Part 3: Habitat selection, diet and territoriality of pine martens reintroduced to a commercial coniferous forest

Introduction

The increase in plantation forestry in Scotland this century is thought to have been an important factor promoting recolonisation by pine martens of parts of their former range. Such commercial forests provide large areas of apparently suitable habitat for reintroductions of this species to England. However, the ecology of pine martens in plantation forests, which are often in the uplands and spruce dominated, is not well known. Dense plantations may not provide sufficient food due to absence of suitable habitat for small mammals, notably field voles *Microtus agrestis,* and other prey items. The availability of sites for dens might also limit pine martens in upland plantations (see Part 4).

This part of the report examines habitat use by pine martens reintroduced to a commercial coniferous forest in Galloway, south west Scotland. We consider both habitats in which pine martens concentrated their activity and those in which dens and lie-up sites were situated. In accordance with current developments in habitat selection theory, we present analyses at a series of spatial scales, from the landscape scale to micro-habitats of core areas within territories. Our results show the extent to which upland coniferous plantations would be suitable for pine marten reintroductions in England. They also highlight the type of forest design and management likely to benefit pine martens.

Methods

Study area

Planting of the Galloway forest began in the 1950s and much of it is now at the end of its first planting rotation. Extensive coniferous plantations comprise the majority of the forest, although there are small areas of ancient oak woodlands.

The territories of tracked martens were contained within a rectangle (325km^2) enclosing most of Glen Trool Forest to the west of the Merrick mountain mass and a small part of Carrick Forest south west of Loch Braddan. To the south, west and north of the study area pastoral farming predominates. Altitude in the study area ranges from 50m to 850m, though most is between 100-400m.

Dense stands of sitka spruce *Picea sitchensis* and some lodgepole pine *Pinus contorta* dominate the forest, especially above 200m. On the lower ground, around Bargrennan and Loch Trool where the risk of wind blow is reduced, other species including Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and larch *Larix* spp. have been planted. Broadleaves are more common on lower ground and include oak *Quercus* spp., birch *Betula* spp. and Rowen *Sorbus aucuparia*. Forest management has created a mosaic of dense, thinned, felled, and regenerating coupes. Felled coupes are usually larger on higher ground and so landscape grain size is coarser there, than at lower altitude. Due to a more varied planting and thinning regime, tree species and forest structural diversity is greater at lower altitude.

Trapping and radio tracking

Following methods used by Balharry (1993), pine martens were caught in cage traps (Tomahawk Ltd.) and lightly anaesthetised using 0.3ml intramuscular injection of ketamine hydrochloride (Vetalar, Parke-Davis) before being fitted with radio collars (Biotrack, Wareham, Dorset; procedures licensed in accordance with the Wildlife & Countryside and Animals [Scientific Procedures] Acts). Collared martens were allowed to recover in wooden boxes for at least four hours before release. Collars weighed approximately 23g, equivalent to 2% of the mass of a female pine marten. Pine martens were subsequently tracked on foot and from a four wheel drive vehicle for 10 or more nights until an asymptote in territory size was reached (Morris, 1988). Tracking was carried out between February 1995 and May 1996. Pine martens were located every five minutes to within 100m with the aid of 1:25,000 Ordnance Survey maps and forest plans. Activity and speed of tracked pine martens were classified according to modulation in frequency and amplitude of transmitter signals as follows: still, moving, moving fast. Minimum convex polygon (MCP; Harris *et. al.* 1990) and grid cell (Siniff & Tester, 1965) territory areas were then calculated using the Ranges V suit of programs (by R.E. Kenward, I.T.E., Furzebrook, Dorset).

Pine martens could be individually recognised by distinctive patterns of light and dark fur on their throats and chests. Breeding status of males was assessed on the basis of size and development of abdominal scent glands. That of females was assessed from on the basis of nipple size (cf Balharry, 1993).

Areas where pine martens were stationary for more than half an hour were considered to be dens or lie-ups. Den sites were distinguished from lie-ups by the presence of a protective structure (tree fall snag, burrow or large bird nest) and frequent prominent midden of scats. Dens were usually day-time retreats, whereas lie-ups were used during day or night.

Habitat surveys

A detailed map of habitats in the study area, with a resolution of 100m, was made with the aid of Ordnance Survey 1:25,000 maps, forest plans and field surveys. Surveys were made of micro-habitat within core areas (see below) and paired randomly selected non-core areas (of the same size) within territories. Percentages of the following ground cover types were recorded: tussock forming grass; berry producing shrubs; moss and non-tussock grass; stream; other ground cover.

Analytical techniques

Total distance travelled by pine martens each night was measured as the sum of straight line distances between successive radio fixes. The greatest linear distance that a pine marten was found from its start den each night was used as another index of movement. Nights with less than five hours of active fixes were excluded from the analysis as were data for two non-breeding (sub-adult) males. Active fixes were location records for which a pine marten was recorded as away from dens or lie-ups. Factors affecting distances travelled, MCP and grid cell territory areas and other range parameters were examined using factorial analysis of variance (ANOVA; Garshelis & Pelton, 1980).

Compositional analysis (Aebischer & Robertson, 1992) was used to examine the selection of territories within the study area and the use of habitat within territories. Territoriality and the use of boundaries was also investigated using this method, as was the selection of habitat 100m around den and lie-up sites. Hierarchical nearest neighbour cluster analysis was used to define core areas, which were the smallest set of minimum convex polygons containing 50% of active fixes.

Scat analysis

Pine marten scats, which were distinguished from those of other mammals by distinctive morphology and odour, were collected during the radio tracking period from tracks, dens and trap sites. After softening in water overnight, individual scat contents were washed through a 1.3mm sieve and the remains identified under a binocular microscope with the aid of published keys. Using the correction factors given by Balharry (1993), estimated weight intake (EWI) of different prey items was calculated from bimonthly samples.

Results

Travel distances and speeds

A total of 123 nights of data were obtained for 11 adult, breeding, pine martens, six males and five females. Data for a further 24 nights for two non-breeding males were also obtained. The greatest distance that a marten was found from its start den was 7.4km and the mean maximum distance was 2.65km (SE 0.28km). Maximum distances were classified by sex and habitat type (upland spruce or lowland mixed conifer) and an ANOVA used to separate the effects of these factors. Maximum distances differed significantly between pine martens of different sex ($F_{1,78}$=5.16, p=0.026) and also between pine martens in habitat of differing quality ($F_{1,78}$=16.36, p=0.001). There was no significant interaction between sex and habitat quality ($F_{1,78}$=0.56, p=0.46). Maximum distances were greater for males and for pine martens in upland spruce habitat (Table 1).

The sum of linear distances between successive radio fixes was used to estimate total distance travelled per night. The greatest total distance travelled was 15.8km and the mean distance 7.33km (SE 0.53). When total distance travelled was classified by sex and habitat type an ANOVA revealed no significant effects (Table 1).

The number of about-turns per night (angles in a movement path of 90-270° *ie* c. 180°) differed significantly between pine martens in lowland mixed conifer and upland spruce habitat ($F_{1,78}$= 4.64, p=0.03). Pine martens in lowland mixed conifer habitat made more about-turns per night (mean 8.4, SE 0.68) than did pine martens in upland spruce habitat (mean 6.77, SE 0.61). Males and females showed no difference in the number of about-turns ($F_{1,78}$= 1.64, p=0.2). Male pine martens did, however, spend more time each night travelling fast (>3km hr^{-1}; mean 20.29 minutes, SE 3.29) than females (mean 5.97 minutes, SE 1.59) ($F_{1,78}$=6.5, p=0.01).

Speed of travel differed significantly in and out of core areas. However, there was significant interaction between the sex and in or out of cores ($F_{1,211}$=12.65, p=0.001). Male pine martens travelled slower when in cores (mean 1.06km hr^{-1}, SE 0.12) than when outside cores (mean 1.65km hr^{-1}, SE 0.13). Females did not show these differences in speed (Fig.2).

Linearity of travel (total distance travelled per night/maximum distance from start den) did not differ between sexes nor in or out of core areas ($F_{1,211}$=2.17, p=0.14).

Territory areas and overlaps

The mean territory area calculated using MCPs was 13.65km^2 (SE 3.92km^2) and that based on grid cells was 7.54km^2 (SE 0.90km^2; Table 2). Grid cell territory areas were generally smaller than MCP territories and

Table 1. Maximum distances travelled from dens where activity began and total distances travelled each night. Means and standard errors are given for male and female pine martens, in upland spruce and lowland mixed conifer habitats. Data for non breeding pine martens (n=2 males) and nights with less than 5 hours of tracking were excluded.

	Mean maximum distance from start den, km (SE).	Mean total distance travelled, km (SE).
Males (n=6)	3.13 (0.39)	7.44 (0.92)
Females (n=5)	2.07 (0.23)	2.70 (0.5)
Upland spruce (n=6)	3.17 (0.36)	7.08 (0.88)
Lowland mixed (n=5)	2.01 (0.24)	7.64 (0.56)

Table 2. Territory areas (km^2) based on minimum convex polygons (MCP) and grid cells. Data are for males, females and non-breeding males in upland spruce and lowland mixed conifer habitats. Mean and standard errors are shown.

	Males upland spruce	Males mixed conifer	Females upland spruce	Females mixed conifer	Males, non breeding
MCP	23.08	5.18	9.78	5.31	3.78
	56.89	8.61	9.04	3.73	9.22
	18.62	11.28	13.03		
Mean	32.86	8.36	10.61	4.52	6.50
SE	12.08	1.77	1.23	0.79	2.72
Grid cell	7.29	3.87	7.56	5.40	2.34
	14.40	6.93	9.09	4.23	8.19
	11.61	9.72	7.47		
Mean	11.10	6.84	8.04	4.82	5.27
SE	2.06	1.68	0.53	0.59	2.93

Table 3. Length of MCP territory boundaries and defended edges. Data are for breeding male pine martens in upland spruce and lowland mixed conifer habitats. MCP boundaries along open moor and lochs were considered to be undefended (cf Balharry, 1993).

Upland spruce habitat			Lowland mixed conifer habitat		
Male no.	Length of MCP boundary, km	Length of defended edge, km	Male no.	Length of MCP boundary, km	Length of defended edge, km
M1	21.5	21.5	M3	9.0	9.0
M7	33.88	12.13	M5	16.25	11.25
M9	11.88	9.25	M6	14.25	14.25
Mean	22.42	14.29	Mean	13.17	11.5
SE	6.37	3.70	SE	2.16	1.52

Table 4. Compositional analysis based on habitat availability in MCP territories compared with habitats in circles of 100m radius around radio fixes. Habitats are ranked in order of utilisation. Ranks sharing letters are not significantly different at the p<0.05 level.

Habitat type	Rank	Mean habitat availability in MCPs, % cover	Mean habitat around fixes, % cover	Significance
Closed	9	64.50	65.30	a
Clear	8	8.13	6.32	a
Track + fire break	7	10.71	7.09	a b
Tussock	6	4.18	2.56	a b
River	5	0.87	0.76	a b
Regenerating	4	3.44	1.25	a b
Open + deciduous	3	6.97	8.86	a b
Pasture	2	1.56	0.09	a b
Lake	1	0.59	0.91	b
Moor	0	3.53	0.25	b c

Table 5. Compositional analysis based on habitat availability in randomly selected areas in MCP territories outside core areas, compared with habitats in core areas. Habitat types were based on ground cover. Habitats are ranked in order of utilisation. Ranks sharing letters are not significantly different at the $p<0.05$ level.

Habitat type	Rank	Mean habitat availability in MCPs territories, % cover	Mean habitat in core areas, % cover	Significance
Stream	4	1.12	2.5	a
Tussock grass	3	4.61	7.75	a
Moss & grass	2	11.83	13.67	b
Other cover	1	82.43	75.86	b
Berry shrubs	0	1.65	0.22	c

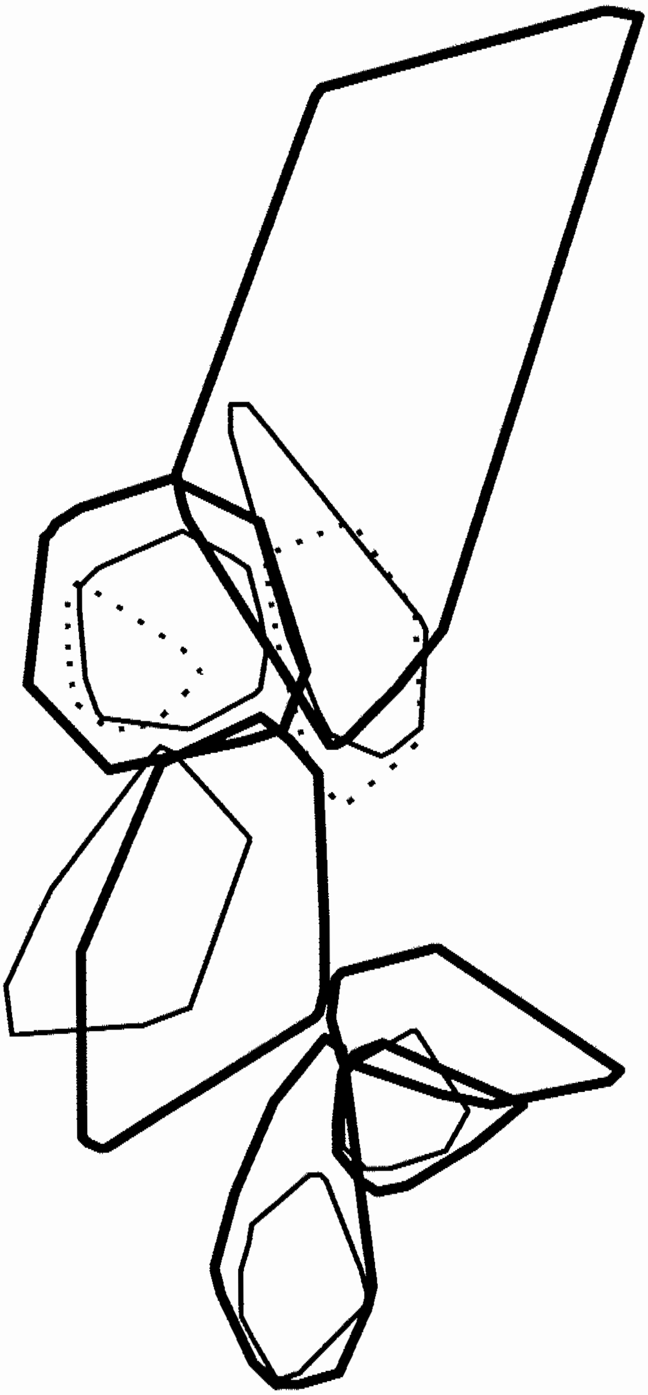
Table 6. Compositional analysis based on habitat availability in the study area compared with habitats in MCP territories. Habitats are ranked in order of utilisation. Ranks sharing letters are not significantly different at the $p<0.05$ level.

Habitat type	Rank	Mean habitat availability in study area, % cover	Mean habitat in MCPs, % cover	Significance
Closed	9	32.15	64.50	a
Clear	8	5.04	8.13	a
Track + fire break	7	14.68	10.71	c
Tussock	6	4.77	4.18	b c
Regenerating	5	6.64	3.44	b c
Open + deciduous	4	2.86	6.97	a b c
River	3	1.93	0.87	b c
Pasture	2	6.04	1.56	b
Lake	1	1.30	0.59	b c
Moor	0	24.59	3.53	d

Table 7. Compositional analysis based on habitat availability in MCP territories compared with habitats in circles of 200m radius around dens. Habitats are ranked in order of utilisation. Ranks sharing letters are not significantly different at the $p<0.05$ level.

Habitat type	Rank	Mean habitat availability in MCPs, % cover	Mean habitat around dens, % cover	Significance
Closed	9	61.74	66.82	a
Tussock	8	4.0	4.70	a b
Track + fire break	7	10.25	6.47	a
Regenerating	6	3.29	5.13	a b
Clear	5	7.78	4.77	a b
River	4	0.83	0.47	b
Pasture	3	1.49	1.28	b
Open + deciduous	2	6.67	9.42	b
Lake	1	0.59	0.64	b
Moor	0	3.38	0.44	b c

Fig. 1. Minimum convex polygon (MCP) territory boundaries, for male (thick lines), female (thin lines) and non-breeding male pine martens (dotted lines).



closely represented the areas pine martens actually utilised. MCP territories included large areas of unused moor and pasture.

Mean overlap between male MCP territories ranged from 0-16% (Fig. 1). The greatest overlap was shown between male 3 and male 5 (16.75%), although this was probably due to tracking at different times. There was no overlap between the territories of female pine martens tracked. Male territories overlapped those of females by 67%-100% (mean 90%, SE 6), whereas female territories only covered 15%-67% of males (mean 43%, SE 8). Males and females sharing the same territory showed little overlap of core areas: the mean overlap of male cores by females being 6.8% (SE 4) and the mean overlap of female cores by males being 1% (SE 0.7).

Length of defended territory edge

Balharry (1993) calculated the length of defended territory boundary by excluding MCP edges along moor and Lochs. He showed that there was no difference in the length of this defended edge in contrasting habitats, despite differences in territory size. The length of defended edges in Kinlochewe, Strathglass (Balharry, 1993) and Galloway were significantly different (Kruskall-Wallace ANOVA; X^2_2= 8.76, p=0.01). However, pairwise comparisons of these study sites showed no significant difference, probably because sample sizes were small and variability high.

In the Galloway study area males had larger minimum convex polygon boundaries in low quality habitat than in high quality habitat. However, if the boundary length is adjusted to consider only that shared by neighbouring males (Table 3), then there is little difference in the length of 'contested' boundaries in high and low quality habitats despite the difference in territory sizes between the areas.

Habitat selection

Woodland areas within the territories of Galloway pine martens (mean 9.49km^2, SE 2.23), were much greater than those in the territories of pine martens tracked in Kinlochewe and Strathglass combined (2.31km^2, SE 0.29; Balharry, 1993) ($U_{11,19}$=199, p<0.001). Even MCP territories in lowland mixed conifer habitat in Galloway had significantly more woodland (4.87km^2, SE 0.81) than those in Balharry's study areas ($U_{5,19}$=85, p=0.008).

Comparison of habitats in a 100m radius of radio fixes with those enclosed by MCPs, indicated that closed canopy forest was utilised most often, but only significantly preferred over pasture, deciduous woodland, lake and moor (Table 4). Areas of moor were significantly avoided relative to all other habitat types except deciduous woodland. Deciduous woodland was only significantly avoided relative to closed canopy woodland, but deciduous woodland was rare within the study area.

Our tracking resolution of 100m would have been insufficient to detect use of linear features. However these might be important foraging habitats in commercial forestry, so we devised a simple 'edge detection' method in an attempt to determine whether linear features were selected. For this, special programming help was provided by Dr R.E. Kenward, ITE, Furzebrook. Comparison of the amount of river, track and fire break in 50m, 100m and 200m radii from radio fixes showed no significant differences in their relative proportions as the distance from fixes increased. The implication is thus that these linear habitat features were not selected by pine martens.

Habitats within core areas were compared with those outside cores but within territories. This showed significant selection for tussock grass and stream, compared with moss and non-tussock grass and other cover (Table 5).

Comparison of habitats in MCPs with those available in the study area showed a significant preference for closed canopy forest and clearfell over all other habitats. Moor was significantly avoided relative to all habitat types (Table 6).

In total 118 den and lie-up sites were found. Habitats in a 200m radius around these sites were compared to habitat availability in MCPs (Table 7). Closed canopy woodland, fire break and track ranked highest utilised for dens and lie-ups, but use differed significantly only from that of moor and lakes. The proportions of track, river and fire break habitats showed no significant change in circles of 50m, 100m and 200m centred on dens and lie-ups. As with active fixes, there was thus no evidence that pine martens selected areas for dens and lie-ups near linear features.

Habitat within a strip 100m wide along MCP boundaries was compared with that available in MCPs. Although tussock grass and closed canopy woodland were ranked highest, the only significant difference in ranks represented avoidance of moor relative to all other habitats. Mean speed and linearity of travel were not significantly affected by position in or out of the boundary strip (for speed: $F_{1.211}=0.62$, $p=0.43$; for linearity $F_{1.211}=0.34$, $p=0.56$); nor did they differ between male and female pine martens ($F_{1.211}=0.97$, $p=0.33$, and $F_{1.211}=0.04$, $p=0.84$ respectively).

Diet

In total 100 pine marten scats were analysed and contained 21 types of prey. Invertebrates and passerine birds were the most common prey items, occurring in 49 and 40 scats respectively. Field vole remains were found in only 14 scats although unidentified vole and small mammal remains were found in 7 and 13 scats respectively. Calculation of estimated weight (EWI) intake showed that carrion (20% EWI), small mammals (23%) and passerines (22%) to be the most important prey in terms of biomass consumed. The relative importance of different prey changed seasonally (Fig. 3). Deer carrion was most important during winter and early spring comprising almost 70% of EWI in March and April. Invertebrates, small mammals and passerines accounted for most EWI during summer. Berries and seeds were most important in September and October when bilberries were abundant (Fig. 3).

When scats from upland spruce and lowland mixed conifer habitats were analysed separately, there was no difference in the frequency of occurrence of prey items.

Discussion

Habitat selection

One problem associated with the study of habitat selection by carnivores is that only a small proportion of an animal's time may be spent hunting. This means that many radio locations may be in habitats not used for foraging, yielding a potentially false view of important habitats. In our analysis of habitat selection this problem should be minimised because radio locations for which a pine marten was recorded as not moving and/or near a den or lie-up site were excluded. We also conducted analyses at a series of nested spatial scales, which should have revealed more subtle patterns of habitat selection.

Pine martens showed a clear preference for woodland both in selection of territories at the landscape scale and in the utilisation of woodland within territories. Such preference has been repeatedly documented (Balharry, 1993; Nyholm, 1970; Pulliainen, 1981) and is likely to represent at least in part avoidance of predation by foxes and large raptors (Storch *et al.* 1990).

Fig. 2. Speeds of travel by male and female pine martens in core areas and outside core areas. Means and standard errors are shown.

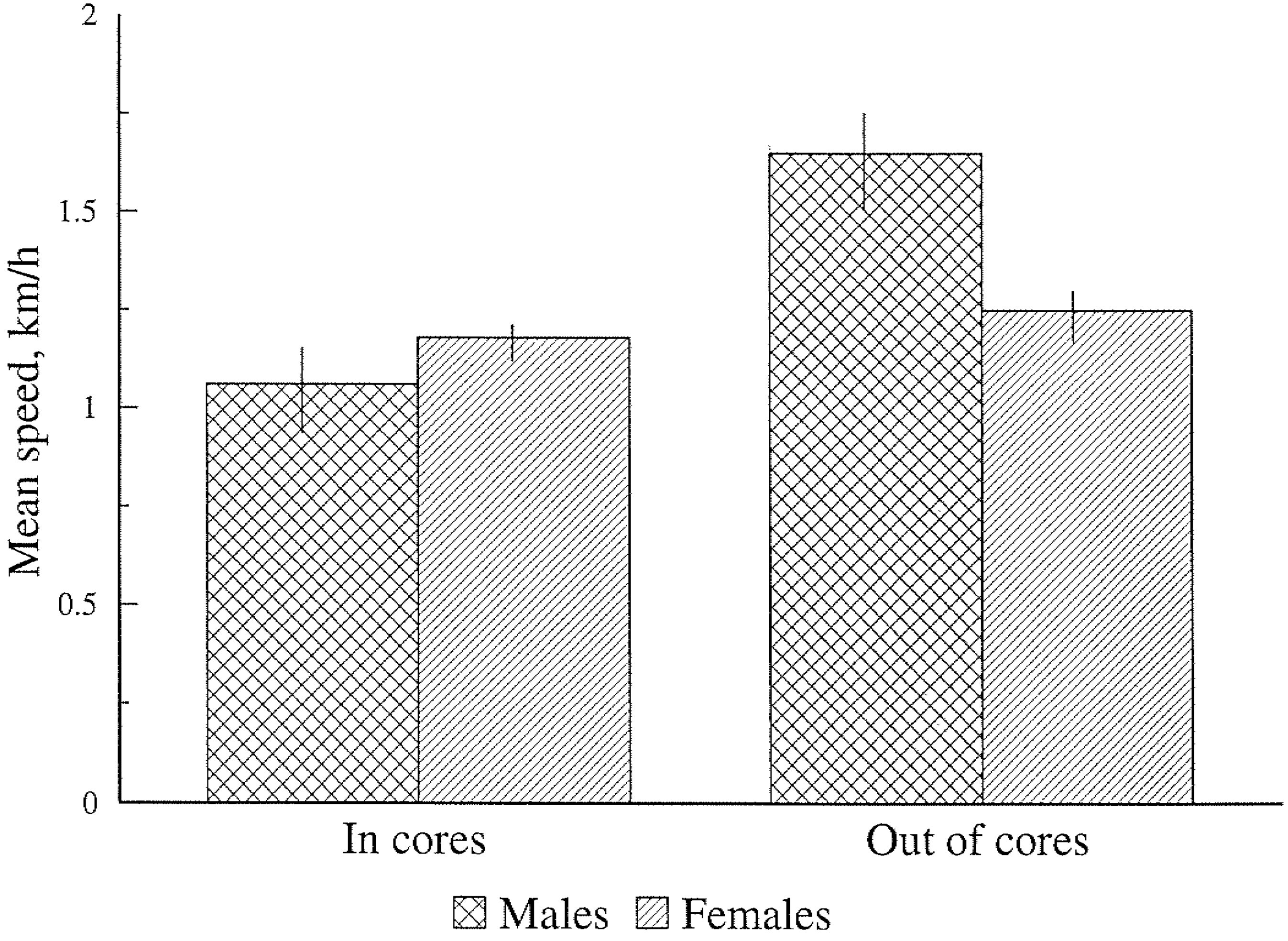
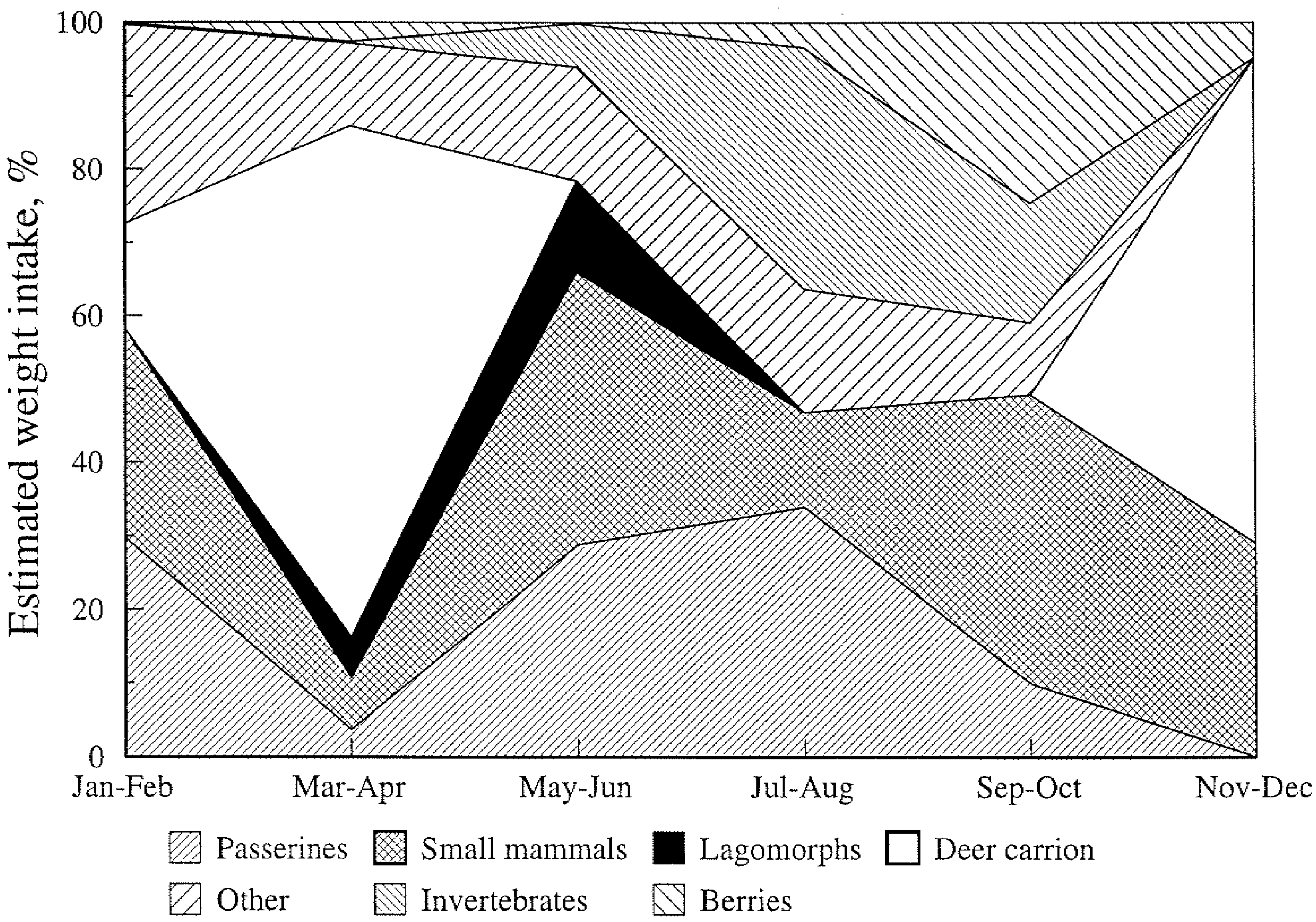


Fig. 3. Estimated weight intake (% biomass) of different prey items by pine martens. Data represent analysis of 100 scats and show the seasonal change in diet, plotted at bi-monthly intervals.



Radio tracking identified a clear preference of pine martens for certain micro-habitats in what appeared to be homogeneous plantation. Selection of these core areas was clearly based on the presence of tussock grass and stream. This was probably related to high abundance of small mammals, as streams were usually bounded by tussock grass the principle habitat of field voles. It may also be related to higher abundance of invertebrates which were a prominent feature in pine marten diet.

Our results suggest that pine martens may not utilise linear features such as fire breaks and rides, at least in relation to foraging or locating dens. This might be due to foxes, predators of pine martens, concentrating their activity along such features. However, although tracks and fire breaks (both being linear tussock grass habitats with high abundance of field voles) were ranked as highly used, their importance was difficult to separate from that of closed canopy forest in which they were embedded. Linear habitats within commercial forest could be important to pine martens, but this might not detectable with our tracking resolution. Pine marten scats were often found on old walls along fire breaks, implying that the latter were important routes for travel. Linear features may thus be less important for foraging, than as travel routes.

Comparison of habitats in pine marten territories with habitat availability in the landscape, suggested that clear felled areas were selected. This was probably an artifact of felling (widespread during the study) occurring after pine martens had established territories. On six occasions female pine martens were tracked along the edge of clear fells and appeared to make detours in excess of 300m to avoid crossing open ground. Males appeared more ready to cross open ground, but moved in a direct line and at high speed between forested areas. One male (M9) several times crossed the open ground between two watersheds, but so rapidly that it was difficult to maintain contact with him in even from a vehicle! This reinforces the suggestion that wooded habitats are of pre-eminent importance to pine martens.

Differences in territory areas and movements by pine martens of both sexes showed that upland spruce plantation offered lower quality habitat than lowland mixed conifer plantation. In particular, pine martens in lowland mixed conifer plantation made significantly more about-turns, these being indicative of foraging in high quality habitat patches. Lowland mixed conifer plantation contained 20% more open canopy woodland (mostly larch dominated) and was therefore likely to support a higher biomass of prey for pine martens.

Balharry (1993) suggested that the area of woodland within a territory was constant irrespective of woodland fragmentation. However woodland areas within territories in Galloway were much greater than those in either of Balharry's study sites. This may well have been due to woodland at Balharry's sites providing higher prey availability; 90% of his woodlands were open canopy, compared with only 3% overall in the Galloway study area (or 7% in MCP territories). Pine martens in Galloway concentrated their activity in core areas of lower canopy cover where tussock grass was abundant. Such habitat patches were more dispersed in upland spruce plantation and pine marten territories were consequently larger than in lowland mixed conifer habitat. It is thus clear that upland spruce plantation formed poor habitat for pine martens compared to that offered by lowland mixed conifer habitat. The former may also offer fewer den sites (see Part 4).

Territorial behaviour

Dispersion of male and female pine martens conformed closely to the intra-sexual territorial system reported by Balharry (1993). This was so even in low quality upland spruce habitat, where territories of pine martens of the same sex might be expected to overlap. There was also no difference in the length of defended territory edge between the current study and those by Balharry (1993). Such findings have profound implications for translocations and reinforce Balharry's (1993) conclusion that the pine marten's social system may be inflexible in respect of habitat quality and fragmentation.

Diet

The abundance of field voles, important prey for pine martens elsewhere (Balharry, 1993), was low during our study. Pine martens would therefore have been expected to consume a wider variety of lower quality prey items, and this appeared to be the case. Composition of the diet varied seasonally, reflecting changing abundance of different prey.

Balharry (1993) found that deer carrion and small mammals contributed 31% and 37% respectively to estimated weight intake (EWI). Passerines and invertebrates contributed only 7.3% and 1.5% respectively to EWI. By contrast, in Galloway passerines (22%) and invertebrates (12%) contributed a greater proportion to EWI. Small mammals were slightly less important in Galloway (23%), but this was probably due to shortage of field voles.

These findings are important because they demonstrate that pine martens are sufficiently generalist predators to survive in upland spruce plantations even when their preferred prey are scare.

Conclusions: implications for reintroductions and forest management

The detailed analysis presented here reinforces a conclusion reached on the basis of pine marten population density (Part 1): lowland mixed conifer plantation provides good habitat for pine martens, but upland spruce plantation is less suitable. More importantly, our analysis suggests why population density is higher in lowland mix conifer plantation: there is a greater area of low tree canopy cover, which leads to a more extensive field layer and probably higher abundance of prey (especially voles) for pine martens. Balharry (1993) reached similar conclusions. Suitable hunting patches appear more dispersed in upland spruce plantation, so foraging there may incur higher energetic costs. It is probably important that hunting patches are present within stands, as we found little evidence that pine martens foraged along forest edges or linear features within forest.

The implication for forest design and management is that more low canopy cover coupes would benefit pine martens, especially in upland spruce plantation. Such coupes will not be desirable in some areas, due to increased risk of damage to more open stands from windthrow. However, current forest management plans for many areas already prescribe some more open stands for second planting rotations. Greater age/structural diversity is also being introduced to many forests and this too will benefit pine martens. Thus the pine marten's requirements are not an additional constraint on forest design. In fact, higher densities of pine martens should be a good indicator of more naturally structured forests that are now the goal of many forest management plans.

Our work has three clear implications for reintroductions. Firstly, upland conifer plantations can support pine martens and, since they offer virtually continuous woodland cover, they will often be large enough to support viable populations. They are thus suitable sites for *trial* reintroductions and also offer several practical advantages *eg* access roads for radio tracking. Secondly, releases should be in areas of lower forest canopy cover as these provide preferred habitat for pine martens. Finally, the intra-sexual territorial system evident even when pine martens are at low population density, means that releases of individual pine martens will need to be very carefully controlled. It will be vital to space and time releases to promote social cohesion and avoid aggressive interactions.

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Part 4: Ecology of den use by pine martens reintroduced to a commercial coniferous forest

Introduction

Being long and thin, having a high surface area to volume ratio, means that martens rapidly loose body heat. Physical protection from inclement conditions during inactive periods is thus of great importance to survival. Consequently, the availability of sheltered dens is likely to be an important component of suitable habitat for martens (Buskirk, 1983; Balharry, 1993). Availability of suitable dens may be especially important to breeding female martens, both for shelter of kits prior to their achievement of thermoregulatory competence and for protection from predators.

This section of the report examines the ecology of den use by pine martens reintroduced to a commercial coniferous forest in Galloway, south west Scotland. In much of this upland forest suitable den sites below ground level may be scarce because soils are often water logged. Arboreal den sites may also be infrequent as there are few tree hollows which elsewhere are often used as dens. Based on the premise that suitable dens may be scarce in upland commercial coniferous forest, we also report on trials of nestboxes specifically designed for pine martens. Nestboxes might be useful conservation aids for pine martens in such habitats and even offer a new way to monitor populations. Our work was based on a duel approach of monitoring the behaviour of radio collared pine martens and determining thermal characteristics of different types of potential den sites.

Methods

Locating dens and lie-ups

Areas where radio collared pine martens were stationary for more than half an hour were considered to be dens or lie-ups. Den sites were distinguished from lie-ups by the presence of a protective structure (tree fall snag, burrow or large nest) and frequent prominent midden of scats. Dens were usually day-time retreats, whereas lie-ups were used during day or night. In addition, dens were generally re-used more frequently than lie-ups.

Availability of denning areas

It was not practical to directly quantify the availability of den sites. However, we were able to sample the availability of areas where dens were often located. These were patches of windthrow (wind-felled trees) and patches of rock at the ground surface. Percentage ground cover of windthrow and rock was determined during surveys of pine marten core areas (50% cluster polygons; Part 3). Additional data on windthrow occurrence was obtained from Forest Enterprise surveys.

Nestboxes

In June 1994, 30 nestboxes of an experimental design thought suitable for pine martens were put up in the study area. Each wooden nestbox had two levels with an entrance hole on the lower level connected to an upper den chamber. A small examination hatch provided access to the den chamber to which dry bedding (usually wood wool)

Table 1. Summary of den and lie-up sites used by 13 pine martens, each radio tracked for about 10 nights.

	Range of height above ground, m	Total number found (%)	Number of marten-days (%)	Re-use (marten-days/no. of dens)
Dens				
Low windthrow	0 - 5	46 (54)	41 (40)	0.9
High windthrow	5 - 15	9 (10)	18 (17)	2.0
Canopy nest	15 - 20	17 (20)	21 (20)	1.2
Root plate	0 - 3	4 (5)	2 (2)	0.5
Nestbox	5 - 15	1 (1)	3 (3)	3.0
Rock crevice	-1 - 0	3 (3)	3 (3)	1.0
Soil crevice	-1 - 0	2 (2)	10 (10)	5.0
Tree hollow	1 - 15	1 (1)	2 (2)	2.0
Timber pile	0 - 3	2 (2)	2 (2)	1.0
Total		85	102	
Lie-ups				
Low windthrow	0 - 5	3 (9)	2 (14)	0.7
High windthrow	5 - 15	8 (24)	5 (36)	0.6
Canopy	15 - 20	22 (66)	7 (50)	0.3
Total		33	14	

was added. Nestboxes were tied with rope securely to trunks of trees at a height of at least 5m above ground.

Temperatures of potential dens

Temperatures in potential dens of five types (three replicates of each) were recorded during winter (January-March 1996) and summer (July-August 1996). Potential den sites were chosen to closely represent den sites used by pine martens. These were: rock cairns, tree brash and tree root plates. Temperatures in pine marten nestboxes and barrels buried in soil were also recorded. The latter were designed to mimic artificial den chambers below ground, which might be provided for pine martens. At each potential den, ambient air temperature and den temperature were recorded every hour for eight days using thermistors attached to data loggers (Squirrel meter/loggers, Grant Instruments, Cambridge).

Results

Den use

In total 118 den and lie-up sites were found by radio tracking pine martens, of which 34 (29%) were classified as lie-ups (Table 1). Lie-up sites invariably had little structure and were used for short periods (c. 1-3 hours), once or twice during a 10 day plus radio tracking session.

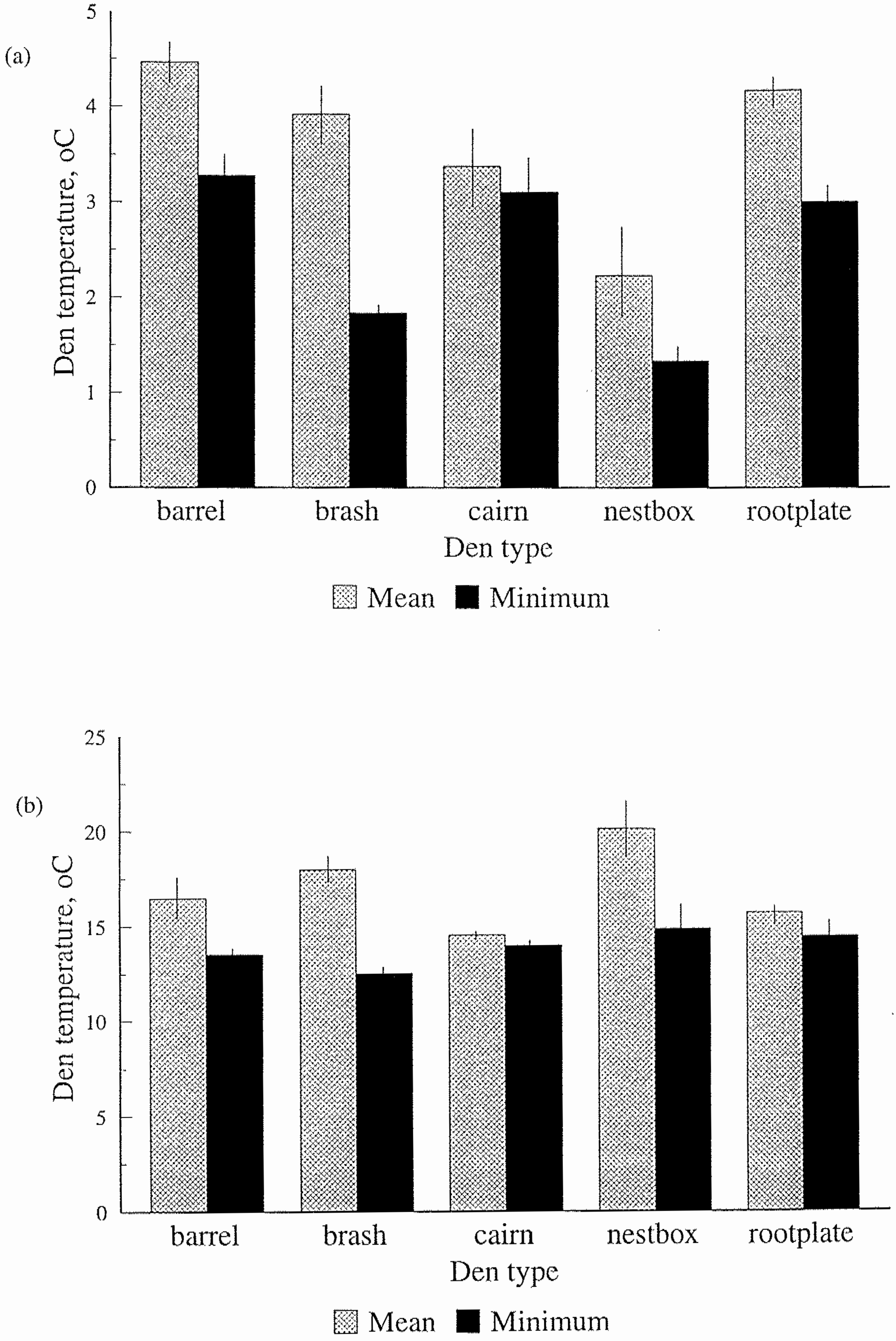
Dens were mostly (54%; Table 1) in areas of low windthrow (*ie* areas of wind blown trees up to 5m in height). Lie-ups were most frequently (66%; Table 1) in the tree canopy. Only five dens (5%) were located below ground in rock or soil crevices and only two dens were in tree hollows or nestboxes. Nine dens (11%) were associated with large bird nests or squirrel dreys, although some canopy lie-ups may have been in nests. The frequency of dens in root plates may also have been under estimated, such dens being miss-classified as in windthrow, because precise dens sites were sometimes inaccessible in windthrow patches.

Den types were divided into two groups dependent upon whether they were above ground (high windthrow, tree hollows, nestboxes) or at ground level (low windthrow, root plates, crevices, timber piles). Fisher's exact test showed no association between the frequency of dens at the two heights and habitat type (lowland mixed conifer or upland spruce; p=0.19). There was also no significant association between den height and season (summer or winter; p=0.35).

An alternative perspective on den use can be obtained by examining the number of radio tracking days spent in different types of dens. In total 102 den-days (88%) were spent in dens and 14 (14%) were spent in lie-ups. There were no significant associations in frequency of den-days between height above ground and habitat type, nor between height above ground and season (Fisher's exact tests: p=0.55 and p=0.22 respectively).

An index of den re-use was calculated by dividing the number of den-days spent in each den type by each pine marten, by the number of dens found. Dens in low windthrow were re-used significantly less often (mean 0.86, SE 0.18) than non windthrow dens (mean 1.78, SE 0.38; Wilcoxon test, z=1.96, p=0.05). Dens in high windthrow, nestboxes and tree hollows were re-used more often. Note, however, that sample sizes of these den types were small. There were no significant differences in re-use between winter and summer, nor in lowland mixed conifer habitat compared with upland spruce habitat (Wilcoxon tests, p>0.2).

Fig. 1. Ambient temperatures in five types of potential pine marten den. Mean and mean minimum diel temperatures are shown, together with standard errors for (a) winter (January-March) and (b) summer (July-August).



Den selection was re-analysed after removal of data for low windthrow dens, which were little re-used and probably sub-optimal (see Discussion). There was a significant association between den height and habitat: more dens were above ground than at ground level in upland spruce habitat (Fisher's exact test: $p=0.049$). Furthermore, more den-days were spent in ground level or subterranean dens in lowland mixed conifer habitat, compared with upland spruce habitat (Fisher's exact test $p=0.002$). During winter more den-days were spent in ground level, than in above ground dens (Fisher's exact test $p=0.038$).

Availability vs use of denning areas

There was no difference in the cover of windthrow areas in MCPs territories in lowland mixed conifer habitat and upland spruce habitat ($U_{8,5}=21$, $p=0.88$). Cover of rock areas was significantly greater in lowland mixed conifer habitat (mean 2.16hakm^{-2}, SE 0.34) than in upland spruce habitat (mean 1.28hakm^{-2}, SE 0.21; $U_{8,5}=34$, $p=0.04$).

Use of different den types by individual pine martens was compared to the availability (cover) of denning areas within MCP territories. There was no correlation between the number, frequency of use (den-days) or re-use of low windthrow dens and cover of windthrow in MCPs. Re-use of low windthrow dens was however negatively correlated with cover of rock areas ($r_S=-0.56$, $n=13$, $p=0.024$). The number of non low windthrow dens used was significantly positively correlated with cover of rock areas ($r_S=0.52$, $n=13$, $p=0.036$).

Use of nestboxes

In July 1995, pine marten scats were present on the roof of three of the 30 pine marten nestboxes put up a year before. In April 1996, five nestboxes had scats and at least one was known to have been used by a radio collared pine marten. The latter nestbox again had fresh scats on the roof in June 1996 and bedding inside had been trampled; the box had clearly been used as a den. Pine martens were radio tracked to bird nestboxes on several occasions. Male 4 spent three den-days in a duck box and male 8 was found in a new owl box on three occasions.

Temperature in potential dens

Mean and minimum temperatures in potential dens in summer were highest in nestboxes (20°C SE 1.52 and 15°C SE 1.3 respectively; Fig. 1a). Mean summer temperatures were lowest in cairns (14°C, SE 0.25) and minimum temperatures were lowest in brash (12°C, SE 0.49). In winter, nestboxes had the lowest mean (2°C, SE 0.49) and minimum 1°C (SE 0.21; Fig. 1b) den temperatures. Barrels buried in soil had the highest mean and minimum temperatures (4°C, SE 0.24; 3°C, SE 0.23, respectively).

Potential dens were randomly distributed at different altitudes, which would have experienced different ambient temperature. We controlled for this in the following ANOVAs by including ambient air temperature as a covariate. There were significant differences between mean den temperatures during summer ($F_{4,119}=9.47$; 0.002), and minimum den temperatures during winter ($F_{4,119}=4.59$; $p=0.02$). Cairns had significantly lower mean summer temperatures than brash or nestboxes (Tukey tests: $p=0.05$ and $p=0.01$ respectively). Nestboxes had significantly higher summer mean temperatures than root plates or barrels ($p=0.05$ and $p=0.05$ respectively). During the winter, however, minimum temperatures were significantly lower in nestboxes than in barrels (p=0.05).

There were no significant differences between mean den temperatures in winter ($F_{4,119}$=0.89; p=0.5) and minimum den temperatures in summer ($F_{4,119}$=0.99; p=0.46).

Discussion

The importance of suitable dens as aids to thermoregulation by American martens experiencing sever (continental) winters has been well documented. Lack of suitable dens has been suggested as one constraint on distribution and abundance (Buskirk, 1983; Buskirk, *et al.* 1988; Buskirk & Macdonald, 1989; Thompson & Colgan, 1991). The maritime climate experienced by pine martens in Britain is much less severe than that in North America. Nevertheless, Speakman & Balharry (1992) showed that energy expenditure would be significantly greater for active pine martens in Scotland in winter than in summer. To compensate, pine martens reduce their activity in winter and spend longer in dens (Speakman & Balharry, 1992). Thus availability of suitable dens is important to pine martens even in Britain's mild climate.

Our measurements of temperature in potential dens suggest that pine martens should select above ground dens in summer (nestboxes being especially warm). In winter, below ground dens in soil, not rock, should be selected (temperature in rootplates and barrel in soil were highest). American martens are known to change selection of dens seasonally in this way (Buskirk, 1983).

Pine martens in Galloway used ground level or subterranean dens significantly more in winter, but this was apparent only if use of low windthrow dens was ignored. The latter were the most frequent den site (54%), but were little re-used. This implies that low windthrow dens were abundant and pine martens not limited to a few such dens, or that low windthrow did not offer optimal conditions for dens. There was no difference in the availability of low windthrow in upland spruce or lowland mixed conifer habitat, but pine martens used low windthrow less in the latter. Our evidence thus suggests that low windthrow does not provide optimal conditions for dens. Furthermore, the availability of ground dens in upland spruce habitat was probably low, soil generally being waterlogged (especially in winter) and little rock being exposed at the surface. This implies that availability of ground dens in upland plantation may constrain pine martens in winter and that artificial ground dens, such as our barrels buried in soil, might be beneficial.

The low use of specially designed pine marten nestboxes was disappointing, but in retrospect not surprising: most of the nestboxes were in upland spruce habitat where pine marten density was low (Part 1). Many of the nestboxes also became very wet inside and this could have discouraged used. A more fundamental problem to providing nestboxes however, is that pine martens clearly require multiple dens distributed throughout their territory. Use of multiple dens is probably one thing that permits pine martens (especially males) to exploit large territories. It might not be energetically feasible for them to be central place foragers. The practical consequence is that several nestboxes would be needed per territory, so that expense and logistics would limit nestbox deployment. Nevertheless we believe that limited trials of nestboxes (above and below ground) would be worth pursuing, especially in relation to reintroductions.

Our findings about den use in upland commercial coniferous forest contrast with those for pine martens in other types of woodland. Tree hollows are frequently used as dens: 70% of dens in a study in Sweden and 37% of dens in Strathglass were in tree hollows (Balharry, 1993; Brainerd *et al.* 1995). Tree hollows were very scarce in the Galloway study area, nestboxes providing a partial substitute. In an upland area with highly fragmented woodland and much rock at the surface (Kinlochewe), Balharry (1993) found that 50% of dens were in rock cairns. Lack of outcropping rock and waterlogged soils would have limited the availability and use of such dens in Galloway.

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