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Marten in highly fragmented landscapes.

MARTEN in the matrix: the importance of non-forested habitats for forest carnivores in fragmented landscapes.

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The intervening landscape between patches of forest (i.e. the ‘matrix’) has enormous potential to mitigate the negative effects of forest fragmentation. However, to release this potential requires greater understanding how individual species perceive the matrix. Here we investigated use of the matrix by pine marten *Martes martes* in a region with low forest cover (Scotland). We radio-tracked 11 marten to determine their habitat preferences, then combined our data with those published from 5 additional Scottish landscapes to examine how home-range size and diet varied with forest edge density, i.e., fragmentation. Our tracking showed that although mature forest was the most preferred habitat, certain matrix habitats (scrub and tussock grassland) were also consistently selected. These 2 habitats provided marten with fundamental resources that are of limited availability within intensively managed plantation forests: den sites and primary prey (*Microtus* voles). The smaller-bodied female marten were more risk-averse than males, avoiding habitats that lacked structural cover near the ground (moorland, agricultural pastures and closed-canopy forest), suggesting that structural complexity is important in maintaining functional connectivity within landscapes. Our synthesis of data across landscapes indicated that marten benefit from supplemental resources in matrix habitats; consumption of small mammals increased with fragmentation and coincided with an initial increase in marten density. However, marten population densities decreased once fragmentation passed a threshold level. Our results demonstrate that habitat complementation at the landscape-scale is essential for some forest-associated species. Resource supplementation from the matrix may be particularly important in regions with a long history of low forest cover or where forest cover is now dominated by afforested plantations, which may lack essential resources.

Keywords afforestation, functional connectivity, habitat complementation, habitat selection, home range, *Martes martes*, foraging ecology, plantation, resource subsidy, Scotland.

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Conceptual models of forest fragmentation that contrast ‘habitat’ patches with a uniformly unsuitable ‘matrix’ (i.e. the ‘non-habitat’ surrounding habitat patches) ignore the importance of heterogeneity within the matrix (Kupfer et al. 2006). While binary fragmentation models may be appropriate for some forest-specialists, for many species the matrix forms a continuum of habitats of varying permeability (Haila 2002; Fischer et al. 2004). Matrix permeability is determined by the structural similarity between matrix habitats and remnant habitats, the perception of which is both species- and context-dependent (Kupfer et al. 2006). As ecological processes within remnants (such as dispersal and foraging) vary as a function of their surroundings, the matrix has great potential to mitigate the negative effects of habitat loss and fragmentation (Dunford and Freemark 2004). Functional connectivity may be maintained even within highly fragmented landscapes depending on how an organism perceives and responds to the intervening matrix between remnants (Ricketts 2001; Bélisle 2005). In some cases, the matrix may provide alternative or supplementary resources (e.g., food or nest sites) that support greater population densities than would be expected within remnants alone ('habitat complementation' e.g., Andrén 1994). Ignoring the ecological qualities of the matrix may therefore result in a gross underestimation of its importance to organisms within remnants, and its potential to serve as functional habitat. To better understand how wildlife populations persist within fragmented landscapes, it is necessary to determine if, how and why animals utilize matrix habitats.

The European pine marten *Martes martes* is often described as a forest-dependent specialist of late-successional forests, an association that may be partly due to a large number of marten-habitat studies occurring within the forest-dominated landscapes of Fennoscandia (Lindström 1989; Brainerd 1990; Storch et al. 1990; Kurki et al. 1998), and to implied similarities with congeneric American marten (*M. americana*) within the equally forested regions of North America and Canada (e.g., Buskirk and Powell 1994). The landscapes of western Europe are much less forested however (FAO 2003), yet marten are present here, occurring in landscapes with as little as 4 % forest cover (Balharry 1993). Though their habitat preferences are much less studied, research has indicated that marten in this region are less dependent on forests than marten elsewhere in their range (e.g. Pereboom et al. 2008). In Scotland for instance, where forest covers just 17 % of land area (Malcolm et al. 2001), the marten’s primary prey are *Microtus agrestis* (Lockie 1961; Balharry 1993; Caryl 2008), a species of vole that is characteristic of open tussock grassland and is absent from forest interiors (Hansson 1978). By contrast, forest-dwelling *Clethrionomys* voles are regarded as the marten’s most important prey throughout the more forested regions of temperate and boreal Europe (Zalewski 2004). Understanding how marten utilize different matrix habitats may facilitate conservation management of this species in regions where forest cover is low. Yet despite this dietary indication that marten are utilizing the non-forested matrix, previous research on habitat use by Scottish marten has focused on their use of forest habitats while treating the matrix as uniformly unsuitable (Balharry 1993; Halliwell 1997).

In this study we investigated how both forest and matrix habitats are utilized by marten by measuring the structural and trophic components of habitats occupied by marten. Predation and winter severity are major limiting factors to European marten populations that directly influence marten habitat selection (Helldin 1998; Zalewski and Jędrzejewski 2006). We therefore predicted that marten would select structurally complex habitats, regardless of whether forest or matrix, which provide protective cover from predators and temperature extremes (Buskirk and Powell 1994). We also predicted that marten would select habitats in which their preferred prey was found (i.e., tussock grassland: Caryl 2008). Matrix permeability is often related to the body size; smaller-bodied species tend to be more prone to predation in the matrix, while large-bodied species view the matrix as less of a barrier to movement (Gehring and Swihart 2003). As there is considerable sexual size dimorphism among *Martes* species, we predicted that the smaller-bodied females would be more risk-averse than males and would avoid those habitats that offered the least structural protection from predators.

Habitat loss and fragmentation are landscape-scale processes, yet few studies of their effects on populations of European mammals have been conducted at an appropriate scale (i.e., where individual landscapes are the study units: Mortelliti et al. 2010). To better understand the landscape-level effects of habitat loss and fragmentation on marten populations, we compiled data from previous studies to investigate how marten diet and population density varied among landscapes with differing amounts of forest cover and forest edge densities (the latter as a measure of fragmentation). Marten populations are vulnerable to fragmentation (Bright 2000), yet increased foraging opportunities in forest gaps may allow population densities to increase with low levels of fragmentation provided that forest habitats remain sufficiently connected, though a sharp population decline is expected once fragmentation reaches a threshold level (Brainerd 1990; Thompson and Harestad 1994).

MATERIALS AND METHODS.

Study area.— The 6000 ha study area was located around Morangie forest, a managed coniferous plantation in NE Scotland, UK (57.8°N, 4.1°W). The surrounding landscape has a low human population density (5 people per km^2) and comprises farmland, woodland and open heath uplands, with elevations ranging 0-400 m a.s.l. The region has an oceanic climate with cool, wet summers (July mean = 13°C) and mild winters (February mean = 0°C: MetOffice, 2008). The forest, which covers around 3000 ha, is dominated by first rotation stands planted on formerly bare ground (61 %) with fewer stands on historically wooded land (34 %, of which just 4% has been continuously forested since c.1900). Lowland areas are dominated by thinned stands of native *Pinus sylvestris* that contain dense ground cover by *Calluna vulgaris* - *Vaccinium myrtillus* heath. Exposed uplands are dominated by unthinned stands of exotic conifers (e.g., *Pinus contorta*, *Picea sitchensis*) managed on a large-scale clear-fell and replant system. Deciduous trees (e.g., *Betula pendula*, *Sorbus acuparia*) are patchily distributed throughout the forest. Shrubby species (e.g., *Ulex europeaus*, *Rhododendron ponticum, Salix* spp.) frequently encroach into open areas. Unplanted areas are dominated by heaths of blanket bogs (e.g., *C. vulgaris* - *Eriophorum vaginatum*) and moorland grasses (e.g. *Nardus stricta*, *Molinea caerulae*) at higher elevations, and by damp grasslands (e.g. *Holcus lanatus* - *Deschampsia cespitosa*: all communities according to Rodwell 1998) at lower elevations.

Marten capture and telemetry.— Between January 2006 and July 2007 we set cage traps (Tomahawk Live Trap Co., WI, USA) at pre-baited locations along forest roads throughout the study area. Captured marten were immobilized with an intramuscular injection of Ketalar and Domitor, antagonized by Antisedan (Pfizer Inc. NY, USA), using dosage rates recommended for similarly sized mustelids (Fournier-Chambrillon et al. 2003). Captured animals were weighed and aged (juvenile or adult ≥ 1 year) according to body size and tooth wear. Adult marten were fitted with VHF-collars (TW-3, Biotrack Ltd., Dorset, UK) and uniquely identified with a passive transponder implanted subcutaneously to the neck. All trapping and handling was carried out under license from Scottish Natural Heritage (Scientific License No.6146) and the British Home Office (PIL60/10174). One animal was tracked per night, on foot or by car, for up to 16 hours. Marten locations were estimated at intervals of at least 20 minutes with simultaneous biangulations. Preliminary tests showed the mean accuracy of this method was 55 m (SE = 9 m) and mean bearing error was 12˚ (SD = 10˚: Zimmerman and Powell 1995). We used Locate III software (Nams 2006) to estimate animal locations and 95 % confidence ellipses from biangulations. Locations with confidence ellipses > 10 ha were excluded from further analysis. Remaining locations had confidence ellipses of 2 ± 0 ha, 58 % of which were ≤1 ha. We entered marten locations into ArcView®GIS (ESRI, California, USA) for analysis with the Home Range Extension (Rodgers and Carr 1998). We used a 95 % minimum convex polygon (MCP: Harris et al. 1990) to estimate the home range of each marten. Marten were tracked until plots of home-range size over time reached an asymptote; those that did not were excluded from further analysis.

Habitat mapping.— We defined the study area as the MCP containing the home ranges of all marten buffered by a distance equal to the average length of female home ranges (1.8km). Within the 5902 ha study area land-cover was classified into 7 habitat types based upon ground, shrub and canopy vegetation using forest inventory maps (Forestry Commission, UK), digital land classifications (LCM2000: Land Cover Map 2000, Centre for Ecology and Hydrology, UK), orthorectified aerial photographs (0.5 m^2 resolution taken 2005: Forestry Commission, UK) before being ground-truthed with field visits. We defined 4 matrix habitats where tree canopy <30% (scrub, tussock, heath, agriculture), and 3 forest habitats where tree canopy >30 % (closed-canopy forest, mature coniferous forest, deciduous woodland: Table 1).

Marten habitat selection.— We determined marten habitat use at 2 spatial scales; first comparing the proportion of habitats found within individual home ranges to their availability within the study area based on the number of hectares of each habitat, referred to herein as 'home-range level' selection (Design II: Thomas and Taylor 1990); then comparing the proportion of locations in each habitat with their availability within home ranges, referred to herein as 'location level' selection (Design III: Thomas and Taylor 1990). Locations were differentiated into 'active' and 'static' depending on the marten's physical state when that location was recorded and separate analyses were conducted for each. To ensure independence of static locations, only one static location was recorded per denning event and subsequent locations were disregarded until the animal moved again. Home ranges were defined by the 95 % MCP buffered by a distance of 55 m (our mean telemetry error). Locations were treated as an ellipse rather than a single point, with the habitat of greatest proportional cover considered that 'used' at that location (Nams 1989). As female marten are morphologically and energetically more constrained than males, they may be more selective (Buskirk and Powell 1994). We therefore examined sex-specific habitat selection rather than pooling data across sexes (Garshelis 2000). Habitat preferences and differences in preferences between sexes were examined with Bonferroniadjusted 90% confidence limits (Cherry 1998). To avoid unequal weighting, we randomly selected an equal number of active locations (males: n = 22; females: n = 28) and static locations (n = 8 for both sexes) from each individual (Thomas and Taylor 2006). Selection of critical resources are likely to be less variable than others, so we determined variability in individual selection strategies by calculating resource selection indices (RSI: % habitat use - % habitat available) from non-pooled data (Thomas and Taylor 1990). We used t-tests to determine sex-related differences in home range size and body mass. We also used t-tests to evaluate intersexual differences in the distance travelled by individual marten into the matrix after measuring the mean and maximum distance of locations outside forest habitats. A chi-square test was used to compare the frequency with which each sex was located outside forest habitats.

Forest fragmentation, home range size and marten diet across Scotland.— We examined marten diet and home range size in relation to forest cover and forest edge-density and extent among Scottish landscapes. We used home range data from studies that have investigated marten spatial ecology in Scotland (Balharry 1993; Bright and Smithson 1997; Halliwell 1997), each of which provided dietary data from scat-content analysis conducted simultaneously with tracking within each landscape. In total, we had home range and dietary data for marten in 6 landscapes across Scotland (including our data from Morangie, dietary data for which came from Caryl, 2008: Table 2, Fig. 1).

We standardized the dietary importance of small mammals in each landscape as the frequency of small mammal occurrences in scats divided by the number of scats analyzed within that landscape to account for inconsistencies in reporting results. We provide a relative measure of the density of resident adult marten in each landscape using the mean sex-specific home range size (100% MCP). We take this measure to be the approximate inverse of breeding marten population density assuming that marten display inter-sexual territoriality; that only adult marten defend territories, and that home ranges within each sex abut each other contiguously (Balharry 1993, Caryl 2008). We recognize that high population density does not necessarily indicate high habitat quality (van Horne 1983), but by focusing on adult resident marten we effectively ignore the juvenile, dispersing or transient individuals that often artificially inflate population densities in poor quality habitat.

Forested extent (%) was calculated within a 9.77 km radius (300 km^2 area) from the centre of each site. Data on forest cover were obtained from the LCM2000 digital land-use layer (Fuller et al. 2005). We included land classified as clear-felled to account for changes to forest cover between the year that this data layer was created (2000) and when marten data were collected among studies. We then calculated the density of forest edges per hectare of forest (m ha^{-1}) as an index of forest fragmentation within each landscape. General Linear Models were used to examine relationships between measures of forest cover and fragmentation with small mammal consumption and marten home range sizes among landscapes. For each analysis a quadratic function of forest cover or edge density was included in the starting model to assess whether this provided a better fit than a linear function; this was removed if non-significant. All statistical tests were conducted in SPSS 17.0 for Windows (SPSS, USA) and MS Excel 2007 (Microsoft Corporation, USA). Data were transformed where necessary to achieve normality and equal variance. All averages and coefficients are presented as means with standard errors unless otherwise stated.

RESULTS

We captured and collared 16 adult pine marten (8 males, 8 females), of which sufficient data were collected for 4 males and 7 females to allow home range estimation. A total of 594 locations were obtained, with 50 ± 4 locations per female, and 54 ± 8 locations per male. Female home ranges reached an asymptote after 29 ± 3 locations and males' after 40 ± 7 locations. Un-buffered female home ranges (95 % MCP) were significantly smaller than those of males, measuring 50 ± 1 ha and 353 ± 7 ha respectively ($t_6 = -4.405$, $P = 0.026$). There was considerable body size dimorphism between the sexes; males weighed 1.88 ± 0.7 kg (range = 1.60–2.30 kg), almost 1.4 times heavier than females (1.37 ± 0.4 kg, range = 1.21–1.55 kg: $t_{14} = 6.195$, $P < 0.001$).

Habitat selection.— Marten clearly selected their home ranges from the landscape in a non-random pattern (Table 3; Fig. 2). Both sexes selected the same 3 habitats at the home range level (mature forest, tussock grassland and scrub), while avoiding the same 2 habitats (closed-canopy forest and agriculture: Table 3). In addition, females strongly avoided heath moorland at the home range level, while males avoided deciduous woodland. Individual selection strategies suggested that female aversions to closed-canopy forest, heath and agriculture at the home range scale were universal to all females (Fig. 2a). Males were more variable in their selection patterns, yet agricultural land was universally avoided (Fig. 2b). No universal preferences were apparent at the home range level except that of female selection for tussock grassland.

There were few significant preferences at the location level, suggesting that once habitats were selected from the landscape they were generally used in accordance to their availability

(Table 3). Exceptions to this were that stationary females avoided heath within home ranges, while stationary males avoided deciduous woodland and active males avoided tussock grassland. Individual selection strategies concur that there was much less selection by active marten than at the home range level, with most resources selection indices lying near zero (Fig. 2a). However, there does appear to be an indication of selection by stationary marten, with females having positive RSI for mature forest and scrub and males having positive RSI for mature forest and closed-canopy forest (Fig. 2).

There were intersexual differences in habitat utilization for all habitats at the home range level except scrub and tussock grassland (Table 3). Scrub and tussock grassland were equally selected by both sexes despite their low availability within the study area. Use of all other habitats appeared to follow a general pattern in which females made greater use of forested habitats than males (63.5 ± 5.0 % of home range forested), while males made greater use of matrix habitats than females (47.2 ± 10.5 % of home range forested). For example, females utilized mature forest and deciduous woodland significantly more than males at the home range level, whereas males used heath and agriculture significantly more than females (Table 3). Within home ranges, active females utilized tussock grassland more than males, and active males utilized heath more than females. There were no significant differences in habitat use at stationary locations.

The males' greater proclivity for open spaces was reflected by significant intersexual differences in both the mean and maximum distance travelled outside forest habitats by individuals ($t_9 = -2.601$, $P < 0.05$ and $t_9 = -2.405$, $P < 0.05$ respectively). Males typically travelled 75.1 ± 18.6 m outside forests habitats, up to an average maximum of 199.6 ± 46.3 m, whereas females typically travelled just 30.4m into the matrix, up to an average maximum distance of 93.7 ± 21.1m. Males also travelled outside forested habitats more frequently than females, 46 % of male locations occurred outside forests compared with just 33 % of female locations (χ^2_1= 8.786, $P < 0.005$).

Forest fragmentation, home range size and marten diet across Scotland.— There was considerable variation in the amount of forest cover among landscapes across Scotland, with an order of magnitude between the least (4 %) and most (47 %) forested, which corresponded to an equally variable degree of fragmentation among landscapes (Table 2). Similarly, there was an order of magnitude difference between the largest (33 km^2) and smallest (3 km^2) male marten home ranges. The frequency of consumption of small mammals varied from 0.34 occurrences per scat to 0.93. Small mammal remains were not identified to species at Minnoch and Glen Trool (Bright and Smithson 1997), but *Microtus agrestis* formed an average 80 % (SE = 5%) of small mammals in the diet within the other 4 landscapes. The relationship between small mammal consumption and forest fragmentation demonstrated a strong positive correlation, indicating that as landscapes became more fragmented, small mammals constituted a greater part of the marten diet ($F_{1,4} = 56.77$, $P = 0.002$, $\beta = 0.007 \pm 0.0009$, R^2 adj = 91.8%; Fig. 3a). A strong positive correlation existed between the extent of forest cover and forest edge-density within landscapes (Pearson correlation r = -0.83, P = 0.042, n = 6). Henceforth we only present results in reference to the latter, as edge-density had a greater functional significance in relation to the consumption of small mammals. Male home ranges were logged prior to analysis. As predicted, the relationship between fragmentation and home range size of female marten was non-linear (edge density $F_{1,3} = 25.53$, $P = 0.015$; edge density^2 $F_{1,3} = 26.23$, $P = 0.014$, R^2 adj =

82.9%; n = 6; Fig. 3b) as what that of males (edge density $F_{1,3} = 13.43$, $P = 0.035$; edge density^2 $F_{1,3} = 14.06$, $P = 0.035$, R^2 adj = 71.1%, n = 6; Fig 3c). Marten home ranges were smallest at intermediate levels of landscape fragmentation (where the forested extent lay between 25 and 30%), and increased in size at higher and lower levels of fragmentation. However, we acknowledge that owing to the small sample size these patterns are sensitive to individual points, particularly at the lowest and highest edge densities, and should be viewed with caution.

DISCUSSION

Our results add support to the suggestion that European pine marten, like other marten species (e.g. Hearn et al. 2010), may be less forest-dependent than previously believed (Pereboom et al. 2008; Mortelliti et al. 2010). Though marten demonstrated a strong preference for mature forest, both sexes showed strong selective preferences for 2 matrix habitats within their home ranges: tussock grassland and scrub. The consistent selection of these habitats suggests that the matrix is not only penetrable but utilized by marten. Furthermore, matrix habitats may provide key resources that are unavailable within forest habitats; the most notable of which being *Microtus* voles, the marten's primary prey (Lockie 1961; Balharry 1993; Halliwell 1997, Caryl 2008), which are absent from forest interiors (Caryl 2008).

Matrix habitats that have a high degree of structural contrast with remnant vegetation are less penetrable to species than low-contrast habitats (e.g. Forman 1995). Marten are commonly described as specialists of old-growth forest (Lindström 1989; Brainerd 1990; Storch et al. 1990), and as such all non-forested habitats have typically been considered to be equally hostile.

Yet evidence increasingly suggests that it is the structural elements within forests rather than forest composition or age that most influences marten habitat selection (Brainerd et al. 1994; Payer and Harrison 2003; Poole et al. 2004; Hearn et al. 2010). Many of the structural features associated with old-growth forests (e.g. multi-layered tree canopies, large diameter trees, standing and fallen deadwood, dense understory vegetation) are required by marten because they help to reduce predation threats (Storch et al. 1990), increase foraging efficiency (Thompson and Harestad 1994; Andruskiw et al. 2008), and offer thermally insulated resting sites (Zalewski 1997). However, these structural legacies are often not available in regions of the marten's geographic range in which much of the original forest cover was removed many centuries ago. For instance, the majority (76 %) of British forests are secondary, i.e. they occupy ground that has not been wooded until recently, and so possess few of the structural features of old-growth forest (Humphrey 2005). In the absence of suitable structural features it seems that marten in our study area were supplementing the resources required to avoid predation, den, and forage from complementary, low-contrasting habitats within the matrix.

Predator avoidance is an important determinant of marten habitat use (Helldin 1998), and structure near the ground is known to provide protective cover for marten (e.g., Slauson et al. 2007). Female marten are smaller than males and subject to greater predation risk and energetic costs, and are thus likely to be more selective in their habitat choice. We found that females were more reluctant to leave forest habitats than males, and typically moved no more than 100 m outside forest edges. Marten have 2 extant predators within Scotland - the red fox *Vulpes vulpes* and golden eagle *Aquila chrysaetos* (Helldin 1998) – both of which were present within the study area (*pers. obs*.). One similarity among those habitats strongly avoided by female marten (i.e., closed-canopy forest, heath moorland and agricultural fields) was that cover near the ground was either absent or greatly reduced in stature. The high shading beneath closed-canopy stands restricts understory vegetation resulting in a ground cover dominated by bryophytes and needle litter (Hill 1986); exposure and heavy grazing of upland heath often results in compact, low-lying vegetation (Grant and Hunter 1962), while continuous grazing has obvious impacts on agricultural pastures. By contrast, ground vegetation was well established in habitats that were preferred by female marten. Thinning to reduce stem density within mature stands (one of our defining criteria) increases irradiance to the ground resulting in a dense understory similar to that found in semi-natural forests (Wallace and Good 1995; Ferris et al. 2000). Scrub habitats provide essential structural features for many small carnivore species within the agriculturally-dominated landscapes of western Europe (Virgós 2001; Rondinini and Boitani 2002; Pereboom et al. 2008; Matos et al. 2009; Santos and Santos-Reis 2010), and so it is not surprising that this habitat is important for marten within our study area. While the *Holcus-Deschampsia* communities that are typical of ungrazed tussock grassland form characteristic tussocks up to a meter in height (Rodwell 1998).

Resource-limited animals may expose themselves to greater risks in order to acquire resources across habitat boundaries (Bélisle 2005). That marten utilized 2 matrix habitats in addition to mature forest suggests that matrix habitats may provide resources that are unavailable within mature forests alone. The most important prey of Scottish marten are *Microtus* voles (Balharry 1993; Caryl, 2008), which is unusual given that *Clethrionomys* voles are numerically dominant within marten home ranges (Balharry 1993; Caryl 2008) and form the bulk of their diet throughout the marten’s range (Zalewski 2004). *Microtus* voles are denizens of ungrazed tussock grassland (Caryl 2008), which undoubtedly accounts for the selection of this habitat by marten within our study area. Interestingly, females made significantly greater use of this habitat while active than males, which may be indicative of resource partitioning between the sexes. A dietary preference for *Microtus* voles may indicate a behavioral trait that has adapted in response to Scotland’s highly fragmented past during which forest-dwelling *Clethrionomys* would have been scarce. Alternatively, low volumes of coarse woody debris (CWD) within plantations may mean that *Clethrionomys* remain unavailable to marten despite their abundance, as CWD is needed to provide sensory cues to marten as to the location of forest rodents (Thompson and Harestad 1994; Andruskiw et al. 2008). Despite management steps to retain CWD within plantations, even volumes of CWD within mature forest stands remain low relative to old-growth forests (Kirby et al. 1998; Humphrey 2005). It is unclear whether further restoration of CWD within plantations will change the vole preference of Scottish marten, but at present they are supplementing their prey resources with subsidies from the matrix. Marten in our study area also seemed to be supplementing den sites from the matrix. Plantation forests have few of the arboreal cavities that are commonly used as den sites by marten in old-growth forests to provide protection from foxes (Birks et al. 2005). Instead, we found that scrub habitat was being used more at female resting locations (23 ± 6 %) than at active locations (13 ± 8 %), which suggests that it may provide important resting habitat. Ground level dens are unusual for maternal dens (*J. Birks pers. comm.*), yet we observed 4 of the 7 females we tracked (3 of which had young) denning within scrub habitat; specifically 2 beneath dense shrubs (*Ulex europeaus* and *Rhododendron ponticum*) and 2 beneath wind-thrown trees or clear-felled debris, such as piles of branches.

Spatially-subsidized predators (i.e. those that gain resources across habitat boundaries) often have abundances that exceed what local resources would otherwise support (e.g. Andrén 1994). The strong positive correlation we found between the consumption of small mammals and forest edge-density among Scottish landscapes suggests that foraging opportunities for small mammal prey increases where fragmentation results in increased availability of edge habitat. As predicted, this initially supported higher marten population densities, as evidenced by smaller home range sizes. Once forest fragmentation passed a threshold level however, marten populations became limited and their population densities decreased (i.e., home ranges expanded). Unfortunately, because of the small sample size of studies used in our synthesis we were not able to investigate the effect of different land-uses within the matrix. However, the composition and configuration of the matrix will undoubtedly influence processes within landscapes. Previous studies into the effects of forest fragmentation on marten population density in Fennoscandia (Kurki et al. 1998) and North America (Chapin et al. 1997; Hargis et al. 1999) have also not accounted for variation within the matrix. Yet as our results demonstrate, the non-forested matrix is not homogenous from a pine marten's perspective. In fact complementary resources from the matrix may be essential for the completion of their life phases depending on local conditions. Fragmentation effects in landscapes composed of matrix habitats that contrast strongly with remnant vegetation are likely to be worse than those in which the matrix is structurally similar (Forman 1995). Therefore to gain greater insight into the landscape requirements of marten (and indeed other forest-dwelling species) we need to account for a more complex perception of habitats than 'forest vs. matrix'. This is particularly so where the length of time since habitat loss has impacted faunal life-histories, or where remaining forest habitats are secondary.

Much of the forest cover in Scotland today comprises afforested plantations in the closed-canopy stage (Malcolm et al. 2001; Mason 2007), which make poor-quality habitat for marten. In addition, a large proportion of the Scottish landscape is dominated by inhospitable matrix habitats (i.e. moorland and agriculture). The marten's reluctance to cross large areas without cover means that even relatively nearby forest remnants may not be used if they are isolated by unsuitable intervening habitats (Ricketts 2001), and as slow-breeding mammals, marten are particularly vulnerable to local extinctions should functional connectivity be lost (Bright 2000). Strategies for conserving marten in these highly fragmented landscapes should seek to restore old-growth conditions within existing forest stands whilst managing the surrounding matrix to ensure that complementary (i.e., low-contrast) habitats are available. As our results have shown, the matrix has enormous potential to mitigate some of the negative effects of habitat loss and fragmentation that should not be overlooked.

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Figure 1. Left: Outline of Scotland showing pine marten distribution (shaded) and locations of 6 landscapes used to examine differences in fragmentation, diet and marten population density: 1. Kinlochewe (Balharry 1993), 2. Strathglass (Balharry 1993), 3. Novar (Haliwell 1997), 4. Morangie (present study: Caryl 2008), 5. Glen Trool (Bright & Smithson 1997), 6. Minnoch (Bright & Smithson). Right: Detail of forest fragmentation shown as forest (black) against matrix (white). Each landscape covers a circular area of 300 km^2.

Figure 2. Individual selection strategies of habitats at the home range level (white bars), at active locations (pale grey bars) and at static locations (dark grey bars) by female (a) and male marten (b). A reference line (y = 0) indicates habitats are used according to their availability (i.e., no selection), data below this line indicate avoidance; data above indicate preference. Boxes show the median (Q2) and interquartile range (IQR: Q3 – Q1). Whiskers indicate the smallest observation within 1.5 IQR of Q1 and the largest observation within 1.5 IQR of Q3. Points lying outside of this range are considered to be outliers (circle) and extreme outliers (star).

Figure 3. The effect of forest edge density (i.e., forest fragmentation) on marten diet and population density among landscapes (n = 6). A positive correlation exists between forest edge density (m ha^{-1}) and an index of small mammal consumption (a). The mean (± SE) home range size of female (b) and male (c) marten is plotted against forest edge density for six 300 km^2 landscapes. Parabolic trendlines are shown for each relationship which fit the data better than

linear trendlines. Owing to the small sample size however, these patterns are highly sensitive to individual points and should be viewed with caution.