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Diversity of den sites used by pine martens *Martes martes*: a response to the scarcity of arboreal cavities?

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ABSTRACT
1. We compiled a sample of 370 pine marten dens to test the hypothesis that a scarcity of sites leads to the use of suboptimal structures.
2. The sample was influenced by detection methods. Radio-tracking revealed cryptic dens but few natal dens; chance encounters revealed dens in buildings and other man-made structures. A total of 82.8% of natal dens were detected by chance encounters.
3. Most dens were associated with trees (44.3%), rocks (27.6%) and buildings (13.8%). The natal den subsample comprised buildings (44.3%), trees (22.8%), other man-made structures (17.1%) and rocks (14.3%). A total of 69.6% of dens were elevated and typically in structures offering limited shelter. Only 9.8% of all dens were in elevated tree cavities.
4. This diversity of dens reflects a scarcity of arboreal cavities. The alternative structures are suboptimal in terms of energetic costs and risks of predation, and this may limit breeding success in some populations.

Keywords: insulation, natal den, predation, resting site, roof void, standing dead wood, suboptimal, thermoregulation

INTRODUCTION
Dens are an important resource for pine martens *Martes martes*, and sites are selected in response to predation risks and energetic constraints (Brainerd *et al.*, 1995; Zalewski, 1997). Pine martens have several predators (Brainerd, 1990; Balharry, 1993), and predation by the red fox *Vulpes vulpes* may limit populations (Lindström *et al.*, 1995; Helldin, 1998). Avoidance of foxes forces pine martens to seek safe shelter above ground (Pulliainen, 1981; Webster, 2001). This may be especially important in Britain because foxes are more abundant now compared with Mesolithic times (Maroo & Yalden, 2000) and pine martens are arguably more vulnerable due to the low and highly fragmented woodland cover (Bright, 2000; Forestry Commission, 2003).

Martens have an elongated body shape that is energetically inefficient (Iversen, 1972). They carry limited fat reserves (Buskirk & Harlow, 1989), and their fur is not highly insulative (Scholander, Waters & Hock, 1950). These features increase the energetic costs of thermoregulation in cold weather (Pulliainen, 1981; Brainerd *et al.*, 1995; Zalewski, 1997). Successful reproduction depends upon the availability of natal dens in structures offering adequate insulation to breeding females and neonates (Brainerd *et al.*, 1995).

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Birks *et al.* (2004) have predicted that, under current woodland conditions in Britain, arboreal dens offering pine martens effective insulation and protection from predators are scarce. We test this prediction by gathering data on dens used by pine martens for resting and breeding. We hypothesize that a shortage of suitable structures would lead pine martens to occupy dens that are suboptimal in terms of the protection they offer, and this may involve compromise between predator avoidance and thermoregulation.

METHODS

We gathered recent information on pine marten dens located in the species' main British range in Scotland from two main sources: first from reports, unpublished work and student theses (see Table 1), and second via a questionnaire survey among naturalists, foresters and estate workers.

Between 2002 and 2004, a questionnaire was distributed by post and email. Respondents were required to supply details of any site or structure used as a den by a pine marten. Information was requested on location, height above ground, evidence of breeding, year of most recent use, the nature of evidence indicating occupancy, surrounding habitat and how the den was discovered.

We use the generic term 'den' to embrace both resting sites and natal dens. We define a den as any site or structure used by a pine marten for a prolonged bout of sleeping or resting. Sites used for brief periods of rest or shelter were excluded (e.g. 'lie-ups' as found by Bright & Smithson, 1997). Following earlier authors (Balharry, 1993; Brainerd *et al.*, 1995), we distinguished dens used for sleeping and resting from natal dens used by breeding females for the birth and initial rearing of young. This distinction is imperfect, however, because a natal den might fall into either category depending upon the season, hence our use of the generic term. Further, even during the breeding season, some natal dens might not be identified as such if juveniles were neither readily visible nor audible.

We categorized all dens according to the structure in which they were situated at two levels of detail. Level 1 involved six broad den categories: 'tree', 'rocks', 'burrow', 'building', 'other man-made structure' and 'open'; definitions are provided in Table 3 in the form of 15 more detailed 'Level 2' categories. If a range of heights was given for a den in reports or theses (e.g. Bright & Smithson, 1997), we assigned the median height. Dens at or below ground level were assigned a height of 0 m.

No data were available for most dens on microclimate or season of occupancy; nor were we able to assess the availability of different den structures, so these factors could not be considered in our analysis.

RESULTS

We obtained information on 370 dens used by pine martens during the period 1983–2004 (Table 1); 70 (18.9%) of these were identified as natal dens. A total of 267 dens were identified via the survey of field studies and 103 by 32 respondents to the questionnaire exercise (four respondents collated information from a further 34 individuals). Within the field studies sample, 263 pine marten dens (98.5%) were detected by radio-tracking. The remainder, as with the entire questionnaire sample, was detected by chance. We recognized that these different methods of detection might influence the structure of the entire den sample.

The composition of the den samples detected by radio-tracking and through chance encounters differed significantly (analysis based on occurrence of 'All dens' in Table 2: $\chi^2 = 249.13$, d.f. = 11, $P < 0.001$). Most of the 107 dens discovered by chance encounter were detected following sightings of pine martens ($n = 67$) or fresh scats ($n = 31$). Predictably, this

Table 1. The six Scottish field studies from which pine marten den data were gathered

Study	Main habitats (altitude)	No. of dens (of which natal dens)	% rocks	% tree	% burrow	% building	% other man-made structure	% open
1. Inverness-shire Velander (1986)	Conifer plantation (50–500 m)	8 (0)	75	25	0	0	0	0
2. Badenoch & Strathspey C. Strachan unpublished	Mountain (300–1000 m)	4 (0)	75	25	0	0	0	0
3. Ross-shire Balharry (1993)	Mountain with limited woodland (100–1200 m)	83 (3)	70	30	0	0	0	0
4. Inverness-shire Balharry (1993)	Native woodland & conifer plantation (100–500 m)	80 (8)	27	54	14	0	0	5
5. Ross-shire Halliwell (1997); Halliwell & Lindley unpublished	Conifer plantation (30–350 m)	7 (1)	0	86	0	0	0	14
6. Dumfries & Galloway Bright & Smithson (1997)	Conifer plantation (30–500 m)	85 (0)	4	90	2	0	4	0
Questionnaire sample – Scotland	–	*103 (58)*	*9*	*11*	*1*	*49*	*30*	*0*

For comparison, the questionnaire sample from the present study is shown in italics.

Table 2. The occurrence of Level 1 pine marten natal and non-natal den categories detected by radio-tracking and by chance encounter

	Radio-tracking subsample		Chance encounter subsample		Entire den sample	
Den category	All dens (%)	Natal den subsample (%)	All dens (%)	Natal den subsample (%)	All dens (%)	Natal den subsample (%)
Rocks	92 (35.0)	3 (25.0)	10 (9.3)	7 (12.1)	102 (27.6)	10 (14.3)
Tree	152 (57.8)	8 (66.6)	12 (11.2)	8 (13.8)	164 (44.3)	16 (22.8)
Burrow	13 (4.9)	1 (8.3)	1 (0.9)	0 (0)	14 (3.8)	1 (1.4)
Building	0 (0)	0 (0)	51 (47.7)	31 (53.4)	51 (13.8)	31 (44.3)
Other man-made structure	3 (1.1)	0 (0)	31 (29.0)	12 (20.7)	34 (9.2)	12 (17.1)
Open	3 (1.1)	0 (0)	2 (1.9)	0 (0)	5 (1.3)	0 (0)
Total	263	12	107	58	370	70

Table 3. Detailed location information for 70 natal dens and 209 other dens for which comparable information was available

Den category		Mean height (m) above ground ± S.D. (n)	
Level 1	Level 2	Natal dens	Other dens
Rocks	Cavity or crevice in rocks, cliff, crag or scree	1.33 ± 3.32 (10)	0.87 ± 2.37 (18)
Tree	Tree cavity above ground	3.22 ± 3.25 (12)	3.82 ± 2.45 (15)
	Rootplate of wind-thrown tree	– (0)	0.50 ± 0.75 (9)
	Snagged branches of wind-thrown tree	2.0 ± 0.0 (1)	3.73 ± 2.80 (56)
	Bird nest	– (0)	15.45 ± 4.04 (38)
	Cavity associated with tree roots	0.0 ± 0.0 (3)	0.0 ± 0.0 (14)
Burrow	Burrow, crevice or cavity in ground not associated with tree or rocks	0.0 ± 0.0 (1)	0.0 ± 0.0 (13)
Building	Occupied house	3.15 ± 1.35 (16)	4.22 ± 1.85 (10)
	Unoccupied house	1.67 ± 2.89 (3)	2.0 ± 0.0 (1)
	Barn, shed or outhouse	3.96 ± 0.69 (12)	2.34 ± 1.39 (8)
Other man-made structure			
	Nest box up tree	3.69 ± 0.26 (8)	3.85 ± 1.78 (18)
	Stone wall	– (0)	1.50 ± 0.0 (1)
	Pile of timber, logs, etc.	0.83 ± 0.58 (3)	1.50 ± 0.0 (2)
	Parked vehicle/boat	1.0 ± 0.0 (1)	3.0 ± 0.0 (1)
Open	'Open' den in ground-level vegetation	– (0)	0.0 ± 0.0 (5)
Total		2.44 ± 2.36 (70)	4.04 ± 5.35 (209)

sample was dominated by dens in buildings and other man-made structures visited by people, such as large bird boxes (Tables 2 and 3). Conversely, the sample revealed by radio-tracking mainly comprised cryptic dens associated with rocks, trees and burrows (Table 2).

The two detection methods differed markedly in the proportion of natal dens revealed (Yates' corrected $\chi^2 = 121.58$, d.f. = 1, $P < 0.001$). Only 4.6% of dens detected by radio-tracking were natal, compared with 54.2% in the chance encounter sample (Table 2). A total of 82.8% of natal dens were detected by chance encounter. The 70 natal dens were typically identified following sightings of an adult female with young ($n = 50$); the remainder were confirmed by audible evidence of marten families within dens and large scat piles found at den entrances during the breeding season.

Dens associated with trees or rocks accounted for 71.9% of the entire sample; a substantial minority (23.0%) of dens was located in buildings or other man-made structures, such as bird boxes and log piles (Tables 2 and 3). Approximately half of the dens in buildings were in occupied houses (Table 3), where most were located in the roof void.

Of 148 tree dens for which Level 2 details were available (Table 3), 64.2% were located in structures offering limited protection against severe weather, such as bird nests or among snagged branches; elevated dens in arboreal cavities comprised only 18.2% of tree dens and 9.8% of all dens shown in Table 3. In a subsample in a conifer plantation (study 6 in Table 1), only one arboreal cavity den was recorded among 85 dens detected; 84.7% of dens in study 6 were located in relatively exposed situations, such as nests or snagged branches. Dens among rocks were the dominant category in the higher altitude studies (studies 2 and 3); at intermediate or lower altitudes, den samples were either dominated by trees (studies 5 and 6), rocks (study 1), or had substantial proportions of each (study 4). A total of 69.6% of dens were located above ground level; the remainder were mainly in rocks, burrows or cavities associated with tree roots (Table 3). Dens in five Level 2 categories (bird nest, occupied house, nest box, tree cavity and snagged branches) had mean heights above ground level of > 3 m (Table 3).

A total of 38.5% of natal dens were located in cryptic sites (expected to be under-represented in this chance encounter-dominated sample), such as rocks, trees and burrows (Table 2). Occupied house was the commonest Level 2 category, representing 22.9% of all natal dens (Table 3); most were located in the roof void. Only 12 elevated arboreal cavity natal dens were reported (mean height > 3 m). The natal den category with the greatest mean height was 'barn, shed or outhouse' (Table 3). Natal dens tended to have lesser heights above ground level than a sample of other dens in which breeding was not observed and for which comparable height data were available ($t = -2.90$, d.f. = 277, $P < 0.01$; Table 3). A total of 27.1% of natal dens were at or below ground level, and most of these were associated with rocks and tree roots; three were within or beneath buildings. In contrast with the 'non-breeding' den sample, almost all natal dens were located in solid structures offering substantial protection from wind and precipitation (Table 3). No natal dens were detected by radio-tracking in a commercial conifer forest (study 6), although natal dens were detected by chance encounter in three owl nest boxes and two barns in this forest. Similarly, in a commercial conifer forest in central Scotland, the questionnaire survey revealed that most natal dens were reported from owl nest boxes.

DISCUSSION

The den sample described here is influenced by the method of detection. However, any biases are counterbalanced as follows: radio-tracking revealed many cryptic dens in 'natural' study areas (dens in rocks or burrows may be under-represented due to radio signal attenuation; E.C.H. personal observation); conversely, chance encounters detected fewer cryptic dens, but revealed many dens in buildings and other man-made structures in areas typically avoided by researchers. Thus, we suggest the entire sample of dens is more representative of the range of habitats occupied by pine martens than that revealed by recent field studies alone.

The diversity of den types in Scotland is greater (even if the chance encounter sample is excluded) than in continental Europe, where dens are predominantly associated with trees and most natal dens are located in arboreal cavities (Brainerd *et al.*, 1995; Achterberg, Bestman, & Wijsman, 2000; Stier, 2000; review by Zalewski, 1997). Although martens commonly used dens associated with trees in this study, most were in structures offering limited insulation or protection against severe weather. The low occurrence of arboreal cavity dens is explained by the domination of Scottish woodland by young trees (88% by area planted after 1950; Forestry Commission, 2002), in which cavities are rare (Newton, 1994). The greater use of rocks, buildings and other man-made structures in Scotland supports the hypothesis that a scarcity of arboreal cavities forces martens to seek alternative sites. This process is likely to operate wherever woodland management limits the availability of such cavities (Brainerd *et al*., 1995).

The alternative den types do not necessarily facilitate both predation avoidance and thermoregulation, so their use may involve some compromise on these critical elements. Dens in elevated rock crevices are comparable with arboreal cavities in their inaccessibility to terrestrial predators (Webster, 2001), and ground-level rock dens may provide some protection against digging predators. However, rock provides poor insulation compared with wood, and the greater energetic costs may necessitate collection of bedding to improve insulation, as observed by Balharry (1993).

Climatic factors influence den selection by pine martens (Zalewski, 1997). For example, ground-level dens beneath snow are used in response to extreme cold (Pulliainen, 1981; Brainerd *et al*., 1995). Such conditions are uncommon in Britain's oceanic climate, so martens here should be less constrained. Nevertheless, nearly one-third of dens (and 27% of natal dens) were at ground level, where the risks of fox predation are greater (Zalewski, 1997). This use of higher-risk ground-level dens probably reflects the scarcity of suitable elevated dens rather than a response to cold weather.

Zalewski (1997) noted that wind speed and humidity influenced den selection, with martens choosing sheltered dens such as tree cavities instead of bird nests on windy or humid days. The pine marten's main range in Highland Scotland has the highest annual mean wind speed (> 6 m/sec), the highest annual mean precipitation (> 210 cm) and the highest mean frequency of annual 'rain days' (> 310 per year) in Britain (Hulme & Barrow, 1997). Thus, compared with arboreal cavities, pine martens face extra energetic costs when using dens in bird nests and branches under these conditions. Nevertheless, such sites predominated in this study, suggesting that the antipredator benefits of resting above ground level outweigh the energetic costs. These costs are greatest for female martens with their energetically less efficient shape, leading them to select more sheltered structures than do males (Zalewski, 1997; Dijkstra, 2000). Therefore, female martens would be more constrained than males by the scarcity of arboreal cavities, especially in commercial conifer forests where such cavities are most scarce (Hodge & Peterken, 1998). Such constraints are most severe for breeding females: exposed structures are unsuitable as natal dens because neonates require good shelter and insulation for their survival (Brainerd *et al*., 1995).

The prominent use of roof voids as natal dens by pine martens is an identical response to that shown by some bats to the scarcity of arboreal roosts (Schofield & Mitchell-Jones, 2003). Roof voids offer insulation, shelter from severe weather and elevation above the reach of terrestrial predators, enabling bats and pine martens to rear young in conditions similar to those in elevated tree cavities. However, unwelcome noise, odours and livestock predation associated with denning in houses are earning the pine marten a reputation as a nuisance (H. Brown, personal communication), with consequent risks of persecution and exclusion by disaffected householders.

We conclude that, as hypothesized, the diversity of dens used by pine martens in this study reflects the scarcity in Britain of high-quality arboreal sites. Compared with elevated arboreal cavities, most of the alternative structures are suboptimal and involve compromising on thermoregulation or the avoidance of predation or human disturbance. Because breeding females are the most likely to be constrained by a lack of high-quality sites, den availability may limit breeding success, especially in commercial woodlands.

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