

Food habits of stoats *Mustela erminea* and weasels *Mustela nivalis* in Denmark

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Stoats *Mustela erminea* Linnaeus, 1758 and weasels *Mustela nivalis* Linnaeus, 1766 exploit the same array of prey species at different frequencies according to body size. The rabbit *Oryctolagus cuniculus*, which typically is the dominant prey for stoats in temperate parts of Europe, is absent in Denmark. The present study based on gastrointestinal tract contents examines the food habits of sympatric stoats ($n = 112$) and weasels ($n = 132$) from Denmark. Rodents were the most important prey group for both stoats and weasels, constituting 77% and 84% of their diet respectively, expressed as frequency of occurrence. No differences were detected in the proportions of major prey groups between sexes within species, but between species the diets differed. Stoats ate birds and birds' eggs more often than weasels did, while weasels ate more insectivores. Stoats ate more often *Microtus* voles and water vole *Arvicola terrestris* than weasels did, while weasels ate more bank vole *Clethrionomys glareolus* and mole *Talpa europaea*. There was a larger dietary overlap between sympatric stoats and weasels in Denmark than in other dietary studies in areas where rabbits were available.

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Introduction

Stoats *Mustela erminea* Linnaeus, 1758 and weasels *Mustela nivalis* Linnaeus, 1766 are two closely related predators with similar appearances and habits. They are sympatric through most of their distribution range across the northern Holarctic region. The two species have

the same fundamental dietary niche but exploit prey species of the size of rabbits *Oryctolagus cuniculus*, water voles *Arvicola terrestris* and smaller rodents at different frequencies according to body size (King 1989). Most previous dietary studies of stoats and weasels have only analysed food habits of one species (eg Erlinge 1975, Tapper 1979, King 1980, Erlinge 1981, Erlinge 1987, Goszczyński 1999, Martinoli *et al.*

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2001). Relatively few studies have considered food habits of both stoats and weasels (Brugge 1977, Day 1968, McDonald *et al.* 2000). Generally, these studies have shown that stoats have a wider and more flexible dietary niche than weasels, which are more specialized on small voles. Stoats and weasels are widespread in Denmark (Jensen and Jensen 1973), but rabbits only occur in small, scattered populations in the southern fringes of the country and on a few small islands where it has been introduced (Jensen 2003).

The coexistence, resource partitioning and character displacement between stoats and weasels has been addressed by several studies. Over their geographic ranges stoats and weasels exhibit a great variation of body sizes, which decrease in size with increasing latitude and altitude in Eurasian populations (Erlinge 1987, King 1989, King 1991), and both species also exhibit a pronounced sexual size dimorphism with males being substantially larger than females (Moors 1980, McDonald 2002). Hypotheses suggest that coexistence between stoats and weasels is explained by a balance of competitive advantages determined by interspecific aggression, differing foraging and reproductive strategies, while sexual dimorphism is correlated to differing energetic requirement in reproduction (King and Moors 1979, Moors 1980, Sandell 1989, McDonald 2002). Dayan and Simberloff (1994) hypothesized that resource partitioning according to prey size explained character displacement, and considered the two sexes of stoats and weasels as four functionally distinct morphospecies.

The present study investigates the food habits of stoats and weasels in a temperate area in Europe outside the distribution range of the rabbit. The dietary niche overlap and body size of stoats and weasels based on the relatively smaller spectrum of prey species in Denmark are compared to food habits of neighbouring populations in temperate parts of Europe. A higher dietary overlap between stoats and weasels and between sexes could be expected in areas outside the distribution range of the larger prey species that typically dominate the diet of stoats.

Material and methods

Stoats and weasels were collected between 1984–2004 in Denmark through private taxidermists and The National Forest and Nature Agency. Most of the animals originated from the northern and central part of the country. All animals but one weasel were collected outside the rabbit distribution range. Stoats and weasels are totally protected in Denmark but a number of animals were killed unintentionally in instant-kill traps for American mink *Mustela vison* and in mole *Talpa europaea* traps (Table 1). Data on site, date and cause of death were noted on site for each animal. Carcasses and data label were sent to the National Environmental Research Institute for necropsy. Body weight was noted and the gastrointestinal tracts were removed from carcasses and frozen until analysis. The animals were grouped into seasons according to date of death: spring, March–May; summer, June–August; autumn, September–November; winter, December–February.

Stomach and intestine were analysed separately. Gastrointestinal tracts were examined in stereomicroscope to collect all small prey remains. Larger volumes of contents were rinsed through a 0.5 mm sieve. All contents were subsequently stored in 70% alcohol. Undigested prey remains were identified to the finest taxonomic level possible according to Day (1966), Debrot (1982) and Teerink (1991). Mammal remains were identified from the cuticle scales, medulla patterns and cross sections of guard hairs. Some mammal remains were identified to genus only: *Apodemus* spp. included yellow-necked mouse *A. flavicollis* and wood mouse *A. sylvaticus*; *Microtus* spp. included field vole *M. agrestis* and common vole *M. arvalis*; *Sorex* spp. included common shrew *S. araneus* and pygmy shrew *S. minutus*. The remains of birds were identified to order from barbule nodes of feathers. Remains of birds' eggs were not identified further. Single hairs and small tufts of stoat and weasel hairs were ignored, as these were assumed to result from grooming or contamination during sample preparation.

The only vegetative materials detected in the guts were small parts of grass and herbal leaves. No remains of

Table 1. Composition of stoats and weasels by sex and cause of death collected in Denmark between 1984–2004. Predation represents carcasses collected by domestic animals, predominately cats.

		Stoat	Weasel
Sex	Males	76	79
	Females	35	39
	Unknown	1	14
Cause of death	Traffic killed	66	41
	Trapped	20	31
	Predation	7	30
	Other	19	28

berries were found. It was assumed that vegetation was ingested coincidentally along with foraging and it was excluded from further analysis. No macroscopic remains of earthworms were found and no attempts were made to detect microscopic prey remains, eg earthworms (Lumbricidae).

The content of gastrointestinal tract usually correspond to one meal in stoats and weasels (Day 1968, Tapper 1979, King 1980). Results are expressed as frequency of occurrence, defined as the number of times a specific prey item occurred as a proportion of the total number of identifiable food items, and as percentage frequency of occurrence to make results directly comparable with other studies. Diets were compared at a low taxonomic resolution comprising the six major groups (rodents, insectivores, other mammals, birds, birds' eggs, and others) and at a higher taxonomic resolution involving the six most frequently occurring mammal genus and species (*Apodemus* spp., water vole, bank vole *Clethrionomys glareolus*, *Microtus* spp., *Sorex* spp. and mole). Birds and birds' eggs were combined for statistical analyses between species. To achieve sufficient sample size the seasons were combined in 6-month periods starting in March (Spring and Summer, where breeding birds and birds' egg are available) and September (Autumn and Winter). Chi-square tests were used to compare variations in the diets between species, sexes within species and between species. Dietary niche breadths at the low taxonomic resolution level of the six major prey groups were estimated by Levins' index (B) (Krebs 1999):

$$B = 1 / \sum_n p_i^2$$

where p_i is the proportions of each prey group i . Dietary niche overlap was estimated using the Pianka index (O_{jk}) and percentage overlap (P_{jk}):

$$O_{jk} = \frac{\sum_n p_{ij} p_{ik}}{\sqrt{\sum_n p_{ij}^2 \sum_n p_{ik}^2}}, \text{ and}$$

$$P_{jk} = \left[\sum_n (\text{minimum } p_{ij}, p_{ik}) \right] \cdot 100$$

where p_{ij} and p_{ik} are the proportion of prey group i used by species j and k , respectively, and n is the total number of prey groups (Krebs 1999).

The statistic error associated with the sampling was estimated with bootstrapping procedures (Reynolds and Aebischer 1991, Krebs 1999). Means and 95-percentile range confidence intervals of percentage frequency of occurrence of prey items and Levins' measure of niche breadth were calculated from 1000 replicate bootstrap estimates. For comparison the dietary niche breadths was calculated for the other European studies considering both stoats and weasels based on the occurrence of the six major prey groups (Day 1968, Brugge 1977, McDonald *et al.* 2000).

Body weights of stoats and weasels were compared by analyses of variance followed by Tukey test between categories.

Results

A total of 112 stoats and 132 weasels were examined (Table 1). Carcasses collected between 1998 and 2003 dominated the sample of both species, 87% and 80% respectively. There was no difference between annual or seasonal distribution of stoats and weasels (Annual: $\chi^2 = 25.9$, $df = 20$, $p = 0.17$; Seasonal: $\chi^2 = 3.0$, $df = 3$, $p = 0.40$). Fewest specimens were collected during the winter season of both species.

Prey remains of nineteen distinguishable taxa or categories were found in the gastrointestinal tracts of stoats and weasels (Table 2). One hundred and two prey remains were found in the gastrointestinal tract of 86 stoats and 127 prey remains were identified in the gastrointestinal tract of 115 weasels. Ten stoats (8.9%) and ten weasels (7.6%) contained remains from two prey species. Three prey items were identified in three stoats (2.7%) and one weasel (0.8%). Due to this relatively large number of individuals with multiple prey items in the gastrointestinal tracts the dietary compositions were described as proportion of prey items in non-empty guts for statistical composition.

Mammals made up the largest proportion of the diet in stoats and weasels, 84.3% and 93.7% respectively. The most frequently encountered mammal remains were rodents, of which most were voles. The overall dietary composition of the major prey groups differed significantly between stoats and weasels ($\chi^2 = 15.44$, $df = 4$, $p < 0.01$). Birds and birds' eggs were a more common food for stoats than weasels, while weasels ate more insectivores than stoats did. No differences were found in the diets between sexes within species (stoats: $\chi^2 = 5.38$, $df = 4$, $p = 0.25$; weasels $\chi^2 = 7.42$, $df = 4$, $p = 0.12$). The dietary variations in 6-month periods were insignificant in stoats ($\chi^2 = 5.59$, $df = 5$, $p = 0.23$) but differed in weasels ($\chi^2 = 11.59$, $df = 3$, $p < 0.01$). There were no difference in the diets of stoats and weasels in spring and summer ($\chi^2 = 6.49$, $df = 4$, $p = 0.17$) but diet composition differed significantly in autumn and winter ($\chi^2 = 27.27$, $df = 4$, $p < 0.001$). The occurrence of birds was higher in the stoat

Table 2. Diet composition of stoats and weasels from Denmark as determined from analysis of prey remains in the gastrointestinal tracts. Percentage frequency of occurrence and 95 percentile range confidence intervals (CI) were calculated from 1000 bootstrap estimates.

Taxa	Stoats			Weasels		
	Freq. of occurrence	% freq. of occurrence	95% range CI	Freq. of occurrence	% freq. of occurrence	95% range CI
Rodents	78	76.61	69.16–83.87	106	83.63	77.42–89.68
<i>Apodemus</i> spp.	11	10.68	5.66–16.51	22	17.44	11.61–23.39
<i>Arvicola terrestris</i>	10	9.77	4.44–15.22	3	2.37	0.00–5.07
<i>Clethrionomys glareolus</i>	8	7.77	2.86–13.25	31	24.43	17.78–30.71
<i>Micromys minutus</i>				1	0.78	0.00–2.64
<i>Microtus</i> spp.	34	33.59	25.93–41.94	26	20.40	13.91–26.89
<i>Mus musculus</i>				2	1.65	0.00–4.07
<i>Rattus norvegicus</i>				1	0.78	0.00–2.64
Unident. rodents	15	14.74	8.60–21.43	20	15.62	10.00–21.54
Insectivores	5	4.97	1.06–9.28	12	9.40	4.76–14.81
<i>Erinaceus europaeus</i>	1	0.98	0.00–3.17			
<i>Sorex</i> spp.	4	3.89	0.85–8.26	4	3.20	0.76–6.35
<i>Talpa europaea</i>				8	6.26	2.38–10.26
Other mammals	3	2.90	0.00–6.36	1	0.78	0.00–2.64
<i>Mustela nivalis</i>	2	1.96	0.00–4.76			
<i>Felis catus</i>	1	0.98	0.00–3.17			
<i>Capreolus capreolus</i>				1	0.78	0.00–2.64
Birds	9	8.83	4.08–14.14	3	2.37	0.00–5.07
Passeriformes	7	6.86	2.27–11.70	3	2.37	0.00–5.07
Falconiformes	1	0.98	0.00–3.17			
Anseriformes	1	0.98	0.00–3.17			
Birds eggshell	6	5.69	1.83–10.78			
Other items	1	0.98	0.00–3.17	5	3.84	0.82–7.20
Invertebrates				5	3.84	0.82–7.20
Unidentified	1	0.98	0.00–3.17			
Total examined guts	112			132		
Total prey items	102			127		
Non-empty guts	86			115		
Empty guts	26			17		

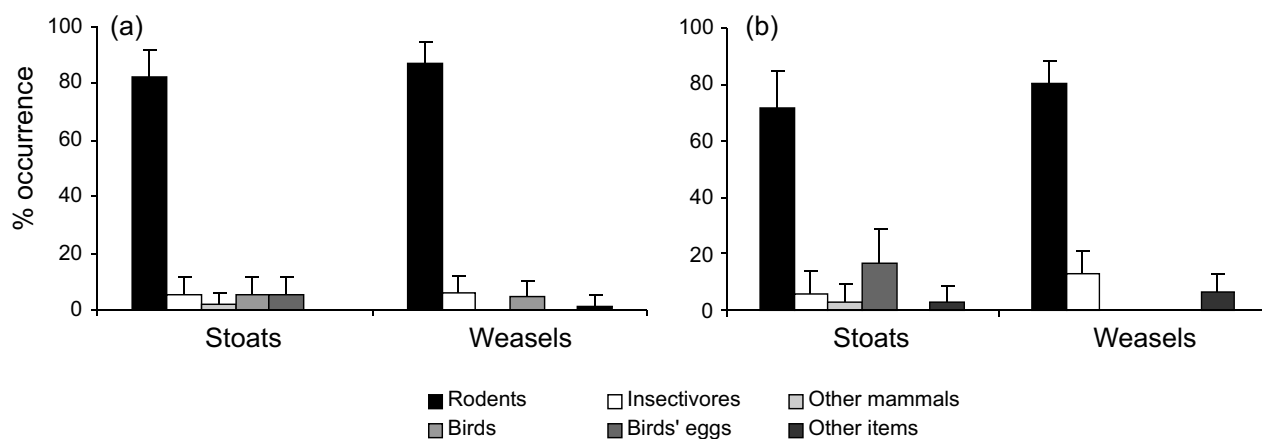


Fig. 1. Seasonal variation of percentage frequency of occurrence of the six major prey groups in the diet of stoats and weasels in Denmark in (a) March–August and (b) September–February. The sexes are combined. Error bars represent the 95 percentile range confidence intervals of 1000 bootstrapped estimates.

Table 3. Bootstrap estimates of Levins' measure for niche breadth of stoats and weasels in Denmark based on the occurrence of the six major prey groups; means and 95 percentile range confidence intervals (CI) calculated from 1000 re-samplings. The sexes are combined for seasonal estimates. n is the number of identified prey remains.

Species	Groups	n	Levins' niche breadth	
			Bootstrap mean	95% range CI
Stoats	All	102	1.67	1.40–1.97
	Males	68	1.72	1.37–2.12
	Females	33	1.59	1.16–2.12
	Spring and Summer	56	1.46	1.18–1.78
	Autumn and Winter	36	1.82	1.37–2.37
Weasels	All	127	1.42	1.27–1.55
	Males	75	1.32	1.13–1.55
	Females	39	1.52	1.24–1.89
	Spring and Summer	61	1.30	1.11–1.54
	Autumn and Winter	60	1.51	1.26–1.79

diet than in the weasel diet during autumn and winter, and weasels ate considerably more insectivores than stoats during autumn and winter (Fig. 1).

The most frequently occurring rodent and insectivore species in the diets of stoats and weasels were *Apodemus* mice, water vole, bank vole, *Microtus* voles, *Sorex* shrews and mole. The overall occurrence of the most important rodents and insectivores differed between stoats and weasels ($\chi^2 = 36.01$, $df = 5$, $p < 0.001$). The difference was also significant when the sexes were considered as morphospecies ($\chi^2 = 102.50$, $df = 15$, $p < 0.001$). Stoats ate more *Microtus* voles and water voles than weasels did. Female stoats ate more water voles and *Apodemus* mice than males did, while males ate more bank voles than females did ($\chi^2 = 19.73$, $df = 4$, $p < 0.001$). The diet of weasels had a higher occurrence of bank voles and moles compared to the diet of stoats. Although female weasels ate moles more frequently than males did, there was no difference in the diet between sexes in weasels ($\chi^2 = 9.25$, $df = 5$, $p = 0.10$). The proportion of females killed in mole traps was not greater than the proportion of females killed by other methods ($\chi^2 = 0.39$, $df = 2$, $p = 0.82$).

Some of the results on prey species and seasonal variations of prey groups must be interpreted with caution however, as sub-sample

sizes of stoats and weasels and occurrences of some prey species were small.

Levins' measure for dietary niche breadth of six major prey groups was slightly larger for all groups of stoats than for weasels (Table 3), but none of the dietary niche breadths indicated notable dietary differences between sexes and species. The diversity of stoat and weasel diets tended to increase from spring and summer to autumn and winter. Dietary niche overlap was high between sexes in stoats (92.9% or Pianka's index: 0.367) and in weasels (90.0% or Pianka's index: 0.494). Overall dietary overlap between stoats and weasels was 85.7% (Pianka's index: 0.423). The dietary overlap was high in spring and summer (92.4% or Pianka's index: 0.524) decreasing in autumn and winter (80.1% or Pianka's index: 0.353).

Table 4. Mean body weight of stoats and weasels from Denmark. All categories differed significantly ($p < 0.001$).

Species	Sex	n	Body weight (g)
			Mean \pm SD
Stoat	Males	62	241 \pm 42
	Females	34	163 \pm 34
Weasel	Males	57	92 \pm 20
	Females	33	53 \pm 16

Body weights of male and female stoats and weasels from Denmark constituted four different categories ($F_{3,182} = 350$, $p < 0.001$, Tukey's test: $p < 0.001$) (Table 4).

Discussion

Frequency of occurrence provides a simple widely used method to describe food habits of stoats and weasels (eg Brugge 1977, Erlinge 1987, McDonald *et al.* 2000). If prey sizes are highly variable diets estimates based on biomass or caloric value of the prey species should also be considered, as the estimates expressed as frequency of occurrence may overestimate the importance of small prey species (Day 1966, Cumberland *et al.* 2001). Considering the biomass of the six most frequently occurring mammalian prey species the importance of water voles and moles increased compared to smaller rodents and insectivores and the overall dietary differences between stoats and weasels increased. Roe deer *Capreolus capreolus*, cat *Felis catus* and hedgehog *Erinaceus europaeus* probably represent opportunistic scavenging of carrion, which are available from road-kills and remains left by hunters.

The major prey group for stoats and weasels were rodents, most of which were voles. Differences in the diets originated in frequencies of secondary prey groups as birds and insectivores. Brown hare *Lepus europaeus* was available as an alternative prey, but no remains from lagomorphs were detected in either stoats or weasels. The larger stoat had more generalised food habits than weasels (King and Moors 1979, King

1989, McDonald 2002). As expected there was a larger niche overlap between sympatric stoats and weasels in Denmark than observed in comparable food studies from areas where rabbits were an important prey species for stoats (Day 1968, Brugge 1977, McDonald *et al.* 2000; Table 5). Dietary studies across the species geographic range illustrate the stoats' adaptable food habits. In southern Sweden water voles and small rodents comprised the primary prey as in Denmark but rabbits were eaten as an alternative prey (Erlinge 1981). In northern Sweden outside the distribution area of rabbits the small stoats almost exclusively ate small voles (Erlinge 1987). Analogous food habits were demonstrated in Switzerland, where stoats ate rabbits in low frequencies only during periods when water vole density was low (Debrot 1981). Martinoli *et al.* (2001) found that stoats frequently ate fruits as a secondary food in Alpine habitats during summer and autumn. The two studies in Great Britain reflect a change in diets between the 1950s in the aftermaths of a crash in rabbit numbers following the myxomatosis and the diets of stoats and weasels the 1990s (Day 1968, McDonald *et al.* 2000). After the rabbit population has recovered the dietary niches of both predators have narrowed as stoats and weasels have specialised on rabbits and small voles, respectively.

The weasel had more specialised food habits. Small voles and *Apodemus* mice were the most important prey species for weasels in Denmark in accordance with other European studies on weasel diet (Day 1968, Tapper 1979, King 1980, Goszczyński 1999, McDonald *et al.* 2000). Insectivores were the second most important prey group, which comprised lagomorphs and birds in

Table 5. Estimates of Levins' measure for dietary niche breadths and dietary overlap for stoat and weasel from European food studies calculated from the occurrence of the six major prey groups.

Country (reference for original study)	Levins' niche breadth		Pianka's index	Percentage overlap
	Stoat	Weasel		
Great Britain (Day 1968)	3.51	2.46	0.096	70.2
The Netherlands (Brugge 1977)	2.51	1.66	0.269	65.0
Great Britain (McDonald <i>et al.</i> 2000)	2.11	1.86	0.145	47.5
Denmark (present study)	1.67	1.42	0.423	85.7

other studies, although shrews also composed a significant proportion of weasels diet in the Netherlands (Brugge 1977). Especially noteworthy was the high occurrence of moles in the weasel diet in the present study. Weasels are often trapped in mole traps and may carry specific mole ectoparasites suggesting that weasels regularly use mole tunnels and nests (King 1989) but consumption of moles has previously only been recorded at very small frequencies.

The results from the present study accord with a general increase in dietary niche breadth increase with increasing body size (McDonald 2002) and a correlation between dietary niche, mean prey size and body size of stoats (King 1991). However, Danish stoats and weasels had similar sizes as specimens from populations at the same latitudes in Sweden where rabbits are available as prey (Erlinge 1975, Erlinge 1987). There was no evidence of resource partitioning according to mean prey size between sexes in either stoats or weasels despite a pronounced sexual size dimorphisms. These results support the hypothesis that resource partitioning between sexes according to prey size should be considered a probably beneficial but secondary effect of the sexual size dimorphism, which has evolved from intrinsic differences in the energetic requirements during reproduction (Moors 1980, Sandell 1989, McDonald 2002).

Closely related species exploiting the same food resources may maintain a stable coexistence in heterogeneous landscapes when both species have a competitive trade-off by different reproductive strategies and capacity, segregation of food resource exploitation, and differential habitat utilization (King and Moors 1979, Bonesi and Macdonald 2004).

Stoat and weasel diets vary according to availability of prey species (Tapper 1979, Erlinge 1981, McDonald *et al.* 2000). Fluctuations in rodent populations in Denmark during the sampling period have not been recorded. Further detailed studies on temporal and spatial variations of food habits and prey selection are needed to characterize the ecological relationship between stoat and weasel populations based on a small food spectrum.

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