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Habitat selection of European pine marten in Central Italy: from a tree dependent to a generalist species

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Abstract

Studies at small spatial scale are often fundamental to highlight the behavioural plasticity of a species and thus have important implications for conservation planning, in particular for species usually considered as habitat specialists. We investigated second-order habitat selection of the European pine marten in an area dominated by deciduous oak forest and open fields in central Italy, by radio-tracking 16 pine martens (eight males, eight females). Pine martens placed home ranges in areas with more open field than in the study area, whereas woodland (oak and conifer forests) comprised a smaller portion of the home range than predominant forest character of the studied area. Although the presence of the species in the open habitats has been documented, to our knowledge, our results provide the first evidence of home range establishment in this cover type by pine marten at population level. The combination of low predation risk and high availability of resources could allow pine martens to occupy open fields in our study area. We highlighted different individual strategies of habitat selection, with some individuals placing home ranges in areas with high forest coverage while others occupying open areas. We found no effects of sex and body condition on habitat selection, and this could indicate that in the study area, both forested and non-forested cover types, such as open fields, shrub and anthropic areas, can provide adequate food, overhead cover and resting sites for all individuals. Pine marten ability to occupy open fields seems thus more related to the behavioural flexibility of the species, rather than to the need to supplement dens and forage from complementary lower quality habitat. The high quality of the Mediterranean continental area studied could also explain the selection of open areas by the pine marten. Our results offer useful information on pine marten ecology and may be helpful for conservation management of this species in southern Europe.

Keywords Carnivore · *Martes martes* · Johnson's second-order selection · Habitat preference · Radio-tracking · Oak forest · Specialist/generalist · Behavioural plasticity

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Introduction

The knowledge of animal habitat selection is fundamental to address issues related to management and conservation of species. Mammals, as other organisms, use habitats that vary across study sites and spatial scales (Devictor et al. 2010; Virgós et al. 2012). Habitat selection is strictly connected to niche width theory, in which specialist/generalist classification is rooted (Moll et al. 2016). Although broad-scale assessments are required to correctly position species along the generalist-specialist continuum (Moll et al. 2016), studies at smaller spatial scale are often fundamental to address the behavioural plasticity of a species and thus have important implications for conservation planning in a specific context (Virgós et al. 2012). Pointing out the habitat adaptability of a species is particularly important for species traditionally considered as

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habitat specialists, such as the European pine marten *Martes martes*.

The pine marten is a medium-sized mustelid distributed throughout much of Europe and northern and central Asia. It is usually described as a forest-specialist species, dependent on late-successional large forest (Pulliainen 1984; Lindström 1989; Storch et al. 1990; Stier 2000; Brainerd and Rolstad 2002). However, the reported specialisation was based upon studies undertaken in the boreal region, characterised by continental climate and forested dominated landscapes. In the last decade, studies conducted in less forested areas of Europe showed a greater adaptability of pine marten, having been registered in edge, Mediterranean maquis, coastal garrigues and woodland fragmented cultivated lands. Such studies highlighted that the habitat niche of pine marten is wider than previously thought (Clevenger 1994; Birks et al. 2005; Pereboom et al. 2008; Balestrieri et al. 2010; Mergey et al. 2011; Caryl et al. 2012; Lombardini et al. 2015a). Despite the fact that the pine marten uses small wood patch and hedgerows, most studies reported that woodlands are preferred and fields constitute the less frequented habitat (e.g. Pereboom et al. 2008; Balestrieri et al. 2015). Only Clevenger (1994) showed that, in the Island of Minorca, introduced pine martens did not exhibit a clear preference for forested over non-forested habitats. In addition, pine marten home range is generally considered dependent on the extension of wooded habitat within its boundaries (Zalewski and Jędrzejewski 2006), indicating this species as a least forest-dwelling species, at least.

The generalist behaviour of the species has been stressed mostly in fragmented or managed habitats (Pereboom et al. 2008; Mergey et al. 2011; Caryl et al. 2012; Balestrieri et al. 2010) or Mediterranean islands (De Marinis and Masseti 1995; Clevenger 1994; Lombardini et al. 2015a). Little is known about the spatial ecology of pine marten in Mediterranean continental areas (Virgós et al. 2012; Balestrieri et al. 2010, 2015; Bartolommei et al. 2016), and to our knowledge, there are no published studies on habitat selection of this species in these areas. In a previous paper on spatial behaviour of pine marten in a deciduous oak forest of central Italy, we showed that pine martens did not occupy home ranges characterised predominantly by forest, and we found no correlation between home range size and area of forest coverage within its boundaries (Bartolommei et al. 2016). As our study area is widely covered by wood, we hypothesised that monitored individuals were able to include a suitable amount of forest in their range to meet their own needs, emphasising the importance of availability of key resources, i.e. food and shelter, rather than plenty of forested habitat for pine martens (Pereboom et al. 2008; Mergey et al. 2011; Caryl et al. 2012). Food availability, thermoregulation and predation pressure are considered the main factors that directly influence habitat selection of pine marten populations (Helldin 1998; Brainerd and Rolstad 2002; Zalewski and Jędrzejewski 2006). Some authors believe that habitat selection of pine marten could also be affected by the coexistence with the congeneric stone marten *M. foina* (Powell and Zielinski 1983; Rosellini et al. 2008; Wereszczuk and Zalewski 2015). This coexistence depends, in turn, on the relative abundance of each predator within the local carnivore guild and food availability (Delibes 1983; Balestrieri et al. 2010). As all these factors strongly vary across pine marten range, it is evident that studies at local geographical scale are necessary. Within a pine marten population, space use may also vary depending on sex and weight of individuals (Zalewski and Jędrzejewski 2006; Mergey et al. 2011; Caryl et al. 2012; O'Mahony 2014), although some authors reported a similar habitat selection by males and females (Brainerd and Rolstad 2002; Pereboom et al. 2008). In a previous paper on spatial behaviour of pine martens, we found no difference between sexes in space use, but our data revealed high individual variability and point out the importance of considering individual pattern in addition to sex and weight-related strategies (Bartolommei et al. 2016).

As pointed out by several authors (Johnson 1980; Boyce and McDonald 1999; McLoughlin et al. 2004), the selection of habitat can be viewed as a multilevel, hierarchical process. An individual first selects a home range in which to live and then makes decision about the use of different habitats inside his home range (McLoughlin et al. 2004). Consequently, analysis of habitat selection can be performed at different orders (Johnson 1980). Second-order selection (sensu Johnson 1980) examines home range placement with the cover type composition of the entire study area. Habitat composition of pine marten home ranges is compared with the actual habitat composition of the study area, and a selection for a habitat corresponds to home range composition in such cover type richer than its relative abundance in the entire study area. Third-order selection (sensu Johnson 1980) examines the use of cover types within the home range. This implies a more 'individual' focus: the baseline is different for each pine marten (while in second-order is shared by all the pine martens), and a selection corresponds to a higher use than what expected on the basis of single pine marten home range composition. Several authors (Rettie and Messier 2000; McLoughlin et al. 2004) suggest that, in mammals, habitat selection patterns that permit animals to avoid the main factors limiting individual fitness should be strongest at the coarsest scale of selection (population range, home range). Less important limiting factors may instead influence selection patterns only at smaller scale (McLoughlin et al. 2004).

In this study, we investigated second-order habitat selection of radio-tracked pine martens in an oak forested area of central Italy. Our objectives were to (1) examine habitat selection for home range establishment by pine martens and (2) highlight possible individual strategies of habitat selection. As we previously assumed that this Mediterranean continental area is a high-quality habitat for the species (Bartolommei et al. 2016), we hypothesise that pine marten selects both open and forested areas for home range establishment. The primary rationale for this hypothesis is that also open areas are able to satisfy food and cover requirements for the species. In this sense, pine martens may occupy open fields regardless of the presence of stone marten. According to previous finding on spatial behaviour of pine marten (Bartolommei et al. 2016), we also hypothesise an individual variability in habitat selection, independently on sex and body condition of individuals.

Materials and methods

Study area

This study was carried out in La Selva Forest (43°13′ N, 11°4′ E), located 45 km from Siena, in central Italy (Fig. 1). The study area mainly consists of a deciduous forest of the sub-Mediterranean zone, managed in the past decades for coppice. The major vegetation types in La Selva are oak forest dominated by *Quercus cerris*, planted and self-sown exotic forest dominated by conifer plantation, evergreen oak matorral, and cultivated and uncultivated fields. There are also small anthropic areas, small lakes and water reservoirs. The altitude ranges from 350 to 700 m a.s.l. The climate is Mediterranean, with warm dry summers and cool wet winters. Mean monthly temperature is about 23 °C in summer and about 4 °C in winter, with average annual rainfall of about 750–1.600 mm per year.

Estimated pine martens population density in La Selva Forest was 0.34 individuals km^{-2} in 2009 (Manzo et al. 2011). The abundance of terrestrial rodents, the main prey of pine martens (Jedrzejewski et al. 1993; De Marinis and Masseti 1995; Zalewski et al. 1995), was estimated at 1150 individuals km^{-2} over 2011–2013 (Gasperini et al. 2016). Meso-mammals acting as competitors and predators of pine martens are stone martens *M. foina* and weasel *Mustela nivalis* as food competitors (Powell and Zielinski 1983), and fox *Vulpes vulpes* as both predator and food competitor (Lindström et al. 1995; Lanszki et al. 2007). Pine martens hunting is forbidden by law.

Capture and handling

Trapping was carried out from January 2008 to March 2013, with the exception of one individual captured in August 2005. Animals were live-trapped using 20 box traps (models TLT108 and TLT206, Tomahawk, WI, USA), baited with fresh eggs and provided with leaf litter. Traps were distributed opportunistically throughout the study area and were checked daily in the morning. Trapped pine martens were weighted and aged as adult or juveniles on the basis of body size. Individuals classified as juvenile were released at their capture point without being manipulated, whereas adult animals were anaesthetised using Zoletil®, individually marked by an Integrated Transponder (PIT), fitted with a unique frequency radio-collar (TW3, Biotrack, Dorset UK), and released at their capture site after complete awakening. For each marked animal, sex and six morphometric measures were recorded (for details see Bartolommei et al. 2014) and the age class was confirmed using tooth wear. Body condition was expressed as body mass index (BMI = body weight (kg) / body length (cm); Wereszczuk and Zalewski 2015). Biological samples (hair) were collected to confirm by molecular analysis the species field identification (for details see Bartolommei et al. 2014), as morphologic and morphometric discrimination between *M. martes* and *M. foina* can be challenging due to their highly similar traits.

Ethics statement

All the work undertaken on pine martens during the study took place under the terms and condition of a licence issued by the Regione Toscana in compliance with the European Council Directive 92/43EEC (Italian law D.Lgs 157/92 and LR 3/1994) and communicated to the Italian Ministry of Health as required by the European Council Directive 86/609/EEC (Italian law D.Lgs 116/92). Animal capture and handling procedures were consistent with guidelines of the American Society of Mammalogist for the use of wild mammals in research (Sikes 2016).

Radio-tracking

Animals were located by standard triangulation techniques (White and Garrott 1990), using a three-element directional Yagi antenna and Sika receiver (Biotrack, Dorset, UK). Individual bearings were taken at 5-min intervals, or less, with location recorded within 15-min intervals to reduce the error caused by the pine martens movement (White and Garrott 1990). Radio-tracking followed a standard protocol to minimise spatial autocorrelation and standardise data collection (Börger et al. 2006). Fixes (at least six fixes per week per individual) were collected at 4-h bouts to provide data throughout the 24-h period within each week, with a minimum interval of 12 h apart. Pine martens were radio-tracked until collars' signals were lost due to device or battery fault, unless they were found dead (by natural causes or killed by humans). Triangulation error was estimated at 41.1 ± 12 m (n = 56) using eight fixed transmitters placed in the different cover types by an independent field operator (Zimmerman and Powell 1995) and located by the seven field workers involved in the data collection. Radio-tracking data were analysed

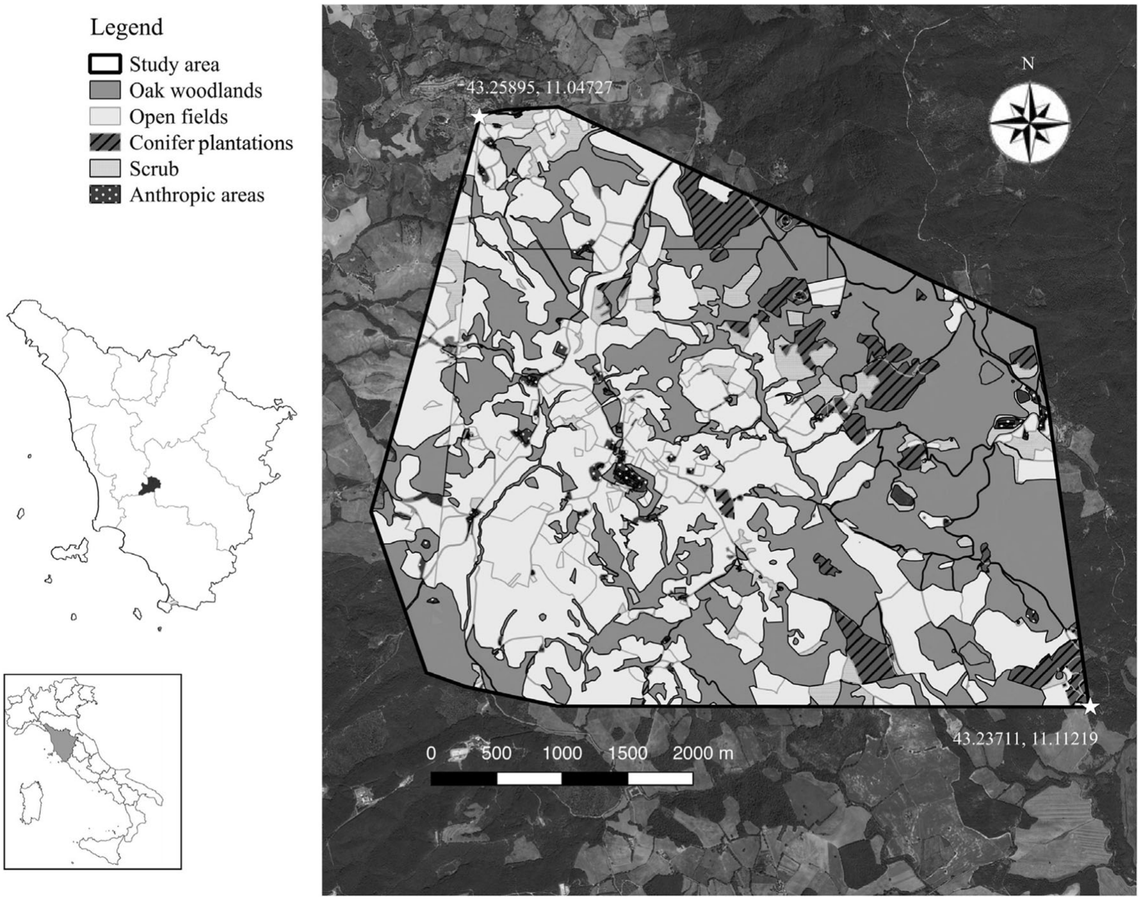


Fig. 1 Location of study area in Tuscany, central Italy (left side). The study area corresponds to the MCP 100% of all monitored individuals and is characterised by five main cover types: oak woodland, open fields (harvested and set-aside fields), conifer plantation, scrub and anthropic areas (streets, rural house, and villages) (right side)

using adehabitatHR (Calenge 2006) of QGIS 2.6 (Team 2014).

Analysis of habitat selection

A detailed map of the coverage of the study area was drafted by E. Manzo based on satellite images (Google Earth 2013) using QGIS 2.6 (Fig. 1). Five main cover types were identified in the study area: (1) oak woodland—*Q. cerris* and *Q. pubescens*—with abundant scrub cover; (2) open fields (harvested—covered by spontaneously growing *Leguminosae* and *Poaceae* hay species—and set-aside areas); (3) artificial conifer woodland—dominated by *Pinus* sp.; (4) scrub—mainly *Rubus* sp., blackthorn *Prunus spinosa* and hawthorn *Crataegus monogyna*, constituting hedges between fields and along roads, or patches covering uncultivated fields; (5) anthropic areas—streets, rural house and villages—usually or occasionally occupied by human (Fig. 1). Habitat availability was measured as percentage of each cover type within the study area, defined by the 100% MCP of fixes of all monitored animals. Home range placement was measured as the percentage of each cover type inside individual home ranges (95 and 50% MCP). $N \geq 45$ locations for each individual were used for the analysis (Kenward 1992).

The analysis of habitat selection based on radio-tagged animals is now a burning theme in ecological research (Fattorini et al. 2014). Despite the rising of sophisticated models to analyse habitat selection, the pioneering approach by Aebischer et al. (1993) is still widely used (e.g. Lashley et al. 2015; Owen et al. 2015; Rhim et al. 2015; Wagner et al. 2015). The compositional data analysis by Aebisher et al. (1993) has the merit of proceeding at animal level (Fattorini et al. 2014): the statistical units are the single animals or, to be more rigorous, the home ranges of the single animals described by the relative percentages of the different cover types. The 1:1 correspondence between individual pine martens and home ranges allows correlating other features of the pine martens (e.g. sex, BMI) to the structure of their home ranges. In this context, Fattorini et al. (2014) proposed an alternative analytical method relying on non-parametric testing strategies. Even if the normality constraints for the applicability of parametric tests are largely overemphasised and explained in De Winter (2013), the low number of statistical units opens the way to spurious results due to the leverage of possible outliers.

This prompted us to base inferential analysis on three different testing paradigms: *t* test, signed-rank test and sign test. This triple approach corresponds to three different hypotheses on the nature of scale: interval, rank and binary, allowing us to eliminate possible biases (Fattorini et al. 2014), while the coherence among three testing strategies is a proof-of-concept of the results robustness. In our work, we decided to use a statistical procedure that benefits from advantages of both methodologies. Following the indications provided by both Aebischer et al. (1993) and Fattorini et al. (2014), we defined the individual home range as a five component vector: (1) OAK: percentage of oak woodland; (2) CONIFER: percentage of conifer plantation; (3) OPEN: percentage of open fields; (4) SCRUB: percentage of scrub area; and (5) ANTHROPIC: percentage of anthropic area. We thus chose DELTAOAK, DELTACONIFER, DELTAOPEN, DELTASCRUB and DELTANTHROPIC as primary variables, which correspond, for each pine marten's home range vector, to the difference between the percentage of each cover type in the individual home range and the percentage of that cover type in the whole study area (that is habitat selection, sensu Johnson 1980). The statistical significance of differential selection was checked by means of both parametric (*t* test) and non-parametric (sign and signed-rank tests) tests against the null hypothesis of no difference between home range composition and cover type availability.

The between-variable correlation was explored by Pearson correlation coefficient and by principal component analysis (PCA), so to highlight (if any) general trends of preference/avoidance of cover types. PCA was applied on the unit/variable matrix having martens as statistical units and delta values relative to the five habitats as variables. An analysis of variance (general linear model, GLM) was applied so to test the effects of sex and BMI on principal component scores. Statistical analyses were performed using SAS software 8.0.

Results

Nineteen adult pine martens were trapped over 620 trap-days, but three males were excluded from the analyses because they were found dead before reaching the minimum criteria deemed necessary for the home range investigation. Eight males and eight females were followed for a minimum of 45 days up to 16 months, for a total of 2513 collected fixes (Table 1). Although not all individuals were tracked in the same season and during the same time span, home range establishment analysis was deemed not affected by the difference in time of pine marten monitoring. In fact, in a previous paper, we showed that in La Selva Forest, pine martens occupy home ranges stable in both size and composition through the year (Bartolommei et al. 2016).

Table 1 Summary of radio-tracking periods and number of fixes used to estimate individual home ranges (ha) of 16 radio-collared pine martens in a sub-Mediterranean deciduous oak forest of central Italy

	Tracking period	N. locations	95% MCP	50% MCP
Males				
M1	02/08/05–06/10/06	216	298.5	105.5
M2	25/10/08–26/03/09	104	684.6	199.7
M3	17/03/10–07/08/10	134	230.4	46.9
M4	10/06/11–13/03/12	255	331.9	17.2
M5	05/11/11–19/03/12	127	214.9	24.1
M6	03/08/12–04/01/13	166	136	76.2
M7	10/10/12–24/01/13	80	74.9	32.1
M8	06/03/13–09/05/13	73	110.7	18.6
Females				
F1	13/01/08–07/05/09	317	173.2	7.5
F2	13/10/08–31/03/09	126	1125.9	218.0
F3	05/05/09–27/09/09	139	59.7	5.9
F4	04/11/09–19/12/09	47	200.0	31.7
F5	21/06/10–10/02/11	192	370.2	6.2
F6	31/10/10–22/12/11	370	412.2	140.5
F7	02/11/12–08/01/13	45	30.5	5.6
F8	07/01/13–10/05/13	122	45.2	4.3

Locations from all individuals (mean = 157.1, SD = 93.0) were recorded and used to calculate the study area (100% MCP), which amounted to 2179 ha. Coverage composition of the study area (habitat availability) was OAK 45.5%, OPEN 41.67%, CONIFER 5.17%, SCRUB 4.82% and ANTHROPIC 2.84%. In fact, although La Selva Forest mainly consists of forest (about 70%), pine martens were caught in areas characterised by both oak forest and fields so that the percentages of these two cover types were similar to each other in the study area. Individual home ranges averaged 281.2 ha (min. = 30.5, max = 1125.9) at 95% MCP and 58.8 ha (min. = 4.3, max = 128.0) at 50% MCP. Oak woodland and open fields were the most represented cover types in home range, although only open areas were included at higher percentage with respect to their availability in the study area (as showed by the positive DELTA value, Table 2). OAK, OPEN and CONIFER were comprised in 95% MCPs differently than a random presence (Table 3), even though a statistically significant avoidance resulted for forested areas, such as oak and conifer woodland (Table 2). OAK and OPEN were comprised differently than a random presence also in 50% MCPs (Table 3), although only open fields were positively selected at core area scale too (Table 2).

The DELTA of two most represented cover types (OAK and OPEN) were negatively correlated (95% MCP $r = -0.90$, $p < 0.001$; 50% MCP $r = -0.84$, $p < 0.001$). A highly significant negative correlation (95% MCP $r = -0.73$, $p < 0.01$; 50% MCP $r = -0.71$, $p < 0.005$) was also observed between

Table 2 Descriptive statistics of cover types in terms of percentage in the individual home ranges (95 and 50% MCP) and DELTA values (difference between the percentage of each cover type in the individual home range and the percentage in the whole study area)

		95% MCP								50% MCP							
		Home range				DELTA value				Home range				DELTA value			
	N	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
OAK	16	31.19	15.88	2	56	− 14.31	15.88	− 43.50	10.50	30.81	17.08	0	61	− 14.65	17.08	− 45.5	15.30
OPEN	16	56.18	18.74	19	88	14.51	18.74	− 22.67	46.33	53.50	20.74	12	80	11.80	20.74	− 29.50	38.70
CONIFER	16	3.06	3.94	0	10	− 2.11	3.94	− 5.17	4.83	3.40	5.82	0	16	− 1.84	5.82	− 5.20	11.20
SCRUB	16	6.25	5.27	1	21	1.43	5.27	− 3.82	16.18	8.63	8.50	0	29	3.75	8.50	− 4.80	24.20
ANTHROPIC	16	3.31	2.41	0	10	0.47	2.41	− 2.84	7.16	3.71	5.18	0	20	0.92	5.18	− 2.80	17.10

OPEN and CONIFER-type selections, confirming that both forested areas were selected oppositely to open areas.

The first two axes of PCA explained the 74% of global variance, with the first component (Factor 1) accounting for 50 and 52% of variance and the second component (Factor 2) explaining the 24 and 22%, for 95 and 50% MCP, respectively. Factor 1 and Factor 2 are mutually independent by construction, pointing out two autonomous modes of habitat selection. Factor 1 orders animals from "individuals selecting open fields" to "individuals selecting forested areas", while Factor 2 orders from selection for OAK to selection for scrub and anthropic areas (Fig. 2, Table 4). No statistically significant effect of sex and BMI was observed on habitat selection of pine martens.

Discussion

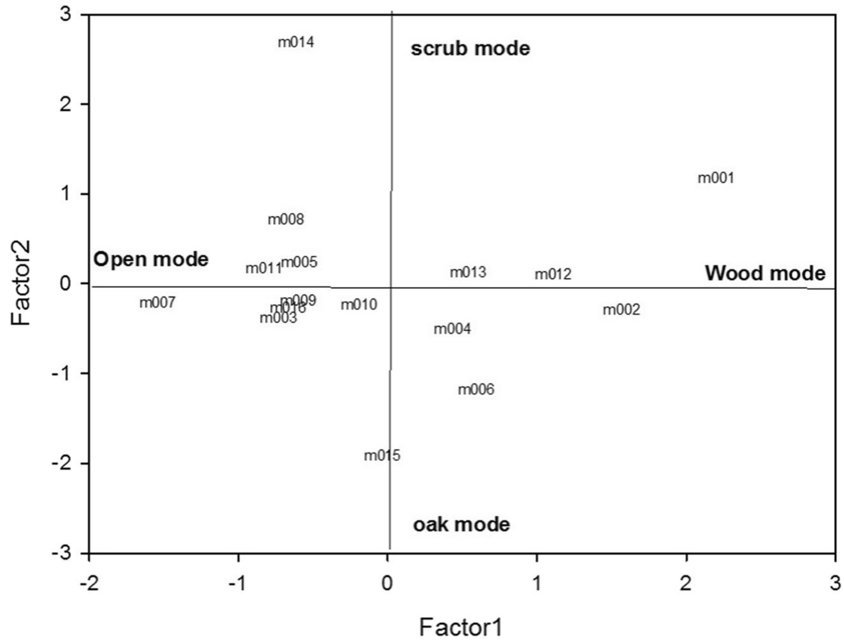
Our results indicate that the pine marten home range includes all the considered cover types in a deciduous sub-Mediterranean oak forest. Although the generalist behaviour of the species was highlighted in previous studies, pine marten is often considered as forest dependent to be inclined to avoid open areas (Stier 2000; Brainerd and Rolstad 2002; Pereboom et al. 2008). Our results draw a quite different picture as, in our study, pine marten selected open fields for home range establishment and tended to avoid woodland (oak and conifer forests), remaining neutral with respect to other cover types. Oak woodland and open fields were the most prevalent cover types (covering 87% of the study area), but only fields were represented in home ranges at a larger proportion than in the study area. Pine marten did not position home range in forested areas, contrarily to what was reported in literature (Brainerd and Rolstad 2002; Zalewski and Jędrzejewski 2006; Pereboom et al. 2008; Balestrieri et al. 2015). Although the presence of the species in the open areas has been documented (Clevenger 1994; Birks 2005; Balestrieri et al. 2010; Caryl et al. 2012; Moll et al. 2016), to our knowledge, our results provide the first evidence of home range establishment in this cover type by pine marten at population level. In previous studies on pine marten habitat selection, fields were avoided or constituted the less frequented habitat (Brainerd and Rolstad 2002; Pereboom et al. 2008; Lombardini et al. 2015a). Only Clevenger (1994) showed that in the Island of Minorca, introduced pine martens did not exhibit a clear preference for forested over non-forested habitats. Interestingly, analyses show that selection of fields is negatively correlated to selections of oak and conifer woodlands, indicating that both forested areas were selected oppositely to open areas. As conifer plantation is a relatively rare cover type in the study area, it is unlikely that correlation is driven by the richness of cover types.

The lack of a strict dependence of pine marten on wooded areas has been showed in fragmented areas of northern Italy, France and Scotland (Pereboom et al. 2008; Balestrieri et al. 2010; Mergey et al. 2011; Caryl et al. 2012) so that pine marten was defined as tree-dependent species rather than forest specialist (Mergey et al. 2011). However, our study was not carried out in a fragmented landscape. Although La Selva Forest mainly consists of forest (about 70%), pine marten did not occupy home ranges covered predominantly by woodland. In a previous paper on spatial behaviour of pine marten in La Selva Forest, we had hypothesised that monitored

Table 3 Habitat selection: Student's *t* test (T), sign test (M), and signed-rank tests (S) against the null hypothesis of no difference between the proportion of the cover type in the home range (95 and 50% MCP) versus proportion in the study area (Johnson's second-order selection). Statistically significant *p* values are italicized

	95% MCP			50% MCP		
	T	M	S	T	M	S
OAK	*0.002*	0.076	*0.004*	*0.004*	*0.021*	*0.008*
OPEN	*0.007*	0.076	*0.009*	*0.038*	0.076	*0.035*
CONIFER	*0.049*	0.076	*0.026*	0.225	0.076	0.299
SCRUB	0.295	0.803	0.291	0.098	0.803	0.231
ANTHROPIC	0.445	0.210	0.396	0.486	0.454	0.733

Fig. 2 Distribution of 16 pine martens in the components space for 95% MCPs. Factor 1 orders animals from individuals selecting open fields (open mode) to individuals selecting forested areas (i.e. oak and conifer woodlands, wood mode), while Factor 2 orders from selection for oak woodland (oak mode) to selection for scrub and anthropic areas (scrub mode)



individuals were able to include a suitable amount of forest in their range to meet their own needs (Bartolommei et al. 2016). Even though forested areas are still considered as higher-quality habitat for the species, many authors stressed the importance of availability of key resources, i.e., food and shelter, rather than plenty of woodland (Pereboom et al. 2008; Mergey et al. 2011; Caryl et al. 2012; Lombardini et al. 2015a). Thus, selection of open fields by pine marten could allow for the best combination of low predation risk, food availability, and access to resting and denning sites.

Predation risk is considered higher in open than in forested areas, because of the lack of escape cover in the first habitat (Storch et al. 1990; Brainerd and Rolstad 2002). Clevenger (1994) assessed that in the absence of predators, open non-forested habitats were equally important as forested ones for pine marten. In La Selva Forest, the red fox *V. vulpes* is the only pine martens predator. Red fox is considered to cause elevated predation pressure to pine marten populations in north Europe (Lindström et al. 1995), even if other researchers questioned the impact of red fox on pine martens (Kurki et al. 1998). In our study, all monitored individuals found dead ($N = 5$) were road-killed or poached, leading us to suppose that the mortality of pine marten might be influenced by human activities more than by predators. A limited predation pressure in our study area might also be supported by the fact that during the study, pine martens were often seen in open fields during daylight. Thus, although we still have not investigated the predator pressure of fox on pine marten, we cannot exclude that the absence of different predator species allowed the selection of fields by pine marten population in La Selva Forest, similarly to what reported by Clevenger (1994). The tree cover could not be an important factor affecting pine marten habitat choice, and structural features of open fields (e.g. presence of bushes) probably could provide adequate overhead cover for this medium-size mustelid. Given the adaptability in resting site selection by pine marten (Brainerd et al. 1995; Zalewski 1997; Birks et al. 2005; Lombardini et al. 2015a), we could hypothesise that features of open areas are able to offer also suitable shelters. In fact, although we have not examined the use of resting sites, during the radio-tracking, pine martens were usually found inactive on rocks, isolated trees and scrub constituting hedges between fields and along roads (unpublished data).

Pine martens feed upon a wide variety of food items, although terrestrial rodents are considered as the main prey (De Marinis and Masseti 1995; Zalewski 2004). Several authors assess that open areas are characterised by a large diversity of small mammals and provide high foraging opportunities (e.g.

Table 4 Loading pattern (correlation coefficients of original variables with components) of the two principal factors explaining most of the variance of pine marten habitat selection (50 and 24% of variance explained by Factor 1 and Factor 2, respectively, for 95 MPC; 52 and 22% of variance explained by Factor 1 and Factor 2, respectively, for 50% MPC). More relevant variables for component interpretation are italicized

	95% MCP		50% MCP	
	Factor 1	Factor 2	Factor 1	Factor 2
DELTAOAK	*0.819*	*− 0.540*	*0.866*	− 0.340
DELTACONIFER	*0.851*	0.264	*− 0.939*	− 0.197
DELTAOPEN	*− 0.977*	0.125	*0.807*	0.053
DELTASCRUB	0.219	*0.729*	0.283	*0.886*
DELTANTHROPIC	0.324	*0.557*	− 0.471	0.391

Clevenger 1994; Pereboom et al. 2008). Also in fragmented landscapes, the use of matrix by pine martens has been explained by the higher abundance of small mammals in grasslands than in hedgerows and forest (Pereboom et al. 2008; Mergey et al. 2011; Caryl et al. 2012). According to density indices reported by Zalewski and Jędrzejewski (2006), terrestrial rodents in La Selva Forest (*Apodemus flavicollis*, *A. sylvaticus* and *Myodes glareolus*) were highly abundant (seven individuals/100 trap-nights, Gasperini et al. 2016). However, density of terrestrial rodents was much lower in fields than in forested cover types (Gasperini 2016), indicating that in our study area, habitat selection of pine marten population does not match habitat preference of their important prey. Due to the plasticity in feeding behaviour of pine and the richness of potential prey species in Mediterranean environment (De Marinis and Masseti 1995; Balestrieri et al. 2011; Lombardini et al. 2015b), we hypothesise that in open fields, pine martens are able to feed on alternative foods, such as other small mammals, birds, insects and fruits. Future studies on pine marten diet and foraging activity will allow us to confirm this hypothesis.

Habitat selection of pine marten can also be affected by the coexistence of competitors, in particular of congeneric *M. foina* (Powell and Zielinski 1983; Rosellini et al. 2008; Wereszczuk and Zalewski 2015). Pine marten and stone marten are morphologically and ecologically similar species, which are prone to separate their spatial niches when they occur simpatrically (Wereszczuk and Zalewski 2015). Although there is little information about habitat selection of the two species in sympatric conditions, pine marten is known to occupy forested areas, whereas stone marten occurs in woodless areas, agricultural land and human settlements when the two species coexist (Larroque et al. 2015; Wereszczuk and Zalewski 2015). In La Selva Forest, pine martens included open fields in home ranges more than they are available in the study area despite the presence of stone marten. Pine martens also did not avoid anthropic areas, showing a spatial behaviour deemed common to its sister species. Even though we have no data on density of stone marten, it appears to be much less common than pine marten in our study area (of 23 martens captured during this study, only four were stone martens); thus, their presence could not affect spatial selection of *M. martes*. Some authors assess that habitat segregation of the two marten species is more likely due to the availability of key resources rather than to any form of intraguild competition (Balestrieri et al. 2010; Larroque et al. 2015; Wereszczuk and Zalewski 2015). In that sense, in a high-quality habitat, pine marten may occupy open and anthropic areas independently on the presence of competitors. In a previous study, we discuss that socio-spatial organisation of pine martens seems to indicate that La Selva Forest is a high-quality habitat where resources are not limiting (Bartolommei et al. 2016), and this hypothesis seems also supported by the relatively high population density of pine marten in the study area (Manzo et al. 2011). Thus, the combination of low predation risk and high availability of resources could explain why in our study area pine martens are able to select open fields for home range establishment.

Although pine martens did not locate their home range in forested areas, it is possible that this habitat was important for the species. The presence and relatively high population density of the species in this study are likely to be a consequence of the large availability of woodland at the landscape scale. Habitat selection is a hierarchical process (Johnson 1980; Boyce and McDonald 1999; McLoughlin et al. 2004); thus, pine marten can first select forested landscape (first order selection by Johnson 1980) and then prefer open areas at home range scale (second-order selection by Johnson 1980). Again, pine marten can use forest cover types within the home range (third order selection by Johnson 1980). At the same time, we cannot exclude that the recorded field selection could be a case of landscape complementation or supplementation (Dunning et al. 1992), with pine marten actually selecting a combination of wooded and open areas. In a landscape composed of different cover type patches each containing different resources, pine martens must travel between patches, since the critical resources are found in different cover types (landscape complementation by Dunning et al. 1992). Otherwise, pine martens could supplement their resource intake by using a substitutable resource in nearby patches of a different cover type (landscape supplementation by Dunning et al. 1992). However, although it would be interesting to investigate the actual use of forest cover type by pine marten in this study area, the fact that pine marten selected open fields for establishment home ranges represents, by a biological viewpoint, a strong form of selection (Rondinini and Boitani 2002). In fact, pattern of selection at the home range scale would likely correspond to factors such as availability of food and cover resources (Rettie and Messier 2000).

In this study, interestingly, some individuals selected areas with more forest cover, while others occupied open areas. In particular, we highlighted two independent trends of selection of cover types. The most marked trend regards animals with a habitat selection ranging from open fields to forested areas, while the other trend regards individuals with a habitat selection ranging from oak woodland to scrub and anthropic areas. Thus, although pine marten preferred and selected fields at population level, our data revealed different individual strategies of habitat selection. Considering the intraspecific competition (Stamps 1994), we could expect a selection of open habitat by individuals in poor body condition. As forested areas are generally considered the highest-quality habitat for the species (Storch et al. 1990; Brainerd and Rolstad 2002; Pereboom et al. 2008), weaker pine martens should be forced out of forest by pine martens in better body condition. Our results did not support this hypothesis, as we found no effect of body condition on habitat selection of pine martens. According to the intersexual niche differentiation hypothesis (Shine 1989), we could also suppose differences in habitat selection among male and female pine martens. In fact, due to the sexual dimorphism of the species, females are deemed subject to grater predation risk and energetic costs, and thus more selective in their habitat choice than males (Caryl et al. 2012). According to Caryl et al. (2012), we could expect that smaller-bodied females would avoid more open cover types, which offer a lower protection from predators. Even though in our study, pine marten exhibits a corporal dimorphism between sexes (Bartolommei et al. 2014), our results did not show any effect of sex on habitat selection. While Caryl et al. (2012) reported that in open habitats avoided by females, the cover near the ground was absent or greatly reduced in stature, in our study area, non-forested cover types were characterised by wide bushes, isolated trees and human structure able to offer dens and shelters for the species. A similar habitat selection by male and female pine martens has been reported in forested and fragmented areas, where both sexes preferred woodland and avoided open areas to increase the chance of survival and reproduction (Brainerd and Rolstad 2002; Pereboom et al. 2008). Thus, the lack of differences in habitat selection among individuals with different sex and body condition recorded in our study area can be due to the fact that in La Selva Forest, both forested and non-forested cover types, such as open fields, shrub and anthropic areas, can provide adequate food, overhead cover and resting sites for all individuals. The individual variability seems thus related to the behavioural flexibility of the species, rather than to the need to supplement the resources required to avoid predator, den and forage from complementary lower quality habitat. Thus, the high quality of habitat (i.e. low predation risk and resources availability) can explain habitat selection strategies at individual as well as at population level, in agreement with what was previously hypothesised (Bartolommei et al. 2016).

Populations are often found in a greater variety of habitat types near the middle of their geographic range compared to the edges (Brown 1984; Hall et al. 1992). Pine marten has a wide distribution in the west and central Palearctic, across most of Europe and northern and central Asia. Nonetheless, in boreal regions, the species is associated primarily with old forest and avoids open areas, being thus considered as habitat specialist, whereas in temperate and southern Europe, it shows a greater adaptability, having been reported in hedges, Mediterranean maquis, coastal garrigues, and woodland fragmented cultivated lands. According to the abundant centre distribution theory (Brown 1984; Hall et al. 1992; Sagarin and Gaines 2002), we would expect a higher selection of wooded areas by pine marten in more stressed environments far from the centre of the range, such as Mediterranean areas. Our results show an opposite pattern of habitat selection, according to what was reported in other studies carried out in the southern Europe (e.g. Clevenger 1994; Balestrieri et al. 2010). Thus, pine marten seems to use a different strategy to cope with more stressful environments at the south of their range, confirming to be a generalist species with a wide ecological niche.

Conclusions

Our study corroborates recent broad- and small-scale indications that the European pine marten is more of a habitat generalist than previously thought. Although the use of open fields has been documented, to our knowledge, our results provide the first evidence of home range establishment in this cover type by pine marten at population level. Contrary to previous studies where dependent forest behaviour has been reported, we detected a negative selection of wooded cover types by pine marten. These findings are particularly interesting because they are relative to a sub-Mediterranean deciduous oak forest consisting of about 70% of woodland. Although the pine marten selected fields at population level, it displayed plasticity in habitat selection at individual level, allowing individuals to occupy all different cover types. The combination of low predation risk and high availability of resource could explain why in our study area, pine martens are able to select both open and forested habitats. Our results offer useful information on the ecology of the pine marten and may be helpful for conservation management of this species in southern Europe.

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Compliance with ethical standards

All the work undertaken on pine martens during the study took place under the terms and condition of a licence issued by the Regione Toscana in compliance with the European Council Directive 92/43EEC (Italian law D.Lgs 157/92 and LR 3/1994) and communicated to the Italian Ministry of Health as required by the European Council Directive 86/609/EEC (Italian law D.Lgs 116/92).

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