

# Resource partitioning among British and Irish mustelids

ROBBIE A. MCDONALD

*The Game Conservancy Trust, The Gillett, Forest-in-Teesdale, Barnard Castle DL12 0HA, UK*

## Summary

1. Seven species of mustelid carnivore live in the British Isles: weasel, stoat, mink, polecat, pine marten, badger and otter. Recent studies have hypothesized that coexistence of these species is facilitated by partitioning of resources according to prey size, particularly that of mammalian prey. This hypothesis has been supported by evidence of character displacement derived from even size ratios in skull length and canine diameter.

2. To test whether this hypothesis is supported by empirical data, 98 studies of the diet of mustelids living in Great Britain and Ireland were analysed. Two main predictions were tested; that larger males ate larger prey than females and that larger species ate larger prey than smaller species.

3. Male mustelids ate larger prey than females but there was no relationship between predator size and prey size, either for all species or when largely vermivorous badgers and piscivorous otters were excluded. There was no difference in dietary niche breadth between the sexes. Dietary niche breadth increased with body size in the assemblage excluding otters and badgers. The dietary niches of mustelids were partitioned along several axes, none of which was clearly related to prey size.

4. The dietary niches of the five species living in Ireland (stoat, mink, pine marten, otter and badger) were more similar to one another in Ireland than in Great Britain and there was no difference in niche breadth between Irish and British mustelids. There was no evidence of competitive release in the diets of Irish mustelids.

5. Resource partitioning according to prey size is apparent between the sexes within species, and this is probably correlated to sexual selection for size dimorphism. Empirical data do not, however, support a hypothesis of resource partitioning according to prey size between species. Interspecific aggression provides an alternative hypothesis explaining character displacement among mustelids.

*Key-words:* character displacement, competition, diet, Mustelidae, size ratios.

*Journal of Animal Ecology* (2002) **71**, 185–200

## Introduction

Competition for limited food resources is a major driving force of evolution within assemblages of related and morphologically similar species (MacArthur & Levins 1967). Analyses of the evolutionary effects of competition have often focused on morphological differences between competing species. Such differences are often accentuated in the region of sympatry, a phenomenon termed character displacement (Brown & Wilson 1956). This is related to Hutchinson's (1959) theory of limiting similarity, a corollary of which was that for species to coexist there must be minimum ratios between them in the size of their trophic apparatus. The

commonplace detection of even size ratios has been widely taken as evidence of the evolutionary importance of competition. None the less, the unqualified interpretation of size ratios has been severely criticized mainly because of a lack of statistical rigour (Strong, Szyka & Simberloff 1979; Roth 1981; Simberloff & Boecklen 1981; Ranta, Laurila & Elmberg 1994). Recently, the development of statistically robust tests (Tonkyn & Cole 1986) has led to something of a revival in size ratio analysis in community ecology (Dayan *et al.* 1989, 1990; 1992; Dayan & Simberloff 1994, 1996, 1998; Jones 1997).

Mammalian carnivores, particularly mustelids living in the British Isles, have had a significant role in the development of character displacement theory (Dayan & Simberloff 1996, 1998). Indeed, Hutchinson (1959) illustrated his case with a description of differences in

**Table 1.** The mass of mammalian prey species and the mass, skull length and canine diameter of mustelids

Common name	Species	Mass/g	Skull length/mm	Canine diameter/mm	Source
Harvest mouse	<i>Micromys minutus</i> Pallas	6			4
Shrews	<i>Sorex pygmaeus</i> L.	10			4
	<i>S. araneus</i> L.				
Water shrew	<i>Neomys fodens</i> Pennant	15			4
House mouse	<i>Mus domesticus</i> L.	17			4
Young small mammal		18			4
Wood mouse	<i>Apodemus sylvaticus</i> L.	19			4
Hazel dormouse	<i>Muscardinus avellanarius</i> L.	20			4
Unidentified small rodent		20			4
Bank vole	<i>Clethrionomys glareolus</i> Schreber	24			4
Unidentified insectivore		30			4
Unidentified vole		30			4
Field vole	<i>Microtus agrestis</i> L.	35			4
Moles	<i>Talpa europaea</i> L.	98			4
Water vole	<i>Arvicola terrestris</i> L.	290			4
Common rat	<i>Rattus norvegicus</i> Berkenhout	500			4
Squirrels	<i>Sciurus carolinensis</i> Gmelin	550			4
	<i>S. vulgaris</i> L.				
Lagomorphs (rabbits and hares)	<i>Oryctolagus cuniculus</i> L.	*800			4
	<i>Lepus europaeus</i> Pallas				
	<i>L. timidus</i> L.				
Weasel	<i>Mustela nivalis</i> L.				
Great Britain		97	36.6	1.61	6, 10
Stoat	<i>Mustela erminea</i> L.				
Great Britain		305	46.9	2.25	6, 10
Ireland		208	44.6	2.07	3, 6
Mink	<i>Mustela vison</i> Schreber				
Great Britain		885	63.1	3.33	4, 6
Ireland		1 002	63.7	3.50	2, 6
Polecat	<i>Mustela putorius</i> L.				
Great Britain		1 113	63.8	3.44	4, 6
Pine marten	<i>Martes martes</i> L.				
Great Britain		1 600	82.1	4.58	4, 6
Ireland		1 500	81.9	4.27	4, 6
Otter	<i>Lutra lutra</i> L.				
Great Britain		8 500	111.5	5.91	4, 7, 9
Ireland		†7 340	113.9	5.91	1, 5, 9
Badger	<i>Meles meles</i> L.				
Great Britain		10 850	126.7	7.47	4, 6
Ireland		9 900	126.2	7.56	4, 6, 8

Sources: <sup>1</sup>Fairley 1972; <sup>2</sup>Fairley 1980; <sup>3</sup>Fairley 1981; <sup>4</sup>Corbet & Harris 1991; <sup>5</sup>Lynch & O'Sullivan 1993; <sup>6</sup>Dayan & Simberloff 1994; <sup>7</sup>Lynch *et al.* 1996; <sup>8</sup>Sadler 1999; <sup>9</sup>A. Kitchener, unpublished data; <sup>10</sup>R. McDonald, unpublished data. \*This figure takes into account an unknown proportion of smaller juveniles. †This figure is based on the weights of skinned animals provided by Fairley (1972) and recalculated according to the formula provided by Jefferies (1986).

the size of stoats (for species names and authorities see Table 1) between Great Britain and Ireland. In Ireland, stoats were reputedly smaller than in Britain and Hutchinson (1959) believed this to be a consequence of competitive release arising from the absence from Ireland of the smaller weasel. Subsequent analyses have shown Hutchinson's argument to be based on incomplete data (King & Moors 1979; Fairley 1981; King 1989, 1991). Nevertheless, his work has become a classic example of competitive release (Williamson 1972) and has been a cornerstone of several other investigations of mustelid assemblages. In common with Hutchinson (1959), several authors have forwarded the proposition that coexistence of several species of

mustelid is mediated principally by selection of differently sized prey (Rosenzweig 1966; McNab 1971; Simms 1979; Dayan *et al.* 1989; Dayan & Simberloff 1994). Holmes (1987) and Holmes & Powell (1994) countered propositions of resource partitioning in the evolution of sexual dimorphism by finding that the carnassials of north American mustelids were less dimorphic than were the rest of their bodies. Meanwhile, other authors studying a range of morphological characters have not found evidence of character displacement among mustelids. Instead, they have explained size variation and sexual dimorphism in this group with hypotheses based on biogeography and sexual selection (Ralls & Harvey 1985), interspecific

aggression (Rosenzweig 1966; Erlinge & Sandell 1988) or from combinations of these factors with stochastic variation in habitat and prey availability (Rosenzweig 1968; King & Moors 1979; Powell & Zielinski 1983; King 1989; Powell & King 1997). In this paper, I test whether empirical data on the diets of mustelids living in the British Isles support a hypothesis of resource partitioning according to prey size, established in particular by the work of Dayan & Simberloff (1994).

The British Isles consists of two main islands. The larger, Great Britain, includes England, Scotland and Wales. Ireland includes Northern Ireland and the Republic of Ireland. Seven species of mustelid live in the British Isles. In order of increasing size (Table 1): weasel, stoat, polecat, pine marten, otter and badger are native to Great Britain. Feral American minks are larger than stoats and slightly smaller than polecats but are not native and are a recent addition to the assemblage, following escapes and releases from fur farms (Dunstone 1993). Of these seven species, only five (stoat, mink, pine marten, otter and badger) live in Ireland. It should be noted that throughout this paper, 'weasel' is used in the British context to mean the species *Mustela nivalis* rather than the North American context where 'weasel' is applied to the three species *M. nivalis*, *M. erminea* and *M. frenata*.

Dayan & Simberloff (1994) defined the mustelids of the British Isles as 'a guild on the basis of limb morphology, which reflects foraging behaviour' (Simberloff & Dayan 1991; Dayan *et al.* 1992). Using museum specimens, they measured skull size (condylobasal length) and the size of the apparatus mustelids used to kill their mammalian prey (the maximum diameter of the upper canine) (Dayan *et al.* 1989). They omitted otters since they held there was virtually no ecological overlap or potential for competition with the native terrestrial mustelids. They conducted their analyses both with and without badgers on the grounds that their largely vermivorous diet may have weakened selective pressure on canine size. All mustelids exhibit pronounced sexual size dimorphism (Moors 1980) and so Dayan & Simberloff (1994) considered males and females to be functionally distinct 'morphospecies' and accorded similar importance to intraspecific and interspecific competition in structuring the assemblage. In Great Britain, they found equal size ratios in skull lengths and canine diameters and concluded that this was evidence of community-wide character displacement. In Ireland, they found that ratios for canine size were even but those for skull lengths were not. They identified differences in the sizes of British and Irish mustelids and this led to their confirmation of Hutchinson's (1959) suggestion that ecological release had taken place in Ireland.

The morphological analyses of Dayan & Simberloff (1994) strongly supported resource partitioning according to prey size, particularly mammalian prey size, among mustelids in the British Isles. What do empirical

studies of the diets of these animals contribute to their argument? If displacement of a trophic character is to be regarded as an evolutionary symptom of competition, evidence for size-related differences in predator diets must be provided. Dayan & Simberloff (1994, 1998) recognized this need. They predicted that males of any species would take larger mammalian prey than females, and that the average prey size for each species would be smaller than that for larger species. These two predictions form the basis of the investigations described in this paper. A relationship between carnivore size and prey size is well established (Gittleman 1985), but this should be examined closely in the specific assemblage under investigation. The data on mustelid diet provided by Dayan & Simberloff (1994) were limited and in several cases did not refer to British or Irish studies (Brugge 1977; Storch, Lindström & De Jounge 1990). This is important because the body sizes of mustelids living in continental Europe and the variety and size of available prey differ markedly from Great Britain and Ireland (Moors 1980; Erlinge 1986; King 1989). Therefore, in this case, as in other character displacement studies (Ralls & Harvey 1985), only local dietary information can be used as supporting evidence. Fortunately, the diet of mustelids in the British Isles is well described and several major studies have been published since Dayan & Simberloff (1994).

In this paper, empirical data on the diets of mustelids living in Great Britain and Ireland have been synthesized to test whether they support a hypothesis of resource partitioning according to the size of mammalian prey. In considering mustelid diet in Britain and Ireland separately throughout, the hypothesis of competitive release among Irish mustelids compared to British mustelids has also been tested. An assessment has been made of whether the seven species living in the British Isles can validly be described, not just as a taxonomic assemblage (Jaksic 1981), but as a guild when defined as an 'arena of intense interspecific competition' (Pianka 1980). In effect, this is a *post hoc* assessment of Dayan & Simberloff's (1994) omission of otters from all and badgers from some of their analyses. This is in accord with the counsel of Simberloff & Dayan (1991) that in defining a guild, the exclusion of sympatric related biota should be justified, where the grounds for exclusion are not self-evident and consist of intuition or simple taxonomy.

## Materials and methods

Data on the diets of all mustelids living in Great Britain and Ireland were collated from the literature. Several studies reported diets from more than one site and in these cases each site was considered a separate sample. The diets of males and females were recorded separately where possible. The reviewed studies used several techniques to investigate diet, including direct observation and analysis of faeces and gut contents. A range of methods, including frequency of occurrence and

estimated weight or volume intake, was then used to describe diet. The raw data do not permit recalculation into a common currency, neither would this be desirable, given differences in foraging ecology within the group. Nevertheless, for smaller mustelids most authors used frequency of occurrence, since guts or faeces generally contained only one item. For larger species, percentage volume was used most often as this took account of the importance of small but common prey, such as invertebrates and fruit. Several studies were not included since they did not provide sufficient detail (Neal 1988), focused on one prey group (Fairley 1984; Kruuk *et al.* 1993; Carss *et al.* 1998) or used data published elsewhere (King 1977; Thompson 1978; Pringle 1982).

Two main analyses were conducted. The first examined the relationship between predator size and prey size at a fine scale and followed the approach of Jones (1997). A weighted-mean prey mass was calculated for each sample by multiplying the mean mass of both sexes of each species of mammalian prey (Table 1) by the prevalence of that species as a proportion of all mammalian prey items. Non-mammalian prey was excluded since Dayan & Simberloff (1994) argued that natural selection acted on canine diameter because of its specific role in killing mammalian prey. Carrion and mustelid hairs from grooming were also excluded. For comparison between species, a mean prey mass was calculated and compared to the species' mean body weight, skull length and canine diameter (Table 1). For comparison between sexes, a paired comparison was made within samples between the mass of prey eaten by males and females. Following Dayan & Simberloff (1994), this analysis excluded otters and was conducted with and without badgers.

For the second analysis of dietary niche relationships at a broader scale, prey items were grouped according to taxonomy, size and requirements for capture (Rosenzweig 1966). Small mammals included shrews, moles, voles, dormice and mice. Medium-sized mammals included rabbits, water voles, rats, squirrels and hares. Large mammals were taken almost entirely as carrion but included sheep *Ovis aries* L. and deer *Capreolus capreolus* L. and *Cervus elaphus* L. Further categories were birds, birds' eggs, fish, herpetofauna, earthworms, other invertebrates and fruit and vegetables. Levins's (1968) measure of niche breadth ( $B$ ) was calculated and standardized across prey categories ( $B_A$ ) (Krebs 1989). To examine resource partitioning among species, a principal component analysis (PCA) was conducted on the prevalence of each food category in the diet of British mustelids (Holmes, Bonney & Pacala 1979). The PCA was conducted on the covariance matrix in order to preserve the relative magnitude of each prey group. The Euclidean distances between the group centroids of each species were calculated as a measure of the differentiation of their dietary niches (Holmes *et al.* 1979). These distances were used to construct a community dendrogram by hierarchical clustering with the average linkage method (Ryan &

Joiner 1994). To test whether the dietary niches of each species were dispersed more widely in Ireland than in Britain, i.e. whether there was evidence of competitive release, PC scores for the Irish samples were calculated by using the loadings from the PCA of the British samples. The Euclidean distances between the group centroids of the Irish samples were then calculated and compared to the British samples. These analyses considered the sexes together and were conducted on the whole assemblage and then repeated omitting otters and badgers. Minitab (Ryan & Joiner 1994) was used for statistical analysis.

## Results

Ninety-eight samples of mustelid diet were analysed (Tables 2–5, summarized in Table 6). Mass of mammalian prey was not related to predator size (Fig. 1). For the British assemblage excluding otters and badgers, there was no significant relationship between the mass of mammalian prey and predator mass ( $r = -0.21$ ,  $n = 5$ ,  $P = 0.73$ ), skull length ( $r = 0.20$ ,  $n = 5$ ,  $P = 0.75$ ) or canine diameter ( $r = -0.18$ ,  $n = 5$ ,  $P = 0.75$ ). For the British assemblage excluding otters but including badgers, there was again no significant relationship between the mass of mammalian prey and predator mass ( $r = 0.30$ ,  $n = 6$ ,  $P = 0.56$ ), skull length ( $r = 0.20$ ,  $n = 6$ ,  $P = 0.71$ ) or canine diameter ( $r = -0.18$ ,  $n = 6$ ,  $P = 0.71$ ). For the Irish assemblage excluding otters, the mean prey mass eaten by badgers was greater than the other three species. The mean mass of prey eaten by Irish martens was, however, less than that eaten by smaller Irish stoats and minks. The mass of prey eaten by Irish stoats was less than British stoats, but greater for Irish minks and martens than for British minks and martens (Fig. 1).

Separate details of the diets of male and female mustelids were provided in 11 samples (Table 7). The mean mass of mammalian prey taken by males was consistently greater than by females ( $t = 5.93$ ,  $n = 10$ ,  $P < 0.001$ ). Sex-related differences in diet were examined statistically in 16 studies (Table 8). In six studies, differences between males and females were statistically significant, but in only five of these were the differences related to prey size. Kruuk & Moorhouse (1990) found the lengths of fish eaten by male otters were greater than female otters. They also found that female otters took differently sized prey depending on whether they were feeding cubs. The differences observed between otters of varying status were, however, not significant when variation in prey availability in their home ranges was taken into account (Kruuk & Moorhouse 1990).

Dietary niche breadth ( $B_A$ ) increased with body size in the assemblage when otters and badgers were excluded ( $r_s = 0.76$ ,  $n = 56$ ,  $P < 0.001$ ), but not when otters and badgers were included ( $r_s = -0.18$ ,  $n = 98$ ,  $P = 0.08$ ). There was no consistent difference in dietary niche breadth between male and female mustelids ( $t = -0.17$ ,  $n = 11$ ,  $P = 0.87$ ). There was no significant

**Table 2.** The diets of (a) weasels (b) stoats and (c) polecats in Great Britain and Ireland

Source	Location	Year	Time	n	Type	Method	Mass	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	B <sub>A</sub>				
(a) Day (1963, 1968)	GB	National	1960–63	Y	115	F,G	F	217.7	59%	20%											0.13			
			Walker (1972)	Hertfordshire	1966	Sp, Au	43	G	F	130.2	71%	18%											0.07	
			Potts & Vickerman (1974)	Sussex	1968–72	Y	186	G	F	141.7	69%	12%											3%	
			Moors (1975)	Aberdeenshire	1971–73	Y	264	F	F	148.7	71%	14%												0.08
			Moors (1975)	Aberdeenshire	1971–72	3–6	82	G	F	188.5	65%	17%												0.10
			Tapper (1976)	Sussex	1971–74	5–6	151	G	F	115.5	61%	8%												0.11
			King (1977)	Northumberland	NS	NS	54	G	F	323.3	51%	33%												0.14
			Howes (1977)	Yorkshire	many	NS	40	O	F	149.3	50%	10%												0.17
			Tapper (1979)	Sussex	1971–77	Y	687	G	F	200.6	60%	17%												0.12
			King (1980)	Oxfordshire	1968–70	Y	344	F	F	29.9	68%	< 1%												0.10
			Armitage (1980)	Yorkshire	1975–78	NS	7	O	F	500.0		14%												0.03
			Pounds (1981)	Aberdeenshire	1976–79	Y	204	F,G	F	229.1	68%	23%												0.08
			McDonald, Webbon & Harris (2000)	National	1995–97	Y	458	G	F	236.6	68%	26%			1%	4%	1%		1%					0.08
			(b) Day (1963, 1968) <sup>1</sup>	GB	National	1960–63	Y	115	F,G	F	427.1	28%	33%											
Hewson & Healing (1971)	Aberdeenshire	1969				NS	16	O	F	800.0		31%											0.07	
Howes (1977)	Yorkshire	many				Y	60	O	F	591.9	5%	38%											0.12	
Armitage (1980)	Yorkshire	1975–78				Y	5	O	F	86.0	80%	20%											0.04	
Pounds (1981)	Aberdeenshire	1976–79				Y	97	F,G	F	386.6	44%	38%												0.15
Pringle (1982)	Sussex	1971–76				Y	282	G	F	617.4	17%	57%			1%	18%	8%		< 1%					0.14
McDonald <i>et al.</i> (2000)	National	1995–97				Y	789	G	F	644.0	16%	65%												0.10
Fairley (1971)	Northern Ireland	1963–66				Y	24	G	F	406.9	29%	7%												0.09
Fairley (1971)	Northern Ireland	1968–70				Y	58	G	F	174.0	7%	67%												0.10
Sleeman (1992)	Ireland	NS				Y	138	G	F	701.7	35%	46%												0.15
(c) Walton (1968)	GB	Wales	NS	NS	38	G	F	NS					33%	13%			25%			23%	7%	0.28		
			Blandford (1986)	Wales	NS	NS	251	F	F	304.4	46%	27%			1%	16%			8%		2%		0.20	
			Birks & Kitchener (1999)	Western England	1990s	NS	83	G	F	712.8	8%	71%				9%		1%	8%	2%			0.08	

<sup>1</sup>This study includes an unknown number of samples from Northern Ireland. NS, not stated in original source, or not in an appropriate format for inclusion in this review. Location: GB, Great Britain; I, Ireland. Time: Y, year-round; Sp, spring; Su, Summer; Au, Autumn; Wi, Winter; 1–5, months of year, e.g. January–May. Type: F, faecal analysis; G, gut contents analysis; O, direct observations; R, prey remains. Method: F, frequency of occurrence; EW, estimated weight intake; DW, dry weight; V, volume or percentage bulk estimate. Mass: weighted mean mass of mammalian prey (Jones 1997). Prey categories: SM, small mammals; MM, medium-sized mammals; LM, large mammals taken as carrion; UM, unidentified mammals; B, bird; E, birds' eggs; F, fish; H, herpetofauna, i.e. reptiles and amphibians; W, earthworms Lumbricidae; I, invertebrates other than earthworms; FV, fruit and vegetable material eaten deliberately and not ingested incidentally; O, other food items. B<sub>A</sub>, Levins's (1968) standardized measure of niche breadth.

**Table 3.** The diets of (a) minks and (b) pine martens in Great Britain and Ireland. For a key to the abbreviations used, see Table 2

Source	Location	Year	Time	<i>n</i>	Type	Method	Mass	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	B <sub>A</sub>			
(a)	Day & Linn (1972)	GB	England and Wales	1964–68	Y	273	G	F	460.5	12%	25%		1%	36%	1%	14%	3%	8%			0.29		
		Scotland	1967–68	Y	88	F,G	F	150.3	25%	7%	1%		21%		46%						0.19		
	Cuthbert (1979)	Scotland	NS	Y	722	F	F	165.9	6%	4%		6%	7%		67%	2%		9%			0.10		
		Scotland	NS	NS	78	F	F	432.1	4%	6%		4%	16%		28%			42%			0.23		
	Chanin & Linn (1980)	Devon	1972–73	Y	475	F	F	269.7	18%	11%		< 1%	11%		54%	3%	2%	1%			0.17		
	Chanin & Linn (1980)	Devon	1972–73	Y	57	F	F	603.1	3%	13%			30%		54%		1%				0.14		
	Chanin & Linn (1980)	Dorset	1972–73	Y	153	F	F	220.5	18%	13%			24%		35%	1%	8%	3%			0.31		
	Jenkins & Harper (1980)	Aberdeenshire	1975–78	Y	185	F	F	652.1	12%	51%		3%	23%		8%	2%					0.18		
	Jenkins & Harper (1980)	Aberdeenshire	1977–78	Y	59	F	F	655.3	15%	68%		4%	7%		6%						0.09		
	Wise, Linn & Kennedy (1981)	Devon	1975–76	Y	513	F	V	459.9	12%	17%			37%		32%	1%	1%				0.23		
	Wise <i>et al.</i> (1981)	Devon	1975–76	Y	448	F	V	584.1	15%	43%			5%		25%	10%	2%				0.23		
	Birks & Dunstone (1984)	Coastal Scotland	1981–82	Y	96	R	F	776.8	1%	60%	1%		38%								0.09		
	Dunstone & Birks (1987)	Coastal Scotland	1980–83	Y	2043	F	F	697.6	5%	35%	< 1%	< 1%	11%		29%			19%			0.26		
	Clode & Macdonald (1995)	Coastal Scotland	1991–93	Su	160	F	F	511.6	3%	5%	4%		8%		46%			34%			0.18		
	Strachan <i>et al.</i> (1998)	Southern England	1994	Y	863	F	DW	380.4	7%	29%			44%		18%				2%		0.20		
	Ferreras & Macdonald (1999)	Southern England	1996	3–8	115	F	DW	442.5	24%	28%			23%		18%			6%			0.30		
	Fairley (1980)	I	Northern Ireland	1975–76	Year	46	G	F	745.5		44%			12%		12%			20%			0.24	
	Ward, Smal & Fairley (1986)	Ireland	1983–85	Year	2510	F	F	622.5	1%	4%		< 1%	18%		17%	8%		50%		2%	0.19		
	(b)	Lockie (1961)	GB	Ross-shire	1956–58	Y	337	F	F	34.2	36%				9%	1%			4%	24%	18%	9%	0.30
			Inverness-shire	1982–83	Y	375	F	F	52.9	29%	1%	3%		14%	< 1%		1%		34%	17%		0.27	
Galloway			1988–89	NS	12	F <sup>2</sup>	F	312.2	32%	18%			23%			9%		9%			0.34		
Ross-shire (Kinlochewe)			1988–89	Y	723	F	EWI	212.0	24%	7%	34%		13%	< 1%		4%		15%	3%		0.33		
Ross-shire (Strathglass)			1989–90	Y	581	F	EWI	33.5	47%		30%		12%	1%		7%		3%	1%		0.19		
Ross-shire			1984–85	Y	240	F	F	39.7	42%	1%	2%			8%		1%	10%	1%	28%	8%		0.23	
Dumfriesshire			1995–96	Y	100	F	EWI	181.4	23%	6%	20%		22%					9%	6%	14%	0.43		
Ross-shire			1993–95	Y	1938	F	F	101.3	29%	3%	5%		16%	2%		1%		24%	9%	10%	0.39		
Highland (Morvern)			1996–98	Y	174	F	F	NS			< 1%	27%	9%		< 1%	1%	8%	34%	21%		0.28		
Clare			1970	Su	NS	F <sup>2</sup>	F	19.0	20%				20%			20%		40%			0.23		
Clare			1974	NS	23	F <sup>2</sup>	F	301.4	13%	9%			7%			4%	29%	22%	16%		0.39		
Clare			1973–77	NS	609	F	F	387.2	6%	6%		1%	18%	2%		2%	25%	23%	17%		0.40		

<sup>1</sup>Some of the figures in this study are estimated from graphs. <sup>2</sup>These samples are piles of faeces.

**Table 4.** The diet of badgers in Great Britain and Ireland. For a key to the abbreviations used, see Table 2

Source	Location	Year	Time	<i>n</i>	Type	Method	Mass	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	B <sub>A</sub>
Middleton (1935)	GB	Oxfordshire	1935	Su	1	G	F	282.7	62%	31%							8%			0.10
Kruuk (1978)	Oxfordshire	1974	Au	39	F	F	NS					5%			57%	17%	21%			0.14
Kruuk (1978)	Oxfordshire	NS	NS	8	G	F	NS								88%		13%			0.03
Kruuk & Parish (1981)	Scotland	1975–78	Y	2159	F	V	654.2	2%	9%	1%		3%		< 1%	2%	58%	7%	18%	< 1%	0.14
Harris (1984)	Avon	1977–80	Y	2376	F,G	V	411.7	< 1%	< 1%			2%		< 1%	< 1%	18%	20%	35%	24%	0.26
Kruuk & Parish (1985)	Scotland	1975–82	Y	3419	F	V	669.7	1%	5%	3%		2%			2%	48%	7%	32%		0.17
Hofer (1988)	Oxfordshire	1982–83	5–11	NS	F	DW	NS								58%	6%	27%	9%		0.12
Skinner & Skinner (1988)	Essex	1984–86	Y	315	F	V	NS				5%	4%	1%		16%	23%	48%	2%		0.19
Shepherdson, Roper & Lüps (1990)	Sussex	1984–85	Y	192	F	V	NS				1%				43%	10%	45%			0.14
Fairley (1967)	I	N. Ireland	1963–64	12–4	33	F,G	F	800.0		6%		20%	3%			37%	23%	11%		0.28

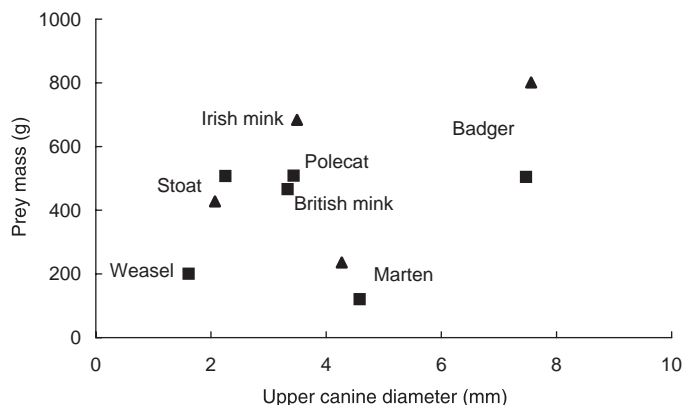
**Table 5.** The diet of otters in Great Britain and Ireland. For a key to the abbreviations used, see Table 2

Source	Location	Year	Time	<i>n</i>	Type	Method	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	B <sub>A</sub>
Stephens (1957)	GB	National	1952–54	Y	110	F,G	F	4%	5%		1%	11%	69%	8%		3%			0-09
Weir & Bannister (1973)		Norfolk	1969–70	Y	1200	F	F			2%	3%	89%				7%			0-02
Webb (1975)		Somerset	1972–74	Y	858	F	F			< 1%	4%	71%	7%			18%			0-08
Weir & Bannister (1977)		Norfolk	1973–74	Y	1060	F	F			2%	2%	93%	2%			2%			0-01
Watson (1978)		Shetland	1976–77	Y	437	F	F				< 1%	92%				8%			0-02
Jenkins, Walker & McCowan (1979) <sup>1</sup>		Aberdeenshire	1975–76	Y	1018	F	F	1%	2%		3%	5%	77%	12%					0-06
Cuthbert (1979)		Scotland	NS	NS	47	F	F				16%	4%	73%				7%		0-07
Jenkins & Harper (1980)		Aberdeenshire (Dinnet)	1975–78	Y	1135	F	F	1%	3%		1%	3%	80%	12%					0-05
Jenkins & Harper (1980)		Aberdeenshire (Dee)	1975–78	Y	1253	F	F	1%	4%	< 1%	1%	1%	88%	4%					0-03
Mason & Macdonald (1980)		Ross-shire	1978–79	Wi	50	F	F					2%	80%			18%			0-04
Wise <i>et al.</i> (1981)		Devon	1974–76	NS	1547	F	V	< 1%	1%			5%	93%	< 1%		1%			0-02
Wise <i>et al.</i> (1981)		Devon	1974–76	NS	675	F	V	2%	4%		1%	2%	82%	5%		4%			0-04
Chanin (1981)		Devon (Teign)	1972–73	Y	253	F	F	1%	3%			1%	92%	1%	2%	< 1%			0-02
Chanin (1981)		Devon (Slapton)	1972–73	5–10	389	F	F	< 1%	1%		< 1%	7%	91%	< 1%					0-02
Herfst (1984)		Shetland	1982	6–8	107	F	F					1%	94%			4%			0-01
Weber (1990)		Aberdeenshire	1987	2–12	919	F	F				3%	2%	73%	21%		2%			0-07
Carss, Kruuk & Conroy (1990)		Aberdeenshire	1989–90	Wi	324	F	F					2%	96%	3%					0-01
Kruuk & Moorhouse (1990)		Shetland	1983–87	Y	2031	O	F		< 1%				97%			3%			0-01
Roche <i>et al.</i> (1995)		Hertfordshire	1992–94	Y	51	F	F				3%	2%	92%	3%					0-02
Clode & Macdonald (1995)		Scotland	1991–93	Su	77	F	F		7%			7%	68%			18%			0-09
Fairley (1972)	I	Galway	1969–71	Y	33	G	F					2%	67%	13%		18%			0-09
Fairley & Wilson (1972)		Londonderry	1970	Au	88	F	F					5%	88%	7%					0-02
Gormally & Fairley (1982)		Mayo (Furnace)	1980–81	8–1	440	F	F					1%	86%	1%		12%			0-03
Gormally & Fairley (1982)		Mayo (Feeagh)	1980–81	8–1	266	F	F					1%	84%	4%		11%			0-03
McFadden & Fairley (1984)		Galway and Mayo	1981	7–12	781	F	F		< 1%	< 1%		5%	66%	13%		16%			0-10
Fairley & McCarthy (1985)		Kerry	1985	5–6	89	F	F					2%	98%						0-00
Murphy & Fairley (1985a)		Galway	1982–83	Y	1026	F	F					< 1%	81%	< 1%		18%			0-04
Murphy & Fairley (1985b)		Western Ireland	1982–83	Wi	394	F	F					< 1%	76%	2%		22%			0-05
Fairley & Murdoch (1989)		Kerry	1987	6	174	F	F					1%	98%	1%					0-00
Kyne, Smal & Fairley (1989)		Midlands	1983–85	Y	2349	F	F					2%	48%	15%		35%			0-15
Breathnach & Fairley (1993)		Galway	1991–92	Y	1709	F	F			< 1%	< 1%	1%	58%	9%		28%		4%	0-13
Tangney & Fairley (1994)		Connemara	1993	Su	316	F	F	< 1%				2%	78%	12%		8%			0-05

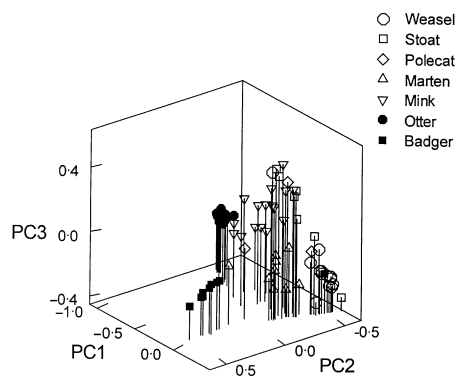
<sup>1</sup>Some of the figures in this study are estimated from graphs.

**Table 6.** Summary of the diets of British and Irish mustelids. Weasels and polecats are absent from Ireland. *n* is the number of samples reviewed. For a key to the abbreviations used, see Table 2

Species	Location	<i>n</i>	Mass	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	B <sub>A</sub>
Weasel	GB	13	200.9	59%	16%		< 1%	21%	1%		1%	1%	1%		< 1%	0.13
Stoat	GB	7	507.6	27%	40%		< 1%	29%	2%	1%		< 1%	1%		1%	0.19
	I	3	427.5	23%	40%			32%	4%							0.19
Mink	GB	16	466.4	11%	26%	< 1%	1%	21%	< 1%	30%	1%	1%	8%		< 1%	0.32
	I	2	684.0	< 1%	24%		< 1%	15%		15%	10%		35%		1%	0.30
Polecat	GB	3	508.6	18%	33%		11%	13%		< 1%	14%	1%	8%		2%	0.38
Pine marten	GB	9	120.9	29%	4%	11%	3%	14%	1%	< 1%	4%	1%	20%	10%	4%	0.44
	I	3	235.9	13%	5%		< 1%	15%	1%		9%	18%	29%	11%		0.43
Badger	GB	9	504.5	7%	5%	< 1%	1%	2%	< 1%	< 1%	< 1%	43%	11%	27%	4%	0.24
	I	1	800.0		6%			20%	3%			37%	23%	11%		0.28
Otter	GB	20	590.3	1%	1%	< 1%	2%	3%		84%	4%	< 1%	4%		< 1%	0.04
	I	12	536.7	< 1%	< 1%		< 1%	2%		77%	6%		14%		< 1%	0.05



**Fig. 1.** Relationship between weighted mean mass of mammalian prey and canine diameter of terrestrial mustelids in Great Britain and Ireland. British samples are marked with a square, Irish samples with a triangle.



**Fig. 2.** Projection of 77 samples of the diets of seven species of mustelid in Great Britain along the first three principal component axes. Axes 1, 2 and 3 account for 55, 18 and 13% of the total variance respectively.

difference in dietary niche breadth between British and Irish mustelids ( $t = -0.39$ ,  $n = 5$ ,  $P = 0.72$ ).

Seventy-seven British samples were included in the initial PCA (Table 9). The species formed groups in multivariate space (Fig. 2) and otters and badgers were distinguished easily from the rest of the assemblage

along the axes described by PC1 and PC2, respectively. There were no apparent trends in the first three components that were related to predator size. The second PCA omitted badgers and otters and was based on 48 samples. The first three components explained a similar proportion of the total variance (Table 9). From the initial analysis including all species, Euclidean distances between dietary niches were not related to predator size (Table 10). This was reflected in the community dendrogram (Fig. 3). Otters were clearly an outlying species since their diet was more distant (0.91) from the rest of the assemblage than the average distance between all species pairs (0.58). The diet of the smallest mustelid, weasel, was most similar to that of one of the larger species, pine marten. Stoats, which are closest in size to weasels, were most similar in their diet to polecats and then to minks. The Euclidean distances among members of the Irish assemblage were significantly lower than among members of the British assemblage ( $W = 4.0$ ,  $n = 10$ ,  $P < 0.05$ ). In the second analysis, omitting otters and badgers, the Euclidean distances were similar to the first analysis (Table 10). There was no significant difference between the two analyses in the distances between species pairs in Britain



**Table 7.** Differences in the diets of male and female mustelids. For a key to the abbreviations used, see Table 2

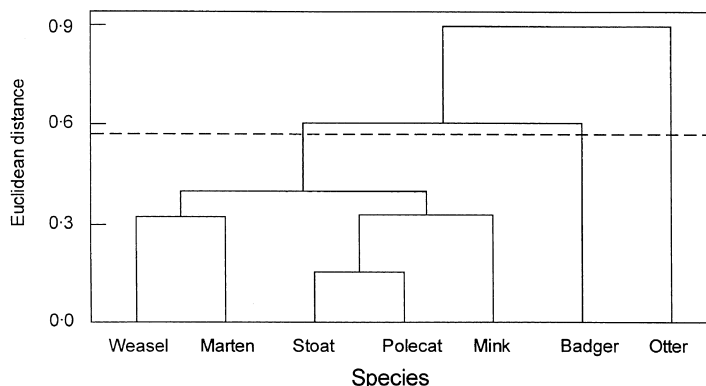
Species	Source	Location	Year	Time	Type	Method	Sex	<i>n</i>	Mass	SM	MM	LM	UM	B	E	F	H	W	I	FV	O	<i>B<sub>i</sub></i>
Weasel	Day (1963, 1968)	GB	1960–63	Y	F,G	F	M	96	255.6	54%	24%			16%				1%	5%			0.15
							F	19	73.0	76%	5%			10%				5%	5%			0.06
Weasel	Pringle (1982)	Sussex	1971–76	Y	G	F	M	146	240.7	47%	10%		1%	15%	1%							0.27
							F	66	208.0	51%	4%		1%	8%	1%		1%					0.24
Weasel	McDonald <i>et al.</i> (2000; unpublished data)	GB	1995–97	Y	G	F	M	381	163.1	66%	26%		1%	5%	1%		1%					0.09
							F	77	83.4	77%	23%											0.05
Stoat	Day (1963, 1968) <sup>1</sup>	GB	1960–63	Y	F,G	F	M	85	443.9	27%	34%			32%				1%	5%			0.22
							F	30	379.9	29%	29%			36%						7%		
Stoat	Pringle (1982)	Sussex	1971–76	Y	G	F	M	138	718.7	14%	61%		1%	18%	6%							0.12
							F	114	550.5	22%	52%		1%	14%	10%			1%				
Stoat	McDonald <i>et al.</i> (2000; unpublished data)	GB	1995–97	Y	G	F	M	503	488.5	8%	73%			12%	6%					< 1%		0.07
							F	286	287.1	26%	55%			16%	4%							
Stoat	Sleeman (1992)	Ireland	NS	Y	G	F	M	58	652.2	25%	53%			23%								0.14
							F	34	568.3	53%	35%			12%								
Polecat	Blandford (1986)	Wales	NS	NS	F	F	M	337	330.7	42%	30%		1%	14%			9%		4%			0.21
							F	251	273.7	50%	24%		< 1%	18%			8%					
Polecat	Birks & Kitchener (1999)	Western England	1990s	NS	G	F	M	53	743.1	5%	77%			7%			9%	2%				0.06
							F	30	652.1	13%	61%			13%			3%	6%	3%			
Mink	Birks & Dunstone (1985)	Coastal Scotland	1980–83	Y	F	F	M	379	731.5	4%	49%		< 1%	7%		20%				19%		0.19
							F	645	608.0	5%	17%		< 1%	11%		38%						29%
Pine marten	Balharry (1993)	Ross-shire	1988–90	Y	F	EWI	M	62	NS	28%		46%		17%			7%		1%	2%		0.20
							F	64	NS	25%		41%		27%			3%		1%	2%		0.20

<sup>1</sup>This study includes an unknown number of samples from Northern Ireland.

**Table 8.** Statistical tests of the differences in the diets of male and female mustelids

Species	Source	<i>n</i>		Test	<i>P</i>		Conclusion
		M	F				
Weasel	Day (1963, 1968)	96	19	$\chi^2$	NS	M = F	No difference in diet. Non-significant tendency for males to take more lagomorphs than females
Weasel	King (1977)	394	118	$\chi^2$	*	M < F	Small rodents
Weasel	Tapper (1979)	199		<i>G</i>	NS	M = F	Lagomorphs and birds
					*	M > F	Lagomorphs in spring only
					*	M < F	<i>Microtus</i> in spring only
Weasel	King (1980)	158	23	Sign	NS	M = F	All groups in summer and winter
					*	M > F	<i>Microtus</i>
					NS	M = F	<i>Clethrionomys</i> , <i>Apodemus</i> , birds, eggs or unidentified rodents
Weasel	Pringle (1982)	146	66	$\chi^2$	NS	M = F	No difference in diet. Non-significant tendency for males to take more lagomorphs than females
Weasel	McDonald <i>et al.</i> (2000)	381	77	LLM	NS	M = F	No difference in diet
Stoat	Day (1963, 1968)	80	35	$\chi^2$	NS	M = F	No difference in diet
Stoat	Pounds (1981)	–	–	$\chi^2$	NS	M = F	No difference in diet
Stoat	Pringle (1982)	138	114	$\chi^2$	NS	M = F	No difference in diet
Stoat	Sleeman (1992)	58	34	$\chi^2$	**	M < F	Shrews
					NS	M = F	All other groups
Stoat	McDonald <i>et al.</i> (2000)	503	286	LLM	***	M < F	Small rodents
					***	M > F	Lagomorphs
					***	M > F	Passerines
					NS	M = F	Birds' eggs and game birds
Polecat	Blandford (1986)	337	251	PIO	–	M = F	Neither sex showed selection in respect of prey size (p. 296)
Polecat	Birks & Kitchener (1999)	53	30	$\chi^2$	NS	M = F	No difference in prevalence of rabbits, other mammals, birds or amphibians
Mink	Birks & Dunstone (1985)	379	645	$\chi^2$	***	M < F	Fish
					***	M < F	Crustaceans
					***	M > F	Lagomorphs
					*	M < F	Birds
					NS	M = F	Small mammals
Pine marten	Balharry (1993)	62	64	$\chi^2$	NS	M = F	No difference in diet
Otter	Kruuk & Moorhouse (1990)	510	660	$\chi^2$	NS	M = F	No difference in prey size or species composition between males and females with cubs, when differences in prey availability taken into account

NS = no significant difference; \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001. LLM = Log-linear modelling, PIO = Pianka's Index of Niche Overlap.



**Fig. 3.** Community dendrogram of the Euclidean distances between the dietary niches of the mustelids living in Great Britain. The dashed line indicates the mean Euclidean distance (0.58) between all combinations of species pairs (*n* = 21) in the assemblage.

**Table 9.** Results of the principal component analysis on the composition of the diets of mustelids in Great Britain. For a key to the abbreviations used, see Table 2

Factor	Whole assemblage			Omitting otters and badgers		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	0.170	0.055	0.041	0.078	0.047	0.027
Proportion of variance explained	0.545	0.176	0.132	0.419	0.252	0.145
Cumulative variance explained	0.545	0.721	0.853	0.419	0.671	0.815
Factor loadings						
SM	0.400	-0.617	-0.549	-0.875	-0.045	0.097
MM	0.211	-0.210	0.619	0.193	-0.800	0.409
LM	0.020	0.007	-0.035	-0.021	0.069	-0.079
UM	-0.008	0.045	0.002	0.043	0.077	-0.045
B	0.140	-0.073	0.488	0.265	-0.212	-0.689
E	0.010	-0.011	-0.001	-0.015	-0.015	0.003
F	-0.877	-0.288	-0.046	0.345	0.422	0.566
H	-0.015	-0.003	-0.002	0.006	0.027	-0.021
W	0.054	0.571	-0.203	-0.002	0.023	-0.003
I	0.007	0.179	-0.104	0.072	0.338	-0.103
FV	0.047	0.352	-0.144	-0.008	0.085	-0.089
O	0.010	0.049	-0.025	-0.003	0.030	-0.045

**Table 10.** Euclidean distances between the group centroids from the first three components of the PCA of dietary composition of British and Irish mustelids. Details of British mustelids are in Roman characters and Irish mustelids in italics. Weasels and polecats are absent from Ireland. The Euclidean distance is a measure of the degree of differentiation between the species' dietary niches. As it increases the similarity between their diets decreases. Distances in the bottom left part of the matrix were derived from the first PCA including otters and badgers. Distances in the top right part of the matrix were derived from the second PCA omitting otters and badgers

	Weasel	Stoat	Mink	Polecat	Pine marten	Badger
Weasel	*	0.396	0.572	0.389	0.320	*
Stoat	0.392	*	0.374	0.149	0.429	*
Mink	0.562	0.372	*	0.291	0.404	*
Polecat	0.394	0.155	0.239	*	0.338	*
Pine marten	0.325	0.391	0.417	0.270	*	*
Badger	0.742	0.705	0.639	0.559	0.426	*
Otter	1.047	0.996	0.633	0.907	0.897	0.985
		0.907	0.624		0.774	0.827

( $t = -0.41$ ,  $n = 10$ ,  $P = 0.69$ ) and in the dendrogram, weasels were again most similar to pine martens and stoats were most similar to polecats and then minks (Fig. 4).

## Discussion

The work of Dayan & Simberloff (1994) has lent substantial weight to Brown & Wilson's (1956) notion of community-wide character displacement and the importance of competition in structuring assemblages of related species. Because of their work, resource partitioning according to prey size has become the estab-

lished hypothesis explaining the coexistence of mustelid assemblages in the British Isles and elsewhere. This analysis of the dietary relationships among British mustelids has confirmed that otters should not be considered part of the same guild as the other six species (Dayan & Simberloff 1994), when adopting Pianka's (1980) definition of an arena of intense interspecific competition. The omission of badgers from certain of Dayan & Simberloff's (1994) analyses was also justified by the distance between this species' dietary niche and those of the other mustelids.

As predicted by Dayan & Simberloff (1994), larger male mustelids consistently took larger prey than females. Outside the British Isles, larger male mustelids have often been observed to eat larger prey than females (Erlinge 1975, 1979; Simms 1979). Previous considerations of such intraspecific differences have supported the resource partitioning hypothesis by following the intuitively appealing notion that dimorphism had arisen primarily as a mechanism for avoiding competition between the sexes (Simms 1979). In contrast, Holmes & Powell (1994), following Holmes (1987), found that the carnassials of male and female mustelids were less dimorphic in size than were the rest of their bodies and concluded that resource partitioning could not have been the driving force in the evolution of size dimorphism. By constructing a model of the optimal body sizes of male and female mustelids, Sandell (1989) concluded that size dimorphism had arisen from differing energetic requirements during the breeding season. Gittleman & Van Valkenburgh (1997) found that the degree of sexual size dimorphism in carnivore canines was best explained by breeding system and not dietary traits and therefore concluded that dimorphism was the result of sexual selection. A sexual selection hypothesis is particularly convincing because male mustelids are always larger than females and this would not be predicted by theories based on prey selection (Gittleman & Van Valkenburgh 1997). Indeed, Dayan

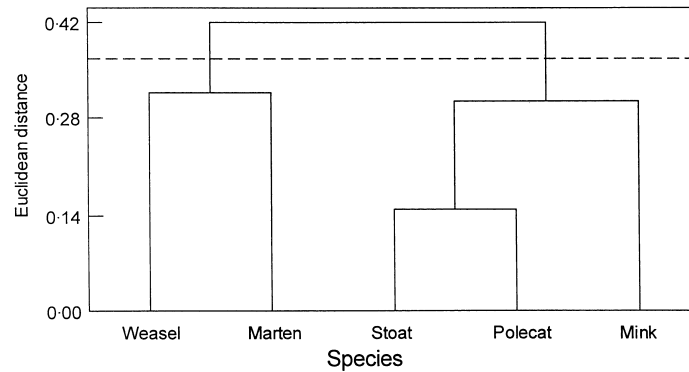


Fig. 4. Community dendrogram of the Euclidean distances between the dietary niches of the mustelids living in Great Britain, omitting otters and badgers. The dashed line indicates the mean Euclidean distance (0.36) between all combinations of species pairs ( $n = 10$ ) in the assemblage.

& Simberloff (1994) themselves did not explicitly claim that sexual size dimorphism was driven primarily by prey size partitioning, but that it might be an additional mechanism of coexistence. Thus, this study and the bulk of previous work accords with Erlinge (1979) and Moors (1980) that differences in diet between male and female mustelids are a secondary consequence of size dimorphism rather than a primary cause of it.

In contrast to the predictions of Dayan & Simberloff (1994), prey size did not increase with predator size and there was no evidence of resource partitioning according to prey size among species. While niche breadth increased with body size (Gittleman 1985), increasing diversity was not explicable solely by increases in the importance of larger mammalian prey. Pine martens ate larger amounts of fruit and invertebrates as well as carrion than smaller mustelids, while polecats and mink diversified their diet into herpetofauna and fish. Dayan & Simberloff (1994) cited a study conducted in the Netherlands (Brugge 1977) in support of their assertion that larger mustelids took larger prey. Nevertheless, a full examination of the British studies they cited (Day 1968; Moors 1975; King 1980; Blandford 1986, 1987; Blandford & Walton 1991) has revealed that these local studies do not support their assertion. The average prey sizes of British stoats, polecats, minks and badgers are similar, yet these predators vary greatly in size and large pine martens take much smaller prey than all of them. As Dayan & Simberloff (1994) are right to point out, pine martens living in continental Europe do eat hares and squirrels (Nyholm 1970; Pulliainen & Hiekkinen 1980). Such medium-sized mammalian prey is, however, rarely eaten by pine martens in Britain or Ireland, even when available in the habitats they occupy (Wray 1992; Hulbert, Iason & Racey 1996; Halliwell 1997). While large mammals make up a substantial proportion of pine marten diet in Britain, these are taken almost entirely as carrion. The empirical data analysed here do not therefore support the established hypothesis of resource partitioning according to prey size as an explanation for even size ratios in the canines of British mustelids.

Irish mustelids exhibit greater variation in canine size and greater size dimorphism than British mustelids. Dayan & Simberloff (1994) took this as evidence of competitive release. In contrast to predictions of competitive release and despite differences in the community of prey species (Corbet & Harris 1991), the diets of Irish mustelids were similar to British mustelids. The Euclidean distances among dietary niches were smaller for Irish mustelids than for British mustelids and the dietary niches of Irish mustelids were no broader than for British samples. These facts suggest that the character release detected by Dayan & Simberloff (1994) was not related to changes in diet. None the less, differences in prey size for Irish stoats and minks, but not pine martens, did correspond to differences in canine size and further studies of mustelid diet in Ireland would be invaluable.

Precise data on the size of individual animals killed by mustelids are required before the possibility of resource partitioning by selecting individuals of varying size within prey species can be ruled out (Kruuk, Conroy & Moorhouse 1987). Gathering these data would be challenging since mustelids often capture their prey underground and remains do not generally permit calculation of prey size. Equally, this analysis may not have fully reflected the extent of niche differentiation among truly sympatric mustelids, since most of the reviewed studies were based on one species and were drawn from throughout the British Isles. Notwithstanding the important issue of scale in defining sympatry and allopatry, a major addition to the current debate would be made by a study of the morphology and prey choice of mustelids living on a single site (Jones 1997; Jones & Barmuta 1998).

The question remains, if resources are not partitioned according to prey size, why do mustelids exhibit character displacement for canine size? Pimm & Gittleman (1990) have pointed out that the process giving rise to even size ratios in carnivore canines must be insensitive to variability in diet, but not to the presence of other carnivores. Interspecific aggression and intraguild predation fit this criterion (Palomares & Caro 1999) and have been considered an obvious alternative hypothesis (Dayan *et al.* 1989; Dayan & Simberloff 1998).

Whitehead & Walde (1993) considered that canine size was an honest signal of threat and demonstrated that a signalling role for canines could lead to even size ratios among morphospecies. Dayan & Simberloff (1994) discounted the role of canines in threat displays since such displays were rarely observed in the Mustelidae. Gossow (1970), Poole (1967), Erlinge (1977) and numerous other studies reviewed by Pruitt & Burghardt (1977) have, however, described threat displays in mustelids that included baring canines. Canines are also involved in biting during conflict between mustelids (Poole 1967; Lüps & Roper 1988). Rosenzweig (1966) did not discount a hypothesis of interspecific aggression and colleagues have highlighted the importance of interference in facilitating the coexistence of weasels and stoats (King & Moors 1979; Erlinge & Sandell 1988). Curiously, Sidorovich, Kruuk & Macdonald (1999) demonstrated an increase in the size of native polecats and European minks *Mustela lutreola* L. in Eastern Europe following the arrival of the larger feral American minks, which have simultaneously decreased in size. Sidorovich *et al.* (1999) suggested that direct aggression between species was leading to enhanced survival of larger individuals of smaller species. Alternatively, Abrams (1986) has suggested that evolutionary 'races' do not always lead to intuitive endpoints. In this case, competing mustelids may find stable strategies not by resource partitioning via scaling of trophic apparatus, but by character convergence (Grant 1972) or they may exhibit no obvious response to the presence of competitors at all. Thus, as suggested by this analysis, patterns in carnivore dentition or body size may not be a dependable index of resource partitioning. While field studies of interactions between carnivores are particularly challenging, examination of alternative hypotheses to resource partitioning is clearly necessary for explaining character displacement among mustelids.

### Acknowledgements

This work was supported by a Royal Society Postdoctoral Fellowship, hosted by the Centre for Biodiversity and Ecology Research, University of Waikato, New Zealand and a Royal Society Conference Grant to attend the European Congress of Mammalogy in Jyväskylä, Finland. I am grateful to Philip Baker, Johnny Birks, Paul Bright, Paul Chanin, James Fairley, Elizabeth Halliwell, Carolyn King, Roger Powell, Rory Putman, Linda Sadlier, Dan Simberloff and Nancy Vaughan for reprints, access to original data and advice and to Andrew Kitchener for measurements of otter canines. The manuscript was greatly improved by the incisive comments of the anonymous referees.

### References

- Abrams, P.A. (1986) Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. *Evolution*, **40**, 1229–1247.

- Akande, M. (1972) The food of feral mink *Mustela vison* in Scotland. *Journal of Zoology*, **167**, 475–479.
- Armitage, J.S. (1980) Notes on hunting techniques and prey of the weasel. *Sorby Record*, **18**, 83.
- Balharry, D. (1993) *Factors affecting the distribution and population density of pine martens (Martes martes) in Scotland*. PhD Thesis. University of Aberdeen.
- Birks, J.D.S. & Dunstone, N. (1984) A note on prey remains collected from the dens of feral mink (*Mustela vison*) in a coastal habitat. *Journal of Zoology*, **203**, 279–281.
- Birks, J.D.S. & Dunstone, N. (1985) Sex-related differences in the diet of the mink *Mustela vison*. *Holarctic Ecology*, **8**, 245–252.
- Birks, J.D.S. & Kitchener, A.C. (1999) *The Distribution and Status of the Polecat Mustela putorius in Britain in the late 1990s*. Vincent Wildlife Trust, London.
- Blandford, P.R.S. (1986) *Behavioural ecology of the polecat Mustela putorius in Wales*. PhD Thesis, University of Exeter.
- Blandford, P.R.S. (1987) Biology of the Polecat *Mustela putorius*: a literature review. *Mammal Review*, **17**, 155–198.
- Blandford, P.R.S. & Walton, K.C. (1991) Polecat. *Handbook of British Mammals*, 3rd edn (eds G.B. Corbet & S. Harris), pp. 396–405. Blackwell Science, Oxford.
- Breathnach, S. & Fairley, J.S. (1993) The diet of otters *Lutra lutra* (L.) in the Clare river system. *Biology and Environment – Proceedings of the Royal Irish Academy*, **93B**, 151–158.
- Bright, P.W. & Smithson, T.J. (1997) Species Recovery Programme for the pine marten in England: 1995–96. *English Nature Research Reports*, 240. English Nature, Peterborough.
- Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **7**, 49–64.
- Brugge, T. (1977) Prey selection of weasel, stoat and polecat in relation to sex and size. *Lutra*, **19**, 39–49 [in Dutch].
- Carss, D.N., Kruuk, H. & Conroy, J.W.H. (1990) Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, **37**, 935–944.
- Carss, D.N., Nelson, K.C., Bacon, P.J. & Kruuk, H. (1998) Otter (*Lutra lutra*) prey selection in relation to fish abundance and community structure in two different freshwater habitats. *Symposia of the Zoological Society of London*, **71**, 191–214.
- Chanin, P.R.F. (1981) The diet of the otter and its relations with the feral mink in two areas of southwest England. *Acta Theriologica*, **28**, 83–95.
- Chanin, P.R.F. & Linn, I. (1980) The diet of the feral mink (*Mustela vison*) in southwest Britain. *Journal of Zoology*, **192**, 205–223.
- Clode, D. & Macdonald, D.W. (1995) Evidence for food competition between mink (*Mustela vison*) and otter (*Lutra lutra*) on Scottish islands. *Journal of Zoology*, **237**, 435–444.
- Corbet, G.B. & Harris, S., eds (1991) *Handbook of British Mammals*, 3rd edn. Blackwell Science, Oxford.
- Cuthbert, J.H. (1979) Food studies of feral mink *Mustela vison* in Scotland. *Fish Management*, **10**, 17–25.
- Day, M.G. (1963) *An ecological study of the stoat (Mustela erminea L.) and the weasel (Mustela nivalis L.) with particular reference to their food and feeding habits*. PhD Thesis, University of Exeter.
- Day, M.G. (1968) Food habits of British stoats (*Mustela erminea*) and weasels (*Mustela nivalis*). *Journal of Zoology*, **155**, 485–497.
- Day, M.G. & Linn, I. (1972) Notes on the food of feral mink *Mustela vison* in England and Wales. *Journal of Zoology*, **167**, 463–473.
- Dayan, T. & Simberloff, D. (1994) Character displacement, sexual dimorphism and morphological variation among British and Irish mustelids. *Ecology*, **75**, 1063–1073.

- Dayan, T. & Simberloff, D. (1996) Patterns of size separation in carnivore communities. *Carnivore Behavior, Ecology and Evolution* (ed. J.L. Gittleman), vol. 2, pp. 243–266. Cornell University Press, Ithaca.
- Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1989) Inter- and intraspecific character displacement in mustelids. *Ecology*, **70**, 1526–1539.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1990) Feline canines: community-wide character displacement among the small cats of Israel. *American Naturalist*, **136**, 39–60.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1992) Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society*, **45**, 315–331.
- Dunstone, N. (1993). *The Mink*. T. & A.D. Poyser, London.
- Dunstone, N. & Birks, J.D.S. (1987) The feeding ecology of mink (*Mustela vison*) in coastal habitat. *Journal of Zoology*, **212**, 69–83.
- Erlinge, S. (1975) Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos*, **26**, 378–384.
- Erlinge, S. (1977) Agonistic behaviour and dominance in stoats (*Mustela erminea* L.). *Zeitschrift für Tierpsychologie*, **44**, 375–388.
- Erlinge, S. (1979) Adaptive significance of sexual dimorphism in weasels. *Oikos*, **33**, 233–245.
- Erlinge, S. (1986) Specialists and generalists among the mustelids. *Lutra*, **29**, 5–11.
- Erlinge, S. & Sandell, M. (1988) Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. *Oikos*, **53**, 242–246.
- Fairley, J.S. (1967) An indication of the food of the Badger in North-east Ireland. *Irish Naturalists Journal*, **15**, 267–269.
- Fairley, J.S. (1971) New data on the Irish stoat. *Irish Naturalists Journal*, **17**, 49–57.
- Fairley, J.S. (1972) Food of otters (*Lutra lutra*) from Co. Galway, Ireland, and notes on other aspects of their biology. *Journal of Zoology*, **166**, 469–474.
- Fairley, J.S. (1975) Summer food of pine martens in Co. Clare. *Irish Naturalists Journal*, **18**, 257–258.
- Fairley, J.S. (1980) Observations on a collection of feral Irish mink *Mustela vison* Schreber. *Proceedings of the Royal Irish Academy Section B—Biological Geological and Chemical Science*, **80**, 79–90.
- Fairley, J.S. (1981) A north–south cline in the size of the Irish stoat. *Proceedings of the Royal Irish Academy Section B—Biological Geological and Chemical Science*, **81**, 5–10.
- Fairley, J.S. (1984) Otters feeding on breeding frogs. *Irish Naturalists Journal*, **21**, 372.
- Fairley, J.S. & McCarthy, T.K. (1985) Do otters rely on breeding natterjack toads? *Irish Naturalists Journal*, **21**, 544–545.
- Fairley, J.S. & Murdoch, B. (1989) Summer food of otters in the lakes of Killarney. *Irish Naturalists Journal*, **23**, 38–41.
- Fairley, J.S. & O’Gorman, F. (1974) Food of pine martens in the Burren. *Irish Naturalists Journal*, **18**, 125.
- Fairley, J.S. & Wilson, S.C. (1972) Autumn food of otters (*Lutra lutra*) on the Agivey River, County Londonderry, Northern Ireland. *Journal of Zoology*, **166**, 468–469.
- Ferreras, P. & Macdonald, D.W. (1999) The impact of American mink *Mustela vison* on water birds in the upper Thames. *Journal of Applied Ecology*, **36**, 701–708.
- Gittleman, J.L. (1985) Carnivore body size: ecological and taxonomic correlates. *Oecologia*, **67**, 540–554.
- Gittleman, J.L. & Van Valkenburgh, B. (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, **242**, 97–117.
- Gormally, M.J. & Fairley, J.S. (1982) Food of otters *Lutra lutra* in a freshwater lough and an adjacent brackish lough in the West of Ireland. *Journal of Zoology*, **197**, 313–321.
- Gossow, H. (1970) Vergleichende Verhaltensstudien an Marderartigen I. Über Lautäußerungen und zum beuteverhalten. *Zeitschrift für Tierpsychologie*, **27**, 405–480.
- Grant, P.R. (1972) Convergent and divergent character displacement. *Biological Journal of the Linnean Society*, **4**, 39–68.
- Gurnell, J., Venning, T., MacCaskill, B. & MacCaskill, D. (1994) The food of pine martens (*Martes martes*) in West Scotland. *Journal of Zoology*, **234**, 680–683.
- Halliwel, E.C. (1997) *The ecology of red squirrels in Scotland in relation to pine marten predation*. PhD Thesis, University of Aberdeen.
- Harris, S. (1984) Ecology of urban badgers *Meles meles* – distribution in Britain and habitat selection, persecution, food and damage in the city of Bristol. *Biological Conservation*, **28**, 349–375.
- Herfst, M.S. (1984) Habitat and food of the otter *Lutra lutra* in Shetland. *Lutra*, **27**, 57–70.
- Hewson, R. & Healing, T.D. (1971) The stoat *Mustela erminea* and its prey. *Journal of Zoology*, **164**, 239–244.
- Hofer, H. (1988) Variation in resource presence, utilization and reproductive success within a population of European badger (*Meles meles*). *Mammal Review*, **18**, 25–36.
- Holmes, T. Jr (1987) *Sexual dimorphism in North American weasels with a phylogeny of the Mustelidae*. PhD Thesis, University of Kansas.
- Holmes, R.T., Bonney, R.E. Jr & Pacala, S.W. (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology*, **60**, 512–520.
- Holmes, T. & Powell, R.A. (1994) Morphology, ecology, and the evolution of sexual dimorphism in North American *Martes*. *Martens, Sables and Fishers: biology and conservation* (eds S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell), pp. 72–84. Cornell University Press, Ithaca.
- Howes, C.A. (1977) A survey of the food habits of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in Yorkshire. *Naturalist*, **102**, 117–121.
- Hulbert, I.A.R., Iason, G.R. & Racey, P.A. (1996) Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. *Journal of Applied Ecology*, **33**, 315–324.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.
- Jaksic, F.M. (1981) Abuse and misuse of the term ‘guild’ in ecological studies. *Oikos*, **37**, 397–400.
- Jefferies, D.J. (1986) Estimation of complete body weights for skinned European otters *Lutra lutra* (L.). *Journal of Zoology, London*, **209**, 282–285.
- Jenkins, D. & Harper, R.J. (1980) Ecology of otters in northern Scotland II. Analyses of otter (*Lutra lutra*) and mink (*Mustela vison*) faeces from Deeside, N.E. Scotland in 1977–78. *Journal of Animal Ecology*, **49**, 737–754.
- Jenkins, D., Walker, J.G.K. & McCowan, D. (1979) Analysis of otter (*Lutra lutra*) faeces from Deeside, NE Scotland. *Journal of Zoology*, **187**, 235–244.
- Jones, M. (1997) Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. *Ecology*, **78**, 2569–2587.
- Jones, M.E. & Barmuta, L.A. (1998) Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. *Journal of Animal Ecology*, **67**, 410–421.
- King, C.M. (1977) The effects of the nematode parasite *Skrjabinylus nasicola* on British weasels (*Mustela nivalis*). *Journal of Zoology*, **182**, 225–249.

- King, C.M. (1980) The weasel (*Mustela nivalis*) and its prey in an English woodland. *Journal of Animal Ecology*, **49**, 127–159.
- King, C.M. (1989) The advantages and disadvantages of small size to weasels, *Mustela* species. *Carnivore Behavior, Ecology and Evolution* (ed. J.L. Gittleman), pp. 302–334. Cornell University Press, Ithaca.
- King, C.M. (1991) Body size–prey size relationships in European stoats *Mustela erminea*: a test case. *Holarctic Ecology*, **14**, 173–185.
- King, C.M. & Moors, P.J. (1979) On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia*, **39**, 129–150.
- Krebs, C.J. (1989) *Ecological Methodology*. Harper Collins, New York.
- Kruuk, H. (1978) Foraging and spatial organization of the European badger *Meles meles*. *Behavioral Ecology and Sociobiology*, **4**, 75–89.
- Kruuk, H., Carss, D.N., Conroy, J.W.H. & Durbin, L. (1993) Otter (*Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia of the Zoological Society of London*, **65**, 171–191.
- Kruuk, H., Conroy, J.W.H. & Moorhouse, A. (1987) Seasonal reproduction, mortality and food of otters (*Lutra lutra* L.) in Shetland. *Symposia of the Zoological Society of London*, **58**, 263–278.
- Kruuk, H. & Moorhouse, A. (1990) Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland. *Journal of Zoology*, **221**, 621–637.
- Kruuk, H. & Parish, T. (1981) Feeding specialisation of the European badger *Meles meles* in Scotland. *Journal of Animal Ecology*, **50**, 773–788.
- Kruuk, H. & Parish, T. (1985) Food, food availability and weight of badgers (*Meles meles*) in relation to agricultural changes. *Journal of Applied Ecology*, **22**, 705–715.
- Kyne, M.J., Smal, C.M. & Fairley, J.S. (1989) The food of otters *Lutra lutra* in the Irish Midlands and a comparison with that of mink *Mustela vison* in the same region. *Proceedings of the Royal Irish Academy Section B – Biological Geological and Chemical Science*, **89**, 33–46.
- Levins, R. (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton.
- 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**, 187–195.
- Lüps, P. & Roper, T.J. (1988) Tooth size in the European badger (*Meles meles*) with special reference to sexual dimorphism, diet and intraspecific aggression. *Acta Theriologica*, **33**, 21–33.
- Lynch, J.M., Conroy, J.W.H., Kitchener, A.C., Jefferies, D.J. & Hayden, T.J. (1996) Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra* L. *Journal of Zoology, London*, **238**, 81–96.
- Lynch, J.M. & O'Sullivan, W.M. (1993) Cranial form and sexual dimorphism in the Irish otter *Lutra lutra* L. *Biology and Environment: Proceedings of the Royal Irish Academy*, **93B**, 97–105.
- MacArthur, J.W. & Levins, R. (1967) The limiting similarity, convergence and divergence of co-existing species. *American Naturalist*, **101**, 377–385.
- Mason, C.F. & Macdonald, S.M. (1980) The winter diet of otters (*Lutra lutra*) on a Scottish sea loch. *Journal of Zoology*, **192**, 558–561.
- McDonald, R.A., Webbon, C. & Harris, S. (2000) The diet of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in Great Britain. *Journal of Zoology*, **252**, 363–371.
- McFadden, Y.M.T. & Fairley, J.S. (1984) Food of otters *Lutra lutra* (L.) in an Irish limestone river system with special reference to the crayfish *Austropotamobius pallipes* (Lereboullet). *Journal of Life Sciences of the Royal Dublin Society*, **5**, 65–76.
- McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.
- Middleton, A.D. (1935) The food of a badger (*Meles meles*). *Journal of Animal Ecology*, **4**, 291.
- Moors, P.J. (1975) The food of weasels (*Mustela nivalis*) on farmland in north east Scotland. *Journal of Zoology*, **177**, 455–461.
- Moors, P.J. (1980) Sexual-dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos*, **34**, 147–158.
- Murphy, K.P. & Fairley, J.S. (1985a) Food and sprainting places of otters on the west coast of Ireland. *Irish Naturalists Journal*, **21**, 477–479.
- Murphy, K.P. & Fairley, J.S. (1985b) Food of otters *Lutra lutra* on the south shore of Galway Bay. *Proceedings of the Royal Irish Academy Section B – Biological Geological and Chemical Science*, **85**, 47–55.
- Neal, E. (1988) The stomach contents of badgers, *Meles meles*. *Journal of Zoology*, **215**, 367–369.
- Nyholm, E.S. (1970) On the ecology of the pine marten (*Martes martes*) in eastern and northern Finland. *Suomen Riista*, **22**, 105–118 [in Finnish].
- Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492–508.
- Pianka, E.R. (1980) Guild structure in desert lizards. *Oikos*, **35**, 194–201.
- Pimm, S.L. & Gittleman, J.L. (1990) Carnivores and ecologists on the road to Damascus. *Trends in Ecology and Evolution*, **5**, 70–73.
- Poole, T.B. (1967) Aspects of aggressive behaviour in polecats. *Zeitschrift für Tierpsychologie*, **24**, 351–369.
- Potts, G.R. & Vickerman, G.P. (1974) Studies on the cereal ecosystem. *Advances in Ecological Research*, **8**, 107–197.
- Pounds, C.J. (1981) *Niche overlap in sympatric populations of stoats (Mustela erminea) and weasels (Mustela nivalis) in northeast Scotland*. PhD Thesis. University of Aberdeen.
- Powell, R.A. & King, C.M. (1997) Variation in body size, sexual dimorphism and age-specific survival in stoats, *Mustela erminea* (Mammalia: Carnivora), with fluctuating food supplies. *Biological Journal of the Linnean Society*, **62**, 165–194.
- Powell, R.A. & Zielinski, W.J. (1983) Competition and co-existence in mustelid communities. *Acta Zoologica Fennica*, **174**, 223–227.
- Pringle, C.R. (1982) *Factors influencing sexual dimorphism in stoats (Mustela erminea) and weasels (Mustela nivalis)*. BSc Thesis. University of Southampton.
- Pruitt, C.H. & Burghardt, G.M. (1977) Communication in terrestrial carnivores: Mustelidae, Procyonidae, and Ursidae. *How Animals Communicate* (ed. T.A. Seboek), pp. 767–793. Indiana University Press, Bloomington.
- Pulliaainen, E. & Hiekkinen, H. (1980) Behaviour of the pine marten (*Martes martes*) in east Finnish forest Lapland in winter. *Suomen Riista*, **28**, 30–36.
- Putman, R.J. (2000) Diet of pine martens *Martes martes* L. in west Scotland. *Journal of Natural History*, **34**, 793–797.
- Ralls, K. & Harvey, P.H. (1985) Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society*, **25**, 119–167.
- Ranta, E., Laurila, A. & Elmberg, J. (1994) Reinventing the wheel: analyses of sexual dimorphism in body size. *Oikos*, **70**, 313–321.
- Roche, K., Harris, R., Warrington, S. & Copp, G.H. (1995) Home-range and diet of re-introduced European otters *Lutra lutra* (L.) in Hertfordshire rivers. *Aquatic Conservation—Marine and Freshwater Ecosystems*, **5**, 87–96.
- Rosenzweig, M.L. (1966) Community structure in sympatric Carnivora. *Journal of Mammalogy*, **47**, 602–612.
- Rosenzweig, M.L. (1968) The strategy of body size in mammalian carnivores. *American Midland Naturalist*, **80**, 299–315.

- Roth, V.L. (1981) Constancy in the size ratios of sympatric species. *American Naturalist*, **118**, 394–404.
- Ryan, B.F. & Joiner, B.L. (1994) *Minitab Handbook*, 3rd edn. Duxbury Press, Belmont, California.
- Sadler, L. (1999) *The behavioural ecology of the badger (Meles meles L.) on pastoral farmland*. PhD Thesis. The Queen's University of Belfast.
- Sandell, M. (1989) Ecological energetics, optimal body size and sexual dimorphism: a model applied to the stoat, *Mustela erminea* L. *Functional Ecology*, **3**, 315–324.
- Shaw, G. & Livingstone, J. (1992) The pine marten – its reintroduction and subsequent history in the Galloway Forest Park. *Transactions of the Dumfriesshire and Galloway Natural History and Antiquarian Society*, **67**, 1–7.
- Shepherdson, D.J., Roper, T.J. & Lüps, P. (1990) Diet, food availability and foraging behavior of badgers (*Meles meles* L.) in southern England. *Zeitschrift für Säugetierkunde*, **55**, 81–93.
- Sidorovich, V., Kruuk, H. & Macdonald, D.W. (1999) Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. *Journal of Zoology*, **248**, 521–527.
- Simberloff, D. & Boecklen, W. (1981) Santa Rosalia reconsidered: size ratios and competition. *Evolution*, **35**, 1206–1228.
- Simberloff, D. & Dayan, T. (1991) Guilds and the structure of ecological communities. *Annual Review of Ecology and Systematics*, **22**, 115–143.
- Simms, D.A. (1979) North American weasels: resource utilization and distribution. *Canadian Journal of Zoology*, **57**, 504–520.
- Skinner, C.A. & Skinner, P.J. (1988) Food of badgers (*Meles meles*) in an arable area of Essex. *Journal of Zoology*, **215**, 360–362.
- Sleeman, D.P. (1992) Diet of Irish stoats. *Irish Naturalists Journal*, **24**, 151–153.
- Stephens, M.N. (1957) *The Otter Report*. Universities Fund for Animal Welfare, Potters Bar.
- Storch, I., Lindström, E.R. & De Jonge, J. (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica*, **35**, 311–320.
- Strachan, C., Jefferies, D.J., Barreto, G.R., Macdonald, D.W. & Strachan, R. (1998) The rapid impact of resident American mink on water voles: case studies in lowland England. *Symposia of the Zoological Society of London*, **71**, 339–358.
- Strong, D.R., Szyka, L.A. & Simberloff, D.S. (1979) Tests of community-wide character displacement against null hypotheses. *Evolution*, **33**, 897–913.
- Tangney, D.E. & Fairley, J.S. (1994) Otter signs and diet in Connemara National Park and its environs. *Irish Naturalists Journal*, **24**, 434–440.
- Tapper, S.C. (1976) The diet of weasels, *Mustela nivalis* and stoats, *Mustela erminea* during early summer, in relation to predation on gamebirds. *Journal of Zoology*, **179**, 219–224.
- Tapper, S.C. (1979) The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. *Journal of Animal Ecology*, **48**, 603–617.
- Thompson, D. (1978) *A comparison of the diets of stoats and weasels found living sympatrically*. BSc Thesis. University of Southampton.
- Tonkyn, D.W. & Cole, B.J. (1986) The statistical analysis of size ratios. *American Naturalist*, **128**, 66–81.
- Velander, K.A. (1985) *A Study of Pine Marten Ecology in Inverness-Shire*. Chief Scientist's Directorate Report 651. Nature Conservancy Council, Peterborough.
- Walker, D.R.G. (1972) Observations on a collection of weasels (*Mustela nivalis*) from estates in south-west Hertfordshire. *Journal of Zoology*, **166**, 474–480.
- Walton, K.C. (1968) *Biology of the polecat, Putorius putorius (L.)*. MSc Thesis. University of Durham.
- Ward, D.P., Smal, C.M. & Fairley, J.S. (1986) The food of mink *Mustela vison* in the Irish midlands. *Proceedings of the Royal Irish Academy Section B – Biological Geological and Chemical Science*, **86**, 169–182.
- Warner, P. & O'Sullivan, P. (1982) The food of the pine marten *Martes martes* in Co. Clare. *Transactions of the International Congress of Game Biologists*, **14**, 323–330.
- Watson, H. (1978) *Coastal Otters in Shetland*. Vincent Wildlife Trust, London.
- Webb, J.B. (1975) Food of the otter (*Lutra lutra*) on the Somerset Levels. *Journal of Zoology*, **177**, 486–491.
- Weber, J.M. (1990) Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. *Journal of Zoology*, **220**, 641–651.
- Weir, V. & Bannister, K.E. (1973) The food of the otter in the Blakeney area. *Transactions of the Norfolk and Norwich Naturalists' Society*, **22**, 377–382.
- Weir, V. & Bannister, K.E. (1977) Additional notes on the food of the otter in the Blakeney area. *Transactions of the Norfolk and Norwich Naturalists' Society*, **24**, 85–88.
- Whitehead, H. & Walde, S.J. (1993) Territoriality and the evolution of character displacement and sexual dimorphism. *Ethology, Ecology and Evolution*, **5**, 303–318.
- Williamson, M. (1972) *The Analysis of Biological Populations*. Edward Arnold, London.
- Wise, M.H., Linn, I.J. & Kennedy, C.R. (1981) A comparison of the feeding biology of mink *Mustela vison* and otter *Lutra lutra*. *Journal of Zoology*, **195**, 181–213.
- Wray, S. (1992) *The ecology and management of European hares (Lepus europaeus) in commercial coniferous forestry*. PhD Thesis. University of Bristol.

Received 18 December 2000; revision received 18 October 2001