BioOne COMPLETE

All forests are not equal: population demographics and denning behaviour of a recovering small carnivore in human modified landscapes

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Landscapes occupied by recovering carnivore populations in Europe are highly modified by human activity. It is unclear how recovering predators will adapt and sustain populations in highly altered landscapes, with most existing research focused on large carnivores. To address this we contrast population demographics and denning behaviour of a small carnivore, the pine marten *Martes martes*, in a semi-natural wooded landscape and a human-modified landscape with limited forest cover composed of conifer plantation, using radio-telemetry on 20 free-ranging individuals in Northern Ireland. In the semi-natural landscape, martens selected old growth, native forest making almost exclusive use of arboreal dens in living trees and standing deadwood. Martens persisted in the human-modified landscape but with lower population density and recruitment, with a male-biased sex ratio. In the human-modified landscape martens denned in marginal habitats such as scrub, heath and property boundaries, while making use of subterranean or man-made structures for dens in response to a lack of above ground denning opportunities. We demonstrate landscape change-induced differences in behaviour and population structure in a recovering carnivore. The results highlight the importance of evaluating the availability of denning sites in carnivore conservation and provide valuable management considerations, key to mitigating human–wildlife conflict as carnivores continue to recover and recolonise Europe.

Keywords: anthropogenic habitats, carnivore conservation, habitat management, land-use change, *Martes martes*, pine marten, predator recovery

The recovery of carnivores in parts of Europe in recent years is well documented, and has been in response to legal protection, improved public opinion and adaptation of management practises making coexistence between carnivores and people possible (Chapron et al. 2014, Ripple et al. 2014). Bears *Ursus arctos*, wolves *Canis lupus*, lynx *Lynx lynx* and small predators such as otters *Lutra lutra* and pine martens *Martes martes* are recolonising areas from which they were once extirpated (Boitani and Linnell 2015, Sainsbury et al. 2019). The existence and recovery of carnivores in Europe is dependent on people's ability to co-exist with carnivores in human dominated landscapes (Chapron and Lopez-Bao 2016, Lopez-Bao et al. 2017). However, this novel co-existence can disrupt social–ecological systems established during the carnivore's absence, resulting in conflict (Treves and Karanth 2003).

Human–carnivore conflict stems from carnivores fulfilling key requirements in modified landscapes; the requirement of food, for example, can result in the depredation of livestock (Kaczensky 1998, Sellenthin and Skogh 2004). Denning sites are another key resource, facilitating sleep, thermoregulation and predator/threat avoidance (Palomares and Delibes 1993, Zielinski et al. 2004, LLaneza et al. 2016). Natural dens such as veteran trees can be lost in anthropogenic landscapes. Denning site selection can directly impact individual survival and reproductive fitness affecting population demography (Garshelis 2000, Morrison et al. 2012, Davies et al. 2016). Availability of denning sites has been suggested as a limiting factor for carnivores such as fishers *Pekania pennanti* (Zielinski et al. 2004), wolverines *Gulo gulo* (Magoun and Copeland 1998) and wolves (Llaneza et al. 2016). Understanding anthropogenic drivers of carnivore population demographics and behaviour is key to the

recovery of carnivores and mitigating associated human–wildlife conflicts.

Despite an emerging literature on large carnivores recovering in human-modified landscapes (Chapron et al. 2014, Carter and Linnell 2016, Morales-Gonzalez et al. 2020), there is a paucity of information pertaining to small carnivores. For example, polecats *Mustela putorius*, which underwent historical decline in parts of Europe, are starting to recover in Britain (Sainsbury et al. 2019). Despite their historical decline being driven by persecution, there has been little research into how to minimize future human–wildlife conflict. Existing research on small carnivore conservation in Europe typically focuses on large-scale modelling of occurrence (Balestrieri et al. 2019, Zub et al. 2018), with limited fine-scale examination of populations and how fulfilling biological requirements in modern human modified environments may affect their recovery.

The European pine marten *Martes martes* is a small carnivore currently recovering in Britain and Ireland following severe historical decline driven by habitat loss and persecution (Langley and Yalden 1977, O'Mahony et al. 2017, Sainsbury et al. 2019). Recent research demonstrates the species may be limited by human disturbance to the more remote, forested parts of Europe (Balestrieri et al. 2019, Twining et al. 2020). There is some evidence that it is the structural elements of ancient forest that are required, not the presence of old-growth forest per se (Brainerd et al. 1995, Caryl et al. 2012). Structural characteristics of ancient woodlands provide elevated denning sites protecting martens from predators (Storch et al. 1990). Above ground dens that offer critical refuge from predation are rare in human-modified landscapes such as managed plantations (Croose et al. 2016), and this has been suggested to limit the distribution and density of the pine marten (Brainerd et al. 1995). In response to a scarcity of natural above ground opportunities, pine martens may use sub-optimal denning sites such as man-made structures (Birks et al. 2005), potentially resulting in human–wildlife conflict.

If availability of suitable den sites constrains small carnivore populations, these effects are likely to be observable in immature commercial plantations. Such habitats are uniform with respect to tree species and age, lack ground cover, and are subject to rotational clear felling. Such forestry practice is typical of Britain and Ireland where over three quarters of the total forest cover is this type of plantation (Forestry Commission 2017). Despite the suspected limiting nature of these plantations, they have previously been considered suitable habitat for the pine marten with all forest cover considered equal in regional populations assessments (O'Mahony et al. 2017). Although the potential importance of marginal habitats such as scrub has been highlighted (Caryl et al. 2012), this has been ignored by forest centred approaches. Such an approach can lead to errors in population estimation and identification of trends, but also can result in inappropriate policy and mismanagement of species.

The aim of this study was to compare the denning behaviour and population demographics of pine marten populations in two landscapes. The objective was to examine denning behaviour and demographics using live-trapping and radio-tracking in: 1) semi-natural lowland, broadleaf setting; and, in contrast, 2) a highly human-modified landscape. We hypothesised that martens occupying the human-modified landscape will make use of non-forested habitats and suboptimal denning sites such as rocky features and man-made structures. Further, we examine the potential effects of habitat alteration on population density and demographics of a small carnivore. Together, this will provide lacking information on a small carnivore recovering in landscapes which are highly modified and shared with humans.

Methods

Study areas

The research was conducted in Northern Ireland, UK (Fig. 1A), at Crom, County Fermanagh (Fig. 1B, Crom) and Slieve Gullion, County Armagh (Fig. 1C, SG). Crom is a 546-ha site with 254 ha native broadleaved woods which constitute the most extensive semi-natural woodlands in Northern Ireland and one of the largest in Ireland (Reeves-Smyth 1989). The woodland is a mix of old-growth oak *Quercus robur*; ash *Fraxinus excelsior* and hazel *Corylus avellana* with extensive areas of alder *Alnus glutinosa* and willow *Salix caprea* carr.

In contrast, Slieve Gullion, is a mountain (573 m) situated in the agricultural landscape of South Armagh. Forest cover in the area is low (10%) and the woodlands present are predominantly commercial plantations. These are formed from immature stands of non-native trees, planted in the last 17–44 years, and some older stands planted more than 44 years ago. The immature stands are predominantly Sitka spruce *Picea sitchensis* and Japanese larch *Larix kaempferi*, and the older stands are native Scots pine *Pinus sylvestris* and non-native lodgepole pine *Pinus contorta*. Dry heath makes up 11% of the area. The remaining three quarters of the area are a mix of agricultural land, tree lines forming field boundaries and scrubland.

Capture procedures

Live trapping was conducted at both sites under license (Home Office, UK; Northern Ireland Environment Agency License 2228) between November 2018–March 2019 and August–November 2019, avoiding the breeding period between March and August when females provide care to dependant kits. Ten Tomahawk 205 live cage traps were deployed at 400 m intervals along two 1.6 km transects at both sites (Fig. 1B–C). Traps were covered with tarpaulin and on top of this hay and moss was used to provide camouflage and insulation. Traps were baited with a mixture of peanuts, raisins, and strawberry jam, a hen's egg, and a handful of grapes. Traps were checked daily after dawn. Trapped animals were anaesthetised with an intramuscular injection of ketamine (25 mg per kg) and midazolam (0.2 mg per kg body mass) and scanned for presence of a microchip using a MiniTracker I (Avid Identification Systems Inc., California, USA). Any animal caught for the first time was fitted with a microchip (Friendchip Mini, Avid Identification Systems Inc.) injected subcutaneously between the shoulder blades. Animals were sexed using anogenital distance and presence of sexual characteristics (nipples, testes, baculum), and aged (adult or yearling) primarily using tooth colouration and
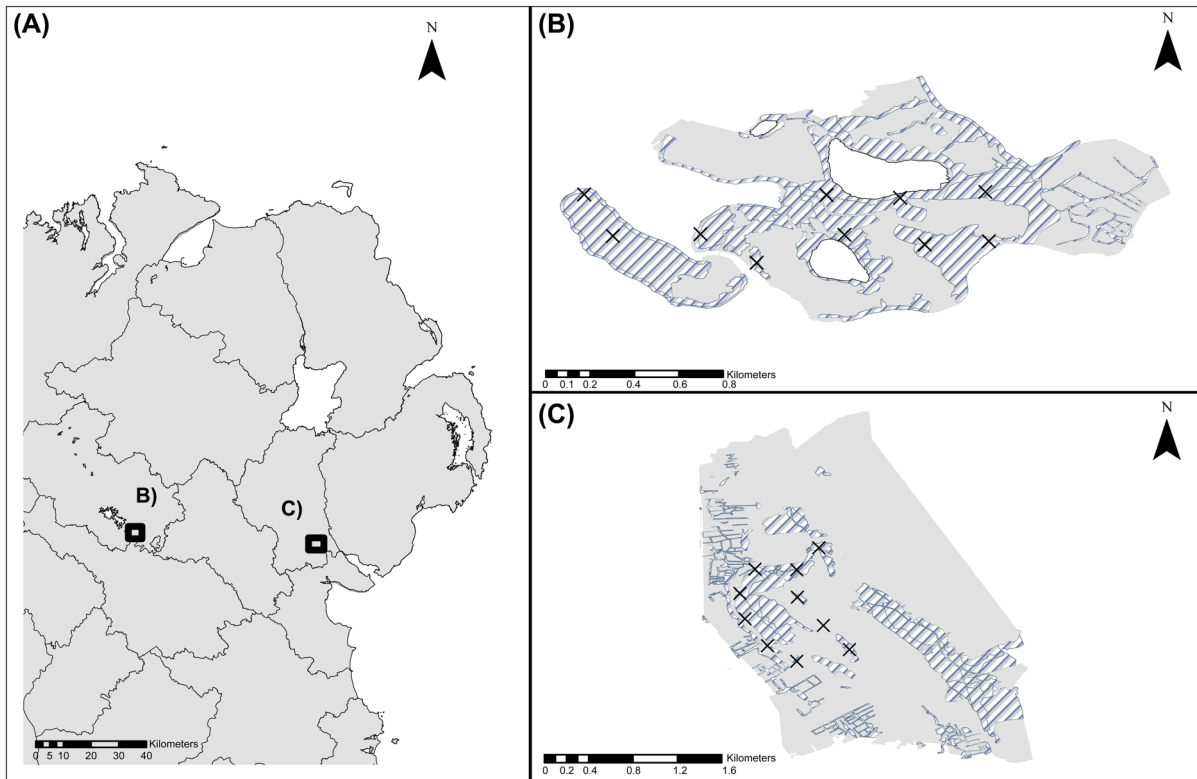
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Figure 1. (A) Map of Northern Ireland showing location of study sites, (B) the semi natural environment of the Crom Estate and (C) the human-modified landscape of Slieve Gullion. Live-trap locations are marked with an X. Dashes areas represent forested habitat and plain grey non-forested habitat, with white representing larger areas of standing water. Study areas were delineated using 95% minimum convex polygons of all pine marten denning locations.

wear (Marshall 1951, Marti and Ryser-Degiorgis 2018). If an animal had been trapped previously and was >1 kg in mass, a 1/3N MX transmitter (7 g, Merlin Systems Ltd) was deployed on a custom leather collar. Total collar weight was approximately 30 g, and, hence, always < 3% bodyweight (Coughlin and van Heezik 2015). Individuals were re-trapped to remove collars.

VHF tracking and den identification

Diurnal tracking of animals (06:00–18:00) commenced 24 h after initial release using a R600 handheld receiver (Communication Specialist Ltd, London, UK) and a folding VHF 5 Element Yagi Antennae (Merlin Systems Ltd, Wrexham, UK). Denning site locations were confirmed using the receiver by disconnecting the antennae and attaining a strong signal. On finding a den, the location was recorded on a hand-held GPS (Garmin GPSMAP 64, Garmin Ltd, Schaffhausen, Switzerland) and den structure (e.g. tree, deadwood, cave, building), level (above, below or ground level) and habitat were recorded. If the den was in a tree, species, diameter at breast height (DBH) and tree height were recorded. Tree height was calculated using a 50 m measuring tape and clinometer using Pythagorean theorem. Additional notes were made on presence of epicormic growth, and percentage of ivy *Hedera helix* cover.

Habitat mapping

Delimiting an area and the availability of habitats available to animals is subjective (Garshelis 2000). Here, the habitat

available to the pine marten were defined as the 95% minimum convex polygon containing all the denning locations. Dens outside this area were excluded from this analysis. Approximately 244 ha at Crom and 499 ha at Slieve Gullion were classified into twelve habitat types based on species composition, ground, shrub and canopy cover (Fossitt 2000), using inventory maps (Forestry Commission, Northern Ireland; National Trust, UK), digital land classifications (LCM 2007) and a ground-truth survey. Six non-forested habitats were present within the study sites: agriculture, buildings, fen, parkland, heath and scrub. Six forested habitats were also present: old-growth oak woodland, wet woodland, ash woodland, closed plantation, mature plantation and property boundary tree lines composed of native deciduous species (Supplementary material Appendix 1 Table A1).

Statistical analysis

Pine marten density was calculated from live trapping at both study sites using spatially explicit capture–recapture (SECR) models (Efford 2017). The use of spatial location information overcomes issues associated with non-spatial estimation techniques, such as edge effects and incomplete detection (Efford 2004, Borchers and Efford 2008). A standardised, four times root square pooled variance (RSPV) of movement was used as a buffer to trapping locations in each density estimation (Efford 2017).

This investigation had two contrasting study areas without replication. Hence, formal statistical analysis of the population demographics was not possible. Observa-

tions on adult sex ratios (ASR) used the proportion of males in the adult population as general measure of ASR ($ASR = (N_{males}/(N_{males} + N_{females}))$, Ancona *et al.* 2017). Similarly, for demographic structure, the proportion of yearlings (juveniles which have survived the first five months of life and are close to adult size) in the total population ($N_{yearlings}/(N_{yearlings} + N_{adults})$), was taken as being indicative of population recruitment.

Fisher's exact tests (FET) were used to compare proportions of den types used between the two study areas. Analysis of variance (ANOVA) was used to examine differences in tree height and diameter at breast height of denning trees between Crom and Slieve Gullion. Minimum convex polygons (MCP 95%) were used to draw an envelope that encompassed all denning sites for each individual to calculate a denning area (ha). Denning area and number of unique dens were modelled against the landscape they inhabited using generalised mixed effects models (GLMMs) with Poisson errors and individual as a random effect. Both response variables were modelled as a function of landscape, sex and age, and the interactions between these fixed effects. Analyses were performed using R ver. 3.2.1 with nlme package (<www.r-project.org>, Pinheiro et al. 2018).

Pine marten habitat selection for dens was determined using the proportional use of habitats relative to their availability. Unique denning locations only were used to ensure data independence. Repeat use of denning sites were discarded. Variability in selection strategies was calculated using resource-selection indexes (RSI) where RSI = % habitat use − % habitat available (Thomas and Taylor 1990). Analysis of Variance (ANOVA) was used to test for differences in RSI between habitat types within sites, and Bonferroni-adjusted 95% confidence limits were used to examine habitat preferences (Cherry 1998).

Results

Population density and demographics

A total of 38 individual pine martens (Supplementary material Appendix 1 Table A2) were caught across the two study sites over the two sampling periods totalling 2195 trap nights; 25 individuals in Crom over 1072 trap nights and 13 individuals in Slieve Gullion over 1123 trap nights. During winter trapping (Nov–March) in Crom, 12 adults, and 4 yearlings were caught. The adult sex ratio was 0.58 and SECR models produced a winter density estimate of 3.64 animals per km² (Fig. 2, CI 95% 2.26–5.86). During summer–autumn trapping (August–November) at Crom the sampled population consisted of 6 adults and 7 yearlings, with an adult sex ratio of 0.5 and a density estimate of 3.34 animals per km² (Fig. 2, CI 95% 1.93–5.80). At Slieve Gullion, winter trapping resulted in eight adults and one yearling. The adult sex ratio of the population was 0.66 and the winter population density was 0.76 animals per km² (Fig. 2, CI 95% 0.374–1.02). In summer–autumn, four adults and two yearlings were trapped at Slieve Gullion. The adult sex ratio was 0.8 and summer–autumn population density was 0.96 animals per km² (Fig. 2, CI 95% 0.39–2.375).

Denning structures

Twenty animals, 12 in Crom, 8 at Slieve Gullion, were collared and radio-tracked to 185 unique dens 277 times (Supplementary material Appendix 1 Table A3). Individuals were tracked for between 8 and 51 days (CI 95% 15–25 days). Most dens were used once (78%), with the remaining 22% of dens being used 2–11 times over the entire study period.

Dens used by pine martens at Crom were almost exclusively above ground in living trees or standing deadwood (99%). While in Slieve Gullion underground dens in rocky crevices, cave systems and burrows were the predominant den type used (57%). Tree use was significantly higher in Crom than Slieve Gullion (Fig. 3, Fisher's exact test, p < 0.001) whilst the use of underground sites was significantly higher in the latter than the former (Fisher's exact test, p < 0.001). Man-made dens including stone walls, woody debris piles and roof-spaces of unoccupied buildings made up 22% of dens used by martens at Slieve Gullion and were used significantly more than at Crom, where they were largely absent (Fig. 3, Fisher's exact test, p < 0.001).

Species of tree used varied between the sites (Supplementary material Appendix 1 Table A4). In Crom, oak was used significantly more than all other tree species (Fisher's exact test, p < 0.001), followed by ash and lime whose usage was not significantly different (Fisher's exact test, p = 0.125), but both were used proportionally more than the next most commonly used tree, silver birch (Supplementary material Appendix 1 Table A4; Fisher's exact test, p < 0.001; <0.001). At Slieve Gullion, when martens used trees as dens, they generally left the conifer plantations and found denning sites in tree lines and field boundaries of the bordering agricultural land. Ash and hawthorn trees were the most commonly used. See Supplementary material Appendix 1 Table A4 for breakdown of tree species usage.

Trees used in Crom were significantly taller than those used at Slieve Gullion (ANOVA, $F_{2,15} = 2.73$, p = 0.001), and also had significantly larger widths at breast height (ANOVA, $F_{2,15} = 15.99$, p ≤ 0.001). All trees used as denning sites either had very high ivy cover (72.69% CI 95% 64.82–80.56%, Supplementary material Appendix 1 Table A4), the presence of internal cavities, in the case of lime, substantial epicormic growth or a combination of the three (Supplementary material Appendix 1 Table A5).

Denning area and number of dens

Pine martens at Slieve Gullion had significantly larger denning range areas than Crom (Fig. 4A; GLMM: site: $F_{1,9} = 4.21$, p = 0.002, age: $F_{1,9} = -1.52$, p = 0.164, interaction between site and age: $F_{1,9} = -2.471$, p = 0.03). Adult pine martens had more unique den sites compared to juvenile animals but there was no significance difference in number of unique denning sites between the two sites (Fig. 4B; GLMM: site: $F_{1,9} = -1.86$, p = 0.096, age: $F_{1,9} = -2.357$, p = 0.042, interaction between site and age: $F_{1,9} = 0.525$, p = 0.612).

Habitat selection

Pine martens in Crom preferentially selected dens in old-growth oak woodland above all other habitat types
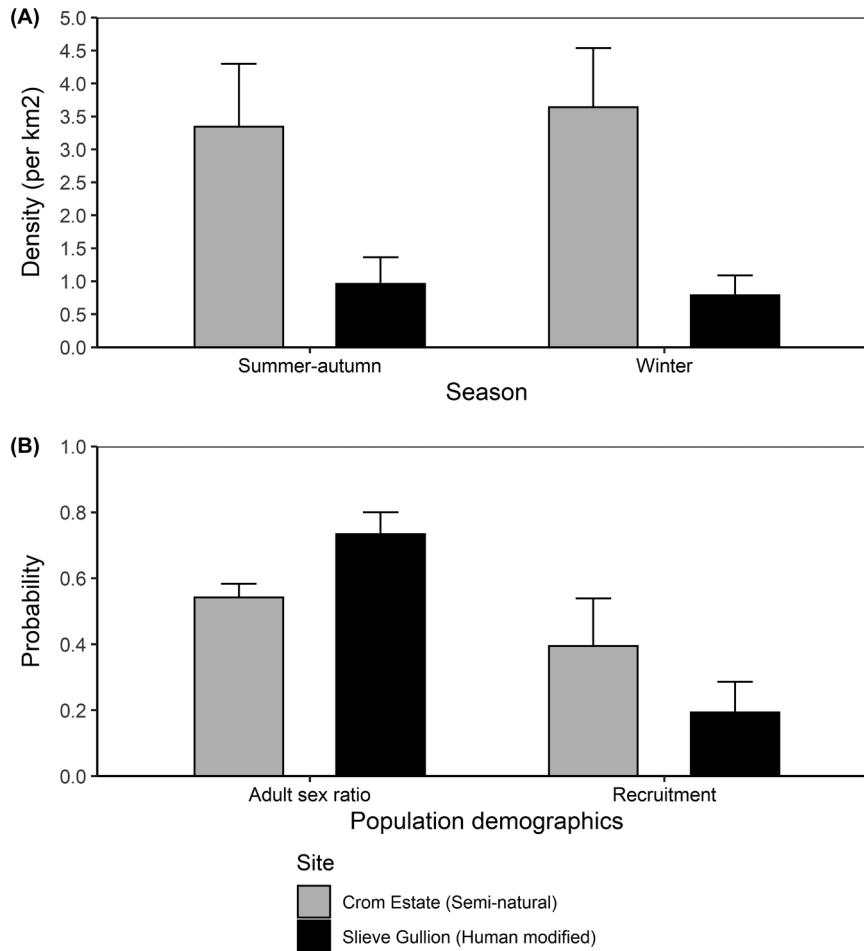
Figure 2. Pine marten (A) summer–autumn and winter density, (B) adult sex ratios and recruitment in populations in the semi-natural environment of Crom (grey), and the human modified landscape of Slieve Gullion (black). Density is displayed in animals per km². Adult sex ratios are displayed as probability of being male within the population, and recruitment is probability of being juvenile within the population.

(Fig. 5A, p = <0.001–0.026, Supplementary material Appendix 1 Table A6–A8 for full Bonferroni 95% CI results), showing avoidance of all non-forested habitats (Fig. 5A). Conversely, in Slieve Gullion dens in mature plantation and tree lines were used above their availability, alongside two non-forested habitats, scrub and heath (Fig. 5B). There was no significant difference between the selection of these habitat types (see Supplementary material Appendix 1 Table A9–A11 for Bonferroni 95% CI results). Agricultural land was the only habitat that showed a significant dif-
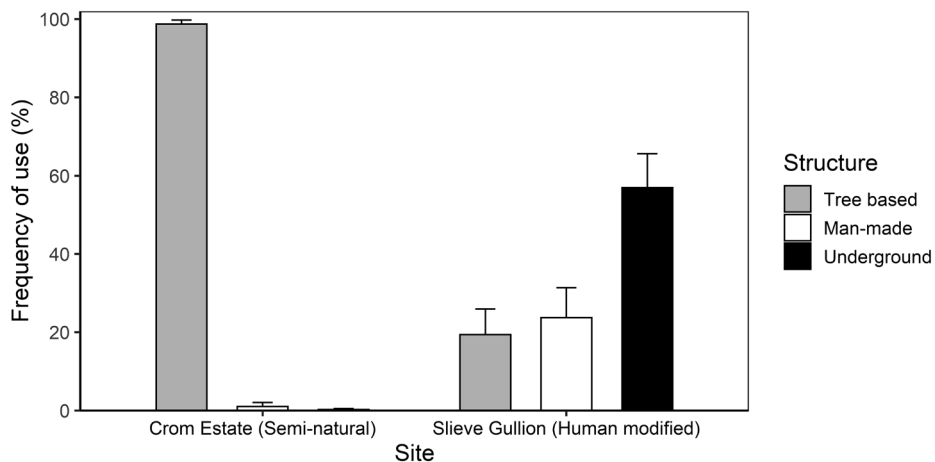

Figure 3. Mean (95% clm) frequency of use (%) of den structures by the European pine marten in lowland broadleaf woodlands at the Crom Estate and upland plantation landscape at Slieve Gullion.
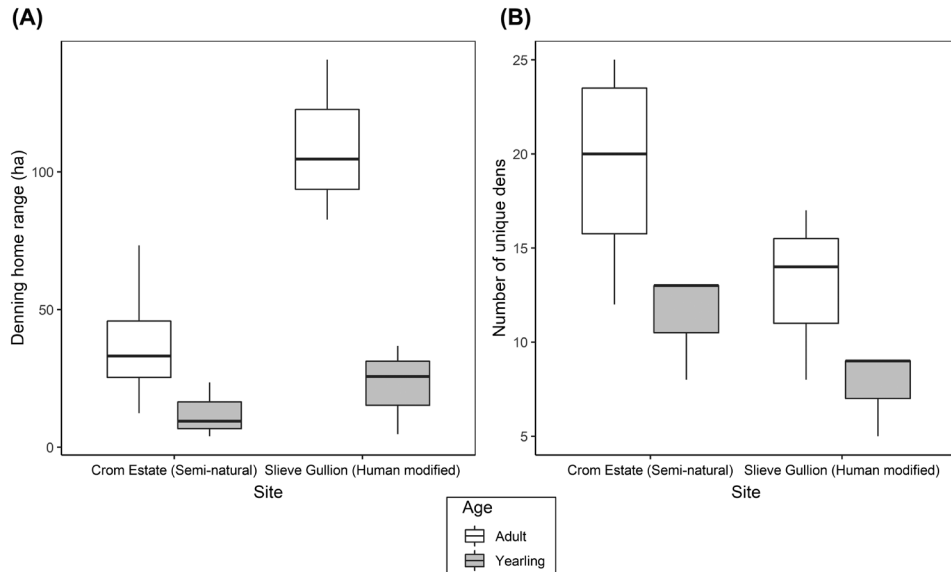
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Figure 4. Boxplots showing landscape and age differences in (A) denning range in hectares and (B) number of unique denning sites per individual in the European pine marten.

ference in RSI to other habitats and was strongly avoided. There were minimal differences in habitat selection of dens between adults and juveniles at Crom (Fig. 5A). However, at Slieve Gullion, age differences were far more pronounced

(Fig. 5B) with pine marten yearlings preferring more structurally complex habitats such as mature plantation and scrub, whilst avoiding the more open heath which was used by adults (Fig. 5B).
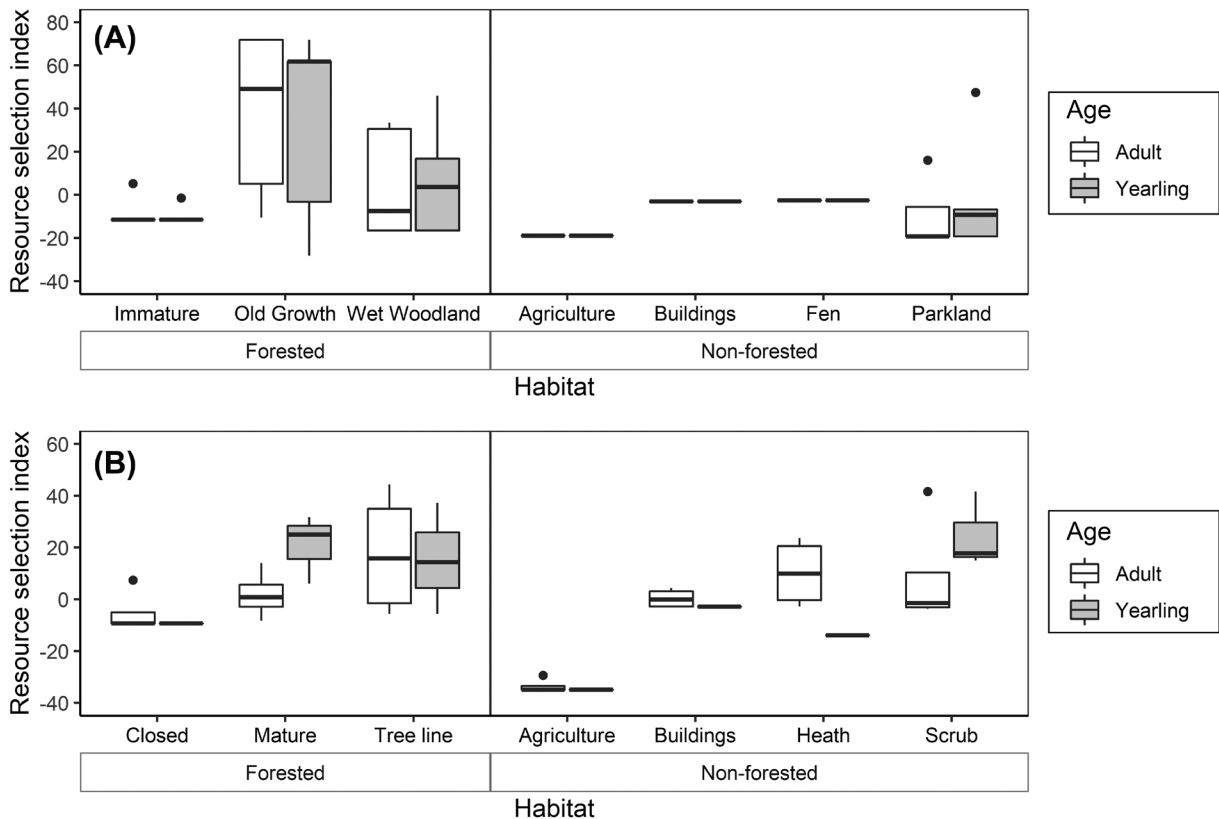

Figure 5. Boxplots showing resource selection index of adult and yearling European pine marten denning sites for (A) habitats present in the Crom Estate and (B) habitats present at Slieve Gullion. Values above zero show use of a habitat above availability, values below zero show use below availability. Significance is shown by the interquartile range not overlapping zero (<0 = positive significance, >0 = negative significance).

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Discussion

This study provides insight into how a small carnivore has adapted to a contemporary human modified landscape when compared with a semi-natural environment. We provide information on how the pine marten is recovering in Ireland and Britain despite an almost complete absence of preferred habitat. The lack of optimal denning sites (veteran trees) does not prevent the pine marten from persisting in human-modified landscapes provided they contain certain structural features e.g. underground or man-made denning sites. However, it is evident from the results that although pine martens can exploit human modified landscapes, these landscapes appear to limit population density and affect both individual behaviour and population structure. Thus, the continued recovery of pine marten, and likely other carnivores in contemporary European human modified landscapes will be limited by the availability of denning sites, unless adequate management actions are undertaken to mitigate their scarcity.

Our results confirm the pine marten to be an old-growth forest specialist (Zalewski 1997, Zalewski and Jedrzejewski 2006). In these habitats, individuals select elevated den sites in living trees and standing deadwood, live at higher densities with higher recruitment, and more balanced sex ratios. In the human-modified landscape of Slieve Gullion, where arboreal den sites are scarce, pine martens were observed denning underground in cave systems and rocky crevices, and in man-made structures, most frequently stone walls and wood debris. They also occasionally used roof spaces in unoccupied buildings and more natural sites such as ash and hawthorn trees along tree lines forming field boundaries. Pine martens rarely denned within immature plantations. Only a single individual made occasional use of above ground dens in plantations, making use of structures constructed by other species in trees e.g. squirrel dreys and bird nests.

The pine marten has been observed to be a forest specialist (Brainerd 1990, Zalewski and Jedrzejewski 2006). Thus, in the past any forest may have been considered potentially suitable and, and by corollary, any non-forested habitat, considered unsuitable (Pereboom et al. 2008, Mortelliti et al. 2010, O'Mahony et al. 2017). On reflection of the findings of our work, and others (Mergey et al. 2011, 2012, Caryl et al. 2012), we argue the habitat requirements of these carnivores are more nuanced than such an approach suggests. Whilst martens may require certain structural elements typical of old-growth forest, where absent, they appear to fulfil biological requirements by making use of marginal habitats. In avoiding immature plantations, pine martens demonstrated use of mature pine plantations and tree lines composed of broadleaf species. Avoidance of immature plantations provides evidence that these forests lack the natural denning sites that are found in mature native woodlands. Thus, all forests should not be considered equal. This is particularly important when considering conservation and recovery and producing populations estimates.

In the absence of old-growth woodland, non-forested marginal habitats are used, mainly scrub, and to a lesser extent, heath. Similar selection for non-forested habitats in landscapes altered by anthropogenic processes, or otherwise lacking in old-growth forest, have been observed in a variety of small carnivores (Revilla et al. 2001, Lozano et al. 2003, Mangas et al. 2008, Caryl et al. 2012). Scrub habitats provide key structural elements for many small predators within human-dominated landscapes in Europe (Virgós and Casanovas 1997, Matos et al. 2009, Santos and Santos-Reis 2010). Heath is not typically associated with the same degree of use as scrub (Mangas et al. 2008, Caryl et al. 2012). However, previous research has reported richness and abundance of small carnivore populations to be positively associated with rock cover (Mangas et al. 2008). The use of heath observed here may reflect Slieve Gullion's topography (mountainous) and geology (granite) which provides abundant rocky refugia, subterranean structural complexity. The present results reiterate the importance of heterogeneity in human modified landscapes and highlight that forest centred approaches to carnivore conservation can lead to mismanagement and ill-informed policy as has been recognised in other carnivores (i.e. *Puma concolor coryi*, Comiskey et al. 2002). This does not undermine the integral nature of woodlands but highlights the importance of accounting for the use of marginal habitats such as scrub and heathland when planning for small carnivore conservation.

Predator avoidance is an important determinant of habitat use by small carnivores (Salo et al. 2008). Red foxes *Vulpes vulpes* which are present at both study sites, are the main predator of the pine marten, and have been reported to alter habitat use and directly reduce densities of pine marten populations (Storch et al. 1990, Lindström et al. 1995). Martens in both study areas showed avoidance of homogenous habitats with little or no ground cover such as agricultural land, parkland and immature plantations. This suggests predation risk may be key to den selection of the pine marten (Storch et al. 1990). This hypothesis is supported by the fact in the absence of predators, pine martens in Minorca were observed to be indifferent to forest cover (Clevenger 1994). Like most mammals, pine martens produce offspring which are small compared to their adult body mass (on average only 10%, Blueweiss et al. 1978). Yearlings, in comparison to adults preferred dens in mature plantation and scrub with high ground cover. Apex predators rarely kill prey individuals at random, with certain sex and age categories at higher risk than others (Hayward et al. 2017). Although adult pine martens have been observed to be predated occasionally by red foxes, kits are particularly vulnerable to fox predation (Brainerd et al. 1995). The requirement for safe refuge where predators cannot access young is critical for successful breeding and recruitment (Brainerd et al. 1995, Lindström et al. 1995). This likely underpins the ubiquitous avoidance of homogenous habitats observed, and the preference of yearlings for mature plantations over more open habitats used by adults (e.g. heath). The species requirement of accessible above-ground refuge provided in the semi-natural landscape likely plays a role in the significantly lower densities observed in the human modified landscape.

Male-biased sex ratios and decreased recruitment were observed in the human-modified Slieve Gullion in comparison to the more natural lowland broadleaf site of Crom. Population differences are consistent with the hypothesis that predation drives differences in the population structure. This

hypothesis, however, based on observed differences between two sites requires testing through further investigation of multiple sites. The current study does not control for food resource abundance which is known to have a strong effect on density and fine-scale distribution. However, food availability is unlikely to result in male-biased sex ratios observed here, whilst increased predation pressure on females and juveniles due to a scarcity of arboreal refugia might. This may hint to the importance of top–down control by apex predators in regulating small carnivore populations, as has been observed previously (Berger et al. 2008, Johnson and VanDerWal 2009, Ritchie and Johnson 2009).

The present density estimates are within known ranges reported for pine marten populations across Europe (0.01–4.42 per km², Zalewski and Jedrzejewski 2006, Sheehy et al. 2013, O'Mahony et al. 2017). Densities of pine marten in Ireland are at the upper end of the spectrum for the species, despite the lack of mature woodland and the unsuitability of much of the land area. The comparatively elevated densities observed in Ireland are likely linked to the absence of large predators, and reduced intra-guild competition compared to mainland Europe.

The pine marten's continued recovery in human-modified landscapes is likely to be hampered by conflict with humans as has been observed in other carnivores (Liberg et al. 2012, Nowak and Mysłajek 2016). The conflation of low densities and low reproductive rates, typical of carnivores, makes them particularly vulnerable to persecution (Ripple et al. 2014). As with large carnivore recovery, it appears managing the human aspects of pine marten recovery in Ireland and Britain are going to be key to its success (Sharpe et al. 2001, Clark and Rutherford 2014). Human–wildlife conflict in Ireland involving martens is growing, and largely arises from martens denning in occupied houses (F. Marnell unpubl.). In the short-term, large-scale deployment of artificial den boxes in commercial plantations may mitigate the main source of human–conflict with the species (Croose et al. 2016). This form of human–wildlife conflict is a symptom of myopic management of landscapes, resulting in a paucity of structurally complex woodland and associated denning opportunities. The continued national afforestation strategies of Ireland and Britain that favour non-native commercial tree crops will only heighten conflict as the species continues to recover. Restoring old-growth conditions to woodlands will be key to reducing conflict associated with this small carnivore's recovery.

The present study has wider implications in demonstrating the potential population consequences of habitat-induced differences in behavioural ecology in a small carnivore recovering in landscapes subject to high anthropogenic change. Suitable denning sites are required for the survival of carnivores; however, behavioural adaptations may enable species to use sub-optimal locations to survive in highly modified landscapes. Dietary and behavioural plasticity alone may not be sufficient to allow such small carnivores to survive to changing environments if scarcity of natural, suitable dens (i.e. sites that protect them from predation, the cold and wet weather, enabling the successful rearing of vulnerable young), drives species into conflict with humans. Habitat restoration and management plans, therefore, must consider the availability of suitable denning sites in order to facilitate the conservation and continued recovery of carnivores in human-dominated landscapes.

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Supplementary material (available online as Appendix wlb-00760 at <www.wildlifebiology.org/appendix/wlb-00760>). Appendix 1.