM that clearly left its home range immediately after release so that analyses were performed on 34 PM and 30 SM. The mean duration of monitoring was 239 ± 191 d for PM (30–719 d, $n = 34$) and 194 ± 155 d for SM (46–882 d, $n = 30$). Individuals were homogeneously monitored over seasons and years (Supplementary material Appendix 1, Fig. A1 and A2).

Identifying resident individuals

For reliable comparisons of the multivariate resting site pattern between and within species, we first sought to identify resident individuals (i.e. individuals showing stable patterns of space use across their life or at least across the monitoring period). Indeed, resident and dispersing individuals of many species exhibit different patterns of habitat use (Selonen and Hanski 2006, Elliot et al. 2014). To identify resident individuals, we used the terminology of movement patterns of McShea and Madison (1992) and adapted it to our species, following previous works of Bray et al. (2007) and Avril et al. (2011) on European hare *Lepus europaeus*.

In a first step, we focused on adult individuals since most spatially stable individuals are found in this age class (Blankenship et al. 2006, Melero et al. 2008, Ruiz-Olmo et al. 2011). We selected adults having a stable spatial pattern of locations over a season (i.e. that did not make obvious excursions and were located several times in the different parts of their overall occupied area during a given period). Seasons were defined following Marchesi (1989) as winter (December to February), spring (March–May), summer (June–August), and autumn (September–November). Based on both climatic conditions and species' life cycles (e.g. mating, gestation), these seasons are long enough to ensure a sufficient number of locations to assess their spatial pattern while matching the main biological phases. To account for seasonal variation of space use, the locations of each individual were split into individual-seasons, pooling locations recorded within the same season for a given individual. The spatial patterns of locations of these individual-seasons were assumed to represent the area typically used for resting by resident adults.

In a second step, we computed, for each individual-season, the centroid across all locations, and calculated the distances of all locations from this centroid from that individual-season. We combined these to produce the overall distribution of the distances between locations and their centroid for all individuals-seasons. We retained as a typical spatial pattern of locations for a resident individual the circle whose radius r encompasses 95% of the distances. Wildlife ecologists are accustomed to working with 95% of the loca-

tions to avoid inclusion of exploratory movements (White and Garrott 1990). We computed r for males and females separately.

In a third step, we identified resident individuals using all their locations recorded during their monitoring as follows. We used an iterative approach to define the position of the centroid (C_i) of resting sites over the entire monitoring for each individual i . To do this we computed a centroid based on the first three locations for an individual. We then added the next location (the 4th one), and if this was within a distance r of the previous centroid, a new centroid was computed using all four locations; we used this to evaluate the next location (the 5th one), and so on. This was iterated until the new location $t + 1$ th evaluated in the process was greater than r from the most recently computed centroid. If this never happened, we took the centroid of all the locations as the centroid of the spatial pattern as a whole, in which case we inferred that the individual was stable throughout the monitoring period. The centroid obtained at the end of the process was defined as the centroid C_i of the spatial pattern of resting sites for individual i . We then calculated the distance between each location and C_i , and any location greater than r was considered either as an exploratory movement or a permanent movement depending on its duration (see below).

We also computed an index of inertia for each location X_t of each individual i , $I(X_t)_{i,r}$. This index allowed us to detect movements from time $t - 1$ to time t that led to a significant change in the spatial distribution of successive locations:

$$I(X_t)_{i,r} = \frac{1}{t} \sum_{j=4}^t d(X_{i,j}, C_{i,t-1})^2$$

where t is the time index of a given location in the monitoring of the i th individuals, $X_{i,j}$ the j th location of individual i , $C_{i,t-1}$ is the centroid computed on the $t-1$ th first locations of the individual i , and $d(X_{i,j}, C_{i,t-1})$ is the distance between the j th location and $C_{i,t-1}$. The stability or instability of $I(X_t)_{i,r}$ over time indicated whether the spatial pattern of locations was temporally stable.

To decide whether an individual was resident, we applied the following two rules: 1) individuals with all their locations within the circle of r radius centered on C_i or individuals for which some locations were beyond r but whose last location was within the circle of r radius; or 2) individuals whose last location was outside the circle of r radius but with a departure from the circle of r radius dating back less than 30 d and not being the movement with the highest magnitude over the monitoring (i.e. the maximum value of the $I(X_t)_{i,r}$ index was reached before this last movement). We chose an arbitrary time span of 30 d because temporary excursions lasted less than 13 d for both species, and hence, individuals leaving the circle of r radius for more than 30 d were considered as having made permanent movement. All individuals that did not fall in these two categories were excluded from the subsequent analyses.

Describing the resting site pattern

We first quantified the number of resting sites per individual-season ($NRS_{i,s}$). Because individuals were located with a

precision of 100 m, we grouped all locations of an individual < 100 m apart, considering that they might constitute a single 'pooled' resting site. To do so, we computed the matrix of distances between each location and we derived a binary neighbouring matrix (0, for two locations < 100 m apart or else, 1). We then used a hierarchical cluster analysis on *R* software (R Development Core Team) with the function `hclust` of the `stats` package to cluster locations less than 100 m apart. Therefore, we took the number of clusters as the $NRS_{i,s}$ used by each individual over its monitoring. We then calculated the $NRS_{i,s}$ for each individual-season (i,s). Although this approach probably underestimated the real number of resting sites, it does so in a similar way for both species.

Secondly, we looked at the pattern of variability of the area covered by all the resting site locations for each individual-season, the area of resting sites ($ARS_{i,s}$) in hectare. We used the minimum convex polygon (MCP 100%) to draw the convex envelope that encompassed all the resting site locations. We used the function `mcp` of the `adehabitatHR` package (Calenge 2006) of the *R* software. Third, we used ArcView GIS 3.2a (Environmental Systems Research Inst., USA) and the Geoprocessing Wizard extension to assign a landscape element to each resting site location to estimate the probability ($RSH_{f,i}$) for an individual-season to be located in forest during resting (i.e. the proportion of locations within the forested habitat). Locations with a precision < 100 m were buffered with a 100 m radius. The cartography of the study area was based on the IGN Bd Ortho 2005 database (French National Inst. of Geography, <www.ign.fr>, January, 2005). Aerial photographs of the study area were precisely redrawn using the software ArcView 3.2a to add missing copses and hedgerows identified during fieldwork to provide the finest possible resolution (< 10 m). Our objective was to investigate more particularly how SM gained access to the forested habitat in this lowly forested habitat (about 21%) which is expected to be mainly occupied by the more specialized species (PM). We thus defined two landscape elements: forest cover (copses ≤ 0.05 ha, forests > 0.05 ha) vs other habitats (open area, hedgerows, buildings, etc.). Buffered locations were assigned to the habitat the most represented in the buffer.

We described the overall resting pattern by using principal component analysis (PCA) to investigate correlations between the three response variables ($NRS_{i,s}$, $ARS_{i,s}$, $RSH_{f,i}$). $NRS_{i,s}$ was standardized by the number of recorded locations for each individual-season. We projected grouping factors (i.e. species, sex, and age classes) on the factorial map to reveal the main factors structuring the variability of the multivariate resting pattern. PCA was made with the *R* package `ade4` (Dray and Dufour 2007).

Statistical modelling

Based on the PCA results (see Results), we chose to separate both species for statistical modelling to limit over-parameterization in the models. We used generalized linear mixed models (GLMM) with a Poisson distribution to assess how the number of resting sites per individual-season ($NRS_{i,s}$) was influenced by several factors. Fixed effects were sex, age, and the season during which locations used

to calculate $NRS_{i,s}$ were recorded, and all their two-way interactions. Given the polygynous mating system and the intra-sexual territoriality of both species, these two-way interaction terms allowed us to investigate whether the resting site pattern was differentially influenced by age in each sex class (age \times sex), whether the two sexes responded differently to the mating season in terms of resting site patterns (sex \times season), and, whether seasonal effect on resting site pattern depended on age (age \times season). The random effect of individual ID was added in the model since locations from one individual were split into several subsets, namely individual-season. The natural logarithm of the number of locations recorded for each individual-season was used as an offset in all models to account for differences in monitoring length (i.e. number of locations) between individuals. Consequently, all fitted values reported from this model are for an offset value of 24 (i.e. the median value of the number of locations per individual-season over the dataset). We used the `lmer` function of the `lme4` package (Bates and Maechler 2009) of the *R* software. We tested for the lack of fit (overdispersion) with Pearson's goodness-of-fit statistics. We used linear mixed models (LMM) with a Gaussian distribution and the same explanatory factors as for $NRS_{i,s}$ (fixed effects: sex, age, season, all two-way interactions; random effect: individual ID) to identify the main factors acting on the resting site surface area per individual-season $ARS_{i,s}$. $ARS_{i,s}$ was log-transformed to reach residual normality and homoscedasticity. The probability for an individual-season to be located in forest during resting ($RSH_{f,i}$) was modelled as a function of both fixed (sex, age, season, all two-way interactions) and random (individual ID) effects using GLMM with a binomial distribution.

Model selection

For all three response variables ($NRS_{i,s}$, $ARS_{i,s}$, and $RSH_{f,i}$), candidate models were ranked according to their second-order Akaike's information criterion ($AICc$), with higher-ranked models having lower $AICc$ values. Because several models with different combinations of covariates performed comparatively well, we averaged parameter estimates for the retained effects from the top-ranked models (i.e. $\Delta AICc < 2$) using standard methods (i.e. multimodel inference, Burnham and Anderson 2002). The candidate model sets were defined from the more complex model $Y \sim \text{age} + \text{sex} + \text{season} + \text{age} \times \text{sex} + \text{age} \times \text{season} + \text{sex} \times \text{season}$, including all simple effects of the fixed factors and their two-way interactions, by reducing the number of parameters through the computation of all possible models (Supplementary material Appendix 1, Table A3, A4, and A5) down to the null model (intercept only). Due to limited sample size in SM (40 individual-season), the fixed interaction term age \times season was not included in the starting model for this species. The random factor individual ID was included in all models of the candidate set, and one parameter for it was included in $AICc$ ranking. Model selection and model averaging were done respectively with the `dredge` function and the `model.avg` function of the *R* package `MuMIn` (Bartoń 2013).

Results

Identifying resident individuals

Twenty-four adult individuals-seasons (16 for PM and 8 for SM) were identified as stable over the three months of our biological seasons, and we calculated r for each of these by sex and species (PM ♂, 1036 m, $n = 10$; ♀, 609 m, $n = 6$; SM ♂, 552 m, $n = 4$; ♀, 44 m, $n = 4$). Based on these values, the classification method enabled us to identify 24 of 34 PM and 21 of 30 SM as resident individuals representing 114 individual-seasons (74 PM/40 SM) for the subsequent analysis with an average of 24.6 ± 9.6 locations (8–49 locations; median = 24) per individual-season and 2.6 ± 2 seasons per individual (1–8 seasons). Most were adults (55) and subadults (53) with a very low number of juveniles (6). Consequently, we pooled juveniles and subadults in a single age class for subsequent analyses.

Describing the overall resting site pattern by PCA

The first two principal components of the PCA on the three variables ($NRS_{i,s}$, $ARS_{i,s}$, $RSH_{f,i}$) describing the resting pattern retained most of the variability (88.42%, PC1 = 61.47%, PC2 = 26.95%). The first axis was clearly associated with $NRS_{i,s}$ and $RSH_{f,i}$ which were highly correlated (Fig. 2). This axis clearly differentiated PM, with high $NRS_{i,s}$ and $RSH_{f,i}$ (and therefore low values on PC1), from SM, with the opposite pattern. Also apparent was the higher $NRS_{i,s}$ and $RSH_{f,i}$

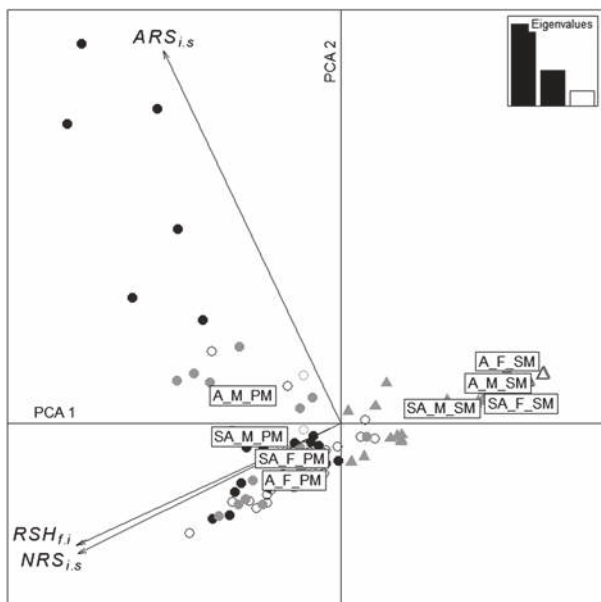


Figure 2. Biplot of the PCA performed on the three variables $NRS_{i,s}$, $ARS_{i,s}$, $RSH_{f,i}$ displaying the grouping factors of sex, age-class, and species. Pine and stone martens are displayed by circles and triangles, respectively. Within each species, males and females are displayed with filled and open symbols, respectively. Sub-adults and adults are displayed in grey and black respectively. The centroid of points belonging to the same age- and sex-classes within a species are displayed within text boxes. 'A_M_PM' denotes adult male pine marten, and 'SA_F_SM' denotes subadult female stone marten, for example.

Table 1. Characteristics of the highest ranked ($\Delta AICc < 2$) models for the number of resting sites ($NRS_{i,s}$), the area of resting sites ($ARS_{i,s}$) and the resting site probabilities ($RSH_{f,i}$) for both PM and SM. Ranking is based on Akaike's information criterion corrected for small sample size ($AICc$), Akaike differences ($\Delta AICc$) and Akaike weights (w). Number of parameters (K) and log-likelihood ($LogLik$) are also shown.

Model	K	$LogLik$	$AICc$	$\Delta AICc$	w
$NRS_{i,s}$					
PM					
Age	4	-36.47	81.51	0.00	0.19
age + sex	5	-35.71	82.31	0.80	0.13
Season	6	-34.63	82.51	1.00	0.12
null model	3	-38.16	82.65	1.14	0.11
season + sex	7	-33.62	82.93	1.42	0.10
Sex	4	-37.18	82.94	1.43	0.10
age + season	7	-33.89	83.47	1.96	0.07
age + season + sex	8	-33.04	84.29	2.78	0.05
SM					
season + sex	7	-23.06	63.62	0.00	0.65
age + season + sex	8	-23.06	66.76	3.14	0.14
$ARS_{i,s}$					
PM					
age + sex + age \times sex	6	-94.09	201.43	0.00	0.39
Sex	4	-96.77	202.13	0.70	0.27
age + sex	5	-96.44	203.77	2.34	0.12
SM					
age + sex + age \times sex	6	-81.71	177.97	0.00	0.60
Sex	4	-85.18	179.49	1.52	0.28
age + sex	5	-85.06	181.89	3.92	0.09
$RSH_{f,i}$					
PM					
age + sex + age \times sex	6	-34.14	81.54	0.00	0.18
Age	4	-36.72	82.01	0.47	0.14
Season	6	-34.40	82.05	0.51	0.14
null model	3	-38.02	82.38	0.84	0.12
season + sex	7	-33.56	82.82	1.29	0.10
age + sex	5	-36.07	83.01	1.48	0.09
Sex	4	-37.40	83.38	1.85	0.07
age + season	7	-34.24	84.18	2.65	0.05
SM					
Season	6	-65.04	144.63	0.00	0.25
season + sex	7	-63.62	144.73	0.10	0.24
age + season	7	-63.68	144.86	0.23	0.22
age + season + sex + age \times sex	9	-60.58	145.15	0.52	0.19
age + season + sex	8	-63.18	147.01	2.38	0.08

estimated for sub-adult male SM relative to other age- and sex-classes of SM. The second axis was associated with the resting site surface area $ARS_{i,s}$ and indicated that male PM (mainly adults, and to a lower extent sub-adults) employed resting sites over a larger area (Fig. 2). Since PM and SM showed clearly differentiated multivariate resting site patterns, we then assessed resting site patterns in greater details for each species separately.

Number of resting sites $NRS_{i,s}$

In PM, seven models, including the null model, were competitive ($\Delta AICc < 2$) in explaining the pattern of variability of $NRS_{i,s}$ (Table 1). Neither the sex, age, nor season influenced the number of sites used for resting

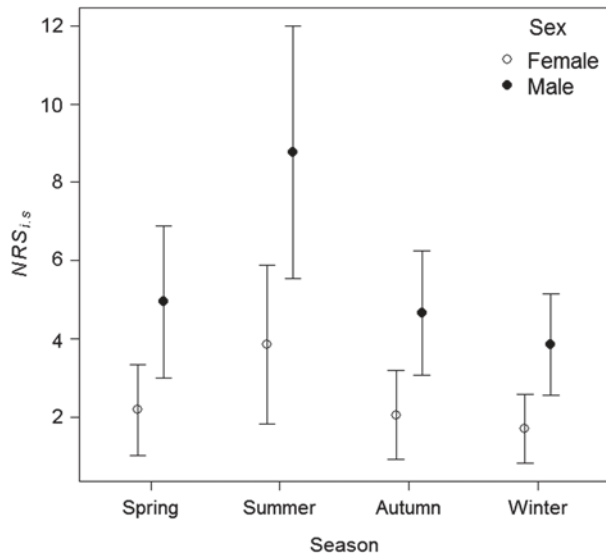


Figure 3. Predicted number of resting sites $NRS_{i,s} \pm 95\%$ confidence interval, fixed effects shown for the median value (24) of the number of locations (model offset) as a function of season and sex in SM.

(e.g. fitted values \pm CI from the model $NRS_{i,s} \sim$ sex: ♂ 13.2 ± 0.86 , ♀ 11.43 ± 0.91 ; and from the null model: 13.03 ± 1.23 , with an offset equal to $n = 24$ locations, Supplementary material Appendix 1, Table A6). In contrast, the single competitive model for SM indicated that sex and season influenced $NRS_{i,s}$ in SM in an additive way (Table 1, Fig. 3, Supplementary material Appendix 1, Table A6). Males used more resting sites than females and the number of resting sites in summer was significantly higher than in other seasons (Fig. 3).

Area of resting sites $ARS_{i,s}$

Two models were competitive in explaining the pattern of variability in $ARS_{i,s}$ in PM (Table 1), and thus averaged (Supplementary material Appendix 1, Table A6). The area of resting sites was strongly associated with sex, with males having larger $ARS_{i,s}$ than females, but the between-sex difference was larger in adults than in subadults (Fig. 4). The same models were retained in SM (Table 1) with male SM having a larger $ARS_{i,s}$ than females, but the retained interaction between sex and age was due to the larger $ARS_{i,s}$ in sub-adult males than in any other age- and sex-classes (Fig. 4, Supplementary material Appendix 1, Table A6).

Resting site habitat RSH_{fi}

The probability of an individual-season being located in forest during resting (RSH_{fi}) was very high for PM, with nearly 98% of locations recorded within forested habitat, regardless of sex, age, or season. Consequently, seven models, including the null model, were competitive in explaining the probability to rest in forest for PM (Table

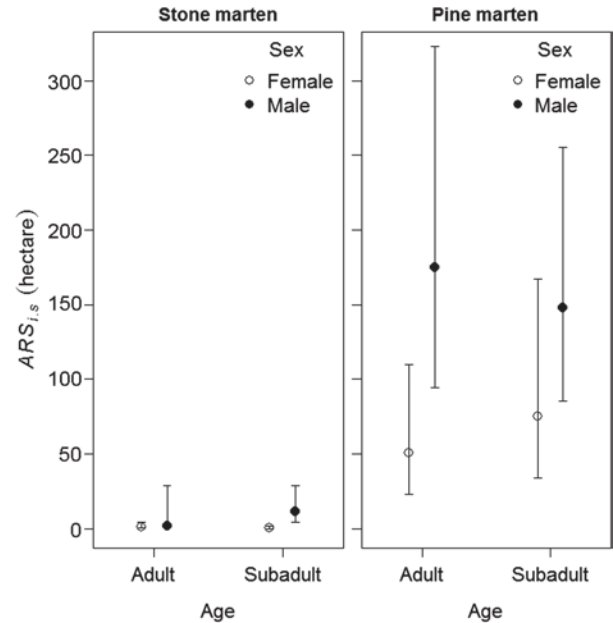


Figure 4. Predicted resting site surface area $ARS_{i,s}$ ($\pm 95\%$ confidence interval, fixed effects only) in SM (left-size) and PM (right-size) as a function of age-class and sex.

1). As with $NRS_{i,s}$, no effect of sex, age, or season explained inter-individual variation in RSH_{fi} (Supplementary material Appendix 1, Table A6). For SM, four models, excluding the null model, ranked within two AIC_c points (Table 1). The averaged model included the single effect of season, and the interaction between age and sex. A clear seasonal pattern was evidenced in the probability to rest in forest RSH_{fi} : it was lower in winter than in other seasons, intermediate in autumn and spring, and significantly higher during summer (Fig. 5A, Supplementary material Appendix 1, Table A6) regardless of age and sex. On average, RSH_{fi} was lower in SM than in PM, with 83% of their resting sites located outside the forest in elements such as human buildings. The significant interaction between the effect of sex and age-class evidenced that sub-adult SM used the forested areas more than adults in both sexes, but that between-age difference was more pronounced in males than in females (Fig 2, Fig. 5B, Supplementary material Appendix 1, Table A6).

Discussion

The resting site pattern, one major component of habitat use for mustelid species (Delibes 1983, Brainerd et al. 1995, Ruggiero et al. 1998, Goszczyński et al. 2007), differed markedly between PM and SM. This result confirms previous observations of habitat segregation when both species live in syntopy (Frechkop 1959, Waechter 1975, Delibes 1983, Herrmann 1994, Remonti et al. 2012). Clearly, resting sites for both species were not located in the same habitat type: SM used mainly non-forested areas to establish resting sites whereas PM used almost exclusively the forest (98%). It has recently been suggested that PM could be less forest specialized than previously thought (Pereboom et al. 2008, Balestrieri et al.

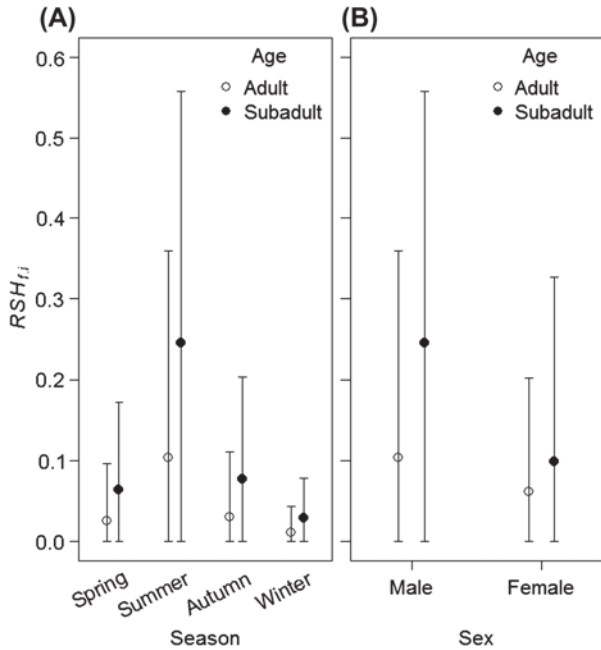


Figure 5. Predicted resting site probability RSH_{fi} (\pm 95% confidence interval, fixed effects only) in SM: (A) effect of season and age-class on RSH_{fi} ; (B) effect of sex and age-class on RSH_{fi} during summer.

2010, Caryl et al. 2012) because of an increasing number of PM observations in non-forested areas, likely due to habitat fragmentation (Mergely et al. 2011). Our results showed that PM used almost exclusively forest patches to establish resting sites even in the highly fragmented habitat of the Bresse region (Mergely et al. 2012).

In contrast, SM resting sites were clearly located in non-forested areas (83%), especially in human buildings as shown elsewhere (Herr et al. 2010). However, since 17% of SM locations were recorded within forested habitat, SM appeared to be less specialised to non-forested habitat than PM was to forested habitat. Two main hypotheses are often used to explain the synanthropic character of SM: this could be either a consequence of thermal preference (Waechter 1975, Lachat Feller 1993, Genovesi and Boitani 1997, Herr et al. 2010) or a consequence of interspecific competition with PM (Delibes 1983, Goszczynski et al. 2007, Remonti et al. 2012). Alternatively, it has also been suggested that this could be a legacy of the late- and post-glacial evolutionary history of the two species in Europe (Sommer and Benecke 2004, Goszczynski et al. 2007), although this scenario could be ruled out based on recent phylogeographic work on PM (Ruiz-González et al. 2013).

We sought to understand whether this pattern of habitat use denoted a preference of each species for a specific habitat type or resulted from interspecific competition. As a starting point, we discuss below the consequence of this habitat segregation for resting on the number of resting sites, and on the surface area they covered, in light of the differences in prey availability (Kruuk 1978, Weber 1989, Yamaguchi et al. 2003, Zabala et al. 2007, Davison et al. 2008) and fragmentation between the forested and the non-forested habitat, but also in light of the behavioural ecology of each species.

On the importance of key resources

First, resting sites of PM are spread over a larger surface area (*ARS*) than those of SM. This pattern could be expected from the larger home range sizes usually reported for the former species (Herr et al. 2009, Mergely et al. 2011) and assuming that resting sites are located throughout the home range of an individual (Brainerd et al. 1995, Ruggiero et al. 1998, Gough and Rushton 2000). If *ARS* and home range size are linked, one has to briefly discuss the likely factors leading to between-species differences in home range size. Basically, home range size represents the minimum area in which an individual finds enough resources for its normal activities (e.g. food, mating, shelters, den, and rest sites; Burt 1943). It has been shown that both the species diversity and the abundance of small mammals (the major prey items for both species, Posluszny et al. 2007, Remonti et al. 2012) are higher in non-forested rural areas (Deplazes et al. 2004, Alain et al. 2006). Having resting sites within or close to human buildings might allow SM to have a smaller home range since the proximity of a human environment may offer 'bed and board', thereby minimizing their resting sites' surface area. We also found that SM used fewer resting sites than PM. This pattern was shown even with a likely underestimation of the number of resting sites for both species (see Methods) and agrees with previous studies (Lachat Feller 1993, Genovesi and Boitani 1997, Zalewski 1997b, Herr et al. 2010). Intraspecific competition for resting sites might determine the number of resting sites used. Indeed, competition among conspecifics might be more intense in SM than in PM, either because the number of available farms potentially containing suitable resting sites might be lower (about 1% of the total study site area) or/and because the SM density might be higher in our study area. In such a competitive context, with a high population turnover rate due to trapping, it could be very costly to leave, even temporarily, a local place containing suitable resting sites without risking permanent loss of these resting sites. Thus, SM may adopt a 'resting site guard strategy' using a small number of resting sites that are easier to defend against conspecifics. Alternatively, the lower number of resting sites in SM than in PM might also reflect the smaller area over which SM placed their resting sites (i.e. resting density could be equal in the two species).

Previous points deal with a relatively low resting site surface area and number in SM, explaining the between-species difference, but other explanations can be proposed conversely. Indeed, PM has already been described to have a wandering behaviour in its territory ('martelism'; Pulliainen 1981), moving according to the spatial availability of food resources. This behaviour, together with the expected less aggregated distribution of small mammals in forest than in non-forested habitat, might contribute to the higher resting site surface area observed in PM. Some studies have also suggested that PM adopts a defensive strategy against parasites (Zalewski 1997b) and predation risks by red fox by diversifying resting sites, hence, increasing their number. To our knowledge, no clear support for this hypothesis has been evidenced (Kleef and Tydeman 2009) and we see no reason why a similar argument could not be made for SM. Alternatively, lower intraspecific competition in PM

might in contrario allow a greater number of resting sites. Unfortunately, the difficulty of estimating population density for these species precludes a deeper assessment of these hypotheses at this time.

Age, sex, and seasonal variation

Beyond the overall between-species differences in various components of the resting pattern described above, we also documented differences between sexes and age classes. In both species males distributed resting sites over a greater surface area (*ARS*) to than did females, with the magnitude of this difference greater in SM than PM. In addition, male SM used more resting sites (*NRS*) than females. These results are consistent with the intra-sexual territoriality that is well described in both species (i.e. female territory is mostly determined by resources whereas male territory overlaps those of several females, Balharry 1993, Herr et al. 2010). Habitat fragmentation was higher for the open habitat than for the forested habitat (Supplementary material Appendix 1, Table A1), and this might explain why the pattern is stronger in SM than in PM. Indeed, female SM territories may not be as contiguous as those of female PM, and assuming that the number of females included in each male territory is the same in both species, male SM may have to cover a larger area, relative to the specific *ARS* of females, to overlap female territories. Alternative hypotheses would be that the number of females monopolized by male is higher in SM than in PM, or that the overlap between females' territories is higher in PM than in SM. Only an exhaustive monitoring of all individuals present in a given area would allow us to better investigate such hypotheses.

The *NRS* was higher in summer for SM, and this pattern was also slightly suggested by modelling of *NRS* in PM (Table 1). This pattern of seasonal change in space use can of course be linked to the reproductive cycle (Sandell 1989). In spring, subadults reach one year of age, become sexually mature, and participate in summer reproduction alongwith adults. However the well-known mating season effect on space use referred almost always to an increase of the surface area used by animals, especially in males, during this period. Here, we did not document such an increase in *ARS* during summer, but rather an increase of the number of resting sites used by resident individuals. These findings call for further investigations to confirm this pattern and to better assess the behavioural processes behind it.

What about interspecific competition?

The focal species differed greatly in resting patterns, and hence in habitat use, one of the three main axes of the niche complementarity hypothesis (Schoener 1974), likely allowing the syntopy of both species. Nocturnal monitoring on few individuals over a short period of time (Larroque et al. unpubl.) during the activity time revealed that PM and SM could cover greater and overlapping areas, in both forested and non-forested habitat, confirming that syntopy occurs with likely behavioural interactions (as previously shown in

Krüger 1990). As outlined above, SM seemed to be more generalist than PM as it used both open habitat and forest for resting. This behavioural plasticity was evidenced more strongly for subadult male SM; when these started to increase their activity in spring and summer, a significant proportion of their resting sites occurred in forest (about 30%, Fig. 5A) and forest appeared to remain a sought-after habitat or a refuge to avoid intraspecific competition. As an example, four young male SM behaved like PM (i.e. with the majority of their resting sites located in forest during spring and summer). However, subadult male SM did not establish later as adults in the forested habitat. Did established PM repel subadult SM out of the forested area (see Remonti et al. 2012 for such a repulsion hypothesis)? We never found evidence of agonistic interactions between these species (behavioural observations, carcass autopsies). In addition, SM are heavier, hence likely more competitive, than PM in the study area (nearly 100 g for adult females and 200 g for adult males, Ruelle et al. unpubl.). Instead of direct aggression, the process of exclusion might be a 'nonaggressive form of territorial defence' (Wolff and Johnson 1979, Pulliainen 1981). For example, PM are known to mark their entire territory but do not actively defend their range against conspecifics in a Finnish forest (Pulliainen 1981, 1982). The function of scent marking may be only to warn against the presence of an individual or to signal that an area already is being hunted. Alternatively, showing that PM and SM used the habitat differently for resting does not necessarily mean they have evolved through competition for this key resource, or that they currently compete for it. Indeed, subadult SM might explore all the available habitats and then choose to establish within the better ones (i.e. the open ones). We cannot rule out the possibility that open, more anthropized habitat, is preferred by SM either because of thermal requirements, evolved synanthropism, or higher resource availability. Such a hypothesis would underline the higher ecological and behavioural plasticity of SM when compared to PM and would not necessarily be linked to interspecific competition. For example, Santos and Santos-Reis (2010) showed that SM may share resting sites with other mesocarnivores of the same size (i.e. the common genet *Genetta genetta* and the Egyptian mongoose *Herpestes ichneumon*) and concluded that the pattern of resting sites in SM was driven by the availability of resources rather than any form of intraguild competition. In that sense, SM may have both spatially and temporarily variable proportions of resting sites located in forest or in more anthropized habitat (from agricultural land to large city center), depending on the relative quality of each habitat type, and, independently, on the other present mesocarnivores. However, SM usually occupies agricultural and more anthropized habitats when living sympatrically with PM (Frechkop 1959, Waechter 1975, Delibes 1983, Herrmann 1994, Remonti et al. 2012) while it also occupies the forested habitat to a much greater extent when PM is absent (Novikov 1962). Hence, one can also argue that the depletion of resources due to the presence of PM within the forest leads to the open, more anthropized habitat becoming more favorable to the SM, which in turn could be a form of exploitative interspecific competition (Schoener 1983).

Conclusion

We documented segregation of space use for resting sites. The differential use of resting sites, a critical resource for mustelids (Brainerd et al. 1995, Ruggiero et al. 1998, Gough and Rushton 2000), could theoretically explain syntopy among these species. Whether past/current interspecific competition or higher ecological plasticity of SM is responsible for this segregation of resting sites is difficult to assess with currently available data. A fine-scale study of habitat selection by both species appears necessary. The consequences of the differential use of resting sites on the home range characteristics and the spatial ecology of other species of the mesocarnivore guild (e.g. red fox) should also be investigated to get a better insight into the coexistence processes as well as the potential exclusion of SM due to expanding PM populations.

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