Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape

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Abstract: Woodland fragmentation through land consolidation practices (the merging of small fields by the removal of separating structures like hedgerows) is recognised as a major threat to biodiversity in Europe. While its impact on the occurrence of species has frequently been the object of focus, its impact on the movements of individuals has rarely been studied. We used paths of radio-tracked European pine martens (*Martes martes* (L., 1758)), a forest-dwelling species, with fixes taken at 3 min intervals to determine their habitat use in fragmented landscape. Our results differ from those generally reported in the literature. Monitored individuals were not confined to large forests, and made additional use of small wood plots and hedgerows. Indeed, individuals moved faster in forests than in all other habitat types, which suggests that martens preferentially foraged in small woods, edges, and hedgerows. Roads and buildings were not avoided; fields, however, were avoided, although they did not act as barriers. Martens stayed close to forest cover when venturing into open ground, which suggests that although not restricted to forests, pine martens exhibit a certain dependence on the presence of trees in the vicinity.

Résumé : La fragmentation du milieu forestier par le remembrement des terres agricoles (le fusionnement des petits champs par le retrait des barrières telles que les haies) est considérée comme une menace majeure pour la biodiversité en Europe. L'impact de cette fragmentation sur la présence des espèces a souvent été évalué, mais son effet sur les déplacements des individus a rarement été étudié. Notre étude avait pour but d'examiner l'utilisation des différents types d'habitats en paysage fragmenté par une espèce forestière, la martre d'Europe (*Martes martes* (L., 1758)). Pour ce faire, nous avons relevé les parcours d'individus équipés de colliers émetteurs sur la base de localisations effectuées toutes les 3 minutes. Nos résultats diffèrent de ceux généralement rapportés dans la littérature. Les martres suivies n'étaient pas confinées aux grands massifs forestiers, mais fréquentaient également les bosquets et les haies. Les martres se déplaçaient même plus rapidement dans les grands massifs que dans n'importe quel autre habitat, suggérant qu'elles chassaient préférentiellement dans les bosquets, les lisières et les haies. Les routes et les bâtiments n'étaient pas évités. Seul le milieu ouvert l'était, sans pour autant constituer une barrière. Les martres restaient à proximité du couvert forestier lorsqu'elles s'aventuraient en milieu ouvert. Soulignant ainsi leur attachement à la proximité du couvert forestier.

Introduction

Loss of natural habitats is one of the main reasons for the decline of biodiversity worldwide (Ramade 1995; Caughley and Gunn 1996; Myers 1997; Noss and Csuti 1997; Wilcove et al. 1998; Lodé 2002). However, while woodlands have been increasing over the past 50 years in both Europe and North America (Food and Agriculture Organization of the United Nations 1995, 2005, 2006), these continents still face local decreases in the number of forest-dwelling species. Accordingly, their fragmentation through the destruction of connecting hedgerows and small wood plots by land

consolidation practices, rather than the reduction of woodlands, is a factor of special importance in the survival of inhabiting species (Saunders et al. 1991; Fahrig and Merriam 1994; Food and Agriculture Organization of the United Nations 1995, 2005, 2006).

One of the main consequences of land consolidation practices is the increasing isolation of remnant wood plots. Such isolation seriously jeopardizes the stability and survival of woodland-dweller populations (Pimm et al. 1988; Reed 2004). Indeed, connectivity between populations crucially depends on the ability of individuals to migrate between forested areas. For terrestrial woodland dwellers, small woods, edges, and hedgerows may be important ecological connecters between larger woodlands. In contrast, fields such as pastures and crops may constitute physical barriers. In addition, the modern landscape has become increasingly urbanized with the construction of roads and buildings. These anthropic structures may form physical barriers to movement and are sources of disturbances through associated human activities.

Habitat specialists are usually considered highly vulnerable to habitat fragmentation (Bright 1993). However, certain forest-dwelling species such as the western roe deer (*Capreolus capreolus* (L., 1758)) have been able to locally colonize open cultivated plains (Marchal et al. 1998; Hewison et al. 2001). It thus appears necessary to determine the sensitivity of each species to habitat fragmentation. Moreover, studies generally focus on the species occurrence in relation to landscape heterogeneity. Thus many empirical studies on forest-dwelling species have been conducted to assess the impact of woodland fragmentation and urbanization on the distribution of populations, e.g., in Eurasian red squirrel (*Sciurus vulgaris* L., 1758) (Verboom and Van Apeldoorn 1990; Van Apeldoorn et al. 1994), wolf (*Canis lupus* L., 1758) (Mladenoff et al. 1995), western grey kangaroo (*Macropus fuliginosus* (Desmarest, 1817)), euro (*Macropus robustus* Gould, 1840) (Arnold et al. 1995), Siberian flying squirrel (*Pteromys volans* (L., 1758)) (Mönkkönen et al. 1997), ungulates (Pearson et al. 1995), and snakes (Luiselli and Capizzi 1997). In contrast, few studies have been conducted at the level of individuals to determine movement patterns within fragmented landscapes (but see Fortin et al. 2005). Such studies are required to understand species sensitivity to habitat fragmentation.

The European pine marten (*Martes martes* (L., 1758)) is a typical woodland-dwelling mustelid. This species is particularly sensitive to changes in its original habitat (Brainerd 1990; Bright 1993; Buskirk and Powell 1994), as a result of habitat specialization and also because it shares a number of traits frequently found in carnivores: it occurs at low densities, adults have low reproductive outputs, home ranges are generally larger than ca. 200 ha and exclusive between males, and subadults usually disperse over long distances (Noss et al. 1996; Sunquist and Sunquist 2001). This territorial and sedentary mustelid could therefore have difficulties dealing with poor environmental conditions.

However, the conclusion that pine martens are dependent on forests is based solely on studies of habitat selection undertaken within large forested areas and focusing mainly on differences between types and ages of forest patches (Pulliainen 1981; Zalewski 1997; Kleef 2000; Zalewski and Jędrzejewski 2006). Marchesi (1989) and Stier (2000) put this supposed vulnerability into question in the conclusion of their papers, and while pine martens mainly inhabit large forests (Balharry 1993; Brainerd and Rolstad 2002; Baltrünaité 2006), individuals are actually sighted in fragmented landscapes (Pereboom 2006).

We assessed the sensitivity of European pine martens to woodland fragmentation by investigating their habitat selection and their movement patterns between successive resting sites in fragmented landscapes. We tested several predictions based on the assumption that the pine marten is a woodland-dwelling species strongly attached to wooded areas. We expected pine martens to preferentially use forests >200 ha, which is the male minimal home range reported in the literature (Labrid 1986; Zalewski 1997; Zalewski and Jędrzejewski 2006). We further expected pine martens to travel preferentially and with high movement speed within groves, edges, and hedgerows, since theses habitats may be used as connecters between forests. Finally, we expected pine martens to avoid nonwooded habitats, i.e., both fields and human constructions.

Materials and methods

Study area

The study was carried out in the Ardennes, a rural region in northeastern France. The area is situated on a clay plateau of woody hills, at an altitude varying between 100 and 300 m above sea-level, and irrigated by two main rivers (the Aisne and the Meuse). It is characterized by a low human population density (<10 inhabitants/km^2) dispersed in isolated farms and very small villages. Climate is semicontinental with wet, cold winters and large variations of temperatures in the summer. Météo France (Belval Station) records about 64 days of frost and only 39 days of temperatures exceeding 25 °C for the area each year. Rainfall (mean 900 mm) is well spread out over the year. Woodlands, dominated by Norway spruces (*Picea abies* (L.) Karst.), deciduous oaks (genus *Quercus* L.), and European beeches (*Fagus sylvatica* L.), cover 27% of the area and are embedded in a matrix of agricultural fields (cereals) and pastures that constitute 72% of the area.

Using FRAGSTAT version 3 (McGarigal et al. 2002), we quantified the level of wood-cover fragmentation of the study area (restricted to an area of 257 km^2 encompassing all location fixes) through indices already used by Hargis et al. (1999) in a study on the American marten (*Martes americana* (Turton, 1806)), namely: percentage of landscape (27%), mean patch size (1.2 ha), patch size coefficient of variation (3047 ha), edge density (72 m/ha), mean proximity index (2411), and mean Euclidian nearest neighbour distance (30 m).

We further defined 6 habitat categories for our analyses on martens: 4 classes of woodlands, i.e., forests (>200 ha, 15% of study area), groves (between 0.5 and 200 ha, 8% of study area), hedgerows (linear elements, 2% of study area), and edges (15 m large bands around forest and grove patches, 4% of study area); the other 2 categories are fields (pastures and crops, 70% of study area) and human constructions, including roads and buildings (1% of study area). The limit between groves and forests (200 ha) was estab-

lished based on pine marten territorial behaviour, since 200 ha is the minimum home-range size of male pine martens reported in the literature (Labrid 1986; Zalewski 1997; Zalewski and Jędrzejewski 2006). Habitat classification was made using GIS software Arcview™ version 3.2 with data derived from IGN maps (1:25000) and recent aerial photographs (precision of 50 cm) to attain higher precision in the fragmented parts of the study area.

Study animals

Eight pine martens (5 males and 3 females) were live-trapped between April 2002 and December 2005. They were caught in baited cage traps (100 cm × 30 cm × 30 cm) placed all year-round in fauna passages. Captured individuals were anaesthetized by intramuscular injection of ketamine hydrochloride (0.15 mg/kg) and medetomidine hydrochloride (Domitor, 0.075 mg/kg) and fitted with activity/inactivity-indicating radio collars (Televilt, about 36 g, between 1.9% and 3.3% of pine marten body mass). All animals were handled and cared for under the supervision of R. Helder, owner of a licence for use of experimental animals (« Certificat d'expérimentation animale ») issued by the Ecole vétérinaire de Maisons Alfort, Paris. Age was estimated by checking teeth, but recapture of individuals showed that this method was not always reliable. Adults and subadults were therefore pooled together. In accordance with the literature (Reig 1992; Holmes and Powell 1994), martens displayed a significant (Mann–Whitney U test: $U = 15$, $P = 0.0236$) dimorphism in body mass with males (1.7 ± 0.3 kg, mean ± SD) being 1.4 times heavier than females (1.2 ± 0.1 kg).

Data collection

Collared pine martens were radio-tracked by two or three fieldworkers from vehicles equipped with 3 m high Yagi antennae. We tracked one pine marten at a time, all through one complete activity period. An activity period was defined as the movement of an individual from one resting site to the next. Animals were considered resting if inactive for more than 30 min. We located them by simultaneous biangulation or triangulation, at <500 m from the individual to minimize localization errors, with a mean (SD) sampling frequency of one location per 3 min 36 s ± 4 min 54 s. The large standard deviation is due to us keeping only the first location in our analyses and discarding the following identical locations to prevent data redundancy if the radio-tracked animal was active but staying in the same place. Azimuths were recorded from two or three positions that could change to increase precision. Animal location was estimated using LOAS™ version 3.03 (Ecological Software Solution 1998–2005) with a bearing error of 5°. Locations completely out of the way and obviously owing to tracking errors were considered outliers and discarded. Finally, as recommended by Pace (2001) and applied by several authors (Dickson et al. 2005; Vokoun and Rabeni 2006), we applied a correction on data to further increase precision, taking a moving window of three locations and obtaining a new position for each window based on averaging.

Data analysis

Movement patterns

Since pine martens were located at short-time intervals in the course of a path, the length of the segment joining two successive locations could be considered a good approximation of the distance really travelled by the monitored individual. Accordingly, we extracted four variables from each path: (1) time elapsed between beginning and end of path, (2) length of path, (3) Euclidian distance between first and last location of path, and (4) straightness of path calculated as the ratio between variables 2 and 3. Because several paths were recorded per individual, mixed-effect ANOVAs, including individual as random factor, were carried out to test for the effect of sex on these four variables using the library nlme version 3.1-79 in R version 2.4.0 (Pinheiro et al. 2006; R Development Core Team 2006).

Habitat selection and corridor use

Habitat selection and corridor use by pine martens were investigated in two ways. First, analyses were performed on the locations within the six habitats (cf. the resource selection function; Manly et al. 2002). Second, analyses were carried out on the segments linking two successive locations in the course of a path to examine distances travelled within the six habitats (cf. the step selection function; Fortin et al. 2005). These are the most appropriate methods when dealing with a large amount of data collected on a few individuals. In the two cases, as detailed below, habitat availability was estimated by generating random paths. Thereafter, habitat use and availability (as well as habitat selection by the two sexes) were compared using the log-likelihood χ^2 statistic, and the associated P value was obtained by the Monte Carlo method.

Random paths

We randomly permuted the order of the segments that composed each path using the Alternate Animal Movement Routes version 2.1 extension for ArcView 3.x developed by Jenness (2004). The first and last locations of paths were maintained so that we respected the global movement patterns of each path (i.e., variables 1–4 described above). This operation was carried out 99 times per path. Thereafter, based on all the random paths thus obtained (or of those corresponding to the individuals of a single sex), we computed the expected total number of locations and the expected total distance travelled within each habitat.

Log-likelihood χ^2 statistic

The observed total number of locations (as well as the observed total distances travelled) within the six habitats were compared with the corresponding expected values, computing the log-likelihood χ^2 statistic (Manly et al. 2002):

$$[1] \qquad L_{\chi^2} = 2 \sum_h O_h \cdot \ln\left(O_h/E_h\right)$$

where O_h is the observed value for habitat h and E_h the expected value for habitat h. If the value obtained for the log-likelihood χ^2 was found to be significant, we then compared observed and expected values within each possible pair of habitats.

To test for the effect of sex on habitat selection, we computed the statistic:

$$[2] \qquad L_{\chi^2} = \left(L_{\chi^2 m} + L_{\chi^2 f}\right) - L_{\chi^2 mf}$$

where $L_{\chi^2 m}$, $L_{\chi^2 f}$, and $L_{\chi^2 mf}$ are the log-likelihood χ^2 statistics computed for males only, for females only, and for the two sexes confounded, respectively. By the general theory of log-likelihood tests, L_{χ^2} is a log-likelihood χ^2 statistic that, in the present case, measures the difference between the sexes in habitat selection (see Manly et al. 2002).

Monte Carlo method

In our case, the log-likelihood χ^2 values obtained did not follow a standard χ^2 distribution under the null hypothesis (of no habitat selection, or of no difference between the sexes), because they were computed on nonindependent locations or on distances (which are not frequencies but continuous variables). Accordingly, the P value of each log-likelihood χ^2 value was obtained using the Monte Carlo method (Manly 1997). The principle of this method is the following. (*i*) Data are permuted in such a way that samples corresponding to the null hypothesis are generated. (*ii*) The log-likelihood χ^2 statistic is recalculated on each permutated sample. (*iii*) The log-likelihood χ^2 values thus obtained and the observed value are ranked together in decreasing order, and the P value of the observed log-likelihood χ^2 value is given by its percentile.

To obtain the P value for the effect of sex on habitat selection (eq. 2), we simply permuted the sex of pine martens. This operation was carried out 55 times, since data were collected on 5 males and 3 females, and the number of possible combinations including the one observed was in this case 8!/(5!3!) = 56.

To obtain the P value of the log-likelihood χ^2 statistic measuring habitat selection (eq. 1), we permuted the habitats at random and independently for each monitored pine marten. This operation was carried out 500 times among the 8(6!) = 5760 possible permutations including the observed one.

Finally, to obtain the P value for each of the 15 possible pairwise comparisons between habitats, we permuted the two considered habitats at random and independently for each pine marten. This operation was carried out 255 times, since there were $2^8 = 256$ possible permutations including the observed one. Since the 15 comparisons involved the same set of data, the threshold of the P values should be corrected following the Bonferroni procedure (α_{cor} = 0.05/15 = 0.0033). However, as the smallest possible P value was 0.004 (i.e., 1/256) rather than 0.0033, we fixed α_{cor} at 0.004 rather than 0.0033 so that the experimentwise error rate was set at 0.06 (i.e., 0.004 × 15) rather than 0.05.

Distance to wooded areas

As the pine marten is known to be a forest-dwelling species, we expected individuals to stay close to wood covers when located within fields. We therefore calculated for each path the mean distance between the locations situated in the fields and the nearest wood cover (i.e., edges of both forests and groves, and hedgerows). We did the same operation with the 99 corresponding random paths (see Random paths above) to obtain the mean distance expected under the assumption that martens moved independently of wood cover. The difference between the observed and expected mean distances obtained per path was then compared with 0, by computing a mixed-effect ANOVA with only the intercept in the fixed-effect part of the model and the individuals as random factor. Another mixed-effect ANOVA with the individuals as random factor was performed to test for the effect of sex on mean distance to nearest wood cover.

Movement speed within habitats

Analyses performed on distances travelled within the six habitats did not indicate whether pine martens exhibited the same movement speed within the six habitats. Nevertheless, we might expect pine martens to move faster within corridors, as these would be used only for transit between preferred habitats, while the reverse might be expected in preferred habitats where individuals might feel more secure and, for example, wander in search for food, look for resting place, or interact with each other.

Since pine martens were located at regular intervals in the course of a path, the faster they were moving within a given habitat the lower was the chance to locate them within this habitat. We therefore approximated movement speed within a given habitat for each path by computing the distance travelled within this habitat divided by the number of locations collected within this habitat plus 1 (the systematic addition of 1 to the number of locations allowed computation of the movement speeds within each habitat crossed, even though no location was collected within it during the path considered).

Mixed-effect ANOVAs including individuals and paths as nested random factors were carried out to test for the effects of sex, habitat, and interaction between sex and habitat. Since mean and variance of movement speeds were correlated, data were log-transformed before analysis.

Results

Each pine marten was radio-tracked during a little more than 5 months (160 ± 127 days/marten; mean ± SD). Paths were collected between June 2003 and May 2006, except from November to January of each year, as no individual could be trapped or satisfactorily radio-tracked during this period of the year. A total of 45 paths (5.6 ± 3.0 paths/marten) consisting of a total of 1 275 locations (28.3 ± 19.6 locations/path) and 95 334 m were recorded.

Movement patterns

Despite the body mass dimorphism recorded between males and females (see Materials and methods), no significant effect of sex was found on time elapsed between beginning and end of path (mixed-effect ANOVA: $F_{[1,6]}$ = 4.2, P = 0.086), length of path ($F_{[1,6]}$ = 0.2, P = 0.703), Euclidian distance between first and last location of path ($F_{[1,6]}$ = 0.7, P = 0.437), and straightness of path ($F_{[1,6]}$ = 0.5, P = 0.517). During the night, pine martens moved from one resting site to the next, on average (SD), for 1 h 38 min (±59 min) while travelling 2.1 km (±1.7 km). Pine martens clearly tended to loop back, as the mean linear distance between first and last location of paths (421.5 ± 438.4 m) was about a fifth of the length travelled (straightness of paths

Table 1. Log-likelihood χ^2 statistic and associated P values of the differences between use of each pair of habitat by European pine martens (*Martes martes*).

Habitat	Edges log-likelihood χ^2	P	Groves log-likelihood χ^2	P	Human construction log-likelihood χ^2	P	Hedgerows log-likelihood χ^2	P	Forests log-likelihood χ^2	P
Groves	1.064	0.332	—	—	—	—	—	—	—	—
Human construction	0.790	0.305	0.205	0.531	—	—	—	—	—	—
Hedgerows	0.021	0.980	0.968	0.969	0.702	0.727	—	—	—	—
Forests	8.935	0.535	5.948	0.723	0.172	0.848	10.197	0.742	—	—
Fields	25.446	**0.004**	28.727	**0.004**	1.110	**0.004**	33.069	0.051	5.374	0.707

Note: Significant P values are in boldface type and are equal to the Bonferroni-adjusted α of 0.004.

Fig. 1. Selection ratios calculated for the six habitats of the study site. Habitats that did not differ significantly in their use intensity by European pine martens (*Martes martes*) are underlined by a single line.
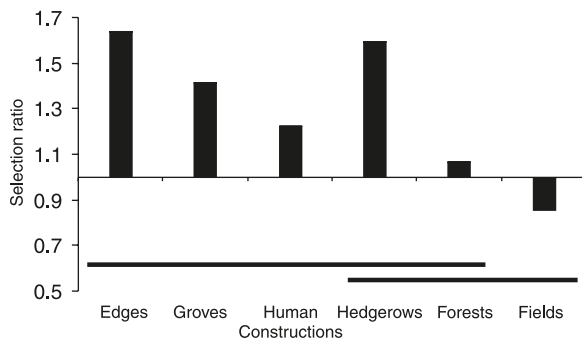
0.24 ± 0.19). Nevertheless, pine martens were never observed to come back to previous resting sites.

Habitat selection

Despite the recorded sexual body mass dimorphism, males and females did not differ significantly in their use of the six habitats (Monte Carlo test: log-likelihood χ^2 = 46.2, P = 0.107). The eight pine martens were therefore pooled in subsequent analyses.

The six habitats distinguished in the study site were not used as expected under the hypothesis that pine martens use the fragmented landscape at random (log-likelihood χ^2 = 74.7, P = 0.026). Pairwise comparisons between habitats (Monte Carlo test with α_{cor} = 0.004) indicated that edges, groves, and human constructions were significantly preferred to fields (Table 1). Hedgerows and forests tended to occupy an intermediate position, since they were neither more nor less intensively used than edges, groves, human constructions, or fields.

Selection ratios (i.e., observed number of locations divided by that expected) revealed no significant differences among the six habitats (Fig. 1). It is worth noting that the selection ratios of the four wooded habitats were very different and that, compared with edges, groves, and hedgerows and contrary to our prediction, pine martens did not prefer forests. Furthermore, pine martens did not avoid human constructions. Finally, fields were the only habitat that was somewhat avoided by pine martens, even though their usage intensity did not differ from both hedgerows and forests (Table 1).

Corridor use

No significant effect of sex was detected concerning the distances travelled within the six habitats (log-likelihood χ^2 = 2887.9, P = 0.107). Furthermore, the distances travelled within the six habitats revealed that distances did not differ significantly from those expected by random use of the six habitats (log-likelihood χ^2 = 4010.4, P = 0.182).

Distance to wooded areas

When pine martens were located within fields, they were significantly closer to nearest wood cover (whatever the size) or hedgerow than expected by chance ($F_{[1,34]}$ = 7.2, P = 0.011). They were located at 41.7 ± 31.8 m (mean ± SD) from the nearest wood-cover habitat. This distance did not significantly depend on sex ($F_{[1,5]}$ = 0.6, P = 0.479).

Movement speed within habitats

While the backward selection procedure performed on the components of the mixed-effect ANOVA revealed neither significant effect of the interaction between sex and habitat ($F_{[5,94]}$ = 0.6, P = 0.675), nor significant effect of sex ($F_{[1,6]}$ = 1.8, P = 0.224), it revealed a very significant effect of habitat ($F_{[5,99]}$ = 26.7, P < 0.0001). In fact (Table 2, Fig. 2), pine martens moved substantially and significantly faster within forests than within the other habitats with the exception of fields. Moreover, they exhibited movement speeds significantly lower within human constructions than within all other habitats.

Discussion

Sexual dimorphism

Martens exhibit a corporal dimorphism between sexes (Reig 1992; Holmes and Powell 1994). According to the intersexual niche differentiation hypothesis (Shine 1990), this dimorphism should lead to differences in energetic requirements. Home-range size of male pine martens is larger than that of females (Labrid 1986; Clevenger 1993; Zalewski et al. 1995). By contrast, our results did not show any significant difference between sexes with regard to characteristics of paths and habitat-selection patterns. This lack of significant difference between the sexes could well be due to the small number of individuals followed. The polecat, however, the mustelid with one of the strongest sexual dimorphisms (1.9), revealed only minor differences in resource selection (Lodé 2003), although females avoided male-occupied zones (Lodé 1996). Our results might also be explained by taking all paths of an individual into consideration. Although both

Table 2. Student's *t* values and associated *P* values of the differences between movement speeds of European pine martens (*Martes martes*) within habitats.

Habitat	Forests		Fields		Groves		Hedgerows		Edges	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Fields	2.584	0.011	—	—	—	—	—	—	—	—
Groves	3.304	**0.001**	1.425	0.157	—	—	—	—	—	—
Edges	4.111	**<0.001**	2.522	0.013	0.862	0.391	—	—	—	—
Hedgerows	4.642	**<0.001**	3.739	**<0.001**	1.834	0.070	1.043	0.300	—	—
Human construction	9.045	**<0.001**	10.421	**<0.001**	7.933	**<0.001**	7.464	**<0.001**	3.739	**<0.001**

Note: *P* values lower than the Bonferroni-adjusted α of 0.0033 are shown in boldface type.

Fig. 2. Box plots (median, first quartile, and third quartile) and outliers (○) of values of movement speeds exhibited by European pine martens (*Martes martes*). Movement speeds between habitats that did not differ significantly are underlined by a single line.
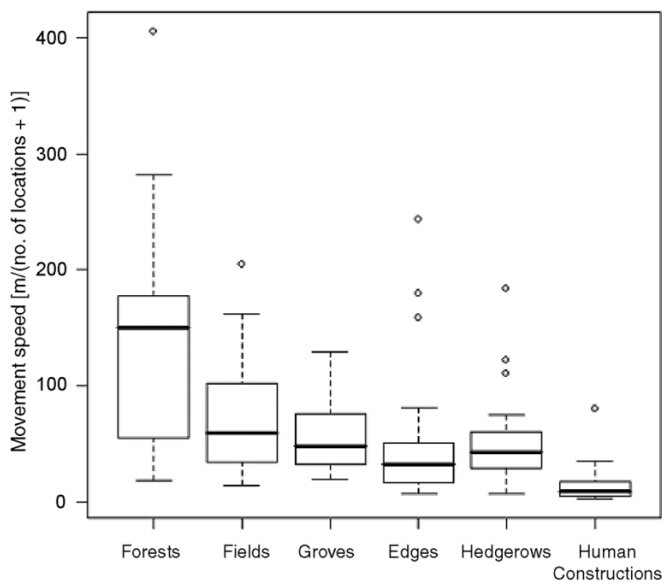
sexes have similar paths, females stay within the same area from night to night, while males tend to shift from one place to another, leading to larger home ranges for males. In a single night, males and females have almost the same space-use pattern; however, over many weeks and months, males are more erratic, moving farther and exploring wider ranges.

Habitat selection

Our results emphasize that the European pine marten shows a habitat-selection pattern less strict than previously observed. A few studies in fragmented landscape, based on a small number of individuals, have revealed a similar pattern (Marchesi 1989; Stier 2000).

In accordance with our predictions, pine martens do not randomly use all available habitat types for their normal activities in fragmented agricultural landscape. Woodlands are preferred and fields constitute the less frequented habitat. In accordance with many authors (Pulliainen 1981; Labrid 1986; Brainerd 1990; Selas 1990), our results indicate that martens are forest-dwelling animals. We found, however, that pine martens are not the forest-specialist species usually described in the literature, i.e., restricted to large forests (e.g., Storch 1988; Schröpfer 1997), as we found no differ-

ence in the use of the four wood-cover types (hedgerows, edges, groves, and forests). Thus the size of forest patches does not appear to be a discriminating factor in habitat selection. Although martens stay at a mean distance of 30 m from forest habitat types, confirming their attachment to forest cover, the presence of trees as units of forest cover seems more significant than the presence of large forests. Small wood plots and hedgerows are suitable for daily activities of foraging and even single trees may be used, at least as a resting site.

Contrary to what was expected, our results suggest that human constructions are not avoided. This may be due to the study area containing <1% of human construction. This low percentage may make its use or avoidance difficult to highlight, the more so as our assessment of habitat availability was very strict. The comparison between used and available habitat is, in fact, highly dependent on the presence of all habitats in the vicinity of paths; the null value of the frequentation index not only indicates an equilibrium between use and availability of one habitat type but may also indicate an absence of this habitat type in the vicinity of the animal's path. If a little-represented habitat type such as human constructions does not appear in an observed path or in the associated simulated paths, the analysis may lead to the erroneous conclusions that this habitat type is used as expected. We actually never observed pine martens visiting buildings or foraging in gardens or around farms. From the eight radio-tracked pine martens, only one crossed a village, and this was over a very short period of time compared with the length of the path.

On the other hand, pine martens do not show any preference or avoidance when crossing the different habitat types. All habitat types in the landscape are crossed: all types of forest cover, fields, and human constructions. This indicates that, on the spatial scale studied, no habitat type plays the role of corridor or barrier for pine marten movements. Although pine martens avoid fields, they do frequently cross them, confirming Stier's (2000) results that these animals do not shrink away from crossing treeless areas.

Finally, the speed of pine marten movement varied with habitat type. Contrary to what was expected, individuals move faster in forests than in other habitat types, with the exception of fields. Taking their habitat-selection pattern into account, this suggests that forests, as one of the preferred habitat types, facilitate their movements, which is in accordance with pine martens being forest-dwelling animals. They do not forage in large forests but rather in groves, edges, and hedgerows. Fields, usually recognised as a barrier for forest-dwelling species, do not constitute a real barrier

for pine martens. We radio-tracked a pine marten in maize fields on several occasions, where it was probably foraging. Finally, the low speed observed in the human-construction habitat might reflect some level of insecurity by the animals in this habitat, with individuals making frequent stops and waiting in hiding places.

Presence in fragmented landscape

The radio-tracked pine martens were present in fragmented landscape for longer than a single-night excursion or while in dispersal transit between two forest patches. We can therefore state that pine marten individuals are settled in this landscape. Their settling in fragmented landscape may derive from the capacity of individuals to lower their level of selectiveness, while retaining their characteristic forest specialization. Most authors believe that habitat selection in pine martens is determined by predator avoidance, foraging success, and (or) thermoregulation (Pulliainen 1981; Thompson and Harestad 1994; Zalewski 1997; Stier 2000; Brainerd and Rolstad 2002). With regard to predator avoidance, we know that in boreal forests, where most studies on pine martens have taken place, there is significant biodiversity with numerous predators such as wolves, lynx, owls, bears, and foxes (Pulliainen 1981; Lindström et al. 1995). Various authors suggest that predation is lower in mature forests than in clear-cuts (Buskirk and Powell 1994; Chapin et al. 1998). Predation by foxes is well known in Scandinavia and has a strong impact on pine marten populations (Brainerd et al. 1995; Lindström et al. 1995). At high latitudes, pine martens hide and rest in burrows under the ground and are thus protected from snow and low temperatures. This habit makes them vulnerable to red foxes and other large terrestrial predators. During our study, however, we never observed pine martens resting under the ground and thus exposed to predators. This may be due to more clement weather. Furthermore, large predators have almost completely disappeared in France, except foxes. For these two reasons — martens not resting underground and low densities of large predators — predation pressure may be significantly lower in France than in northern countries.

With regards to foraging success, many studies have shown that open areas such as clear-cuts and meadows are characterized by a large diversity of small mammals and provide high foraging opportunities (Thompson and Harestad 1994; Huggard 1999). Simon (1980) and Spencer et al. (1983) showed that American martens select meadow edges for foraging, and although they avoid venturing in the interior of open areas, they frequently hunt up to 10 m from the forest edge. Thus, in the absence of predators, pine martens may tend to hunt in open areas where small mammals are much more abundant than under forest cover. This is what Clevenger (1994) demonstrated on the island of Minorca. Finally, with regards to thermoregulation, pine martens are characterized by an elongated body and a highly conductive fur, which raises the energetic costs of thermoregulation (Buskirk et Powell 1994; Brainerd et al. 1995). Consequently, resting and denning sites are selected to overcome this drawback, with a preference for arboreal cavities and bird and squirrel nests (Pulliainen 1981; Marchesi 1989; Brainerd et al. 1995; Zalewski 1997). In our landscape, hedgerows are made of trees (willow (*Salix* L.), ash (*Frax-*

inus L.), oak, apple (*Malus* P. Mill.), etc.) and shrubs (singleseed hawthorn (*Crataegus monogyna* Jacq.), chokecherry (*Prunus* L.), and common filbert (*Corylus avellana* L.) for the most part) that provide quantities of adequate shelter against both low temperatures and predators. All these parameters furnish a possible explanation for the use of space by the pine martens observed in our study, with individuals using hedgerows and wood plots <200 ha more than was expected.

Our work did not, however, show that pine martens can proliferate in fragmented landscape without the presence of large forested areas. We therefore stress the need to undertake long-term studies to gain information on the capacity of populations to maintain themselves in hedged farmland. We may already hypothesize that to reproduce martens require an area of forest cover many times larger than the size of their home range, as is the case for area-sensitive forest birds (Robbins et al. 1989). We therefore conclude that further research is required on their home range and reproductive success in fragmented landscape, as well as with further investigation into areas where forest cover is sparser than our study site.

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