THE DIET OF THE PINE MARTEN (*MARTES MARTES*) IN KILLARNEY NATIONAL PARK

Áine B. Lynch and Yvonne McCann

ABSTRACT

This study examined the diet of a re-established population of pine marten *Martes martes* in the broadleaf woodlands of Killarney National Park between 2003 and 2005. In contrast to previous dietary studies of pine marten, fruit formed the greater part of the diet, not small mammals. Except in summer, fruit was the most frequently consumed item and it also contributed the most in terms of percentage mass and percentage fresh weight ingested in the diet. The Mammal Group was the next most important food group overall, particularly in summer. No significant difference was observed in the frequency of occurrence of the wood mouse and the recently introduced bank vole in the diet. Birds were only consumed in spring and summer. Frogs were important throughout spring, summer and autumn, while earthworms were only important in winter. The overall dietary niche breadth was wide, and the narrowest seasonal niche breadth was recorded in autumn. The maintenance of woodlands with good fruiting species diversity, which in themselves provide the habitat for the other prey items that the pine marten consumes, is desirable for marten conservation.

Áine B. Lynch (corresponding author; e-mail: lynch_aine@hotmail.com) and Yvonne McCann, School of Natural Sciences, Department of Zoology, Trinity College Dublin, Dublin 2, Ireland.

Received 4 May 2006. Accepted 15 February 2007. Published 30 April 2007.

INTRODUCTION

A fundamental aim in mammal ecology is to determine what resources a particular species requires to exist, and an understanding of the dietary needs of that species is essential to address this objective (Reynolds and Aebischer 1991; Begg *et al*. 2003; Estes *et al*. 2003; Barrientos and Virgos 2006). Many techniques exist for assessing the diet of a species, and the behaviour of the species and what is required of the data set (Litvaitis 2000; Madsen *et al*. 2002) will determine which technique is most appropriate.

Wild-living carnivores are typically alert, highly mobile and elusive, and may be predominately nocturnal, so the analysis of the components of their diets is often restricted to indirect observations. These include the examination of the gut contents of dead animals or the collection and examination of faecal material left behind by the animal (Powell *et al*. 1997). The examination of gut contents is generally restricted to a short time-frame during which the target species can be legally hunted or culled; although this can give additional information such as sex and age (Goszczyński 1986), it is obviously destructive in nature. The collection of faecal material, while not as informative, is often favoured as it is non-invasive and is the cheapest means by which diet can be described. There are drawbacks to this method, and these should be taken into account. Results from faecal analysis may misrepresent the diet of the species under investigation owing to some dietary groups being more readily distinguished than others. Moreover, dietary analysis from faecal samples gives only a relative estimate of the foods ingested as opposed to an absolute estimate (Roper and Lüps 1995).

Despite being classed as carnivores, marten species (the fisher (*Martes pennanti*), American marten (*M. americana*), stone marten (*M. foina*) and pine marten) studied so far have a surprisingly catholic diet and are often referred to as opportunistic general feeders (Marchesi and Mermod 1989; Nagorsen *et al*. 1991; Genovesi *et al*. 1996; Powell *et al*. 1997; Ní Neachtain 1998). The diet of the pine marten has been investigated throughout Europe (Finland, Poland, Russia, Scotland, Spain and Switzerland), and the consensus across studies is that small mammals, particularly voles (*Microtus* and *Cleithrionomys* spp), are the most important prey items throughout the year, with other groups (birds in spring/summer, insects in summer/autumn, fruit in autumn/winter and amphibians/reptiles in spring/summer) being seasonally important (Goszczyński 1976; 1986; Pulliainen 1981; Lindström 1989; Marchesi and Mermod 1989; Jedrzejewski *et al*. 1993; Clevenger 1993a; Putman 2000).

However, studies carried out on certain islands (Minorca and Ireland) have shown that mammals are not the main component of the diet over the whole year—each of the main food groups (fruit, mammal, bird and arthropods) occur with equal frequency (though they may differ seasonally in their importance), while the other groups (reptiles, amphibians and earthworms) occur throughout the year but at a lower frequency

(Warner and O'Sullivan 1982; Clevenger 1993a, 1993b; Ní Neachtain 1998).

Clevenger (1993b) found that small mammals, fruit, birds and insects were equally important in the annual diet, with all four showing seasonal peaks. Furthermore, in a comparison of insular and mainland populations in Spain he found that the pine marten consumed a more diverse set of prey items, indicated by a wider niche breadth (BS = 0.754 *cf* 0.38 respectively), on the island compared with the mainland, where mammals were the dominant prey items (Clevenger 1993a). Both Ní Neachtain (1998) and Warner and O'Sullivan (1982) found a similar pattern in Ireland. It has been suggested that the consumption of a diverse set of prey items results from a depauperate mammal fauna, as is commonly associated with islands (Warner and O'Sullivan 1982). Conversely, this pattern has been attributed to the species exploiting the food available to it (this has been shown to be the case with other species, such as the genet *Genetta genetta*) and supports the suggestion that the pine marten is a generalist predator (Virgós *et al*. 1999).

Prior to the introduction of bank voles (*Cleithrionomys glareolus*) to Ireland, *c*. 1955 (Smal and Fairley 1984), the small mammal fauna comprised wood mouse (*Apodemus sylvaticus*), pygmy shrew (*Sorex minutus*), house mouse (*Mus musculus*) and rat (*Rattus norvegicus*). The latter two species are not common components in the diet of pine marten in Ireland (Warner and O'Sullivan 1982; Ní Neachtain 1998). The bank vole's range has not yet extended to any areas covered by research into the diet of martens, with the exception of the areas studied by Ní Neachtain (1998). Ní Neachtain concluded that the bank vole population was just becoming established in the area of the Burren where she carried out her research; she was unable to calculate vole densities from her small mammal trapping data as trapping success was so low (total numbers of individuals: $n = 78$ wood mice and $n = 11$ bank voles). In contrast, bank voles have been present in Killarney National Park since at least 1965 (Smal 1978) and now have a large and well-established population, although their population density is restricted by ground cover (Lynch 2002). An opportunity to observe whether the pine marten will incorporate introduced mammals into its diet was afforded by our research at Killarney National Park.

In this study we assessed the annual and seasonal diet of pine marten in the broadleaf woodlands of Killarney National Park over a two-year period and investigated whether the pine marten will consume an introduced small mammal, the bank vole.

STUDY AREA

This study took place in Killarney National Park (Irish national grid reference V9487), in the south-west of Ireland (Fig. 1). Killarney National Park, established in 1932, is now approximately 10,289ha, of which 14% is semi-natural woodland (native oak woodland (1200ha), yew woodland (25ha) and wet broadleaf woodland (155 ha)). The remainder is made up of lakes (24%) and upland blanket bog, heathland, rivers and streams (62%). All the woodlands in Killarney National Park are to a greater or lesser extent infested with rhododendron (*Rhododendron ponticum*) and are or have been overgrazed by deer: they show little sign of natural regeneration.

The park was once managed as a game reserve (with vermin being trapped or poisoned) and for commercial forestry: as a result there are some areas of conifer plantation, which are for the most part are surrounded by broadleaf woodland or are now semi-naturalised themselves. Killarney National Park is now under the management of the National Parks and Wildlife Service (NPWS). Until recently pine marten were considered either extremely rare or absent from the park following centuries of exploitation for their fur in the locality (O'Sullivan 1983). The population was augmented or re-established between 1987 and 1995, with *c*. 30 animals being translocated from County Clare (exact numbers unknown (P. O'Leary and P. O'Sullivan, pers. comm.)). The population is now fully established (Lynch 2006).

METHOD

Twelve sites within Killarney National Park were selected as possible sites for collecting scats, and a walking transect was established in each (Fig. 1). Transect lines were approximately 2.5km in length ($\mu = 2.05$km, SD = ± 0.28), and the same route was walked on each occasion. It was not possible to collect scats from all transects at the same frequency due to the lack of accessibility to some areas. Transects 1–10 were cleared of all faeces on day one and then walked every second day over six days. Each of these transects was visited three times during the period April to September in 2003 and 2004. Transects 11 and 12 were walked fortnightly and monthly, respectively, during April to September in 2003 and 2004, owing to their remote location. Scats were also collected during February 2003 (Transects 1–5) and November 2004 and January 2005 (Transect 4 and 10). Transect 4 was chosen as it was representative of all the other transects that could not be sampled during this time. No scats were collected in October or December 2004 as many scats were

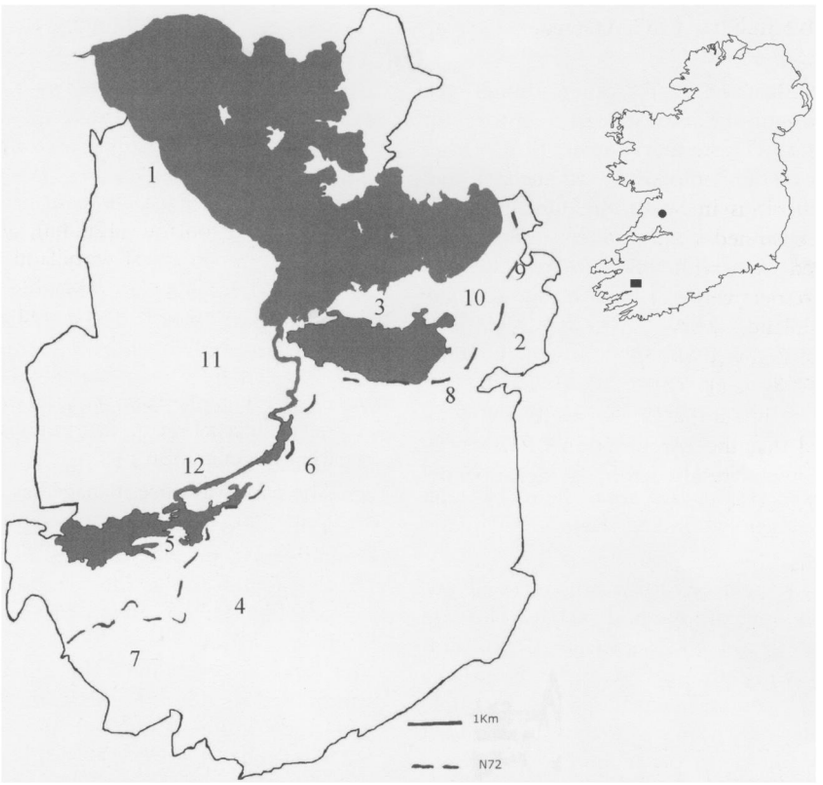

Fig. 1 — Map of study area showing the location of Transects 1–12 within Killarney National Park. Shaded area is the area covered by the lakes of Killarney National Park. The inset shows the location of the park within Ireland.

washed away during very wet weather and it was not possible to determine if remaining scats were those of pine martens.

Recent work in the UK reported that, even in the case of experienced field workers, confusion with the scats of other species, primarily fox (*Vulpes vulpes*), may arise when identifying pine marten scats in the field (Davison *et al.* 2002). In Ireland, pine marten scats may be confused with those of fox, stoat (*Mustela erminea*), badger (*Meles meles*) and mink (*Mustela vison*), all of which occur in Killarney National Park. Pine marten scats were distinguished from the above species initially by their smell, which Ní Neachtain (1998) described as aromatic, but not pungent or unpleasant, and secondly by their size and shape. Davison *et al.* (2002) suggest that scats from wild captive pine martens may be used to train field workers in their correct identification in the field. As part of a larger study, animals were also live trapped during this period, and scats found in the cages were compared to scats collected for dietary analysis to ensure correct identification. Scats were collected following inspection and wrapped in tinfoil. The date and grid reference were recorded for each scat, and they were preserved at −28°C until analysis in the laboratory. All scats except those collected in November 2004 and January 2005 (by the second author; $n = 43$) were identified and collected by the first author, who also carried out all live trapping and provided training for the other field worker.

Each scat was defrosted in the lab and dried to a constant weight in a 50°C oven and the weight noted. The dried scat was soaked overnight in detergent (Steradent) to help break it up and then washed through two sieves placed on top of each other, with pore sizes of 500μm and 125μm, respectively. The microscopic component was considered to be that fraction retained in the 125μm sieve. This was collected and allowed to settle and was later investigated for the presence of earthworm chaetae. The macroscopic fraction was collected in the top sieve and was examined under a dissecting microscope. This fraction was divided into its separate components and identified using the first author's own reference collection and following published keys (Day 1966; Yalden and Morris 1990; Teerink 1991; Chinery 1993). Each of these components was then dried and weighed separately (Goszczyński 1976; 1986). An attempt was made to identify each component to order level (invertebrates, birds and mammals) or species level (mammals, fruit, amphibians), although this was not always possible.

STATISTICAL ANALYSIS

To allow comparison with other studies the data were categorised into six main groups for analysis: Arthropod, Fruit, Mammal, Bird, Other (amphibians, reptiles, molluscs and debris) and Earthworm. In keeping with the literature, the percentage frequency of occurrence (% FO)—the number of times a given item occurs over the total number of items—was used to assess the components of the diet. Percentage FO tends to place importance on those items that turn up often in the diet rather than or those that contribute the most in terms of mass or energy to the individual, so percentage Mass (% M, biomass) and the percentage fresh weight ingested (% FWI) were calculated for comparison, using the total mass of each component and digestibility factors following Lockie (1961).

The fresh weight of earthworms ingested was calculated following the method of Reynolds and Aebischer (1991) and Ní Neachtain (1998). This involved removing the excess water from the microscopic fraction and centrifuging each sample for two minutes (1000rpm). Water was then added so that the volume of the pellet and the water were equal. One cubic centimetre of the mixed solution was added to a Petri dish of known area, and the number of chaetae in eight $1cm^2$ boxes counted. From this the number of chaetae were estimated and thus the number of segments. The mean fresh weight of an earthworm segment was taken to be 15mg (Reynolds and Aebischer 1991).

Chi-square analysis was used to investigate whether there was any interannual variation for months for which two years of data were available, prior to assessing whether there was a seasonal difference in diet. For seasonal investigations all data were pooled and divided into the following seasons: spring (February–April), summer (May–July), autumn (August–October) and winter (November–January). Chi-square analysis was used again to isolate differences in the diet due to season. The dietary niche breadth (BS) was calculated using the formula described by Hespenheide (1975).

$$BS = (B - 1)/(n - 1)$$

where $B = 1/(\Sigma p_i^2)$, n = number of groups and p_i = number of items in group i/total number of items. The closer BS is to 1 then the wider the dietary niche (each group being equally represented), while the closer BS is to 0 then the narrower the niche (with one food group becoming more and more important).

RESULTS

Based on the analysis of the total sample of scats ($n = 387$), the diet of the pine marten in Killarney National Park consists of a wide variety of food items ($n = 30$) (Table 1). In total there were 883 components, with each scat containing approximately two components on average ($\mu = 2.28$, SD = 0.99). In our overall description of diet, the data will be presented in decreasing importance of % FO. The % Mass and % FWI are discussed directly afterwards for each group to indicate whether items that were consumed frequently actually contributed to the same in terms of energy. Only % FO will be used to illustrate the differences in the diet for each group across the four seasons.

Fruit was the most frequently consumed component in the diet (30.01% FO; Table 1): ivy (*Hedera ilex*) was the most frequently consumed item followed by yew (*Taxus baccata*) and blackberry (*Rubus* spp). None of the remaining fruit species consumed by the pine marten contributed significantly to the diet. Fruit was also the largest group consumed in terms of % Mass (47.95%) and % FWI (51.44%) (Fig. 2). Arthropods were the next most frequently consumed item (29.22% FO) but contributed little overall in terms of mass (5.07% M) or FWI (1.97% FWI). Among the Arthropod Group, the order Coleoptera was the most frequently consumed group (22.9% FO).

Mammals were the next most frequently consumed group (20.27% FO) in the diet of the pine marten, with wood mouse (*Apodemus sylvaticus*) and bank vole being the most notable prey items in this group (5.77% and 4.42% FO, respectively). There was no significant difference in the occurrence of these two species in the diet of the pine marten (Chi-square: $\chi^2 = 2.14$, d.f. = 1, $P = 0.15$). In terms of % Mass (15.29%) and % FWI (26.73%), mammals were the second most important group in the diet, after fruit (Fig. 2).

Birds were the next most frequently consumed group, with passeriformes being the most noteworthy order among the birds (3.17% FO), although a large number of birds remained unidentified (5.32% FO; Table 1). Based on % Mass and % FWI, Birds were the third most important prey group in the diet of the pine marten (Fig. 2).

Frogs (*Rana temporaria*) were the main component of the Other Group (5.44% FO), while earthworms were present in the diet, albeit in small amounts (3.05% FO and 1.67% FWI).

Overall there was a trend for one or two items within each group to dominate the majority of prey consumed within that group. On the whole the

Table 1—Components ($n_{total} = 883$) found in the scats ($n = 387$) of pine marten in Killarney National Park expressed as the percentage frequency of occurrence (% FO), percentage mass (% Mass) and percentage fresh weight ingested (% FWI). No value was computed for % Mass for Earthworm as the chaetae were too light to weigh. *n* is the number of components for each group.

Group	*Component*	*n*	*% FO*	*% Mass*	*% FWI*
Arthropoda	Beetles (Coleoptera)	203	22.99	4.19	1.61
	Bees & wasps (Hymenoptera)	7	0.79	0.16	0.06
	Butterflies (Lepidoptera)	6	0.68	0.06	0.05
	Wood-lice (Isopoda)	8	0.91	0.06	0.02
	Larvae	1	0.11	0.03	0.01
	Not identified	33	3.74	0.56	0.22
	Total	**258**	**29.22**	**5.07**	**1.97**
Fruit	Blackberry (*Rubus* sp.)	20	2.26	2.92	0.03
	Bilberry (*Vaccinium myrtilius*)	13	1.47	2.08	2.23
	Ivy (*Hedera ilex*)	147	16.65	26.18	28.12
	Rowan (*Sorbus accuparia*)	8	0.91	0.3	0.3
	Yew (*Taxus baccata*)	54	6.12	15.65	16.8
	Apple (*Malus* sp.)	5	0.57	0.14	0.15
	Hawthorn (*Crategus monygna*)	1	0.11	0.09	0.09
	Pine (*Pinus* sp.)	4	0.45	0.03	0.03
	Not identified	13	1.47	0.56	0.6
	Total	**265**	**30.01**	**47.95**	**51.44**
Mammal	Woodmouse (*Apodemus sylvaticus*)	51	5.77	4.44	7.49
	Bank vole (*Cleithrionomys glareolus*)	39	4.42	3.85	6.49
	Pygmy shrew (*Sorex minutus*)	11	1.24	0.99	0.02
	Rat (*Rattus norvegicus*)	4	0.11	0.43	1.41
	Red squirrel (*Sciurus vulgaris*)	1	0.45	0.07	0.12
	Rabbit or hare (*Lagomorph* spp)	4	0.45	0.18	0.3
	Deer (*Cervus* spp)	2	0.23	0.09	0.43
	Not identified	67	7.59	5.24	8.85
	Total	**179**	**20.27**	**15.29**	**26.73**
Bird	Song birds (Passeriformes)	28	3.17	1.02	2.89
	Falcons (Falconiformes)	1	0.11	0.29	0.83
	Egg shell	3	0.34	0.008	0.001
	Not identified	47	5.32	3.14	8.94
	Total	**79**	**8.95**	**4.47**	**12.66**
Other	Snail (Mollusca)	8	0.90	0.03	0.037
	Common frog (*Rana temporaria*)	48	5.44	3.89	5.38
	Debris	19	2.15	1.49	0.11
	Total	**75**	**8.49**	**5.42**	**5.41**
Earthworm	Chaetae (*Lumbricus terrestris*)	27	3.05	–	1.67

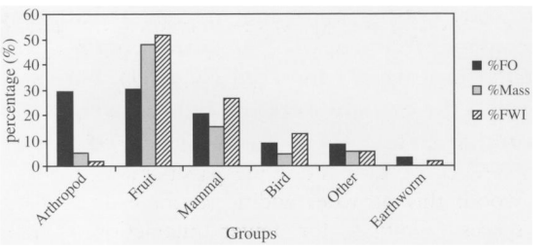

Fig. 2—% FO (frequency of occurrence), % Mass and % FWI (fresh weight ingested) for each group in the diet of the pine marten in Killarney National Park.

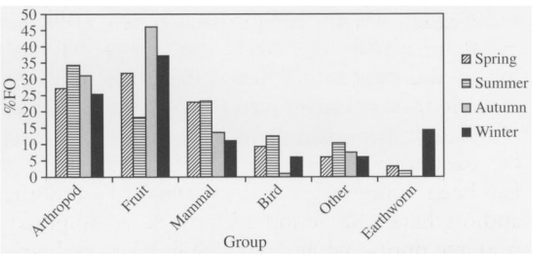

Fig. 3—Seasonal variation in the % FO (frequency of occurrence) of each dietary group for the four seasons.

pine marten showed a wide dietary niche breadth, with the BS value = 0.659. This indicated that four groups (Fruit, Mammals, Birds and Arthropods) were more important than the remaining two (Other and Earthworm).

No significant interannual variation was found for the diet of the pine marten for any of the months for which there were two years of data available (Chi-square: April: $\chi^2 = 5.94$, d.f. = 5, $P = 0.3$; May: $\chi^2 = 8.7$, d.f. = 5, $P = 0.1$; June: $\chi^2 = 6.6$, d.f. = 4, $P = 0.19$; July: $\chi^2 = 7.2$, d.f. = 4, $P = 0.1$; August: $\chi^2 = 0.9$, d.f. = 4, $P = 0.9$). As such it was possible to pool the data for both years and compare the seasonal trends for the diet of the pine marten.

Fruit was the most important dietary group in spring time, while earthworms were the least ($\chi^2 = 216.9$, d.f. = 5, $P < 0.001$). During the summer months arthropods and mammals were the chief prey items in the diet while earthworms were the least common ($\chi^2 = 114.85$, d.f. = 5, $P < 0.001$). Once again, fruit was by far the most notable food group in autumn, followed by arthropods; earthworms were absent from the diet ($\chi^2 = 97.856$, d.f. = 5, $P < 0.001$). Fruit was by far the most important group in winter too, with the groups of Bird and Other contributing little to the diet at this time ($\chi^2 = 73.89$, d.f. = 5, $P < 0.001$).

Overall the % FO of arthropods in the diet did not vary among seasons: 25%–34% of the diet came from this group throughout the year (Fig. 3; $\chi^2 = 5$, d.f. = 3, $P = 0.13$). In contrast, a significant result was recorded for fruit, with peak intake occurring during autumn, although this group was also important in the diet during winter and spring ($\chi^2 = 47.69$, d.f. = 3, $P < 0.005$). Mammals were consumed significantly more in spring and summer than they were in autumn and winter (Fig. 3; $\chi^2 = 20.8$, d.f. = 3, $P < 0.005$). Birds were primarily taken in the diet during spring and summer and hardly ever during autumn and winter (Fig. 3; $\chi^2 = 11.36$, d.f. = 3, $P = 0.01$). There was no difference observed between the seasons in the % FO of the Other group, comprising frogs, mollusca and debris ($\chi^2 = 4.5$, d.f. = 3, $P = 0.2$). Earthworms were largely taken during the winter, with small occurrences in the diet during spring and summer and no intake during autumn (Fig. 3; $\chi^2 = 41.17$, d.f. = 3, $P < 0.005$) (Fig. 3).

A similar dietary niche breadth (BS) was observed for spring, summer and winter (BS = 0.63, BS = 0.67 and BS = 0.62, respectively). For these seasons the diet, while dominated by one or two groups, contained all six. The dietary niche breadth for autumn was much narrower than that recorded for the other three seasons, indicating that one food group, fruit (46.25% FO, 89.46% M and 91.46% FWI), dominated the diet (BS = 0.39).

DISCUSSION

The composition of the diet of pine marten in this study differs from that reported for the pine marten throughout mainland Europe. Most studies refer to small mammals as the most outstanding component of the diet in terms of mass, with other groups being seasonally important (Goszczyński 1976; Marchesi and Mermod 1989; Balharry 1993; Jedrzejewski *et al.* 1993; Halliwell 1997). In this study a different pattern of resource use was observed. Fruit was the most important diet item to the pine marten, followed by mammals, particularly wood mouse and bank vole, throughout the year. Birds were the next most important item, followed by frogs and earthworms, respectively. Arthropods, in particular the order Coleoptera, were ingested frequently, as has been found with all dietary studies on pine marten, but they contributed very little in terms of overall mass and fresh weight ingested. The pine martens' diet was characterised by a wide niche breadth, indicative of an opportunistic and general feeder.

Fruit was found to be the most commonly ingested component and the item that contributed most to the diet of the pine marten in Killarney National Park in terms of % Mass and % FWI. While Killarney National Park has many fruiting species (Kelly 1975), it is evident that the pine marten focused on three main fruits (ivy, yew and blackberry) and largely ignored the rest. Ivy was a principal food item in the diet of the pine marten

throughout winter and spring, as noted previously by Warner and O'Sullivan (1982). Yew is only locally abundant in one area of the park, but it was evident that wherever yew fruit occurred it was consumed, while blackberries available throughout the park were taken when ripe (in September), as has been found elsewhere (Fairley 1970). Other authors have also found fruit to be an important resource during winter and spring, with the berries consumed being those abundant in the study area (Goszczyński 1976; Marchesi and Mermod 1989).

While there was a seasonal pattern to the intake of fruit in the diet (peaking in autumn with smaller peaks in winter and spring), this was not obvious. Fruit was always more frequently consumed than mammals and contributed more to the diet of the pine marten in Killarney National Park, except in summer: this pattern is similar to that found by Ní Neachtain (1998) for broadleaf scrub woodland in the west of Ireland. In contrast, Warner and O'Sullivan (1982) found that overall the intake of birds was marginally greater than fruit, which was the main food item throughout autumn and winter. Similarly, Clevenger (1993b), when investigating an island population on Minorca, found that while one group may be the most important overall (highest % FO for the overall diet), no one group dominated throughout the year, each being seasonally important. Studies on genets have also revealed two differing dietary patterns. Reports on the diet of populations of genets at northern latitudes show the diet is dominated by small mammals, while those on southern populations report a diverse set of prey items, which the authors suggest is indicative of the wide set of prey items available to this species and its generalist opportunistic nature (Virgós *et al*. 1999).

Mammals were the most important food item after fruit, with peak intake occurring in the spring and summer, the summer season being dominated by mammals. A pattern observed in many other studies but absent from this study is the dominance of the vole species (*Microtus* or *Clethrionmys* spp) in the mammal prey category over other items (e.g. wood mouse, shrews, rats and squirrels) (Lockie 1961; Storch *et al*. 1990; Balharry 1993; Jedrzejewski and Jedrzejewska 1993; Gurnell *et al*. 1994; Zalewski 1996; Putman 2000). In the Killarney National Park pine marten population, the wood mouse was the most frequently consumed mammal, with bank voles a close second.

The average estimate of bank vole density for the yew wood of Killarney National Park in 2001 carried out over a three-month period (July, August and September) and based on minimum number alive was approximately 26 bank voles compared with 19 wood mice per 0.002km^2. In contrast, in the neighbouring oak wood, wood mouse density was higher than that of bank voles. As the majority of woodland sampled in this current study was oak wood, this reflects a truer picture of the dynamics of these two small mammal species.

The difference in density between the yew woods and oak woods can be accounted for by the presence of karst limestone pavement in the yew wood: this provides additional three-dimensional spaces, allowing for fewer interactions among individuals (frequency of interactions is known to regulate bank vole populations) and protection from predation (Alibhai and Gipps 1985). However, it is worth considering that the difference in % FO between the wood mouse and bank vole in the diet of the pine marten may be due to the pine marten actively selecting one species over another. This is speculative, and a more in-depth study of prey availability and selection would be needed to prove this hypothesis. Nevertheless, it is evident that the bank vole is an important prey item for the pine marten in Killarney National Park.

Birds accounted for 20% of the diet of pine marten in Warner and O'Sullivan's study (1983), which the authors hypothesised was a result of the depauperate mammal fauna in their study area. A similar pattern was observed in Minorca, another island population, where birds accounted for approximately 20% (FO) of the overall diet (Clevenger 1993b). Most authors cite an intake of about 10%–15% (Lockie 1961; Goszczyński 1976; Balharry 1993; Jedrzejewski and Jedrzejewska 1993; Ní Neachtain 1998). In this study birds accounted for 8.95% FO and 12.65%. As is the case with all studies on pine marten, passerines made up the bulk of the avifauna taken, and these were primarily consumed in spring and summer. Most studies also report birds being consumed in spring and summer, when naive juveniles, nestlings and fledglings are present in the environment (Goszczyński 1976; Marchesi and Mermod 1989; Balharry 1993; Ní Neachtain 1998). Some studies report them as chiefly a winter food, easily taken when weakened by the winter weather (Warner and O'Sullivan 1982). A high percentage of bird remains were not identified to order level due to a lack of diagnostic features (barbules), which tend to be destroyed when passing through the gut (Reynolds and Aebischer 1991).

Arthropods did not contribute much to the diet in terms of % Mass or % FWI, but after fruit, these were the most frequently consumed item. Within the Arthropoda, the order Coleoptera was the most important food item, with Hymenoptera, Isopoda and Lepidoptera all consumed in equal but low amounts. Other authors have found that though Coleoptera always dominate, the order Hymenoptera was also important (Marchesi and Mermod 1989; Balharry 1993). In these studies animals had been reported robbing hives for honey, particularly at night when the inhabitants were

immobile, but no incidents of hive robbing were found in Killarney National Park.

Interestingly, there was no distinguishing seasonal peak for arthropods, this group being consumed in equal amounts throughout the year. Ní Neachtain (1998) reported such a pattern for pine martens in County Clare (Ireland), although Warner and O'Sullivan (1982) found that consumption of this group peaked in summer and autumn in the same county. Clevenger (1993b) reports a similar peak in autumn for Minorcan pine martens, but once again consumption of arthropods is not profoundly different in other seasons. Other studies show peaks for arthropods in summer and autumn, with little or no consumption in the spring and winter (Marchesi and Mermod 1989; Balharry 1993). It is likely that the relatively mild climate in the south-western part of Ireland is conducive to arthropod activity throughout the year.

The main component consumed of the 'other' group was the common frog (Ireland has only one frog species, and toads are absent from the Killarney National Park area). Though frogs are not taken in large amounts at any time of the year, they are eaten throughout the spring, summer and autumn. Balharry (1993) and Marchesi and Mermod (1989) also report a similar pattern, indicating that frogs are a resource that the pine marten exploits year round, albeit at low frequency.

In contrast, earthworms were found to be important during the winter months only, despite the two previous Irish studies reporting them as an important part of the diet of the pine marten throughout the year (Warner and O'Sullivan 1982; Ní Neachtain 1998). In other studies the importance of earthworm in the diet has been overlooked as it is thought chaetae can be ingested when the animal is preying upon birds or through the accidental ingestion of soil when consuming berries (Warner and O'Sullivan 1982). While we could attribute chaetae found in samples during the spring and summer as indirect ingestions through the consumption of birds (birds were most frequently taken in spring and summer) we cannot reconcile this with the data for winter (no chaetae were found in autumn). Chaetae may be ingested accidentally when foraging for other food stuffs, namely bird and berries, as shed chaetae are present in the soil or in the guts of birds having preyed on earthworms themselves; however, this could not account for all the occurrences of chaetae in the samples, especially in winter samples. Marchesi and Mermod (1989) also found many remains of earthworms in their samples and report that the earthworm to be important in the diet, although theirs was the only mainland European study to do so.

The diet niche breadth (BS = 0.659) of the pine marten population investigated in this study is the lowest recorded for Ireland thus far. Ní Neachtain (1998) reports a BS of 0.798 (based on the six categories) for her population of pine marten in hazel–scrub woodland, while Warner and O'Sullivan (1982) report a BS of 0.803 (based on six categories) for pine martens in lowland broadleaf woodland. The higher BS in both these studies results from a more even intake of all prey items, contrasting with this study, where fruit, mammals, birds and insects made up the bulk of the diet and the other two groups were very much secondary (Other and Earthworms). The observed reduction in the niche breadth compared with other Irish studies, although speculative, may be due to the presence of the bank vole in the diet (bank voles were not present at the sites of the previous studies). Thus the two groups Other and Earthworm are not as important. A comparative study investigating the diet of the pine marten in woodlands with or without the bank vole may give weight to this argument.

Clevenger (1993a) reports a similarly wide niche breadth for the island population of Minorca (BS = 0.754 based on five categories, no earthworm; *cf* 0.829 this study, excluding the earthworm category) but a much narrower niche breadth for the mainland population studied (BS = 0.38, based on same five categories). This he attributes to a poorer mammal prey base and reduced interspecific competition on the island as compared with the mainland population. However, the wide niche breadth may also be indicative of a generalist predator that preys upon food items that are readily available to it. Thus the prey available to an individual species will be determined not only by location but by climatic and altitudinal factors (Virgós *et al*. 1999). Hence it is hardly surprising that the dietary pattern of the pine marten differs across its geographic range. The mild climatic conditions in Ireland, particularly during the winter months, are conducive to a diverse set of prey items being available to the pine marten throughout the year. The role that the other carnivore species (fox, badger, stoat, mink and feral cat) play in shaping the diet of the pine marten through competition or sequential resource utilisation remains to be investigated.

A similar BS (0.62–0.67) was recorded for all seasons except for autumn (0.39), which was dominated by the fruit group; approximately 50% of the autumn diet was fruit. Ní Neachtain (1998) also recorded a seasonal drop in the BS during summer and autumn, but this drop was not as obvious as that observed in our study.

With the exception of the summer months, when mammals were the most important food group, fruit was the most notable food item

consumed throughout the year. Though mammals were not the major part of the diet (in contrast to many other studies), they were consistently taken. The bank vole, firmly established within Killarney National Park, is now an integral and important component of the mammal prey consumed by the pine marten. This species is also likely to be important in the diet of pine marten wherever it occurs within Ireland. Insects were important all year round, and birds were important when at their most vulnerable, spring and summer. The wide niche breadth found in this study is consistent with those reported for other island populations. The implications of woodland management with regard to the conservation of the pine marten are highlighted in these findings. The maintenance of woodlands with good fruiting species diversity, which in itself will provide the habitat for the other wide range of prey items that the pine marten consumes, is essential for marten conservation.

ACKNOWLEDGEMENTS

This study was part of research funded by the Irish Research Council for Science Engineering and Technology (IRCSET) under the Embark initiative and generously supported by NPWS. We would like to thank the following people for their support, advice and encouragement: Peter Stafford and Alison Boyce, Ailbhe Kavannagh and Grainne Cleary (TCD), Paddy O'Sullivan, Paudie O'Leary and especially Peter O'Toole (NPWS), Killarney National Park rangers and volunteers (particularly Katharina Meinhardt and Roelof Jan Koops). We would also like to thank the two referees for their helpful comments.

REFERENCES

Alibhai, S.K. and Gipps, J.H.W. 1985 The population dynamics of bank voles. *Symposium of the Zoological Society of London* **55**, 277–313.

Balharry, D. 1993 Factors affecting the distribution and population density of pine martens (*Martes martes* L.) in Scotland. Unpublished PhD thesis, University of Aberdeen, Scotland.

Barrientos, R. and Virgos, E. 2006 Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. *Acta Oecologica* **30**, 107–16.

Begg, C.M., Begg, K.S., Du Toit, J.T. and Millis, M.G.L. 2003 Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger. *Journal of Zoology London* **260**, 301–16.

Chinery, M. 1993 *Collins guide to the insects of Britain and western Europe*. London. Harper Collins.

Clevenger, A.P. 1993a Pine marten (*Martes martes*) comparative feeding ecology in an island and mainland population of Spain. *Zeitschrift für Säugetierkunde* **58 (4)**, 212–24.

Clevenger, A.P. 1993b Spring and summer food habits and habitat use of the European pine marten (*Martes martes*) on the island of Minorca, Spain. *Journal of Zoology, London* **229**, 153–61.

Davison, A., Birks, J.D.S., Brookes, R.C., Braithwaite, T.C. and Messenger, J.E. 2002 On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. *Journal of Zoology, London* **257**, 141–3.

Day, M.G. 1966 Identification of hair and feather remains in the gut and faeces of stoat and weasels. *Journal of Zoology, London* **148**, 201–17.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T. and Lyon, B.E. 2003 Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* **72**, 144–55.

Fairley, J.S. 1970 Blackberries as food of pine marten. *Irish Naturalists' Journal* **16 (10)**, 317–18.

Genovesi, P., Secchi, M. and Boitani, L. 1996 Diet of stone martens: an example of ecological flexibility. *Journal of Zoology, London* **238**, 545–55.

Goszczyński, J. 1976 Composition of the food of martens. *Acta Theriologica* **21**, 527–34.

Goszczyński, J. 1986 Diet of foxes and martens in central Poland. *Acta Theriologica* **31**, 491–506.

Gurnell, J., Venning, T., MacCaskill, B. and MacCaskill, D. 1994 The food of pine marten (*Martes martes*) in west Scotland. *Journal of Zoology, London* **234 (4)**, 680–3.

Halliwell, E.C. 1997 Red squirrel predation by pine marten in Scotland. In J. Gurnell and P. Lurz (eds), *The conservation of red squirrels (Sciurus vulgaris)*, 39–47. London. Peoples Trust for Endangered Species.

Hespenheide, H.A. 1975 Prey characteristics and predator niche width. In M.L. Cody and J.M. Diamond (eds), *Ecology and evolution of communities*, 158–180. Cambridge, Massachusetts. Harvard University Press.

Jedrzejewski, W. and Jedrzejewska, B. 1993 Predation on rodents in Bialowieza National Park, Poland. *Ecography* **16 (1)**, 47–64.

Jedrzejewski, W., Zalewski, A. and Jedrzejewska, B. 1993 Foraging by pine marten (*Martes martes*) in relation to food resources in Bialowieza National Park, Poland. *Acta Theriologica* **38 (4)**, 405–26.

Kelly, D. 1975 Native woodland in western Ireland with especial reference to the region of Killarney. Unpublished PhD thesis, University of Dublin (Trinity College).

Lindström, E. 1989 The role of medium-sized carnivores in the Nordic boreal forest. *Finnish Game Research* **46**, 53–63.

Litvaitis, J.A. 2000 Investigating food habitats of terrestrial vertebrates. In L. Boitani and T.K. Fuller (eds) *Research techniques in animal ecology: controversies and consequences*, 165–90. New York. Columbia University Press.

Lockie, J.D. 1961 The food of the pine marten (*Martes martes*) in West Ross-Shire, Scotland.

Proceedings of the Zoological Society of London **136 (2)**, 187–95.

Lynch, A. 2002 The effects of density and spatial distribution of small mammals (*Apodemus sylvaticus* and *Cleithrionomys glareolus*) on yew (*Taxus baccata*) regeneration in Killarney National Park. Unpublished Mod thesis, Trinity College, Dublin.

Lynch, A.B. 2006 An investigation into the ecology of the pine marten (*Martes martes*) in Killarney National Park. Unpublished PhD thesis, Trinity College, Dublin.

Madsen, S.A., Madsen, A.B. and Elmeros, M. 2002 Seasonal food of badgers (*Meles meles*) in Denmark. *Mammalia* **66**, 341–52.

Marchesi, P. and Mermod, C. 1989 Regime alimentaires de la martre (*Martes martes*) dans le Jura suisse. *Revue suisse de Zoologie* **96 (1)**, 127–46.

Ní Neachtain, R. 1998 *Martes martes* (an cat crainn) in the Burren, Co. Clare: an investigation of its population structure and its diet. Unpublished MSc, Trinity College, Dublin.

Nagorsen, D.W., Campbell, R.W. and Giannico, G.R. 1991 Winter food habits of marten (*Martes americana*), on the Queen Charlotte Islands. *The Canadian Field-Naturalist* **105**, 55–9.

O'Sullivan, P. 1983 The distribution of the pine marten (*Martes martes*) in the Republic of Ireland. *Mammal Review* **13**, 39–44.

Powell, S.M., York, E.C. and Fuller, T.K. 1997 Seasonal food habits of fishers in central New England. In G. Proulx, H.N. Bryant and P.M. Woodward (eds), *Martes: taxonomy, ecology, techniques, and management*. Proceedings of the Second International Martes Symposium. Canada. The Provincial Museum of Alberta.

Pulliainen, E. 1981 Food and feeding habits of the pine marten (*Martes martes*) in Finnish forest Lapland in winter. *Proceedings of the Worldwide Furbearer Conference* **2**, 1068–87.

Putman, R.J. 2000 Diet of pine martens *Martes martes* L. in west Scotland. *Journal of Natural History* **34**, 793-797.

Reynolds, J.C. and Aebischer, N.J. 1991 Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations based on the study of the fox *Vulpes vulpes*. *Mammal Review* **21 (3)**, 97–122.

Roper, T.J. and Lüps, P. 1995 Diet of badgers (*Meles meles*) in central Switzerland: an analysis of stomach contents. *Zeitschrift für Säugetierkunde* **60**, 9–19.

Smal, C.M. 1978 The role of small mammals and the regulation of their numbers in Killarney woodland ecosystems. Unpublished PhD thesis, University College Galway, Ireland.

Smal, C.M. and Fairley, J.S. 1984 The spread of the bank vole *Cleithrionomys glareolus* in Ireland. *Mammal Review* **14 (2)**, 71–8.

Storch, I., Lindstrom, E. and de Jounge, J. 1990 Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica* **35 (3–4)**, 311–20.

Teerink, B.J. 1991 *Hair of west-European mammals*. 1st edn. Cambridge University Press.

Virgós, E., Llorente, M. and Cortés, Y. 1999 Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. *Mammal Review* **29**, 119–28.

Warner, P. and O'Sullivan, P. 1982 The food of pine martens *Martes mart*es in Co. Clare. *Transactions of the International Congress of Game Biologists* **14**, 323–30.

Yalden, D.W. and Morris, P.A. 1990 *The analysis of owl pellets*. London. The Mammal Society.

Zalewski, A. 1996 Choice of age classes of bank voles *Cleithriomys glareolus* by pine marten *Martes martes* and tawny owl *Strix aluco* in Bialowieza National Park. *Acta Oecologica* **17 (3)**, 233–44.