

Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes

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Abstract Studies on the distribution of mammalian carnivores in fragmented landscapes have focused mainly on structural aspects such as patch and landscape features; similarly, habitat connectivity is usually associated with landscape structure. The influence of food resources on carnivore patch use and the important effect on habitat connectivity have been overlooked. The aim of this study is to evaluate the relative importance of food resources on patch use patterns and to test if food availability can overcome structural constraints on patch use. We carried out a patch-use survey of two carnivores: the beech marten (*Martes foina*) and the badger (*Meles meles*) in a sample of 39 woodland patches in a fragmented landscape in central Italy. We used the logistic model to investigate the relative effects on carnivore distribution of patch, patch neighbourhood and landscape scale variables as well as the relative abundance of

food resources. Our results show how carnivore movements in fragmented landscapes are determined not only by patch/landscape structure but also by the relative abundance of food resources. The important take-home message of our research is that, within certain structural limits (e.g. within certain limits of patch isolation), by modifying the relative amount of resources and their distribution, it is possible to increase suitability in smaller/relatively isolated patches. Conversely, however, there are certain thresholds above which an increase in resources will not achieve high probability of presence. Our findings have important and generalizable consequences for highly fragmented landscapes in areas where it may not be possible to increase patch sizes and/or reduce isolation so, for instance, forest regimes that will increase resource availability could be implemented.

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Introduction

Habitat loss and fragmentation are widely recognised as a major threat to biodiversity (Fahrig 2003; Foley et al. 2005) affecting individuals, populations, and species at multiple scales depending on their biogeographic, demographic and ecological traits (Swihart

et al. 2003; Henle et al. 2004). For some species, remnant patches will be a habitat for whole populations (or local populations in a metapopulation) or part of an individual's home-range, therefore movements between remnant habitat fragments may range from day-to-day movements (patch use), to dispersal or seasonal migrations (Fischer and Lindenmayer 2007). In the first case (day to day movements), size and spatial configuration of habitat patches will have profound effects on their use by the individuals. Habitat isolation, for instance, may impair the ability to utilise spatially isolated resources (Lindenmayer and Fischer 2006).

Despite their high mobility, mammalian carnivores have long been considered particularly sensitive to habitat loss and fragmentation (Carroll et al. 2001; Crooks 2002). Distribution patterns of mammalian carnivores in fragmented landscapes have been investigated by various authors (e.g. Crooks and Soulé 1999; Swihart et al. 2003): probability of patch use decreases with increasing patch isolation and decreasing patch size (e.g. Crooks 2002; Virgós et al. 2002). These studies, however, focus on the structural constraints (such as patch size and isolation) thought to impede or limit movement of individuals, rather than biotic influences such as abundance of food (Paquet et al. 2006). Consequently some important aspects of species' biology are ignored. From a behavioural ecology perspective (sensu Lima and Zollner 1996), patch use could be determined by a costs/benefits trade-off between the cost of reaching the patch and the benefit of resource availability in the patch: giving up on a site and moving to another imposes energetic costs (Stephens and Krebs 1986). Impaired foraging resulting from spatial isolation of food resources has been observed in frugivorous birds: visitation rates of fruit trees decreased with their isolation (Guevara et al. 1998; Luck and Daily 2003).

Nevertheless, this bias towards structural components of the landscape has had important consequences on connectivity measurement and assessment (Kramer-Schadt et al. 2004). Connectivity is defined as the "degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993). Landscape connectivity is assessed by determining how organisms move and interact (functional connectivity) with the structural heterogeneity of the resulting landscape (structural connectivity) (With and Crist 1995; Taylor et al.

2006). However, most researchers focus only on the structural components ignoring other aspects that may influence individuals' perspective of the landscape (Taylor et al. 2006) such as resource abundance.

Functional connectivity could be implemented by modifying resource abundance / availability; inversely, under certain spatial constraints an increase in resource availability may not improve patch suitability. Ignoring such an important aspect (foraging ecology) in connectivity assessment may lead to unsuccessful conservation planning. This may have broader implications, since mammalian carnivores are often advocated as focal-umbrella species for conservation planning (Carroll et al. 2001; Hunter et al. 2003) and, most of all, play an important role in ecosystems functioning as predators.

We chose as model species for our study the badger (*Meles meles*) and the beech marten (*Martes foina*) that, in mediterranean agricultural landscapes, inhabit mainly forest habitats (Genovesi 2003; Genovesi and De Marinis 2003) and have shown sensitivity to habitat loss and fragmentation (Virgós et al. 2002). Given the size of patches and home-range sizes of the target species it is likely that individuals' incorporate more than one patch in their home-range, therefore we carried out a patch-use survey. The overarching aim of this study is to test if food availability can overcome structural constraints on patch use by the two species. We followed a multiple hypothesis testing framework, where landscape, patch and resource abundance were used as predictor covariates.

Definition of resources was based on available literature. The diet of the beech marten in rural areas of Italy (and Tuscany) has been extensively studied: beech marten is considered the most frugivorous of small carnivores (Genovesi 2003), since fruit is the most abundant item in scats (Serafini and Lovari 1993) as elsewhere in Europe (Clevenger 1994). The badger, instead, predaes mainly on invertebrates (particularly Coleoptera) that are consumed all year round (Melis et al. 2002; Genovesi and De Marinis 2003); fruit, and to a less extent field mice (*Apodemus* sp) are also important in badger diet (Melis et al. 2002; Genovesi and De Marinis 2003).

We predict that under spatial constraints an increase in resource availability will not improve patch suitability. We then interpret the models comparing the response of the two species.

Methods

Study area

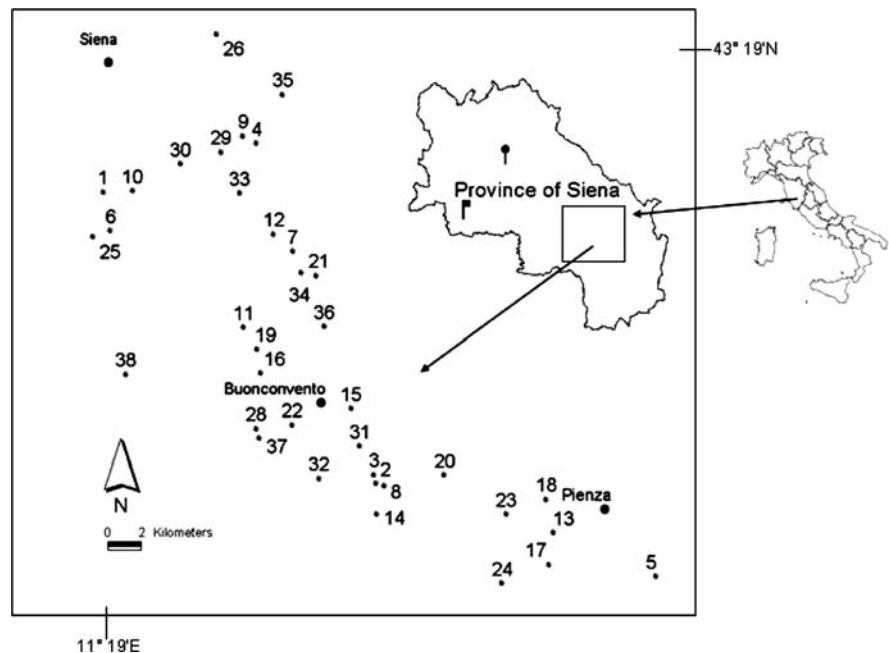
The Province of Siena, Tuscany, central Italy, covers a surface of 3821 km² and is mostly between 200–500 m asl (Fig. 1). The western part (Farma-Merse valleys) is dominated by continuous forests of *Quercus cerris* mixed with *Quercus pubescens*, in some portions substituted by artificial plantations of conifers and semi natural plantations of *Castanea sativa*. The north-eastern part (Chianti) is dominated by continuous forests of *Quercus pubescens* interspersed with vineyards. The south-eastern part, which is divided across three main valleys (Val d’Orcia, Val d’Arbia, Crete Senesi), has been extensively cultivated since the Middle Ages, therefore it is a highly fragmented landscape with a cultivated matrix and small residual woodland patches dominated by *Quercus pubescens* with *Quercus cerris* and rich understorey vegetation. A peculiarity of the landscape is a generalized lack of linear “corridor” features connecting patches, therefore the landscape is structured as discrete patches surrounded by an agricultural matrix. The matrix is bare ground for at least 6 months/year due to ploughing.

Field surveys

Mammal sampling took place in 36 woodland patches and 3 continuous non-fragmented areas (Chianti, Alto Merse, Campriano) from spring 2005 to winter 2007 (Fig. 1). Patches varied in size (range: 0.41–102 ha, mean = 12.99) plus the three non-fragmented, continuous areas), isolation (proximity index within 1000 m from patch edge: 0–29.2, mean = 1.27), and age (years since last cut: range 7–45, mean 12), Appendix 1. Dominant arboreal species are: *Quercus pubescens* and *Quercus cerris*, whereas the surrounding matrix is composed of corn (*Triticum* sp.) or *Medicago sativa* fields. Sampled patches are widely distributed across 3 valleys (Val d’Orcia, Val d’Arbia, Crete Senesi), (mean nearest sampled patch distance = 1,624 m; range 350–6,039 m) and are included in an area of 45,000 ha (area of the convex polygon surrounding patches: <15% of residual woodland habitat).

The patch and neighbourhood landscape features were measured using Arcview 3.3, and “identify features within distance” extension for Arcview (Jenness 2003). Landscape scale metrics were measured in 3 circular landscapes surrounding the patch (150, 300 and 500 ha) through Patch Analyst extension for Arcview (<http://flash.lakeheadu.ca/~rrempe/patch/>).

Fig. 1 Map of the study area with location of the 39 sampled sites. The square flag on the province of Siena map locates Alto Merse reserve, circled flag locates Chianti site



These buffers were chosen as rough indicators of the home-ranges of the studied species (Genovesi 2003, Genovesi and De Marinis 2003).

Carnivore distribution was investigated with various techniques: scent stations, camera traps, track surveys, interviews with local people (gamekeepers, hunters, stakeholders). Scent-stations consisted of talcum powder sifted on a permanent circular base of gypsum used to accustom animals and ameliorate isolation from soil. Scent-stations were activated for five consecutive days each season (with 1–5 patches activated simultaneously); rotten fish was used as lure and placed on a flat stone at the centre of the scent-station. A total of 1750 scent-stations nights was performed.

Field signs surveys were conducted in each habitat patch each season, on various occasions (and at least once after rainfall) with sampling effort increasing with increasing patch size. 100 m transects (number approximately proportional to patch size, minimum 60 in 1-ha patches) were located on footpaths inside the patch, cross country (away from footpaths), in the matrix immediately surrounding the patch (in a 2–5 m strip of non cultivated bare ground surrounding the perimeter of the patch) and on footpaths leading to the site. If a supposed beech marten (*Martes foina*) track or faeces were found, we placed a camera trap (Camtrakker 35 mm, Stealth Cam WD2X) with rotten fish as lure in the area to confirm identification since tracks and faeces of this species cannot be distinguished from those of pine marten (*Martes martes*), (however, this species was found only in two continuous areas: sites 27 and 38). This data provided further confirmation also for badger presence; camera-traps were activated up to 2 weeks. Moreover, since extensive field research was being carried out in the area, every occasional data were recorded.

A more detailed description and an evaluation of sampling methodologies is provided elsewhere (Mortelliti and Boitani 2007a). In brief: 26 patches were sampled with all the above mentioned techniques (from March 2005 to February 2006); we applied occupancy models (MacKenzie et al. 2002) to scent-stations detection history data and compared the estimate of proportion of sites occupied with the proportion of sites where the species was found with the other methodologies (track and signs surveys and camera trapping). Similar estimates were obtained for the beech marten, suggesting that the distribution estimate was relatively unbiased (Mortelliti and

Boitani 2007a). On the contrary scent-stations data, even when treated with the occupancy models, provided biased occupancy data (underestimation) for badgers. Following these results, surveys during the second year (patches 27–39) were continued only with field signs and camera traps (Appendix 1). The badger signs of presence are rather conspicuous, easy to identify and scattered throughout the territory and have successfully been used in the past to study abundance and distribution of this species (Tuytens et al. 2001, Sadlier et al. 2004).

Distribution data and spatial autocorrelation

Binary response data (use – non use of a patch) was modelled as a function of explanatory variables through the logistic model using software Spss (SPSS Inc., Chicago, IL, USA). Residuals were tested for spatial autocorrelation using Moran I test implemented in the software SAM 1.1, using a Monte Carlo randomisation test (999 permutations) (Rangel et al. 2006).

Resource availability explanatory variables

We used direct and indirect methods to estimate resource relative abundance in the sampling sites. Resources were divided into three categories: small mammals, fruit, terrestrial invertebrates. This subdivision was based on the available bibliography on the diet of the target species in the study area (Serafini and Lovari 1993; Genovesi 1993; Melis et al. 2002; Genovesi 2003; Genovesi and De Marinis 2003).

Rodents were live-trapped using Sherman trap transects (Sherman Traps, Tallasee, Florida), 10 traps per transect (trap distance = 10 m), the number of transects being proportional to patch size. Trapping was carried out once per season (Spring, Summer, Autumn, Winter), for a total of 22,390 trap nights. Traps were baited with a mix of peanut butter, sunflower seeds, flour, fish liver oil. Further details on rodent sampling are provided in Mortelliti and Boitani (2007b). A rough index of *Apodemus* annual abundance was calculated as the number of unique individuals caught / total number of trap nights.

We used insectivore (shrew) abundance as a surrogate indicator of terrestrial invertebrate abundance.

Shrews mainly feed on a wide variety of terrestrial invertebrates (e.g. earthworms, Carabidae) (Churchfield 1990; Churchfield and Rychlik 2006). Shrew abundance has been found to be positively related with invertebrate abundance (Holling 1955; Platt and Blakley 1973; Butterfield et al. 1981; Churchfield 1990; Innes et al. 1990); Shore and MacKenzie (1993) report correlation coefficients for *Sorex minutus* and different invertebrate preys (range 0.47–0.74 $P < 0.1$; $R^2 = 0.911$, $P = 0.027$ for multiple regression model of total invertebrate abundance and lime presence/absence on shrew abundance), Santillo et al. (1989) found a significant reduction ($P < 0.01$) in overall shrew abundance after reduction in invertebrate density. Shrews were trapped with permanent pitfall traps made from plastic water bottles activated for 12 months. A rough index of annual shrew abundance was calculated as the number of unique individuals caught/number of traps. Removal trapping was necessary since a pilot study showed that live trapping in the area was extremely difficult due to low capture probability and low survival in traps; moreover, in this way accurate species identification through skull examination was possible (necessary for co-occurring studies). The number of pitfall traps was proportional to patch size, from a minimum of 3 to a maximum of 30. Less than 0.7% of available patches in the area were sampled so we strongly believe our sampling had no significant impact on the populations. Necessary permits were obtained: Regione Toscana prot. 123/17035/152.

Since the majority of understorey shrubs of the termophilous *Quercus pubescens* forests are constituted by fruit-bearing shrubs (*Rubus*, *Malus*, *Sorbus*, *Rosa*, *Prunus*, *Pyrus*, and *Juniperus*; Arrigoni 1998), we used the sum of shrubs and *Juniperus* cover as a proxy for fruit relative abundance. Cover was estimated in quadrat plots (number of plots proportional to patch size).

Patch and landscape structure explanatory variables

We measured variables at the patch, patch neighbourhood and landscape scale. A list of variables is shown in Appendix 2. Patch and landscape variables were tested for correlation using Spearman correlation coefficient. We followed two approaches to

tackle potential collinearity problems: (1) explanatory variables were aggregated through Principal Component Analysis (hereafter PCA); only interpretable components were retained as explanatory variables; (2) single variables (e.g. proximity index) were used as distinct predictors, together with other variables in the model (e.g. patch size). We used residuals of patch size regressed on proximity index to obtain a new variable accounting for habitat amount not correlated with the proximity index (see McGarigal and Comb 1995 for an application). It should be underlined that such use of residuals does not allow us to separate the joint variance of the two correlated variables (Freckleton 2002; Koper et al. 2007). However, simultaneous use of both predictors in the model, retains all the covariance, avoids collinearity but, as a drawback, does not allow clear separation of their effects.

Both patch neighbourhood and landscape variables were measured within various threshold distance classes: 500, 1,000, 1,500, 2,000 meters (edge to edge distance), and a 150, 300 and 500 ha buffer around patches. Since only slight differences occurred in the model fit, we here report results of the 1,000 m distance class—a scale compatible with average travelling distances of the studied species (Van Apeldoorn et al. 1998; Rondinini and Boitani 2002) - and 500 ha as a landscape buffer.

Model selection

We followed an information-theoretic approach for model selection. Models were first ranked according to AICc (second order Akaike Information Criteria) values. We then calculated $\Delta AICc$ and Akaike weights (Burnham and Anderson 2002).

We calculated Nagelkerke R^2 as a goodness-of-fit measure; departure from the logistic model was assessed through the Hosmer- Lemeshow test on the global model (Hosmer and Lemeshow 2000).

Results

Distribution data

We found beech marten and badger in 43% and 46% of the sampled sites, respectively. The two species

co-occurred in 13 sites. Other carnivores found were: fox (*Vulpes vulpes*), domestic cats (*Felis silvestris f. catus*) and pine marten (*Martes martes*); the latter was found only in the continuous areas (sites 27, 38 and 39; Appendix 1).

Principal components analysis

Through the PCA we aggregated variables in a component that explained 84.26% of variance; factor loadings are shown in Appendix 2, factor scores in Appendix 1. The component describes the size and the neighbourhood of the focal patches creating a gradient from big non isolated patches, to big relatively isolated patches, to smaller non isolated patches to small isolated patches.

Relative resource abundance

Small mammals (*Apodemus* sp) and fruit-bearing shrubs were found in every patch, with variable abundance (Table 1). Shrews were not captured only in 25% of patches; in 4 of these (sites 22, 27, 38, 39) wild boars (*Sus scrofa*) repeatedly inactivated pitfall traps, therefore no captures occurred. A co-occurring study on barn owl pellets (Mortelliti et al. 2007) revealed that shrews were present in these sites, therefore a capture index of 0 is not reliable.

Resource variables were not correlated with patch size and isolation variables (Spearman correlation coefficient, Table 1). We also tested if resource abundance differed among patch size-isolation classes using the Kruskal–Wallis test with the following patch size-isolation classes: small isolated ($pn_{1000} < -0.35$), small less isolated ($-0.35 < pn_{1000} < -0.1$), big relatively isolated ($= 0.1 < pn_{1000} < 0.00$), and large non-isolated ($pn_{1000} > 0$). No

significant difference was found for fruit cover ($\chi = 3.78$, $df = 3$, $P > 0.05$, $N = 39$); *Apodemus* sp abundance ($\chi = 3.25$, $df = 3$, $P > 0.05$, $N = 39$) and insectivore abundance ($\chi = 3.27$, $df = 3$; $P > 0.05$, $N = 34$).

Distribution models

The top ranked beech marten regression model found that probability of presence was related to fruit abundance ($\beta = 69.92$; $SE = 47.58$) and the PCA patch component ($\beta = 5.65$; $SE = 4.64$; Table 2). This model had a high goodness of fit ($R^2 = 0.945$) and was not affected by spatial-autocorrelation (Fig. 2).

Probability of beech marten's presence increased with relative fruit abundance and decreased from large non-isolated patches, to "large relatively isolated patches", to "smaller non isolated patches" to "small isolated patches" (Fig. 3). The other candidate models ($\Delta AICc > 10$) received little support in the model selection procedure (Burnham and Anderson 2002). Modeling beech marten probability of presence expressed as a function of fruit cover, while controlling for patch size and isolation, predicted that increasing resources would increase presence probability in relatively small and isolated patches (e.g. factors 0.1–0.4, Fig. 3). A threshold occurred (factors 0.5–0.6) where even extremely high values of fruit cover (e.g. 7) were not predicted to increase presence probability to relatively high values.

Since preliminary analyses revealed that insectivore abundance was an important explanatory variable for badger distribution, we did not include sites 22, 27, 38, 39 in the analyses (that is the continuous areas and patch 22), since, as explained before, the capture index is not reliable due to wild boar inactivation of the traps.

Table 1 Results for the Spearman correlation coefficient on resource abundance and patch size (log_ha), patch isolation (pi_1000) and the patch and neighbourhood factor (pn_1000). In the first column are reported the range of values for the

resource covariates in studied patches, mean and standard errors are reported in the second column. In the last three columns are reported Spearman correlation coefficients with P value in brackets

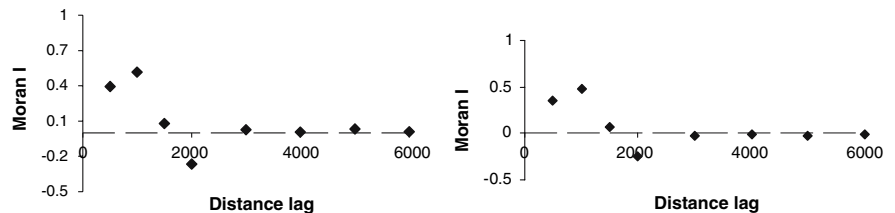
	Range	Mean and SE	Patch size (log_ha)	PI_1000	Pca_factor 1000
Fruit cover	0.65–7.08	2.93 (1.24)	0.109 (0.51)	−0.032 (0.84)	0.052 (0.75)
<i>Apodemus</i> sp abundance	0.01–0.21	0.07 (0.048)	0.16 (0.31)	−0.12 (0.43)	−0.22 (0.16)
Insectivore abundance	0–2.8	0.72 (0.72)	0.23 (0.15)	−0.079 (0.63)	−0.127 (0.43)

Table 2 Top logistic regression model set to predict beech marten and badger probability of presence in woodland patches. Models are ranked according to AICc and may be compared using Δ AICc

Model form	-2LL	Δ AICc	w	R ²
<i>Martes foina</i>				
PCA_factor 1000 + fruit cover	5.96	0	1.00	0.945
PCA_factor 1000	19.04	10.73	0.00	0.788
PCA_factor 1000*fruit cover	41.92	33.6	0.00	0.352
Fruit cover	45.67	37.35	0.00	0.252
Edge density 300 ha	53.83	43.73	0.00	0.06
Class Area 300 ha	53.68	45.37	0.00	0.005
<i>Apodemus</i> abundance	53.70	45.39	0.00	0.004
Index_Insect.	53.82	45.51	0.00	0.000
<i>Meles meles</i>				
Patch size resid + PI_1000*index_insect	24.60	0	0.58	0.641
Patch size resid + PI_1000*index_insect + Fruit cover + <i>Apodemus</i> abundance	20.31	0.99	0.35	0.723
PCA_factor_1000	31.08	4.08	0.05	0.497
PI_1000*index_inset	34.15	7.15	0.02	0.418
PI_1000	39.21	12.21	0.00	0.27
Patch size resid	42.01	15.16	0.00	0.183
Fruit Cover + <i>Apodemus</i> abundance	46.87	22.26	0.00	0.09
Class Area 300 ha	46.78	22.18	0.00	0.013

Goodness-of-fit was assessed with Nagelkerke R². PCA-factor = principal component analysis factor; PI_1000 = proximity index with a 1000 m threshold; Index_insect. = insectivore abundance index; patch size resid = residuals of patch size regressed on proximity index; class area = residual habitat in 300 ha landscape

Fig. 2 Moran I correlogram of residuals from first ranked logistic model for the beech marten (left) and badger (right). None of the values was statistically different from 0 ($P > 0.05$)



The top ranked badger regression model found that badger probability of presence was related to patch size residuals ($\beta = 2.84$; $SE = 2.27$) and interaction of proximity index and insectivore abundance ($\beta = 5.70$; $SE = 2.75$); the second ranked model also includes rodent abundance and fruit cover (Table 2). Both models have high goodness of fit ($R^2 = 0.641$ and $R^2 = 0.763$ respectively). The other candidate models show considerably less support when compared to the first: Δ AICc > 4 (Table 2).

In Fig. 4a we represent badger probability of presence expressed as a function of the insectivore abundance index (proxy for terrestrial invertebrates abundance) controlling for patch isolation. In Fig 4b, inversely, we represent badger probability of presence expressed as a function of patch isolation controlling for insectivore abundance index. The model predicted that increasing resources would

increase presence probability in relatively small and isolated patches (e.g. PI = 0.4, Fig. 4a). A threshold occurred (e.g. PI = 0.05) where even extremely high values of insectivore abundance index (e.g. 2.8) were not predicted to increase presence probability to relatively high values. An examination of Fig. 4b leads to analogous conclusions: non isolated patches but with low resource abundance will still have low probability of presence values.

No significant autocorrelation was found on the residual of the first ranked model (Fig. 2), consequently no spatial autocovariate was introduced (e.g. Lichstein et al. 2002).

The Hosmer-Lemeshow test on the global model for both species showed that data did not depart from a logistic regression model (beech marten: $\chi^2 = 8.42$, $df = 8$, $P = 0.394$; badger: $\chi^2 = 7.87$, $df = 7$ $P = 0.344$).

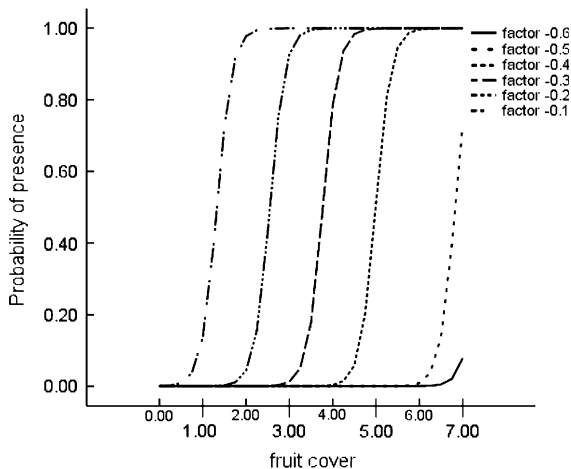


Fig. 3 Beech marten probability of presence expressed as a function of fruit cover controlling for patch size and isolation. Each line represents a fixed factor value: factor -0.6 equivalent to patch 4 or 30 corresponds to an extremely small and isolated patch while factor -0.1 corresponds to a relatively big and non isolated patch, equivalent to patch 37. An increase in resources can increase probability of presence in relatively small and isolated patches, but after a certain threshold (e.g. factors -0.5 and -0.6) even extremely high values of fruit cover will not increase probability of presence to relatively high values

Discussion

Our results show how both spatial features (patch and patch neighbourhood characteristics) and resource availability determine patch use patterns of the badger (*Meles meles*) and beech marten (*Martes foina*) in a patchy landscape in the Province of Siena, central Italy. Interestingly we did not find signs of presence in the smallest and most isolated patches, despite availability of resources: this could suggest a costs/benefits trade-off or lower chances of remote patches being sighted by animals. These results have clear implications not only for the biology of the species but also for connectivity assessment.

Reliability of field data

Our field survey included a variety of methods which, if used concurrently, can provide reliable distribution estimates, for the two examined species in our study area (Mortelliti and Boitani 2007a). Scent stations and field signs are often used to monitor badgers and martens both in continuous (Wilson and Delahay 2001;

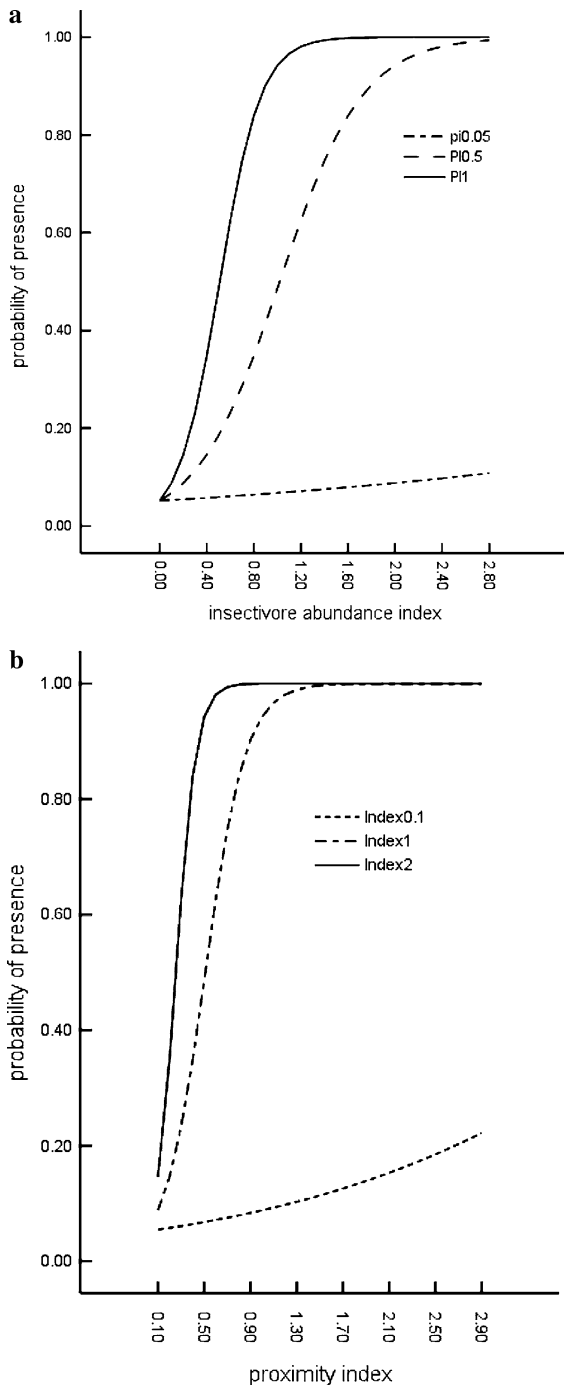
Zielinski and Stauffer 1996, Barea-Azcon et al. 2007) and patch-level studies in fragmented landscapes with similarly sized sampling sites (e.g. Crooks 2002; Virgós et al. 2002). Caution should be exerted since smaller patches, if visited for shorter time periods by animals, could have less chance of “receiving” a field sign. However, the variety of methodologies we have adopted (particularly scent-stations and camera trapping), the extended period of sampling and allocation of visits (high number of repeated visits each season), together with the peculiarity of the clayish soil surrounding patches (ease of finding/recognising the prints), strongly support that we had high chances to detect occasional visits. Nevertheless, rather than non-use of a patch it should more realistically be underlined that sporadic visits in the smaller patches could have occurred and been non-detected. This, however, would not affect our conclusion, as will be discussed later.

Estimation of resource abundance was either direct (*Apodemus* sp) or using proxies (e.g. insectivore abundance as an indicator of terrestrial invertebrate abundance). No correlation was found between resources variables. We acknowledge a potential lack of suitability of invertebrate abundance estimation, since the positive relation between insectivore and invertebrate abundance was based on the literature and not directly verified in our study area. Future studies should attempt a more direct estimation of resources, particularly if a straightforward application to management problems is planned.

Beech marten models

The first model fits particularly well to the data, as confirmed by high values of Nagelkerke R^2 ; Akaike weights provide substantial evidence for it when compared to the others. Therefore both patch size/isolation and resource relative abundance contribute to the determination of the beech marten’s patch use. The preference of beech marten for relatively big non isolated patches has been previously found (Virgós and Garcia 2002), and radiotracking showed how arable land is a seldom traversed barrier by beech martens (Genovesi 1993; Herrmann 1994; Rondinini and Boitani 2002).

The second ranked prey items in diet studies (Genovesi 1993; Serafini and Lovari 1993) are *Apodemus* mice, that are relatively abundant in all



the patches. In smaller patches populations of *Apodemus* occasionally face local extinctions in spring-summer (Mortelliti, unpublished data) and may therefore be a less reliable (unpredictable) resource, thus not crucial in determining patch use. Fruit is a seasonal item, but dietary studies show how

◀ **Fig. 4** (a) Badger probability of presence expressed as a function of abundance of insectivores (proxy for terrestrial invertebrate abundance) controlling for patch isolation (proximity index with 1000 m threshold). Patch size residual was held constant = 0.4. Each line represents a fixed patch isolation value (0.05 = high isolation, 1 = medium isolation, 2 = low isolation). Increasing resource abundance can increase probability of presence in relatively non isolated patches, but after a certain threshold (e.g. proximity index = 0.05) even extremely high values of resource abundance (such as 2.8, observed only in patch 15) cannot lead to high values of probability of presence. (b) Badger probability of presence expressed as a function of proximity index controlling for insectivore abundance (proxy for terrestrial invertebrates abundance). Patch size residual was held constant = 0.4. Each line represents a fixed insectivore abundance index value (0.1 = low, 1 = intermediate, 2 = high). A decrease in isolation (increasing proximity index) can increase probability of presence in patches with higher resource abundance, but after a certain threshold (e.g. shrew abundance = 0.1) decreasing isolation cannot lead to high probability of presence values

fruit is consumed even during the winter moreover some berries, such as *Juniperus* berries, are available all year round since they are extremely slow in decomposition. A seasonal shift to *Apodemus*, available in most patches during the winter, is possible; it is important to note that, through the analysis of scent-stations only data, we were not able to identify seasonal patterns of patch use. The modelling exercise in Fig. 3 shows how, within certain limits of patch size/isolation, an increase of resources could lead to an increase in patch probability of presence, but also that the smallest and most isolated patches will never reach high presence probability despite an increase in resources.

An interesting field of investigation could be a possible inter-patch seed dispersal operated by the beech marten, dispersal of *Juniperus thurifera* by the beech marten is discussed by Santos et al. (1999).

Badger models

The first ranked model expresses probability of badger presence as a function of two non correlated but strictly related variables. The probability of presence increases with increasing patch size or, more specifically, with residuals of patch size regressed on the proximity index (that accounts only for the variance explained by patch size *per se* -see Koper et al. (2007) and Freckleton (2002) for discussion). The probability of presence also depends

on the interaction between proximity index and insectivore abundance, that is, probability of presence is higher in patches that are relatively rich in resources and non isolated: more accessible resources. Again, the proximity index includes, also, the joint variance of both variables (patch size and isolation).

Patch isolation, size and habitat type have been found to influence badger presence or abundance (Virgós 2001; Virgós et al. 2002). Our results extend previous findings by showing how the isolation of resources (invertebrate abundance) can determine probability of patch use. In addition to invertebrates, fruit and *Apodemus* sp abundance both contribute to a better fit of the model.

The most interesting result with clear implication for connectivity is the fact that resource-rich patches (e.g. patches number 4, 9 and 19, Fig. 2) may not be visited due to their isolation, which from an animal ecology perspective can suggest a trade-off of costs/benefits of reaching the patch and/or the possibility of being sighted of remote patches. The dispersion of resources is known for being an important factor both for territory size (increase of home-range size with higher resource dispersion) and sociality of the badger (*resource dispersion hypothesis*: Macdonald 1983; Rodriguez et al. 1996; but see Revilla 2003 for debate).

Comparison of the two species

The two examined species showed similar response to relative abundance of food resources, with the difference that the badger showed higher capability of using smaller-non isolated patches (Appendix 1). This could depend on many possible reasons: resource absolute abundance (that will depend also on patch size), different characteristics of the resources (higher density of invertebrates in smaller patches relatively to fruit or higher trophic value) or matrix tolerance. Testing such hypothesis will require further studies, possibly combining diet and radio-tracking data.

Scale of the study

Patch use data has been widely used as an indicator of species sensitivity to fragmentation (Crooks 2002) we

believe it is the appropriate scale to examine individual's response to landscape structure. Following categorisation of McGarigal and Cushman (2002) our study can be defined as a patch-landscape scale study: the patch is the experimental unit but independent variables include landscape structure within a specified "neighbourhood" distance surrounding patches. Landscape level explanatory variables were never included in our top models, rather patch neighbourhood (e.g. patch isolation measures). Patch isolation measures have been tested by various authors (Hargis et al. 1998; Bender et al. 2003): area-informed metrics (such as proximity index) seem to perform better (Bender et al. 2003).

We did not attempt to disentangle the effects of patch size and isolation. Feasibility and methodologies for such separation are currently debated (see Fahrig 2003; Koper et al. 2007 for discussion). We believe that in our case this separation may not be so important, if one realistically considers that in a patchy landscape most considerably isolated patches will be small (and viceversa), therefore the two above mentioned aspects will occur concurrently.

Implication for connectivity implementation

Our results show how resources complement patch size and isolation as factors influencing species perception of fragmented landscapes. We agree with Paquet et al. (2006) that patch size probably means higher absolute abundance of resources, therefore in the smallest and relatively isolated patches the amount of resources may be crucial in determining its choice as foraging area. The relationship between patch size and resources (variety and abundance) is well discussed in the literature (see Forman 1995; Lindenmayer and Fischer 2006).

Implementation of functional connectivity in fragmented landscapes should incorporate resource assessment. This is seldom done, mainly due to the GIS-based approach often used (e.g. Bani et al. 2002) symptomatic of bias towards structural connectivity (Taylor et al. 2006). With such an approach there is a concrete risk, however, to miss some important aspects of the biology of the species.

The important take-home message comes from Figs. 3 and 4a–b, that show how, within certain structural limits, by modifying relative amounts of

resources and their distribution, it is possible to increase probability of presence in smaller/relatively isolated patches. Conversely, there are certain thresholds above which even an increase in resources will not achieve relatively high levels of probability of patch use. This has important consequences particularly for highly fragmented landscapes in areas where it may not be always possible to increase patch sizes and/or reduce isolation; thus, for instance, forest regimes that will increase resource availability (in this case increase of shrub cover and terrestrial invertebrates) could be implemented. Clearly this practice should not be alternative to halting habitat fragmentation, but supportive to habitat restoration.

From a broader perspective, our results support the fact that patch quality should be considered when studying the distribution of species in fragmented landscapes (Fleishman et al. 2002, Holland and Bennett 2007); this highlights the fact that the vision of binary landscapes (patch - matrix) is not adequate to approximate the more complex perception of animals (Fischer and Lindenmayer 2007).

To understand the underlying mechanisms determining mammals' response to landscape structure and quality we envisage a combination of field sign surveys and radiotracking that will help to understand the extent to which perceptual range (the possibility of remote patches being sighted) may act as a determinant of patch use (Zollner and Lima 1999; Schooley and Wiens 2003) or costs/benefits tradeoffs determine exploitation of remote resource-rich patches.

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Appendix 1 Carnivore distribution and patch characteristics

Summary of the distribution of beech marten and badger in the sampled patches, including patch size and one measurement of patch isolation (proximity index, threshold 1,000 m). 0 = not found, 1 = detected. Scent-stations were used only for sites

1–26. Patch location (by ID in first column) is shown in Fig. 1

Patch ID	Hectares	Proximity index (1,000 m)	PCA component (1,000 m) factor scores	Beech marten (<i>Martes foina</i>)	Badger (<i>Meles meles</i>)
1	0.48	0.12	-0.45	0	0
2	0.41	0.23	-0.41	0	0
3	1.38	0.24	-0.31	0	1
4	1.32	0.01	-0.58	0	0
5	1.53	0.00	-0.79	0	0
6	0.85	0.58	-0.33	0	0
7	1.15	0.51	-0.25	0	0
8	1.80	0.21	-0.29	0	1
9	2.20	0.01	-0.52	0	0
10	2.24	0.00	-0.59	0	0
11	2.22	0.14	-0.33	0	0
12	2.15	0.36	-0.30	0	0
13	4.51	0.14	-0.28	1	0
14	3.86	0.15	-0.27	1	0
15	5.09	0.15	-0.28	0	1
16	3.56	0.07	-0.35	0	0
17	6.37	0.02	-0.34	1	0
18	8.59	0.25	-0.15	1	1
19	8.17	0.08	-0.27	0	0
20	15.65	0.91	-0.04	1	1
21	14.79	0.94	-0.05	1	1
22	20.85	1.28	-0.01	1	1
23	27.27	0.13	-0.10	1	1
24	53.00	4.92	0.37	1	1
25	65.56	29.22	0.61	1	1
26	79.86	0.21	-0.01	1	1
27	30,000	30.00	3.33	1	1
28	0.32	1.17	-0.31	0	0
29	1.07	0.05	-0.46	0	0
30	1.39	0.00	-0.63	0	0
31	2.43	0.11	-0.33	0	0
32	2.52	0.03	-0.51	0	0
33	3.00	0.06	-0.38	0	1
34	4.43	0.30	-0.21	1	0
35	7.72	0.00	-0.58	0	1
36	8.16	0.86	-0.13	1	1
37	101.72	2.44	0.13	1	1
38	8000	30.00	3.22	1	1
39	27,500	30.00	3.32	1	1

Appendix 2 Covariates

List of covariates used as predictor variables for the logistic regression models. Covariates are patch attributes measured in a sample of 39 patches in the Province of Siena, central Italy

Covariate types	List of covariates
Patch geometry (variables measured in metres or hectares and log-transformed)	Patch size; patch shape (Area/perimeter); average edge distance (in metres) of patches within 1000 m (<i>dist_1000</i>), sum of the areas of the patches within 1000 (<i>sum_1000</i>); proximity index (<i>PI_1000</i>); Mean Proximity Index (<i>MPI_1000</i>); distance to nearest farm; distance to nearest non-fragmented area
Resource availability/abundance (shrub cover was estimated according to Braun-Blanquet classes)	<i>Apodemus</i> sp abundance index, insectivore abundance, fruit (shrubs and <i>Juniperus</i> sp)
Patch and neighborhood PCA factor (1000 m) (factor loadings in brackets)	Log_ha (0.924); <i>sum_1000</i> (0.809); <i>dist_1000</i> (–0.961); <i>PI_1000</i> (0.916); <i>MPI_1000</i> (0.972)
Landscape scale variables	Residual habitat cover (<i>class area</i>), edge density, mean shape index, median patch size

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