Diet of stoats (*Mustela erminea*) in an Alpine habitat: The importance of fruit consumption in summer

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Abstract – The diet of stoat, *Mustela erminea*, in the Italian Alps was studied from May to October 1996 and 1997 through faecal analysis. Scats were collected along twenty transects and near dens within a 10-km^2 study area. In the same area, seasonal variation in the available biomass of different prey types was estimated using capture-mark-recapture (small rodents), pitfall trap grids (insects), and fruit counts. About 60 % of scats ($n = 734$) contained small rodents, indicating that they were the main prey for stoat. However, the frequency of occurrence of fruits in the diet increased significantly in August, after rodent biomass had dropped by more than 50 % in July, but increased again to previous August levels. Fruit consumption decreased in September and October, although available biomass of fruits remained constant. Thus stoat included a large amount of alternative food in their diet when fruits were mature and their availability, and probably their profitability, increased. We were, however, unable to measure absolute consumption of prey. We conclude that primary prey, rodents, is always harvested, suggesting that the costs of harvesting rodents, abundant throughout spring–autumn, are never high. The consumption of alternative prey is independent of its availability, and increases only when relative benefits of harvesting alternative prey (fruits) increases, which is consistent with optimal foraging theory. © 2001 Éditions scientifiques et médicales Elsevier SAS

alternative feeding strategy / diet / food specialist / *Mustela erminea* / trophic ecology

1. INTRODUCTION

Optimal foraging theory states that a predator should choose prey types based on a trade-off between costs and benefits that will give the maximum net benefit to the individual [27]. The profitability of certain prey types might change in time. As long as the most profitable prey is very abundant, the predator should specialise on that prey alone, independent of the availability of the secondary prey type. Only when the energy intake rate of foraging solely on primary prey falls below the profitability of harvesting alternative prey will the diet be expanded (e.g. [13, 28, 33]). Since handling time will have great effects on prey profitability, a decrease in prey numbers (biomass) will increase foraging costs. Other factors involved can be: (i) nutrient quality of different prey types; (ii) risk of the predator being attacked by larger predators; and (iii) increased energy demands, e.g. breeding (lactation in females, increased mobility in males searching for a partner), winter fattening, increased costs of thermoregulation, or migration. Finally, a breeding female might change the spatial pattern of hunting behaviour in order to always stay close to its den, covering its territory in a patchy manner. In this case profitability of primary prey, as a result of local depletion and increased handling time, may decrease rapidly in a given patch close to the den.

The dietary choices of small carnivores, such as the stoat (*Mustela erminea* L., 1758), will depend primarily on the temporal variation of foraging costs [13, 33, 41], which are mainly affected by availability of the primary prey species. Stoats primarily feed on small mammals throughout the year [7, 9, 13]. Even though some authors use the term 'semi-generalist' [26, 36], the results of theirs and other similar studies indicate that the stoat is a 'specialist' predator, feeding mostly on small rodents or on other food resources of animal origin [9, 8, 13]. Moreover, small rodent availability not only determines the presence of small mustelids, but also their activity and spacing behaviour, and

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annual variation in small rodent numbers and biomass is the driving factor causing the fluctuations in weasel and stoat population densities [12, 13, 23, 26, 32, 39].

In contrast with the extreme importance of small rodent biomass, the availability of alternative prey has always been considered of minor importance for stoats. Only few authors recorded fruit presence in stoat diet, and fruits are reported as a poorly utilised food resource, even in summer when fruit availability is at its maximum [9, 25, 38]. In subartic conditions, however, juniper berries formed an important part of the diet during a dramatic small rodent decline in Lapland (Nasimovich, 1949 in [23]), while in temperate habitats, with high densities of songbirds and rabbits, a decline in small rodents caused a home range increase and/or exploitation of the alternative prey species [13, 31].

In Italy, stoats are present only on the alpine ridge, and exclusively above the treeline limit. This study aims to investigate to what extent stoat diet changed seasonally with the temporal availability of small rodents, and to what extent seasonal variation in consumption of small rodents was affected by changes in the availability of alternative prey. Based on optimal foraging theory, we predict that monthly frequency of occurrence of alternative food types, fruits and insects, in the stoat's diet will increase only in those periods when their profitability exceeds the rate of energy intake of foraging solely on primary prey, small rodents. Hence, the consumption of alternative prey will not be closely related to temporal variation in its availability, but will increase when the benefits of harvesting rodents decrease.

2. STUDY AREA

The study area was located in the Adamello-Brenta Natural Park, mid-eastern Alps (N Italy, 46°10' N, 10°45' E). It extends to about 10 km^2, at heights varying from 2 200 to 2 500 m a.s.l. The landscape is a typical alpine habitat, with a great variety of glacial morphologies such as moraines and consolidated screes. Several streams feed Lake Cornisello, a small basin (0.07 km^2) located approximately in the centre of the study area. The most common habitats are alpine grassland and screes studded with dwarf shrubs of limited cover, mostly composed of *Juniperus communis*, *Vaccinium* sp., *Rhododendron ferrugineum* and *Alnus viridis*.

3. MATERIALS AND METHODS

We carried out field work between May and October in 1996 and 1997. During both summers, we placed 52 mustelid live traps ($17 \times 17 \times 90$ cm, built in plywood), that were activated monthly for a total of seven trapping days, following a 3-d pre-baiting period. These trapping methods, allowed to ascertain the absence of weasel, *Mustela nivalis* [22, 24]. Each trapped stoat was sedated (Inoketamm 500, Virbac; 0.4 mL intramuscular), sexed and marked by ear clipping (Research permit by Trento Province No. 125-1995 after approval by the National Wildlife Institute). It was weighed to the nearest 5 g using a Pesola spring balance (500 g) and measured (body length and tail length) to the nearest mm using 1/10-mm calipers. The animals were classified as juveniles or adults on the basis of body mass and size.

Stoat scats were collected along twenty randomly chosen transects (1 km long and 4 m wide), covering the entire study area for a total length of about 20 km. We checked each transect at approximately 2-week intervals. During the first visit all scats were removed, so that, at later visits, only fresh scats were collected for analyses. The absence of weasel from the study area was indicated by the fact that no weasels were caught in the life traps. Moreover, scats being found near burrows used by stoats, clearly shows that the samples we analysed consisted of stoat scats. Stoat scats were easily separated from those of marten due to their smaller dimensions (scat length stoat 25–50 mm; marten > 70 mm). Diet analysis was carried out according to the method described by Kruuk and Parish [29]. Relative frequency of food item (a) was calculated by dividing the number of scats containing item a by total number of scats collected. Volume of food item (a) was defined as the average volume of item a (sum of bulk-scores containing item a divided by the total number of scats as described by Kruuk and Parish [29]). Undigested remains found in stoat faecal samples were identified by comparison with reference collections made with specimens collected inside the study area. We relied on comparison with reference atlases [6, 10, 40] for mammal hair identification, considering scale pattern and observing the composition and structure of the medulla in cross-section. Fruit consumption was determined based on the remains of undigested seeds and parts of the fruit cuticle appearing in the scats.

Food availability estimates were carried out from May to October in the same area where faeces were collected. Small mammal densities were estimated by capture-mark-recapture sessions on three trapping grids [1, 2], distant by 0.8–1 km from one another. Each grid consisted of sixteen Sherman live-traps, arranged in a 4×4 square, with 4 m spacing between

traps. Grid size was 545 m², calculated by adding a 6-m wide grid margin, and supposing circular areas of influence for each corner trap. Each month, the traps were pre-baited for two nights and then activated for three nights. All trapped rodents were individually marked, sexed, aged (juveniles or adults) and body mass was taken to the nearest 0.5 g. Insect availability was estimated using three pitfall trap grids. Each grid consisted of nine pitfalls, of 6 cm diameter, arranged in a 3×3 design with 2-m spacing (64 m² per grid), activated for a week each month. Monthly counts of insects on all three grids (total area sampled 192 m²) were converted to densities·ha⁻¹. Fruit presence of *Juniperus communis* and *Vaccinium uliginosum* was evaluated monthly along twelve transects (50 by 4 m), counting both ripe fruits on the ground and fruits still on the plants. Bird densities were not estimated.

We converted prey density estimates into available biomass to allow comparisons of availability between the different prey types. Rodent, insect and fruit densities were converted into available biomass using the average biomass for each food item, calculated from the samples we collected on the study area. Mean biomass per prey item was for: *Clethrionomys glareolus* 25.6 g (SD 5.6, $n = 102$); *Chionomys nivalis* 34.1 g (SD 12.0, $n = 49$); *Microtus arvalis* 20.9 g (SD 7.8, $n = 23$); *Apodemus* sp. 25.9 g (SD 7.7, $n = 12$); juniper berries 0.17 g (SD 0.02, $n = 376$); bilberries 0.17 g (SD 0.01, $n = 284$); insects (Coleoptera) 0.12 g (SD 0.03, $n = 341$). Energy value of rodents and fruits was determined by calorimetry. Fresh weight was determined, samples were dehydrated under vacuum at –50 °C for 72 h and weighed dry. Dry samples were ground in a blender and reduced to a fine powder in a mortar. For each sample, one gram of powder was burned in a bomb calorimeter (Berthelot-Mahler model CBM, Vittadini Instruments, Milan) to obtain an estimate of weight specific energy value (in kJ·g⁻¹). Energy value of prey were estimated by multiplying the energy value per gram of dry mass with average dry mass. Our estimates of weight specific energy content of prey were comparable with those of other small mammal species reported elsewhere [33]. Energy value of snow vole was extrapolated from its mean fresh body mass, using the average percentage dry mass and average weight specific energy value of bank vole and wood mice.

Niche width of the monthly diet of stoats was calculated using the standardised Simpson's index $Bs = (B - 1)(n - 1)^{-1}$, where n is the number of prey classes used in a single month, and B the $(p_i^2)^{-1}$, with p_i the proportion of ith prey class in the diet [9].

Selectivity between mammals and fruits was measured using Ivlev's electivity index [18]. We used the frequency of occurrence of different prey types, excluding birds, as a measure of monthly proportions of prey utilised, and our monthly estimates of mammal, insect, and fruit biomass to calculate the proportions of different prey types available.

We used both literature data, and radiotracking to estimate time spent active per day, and time spent foraging per day by stoats. In July and August, we radiotracked three individual stoats (two males, one female) for 6-h periods, taking a fix every 15 min. Each fix was classified as active or non-active, based on distance moved, and on signal intensity and frequency [12, 34, 42]. Our data (unpubl.) agreed with data from southern Sweden, where stoats were active from 19 % (autumn) to 34 % (spring) of the circadian cycle, or for about 4.5 to 8 h [12, 34, 42]. In weasels and stoats, locomotion is closely linked to hunting and feeding [12, 34, 41, 42]. In spring-summer, 75 % of active time was spent foraging, thus hunting for prey, and 25 % on other activities (long-distance movements, territory patrolling, food consumption in the burrow, grooming) [12]. Therefore we estimated that our stoats spent about 6 h·d⁻¹ foraging in spring-summer, the period we monitored food choice.

Cluster analysis of distance between consecutive active fixes ($n = 417$) of radiotracked stoats revealed three distinct classes, related to three types of foraging/travelling activity. (1) Active stoats found at two or more consecutive fixes nearly at the same location (< 20 m between one fix and the next), associated with foraging for fruits; (2) short distance movements within a 1-ha patch, associated with foraging for small mammal prey; and (3) fast, long distance movements (> 300 m) when stoats travelled from one patch to another (ANOVA of three clusters: F = 1 486, df = 2,414, $P < 0.0001$, $R^2 = 0.88$).

4. RESULTS

Only seven stoats were caught and marked during the study period (six animals in 1996, one in 1997), two females, and five males (*table I*). We caught no weasels or martens. Thus, only few stoats occurred in the study area (minimum density in summer 1996 of 0.6 animals·km⁻², *table I*), despite high densities of microtine rodents (*figure 1*).

We had 65 series of 15-min active fixes that could be used to calculate the average time spent in each type of behaviour. Another four series of consecutive fixes with 0-m distance between one fix and the next

Table I. Number of stoats captured and marked during the study period. Stoats No. 5 and 8 escaped during handling. For each anaesthetised stoat, weight, body length and tail length were recorded. Only stoat No. 2 was recaptured twice on a single day (10 July 1996).

No.	Date	Age class	Sex	Weight (g)	Body length (mm)	Tail length (mm)
1	9 July 1996	Young	Female	70	165	59.0
2	9 July 1996	Adult	Male	156	243	68.0
3	11 July 1996	Young	Male	75	190	61.2
4	12 July 1996	Young	Male	65	187	56.0
5	13 July 1996	–	–	–	–	–
6	14 July 1996	Adult	Male	155	240	82.6
7	30 August 1996	Young	Male	75	160	69.7
8	29 September 1997	Young	–	–	–	–
9	30 September 1997	Adult	Female	85	170	66.7

were clearly related to resting or sleeping in a den (mean duration $\pm$ SD = 173 $\pm$ 61 min, range 120–255 min). Bouts of long distance movements lasted on average 31 min ($n = 11$, SD = 24 min). Duration of active bouts associated with foraging on fruits was on average 55 min ($n = 37$, SD = 20 min), while stoats hunting small rodents spent between 45 and 240 min active ($n = 17$, mean $\pm$ SD = 118 $\pm$ 58 min).
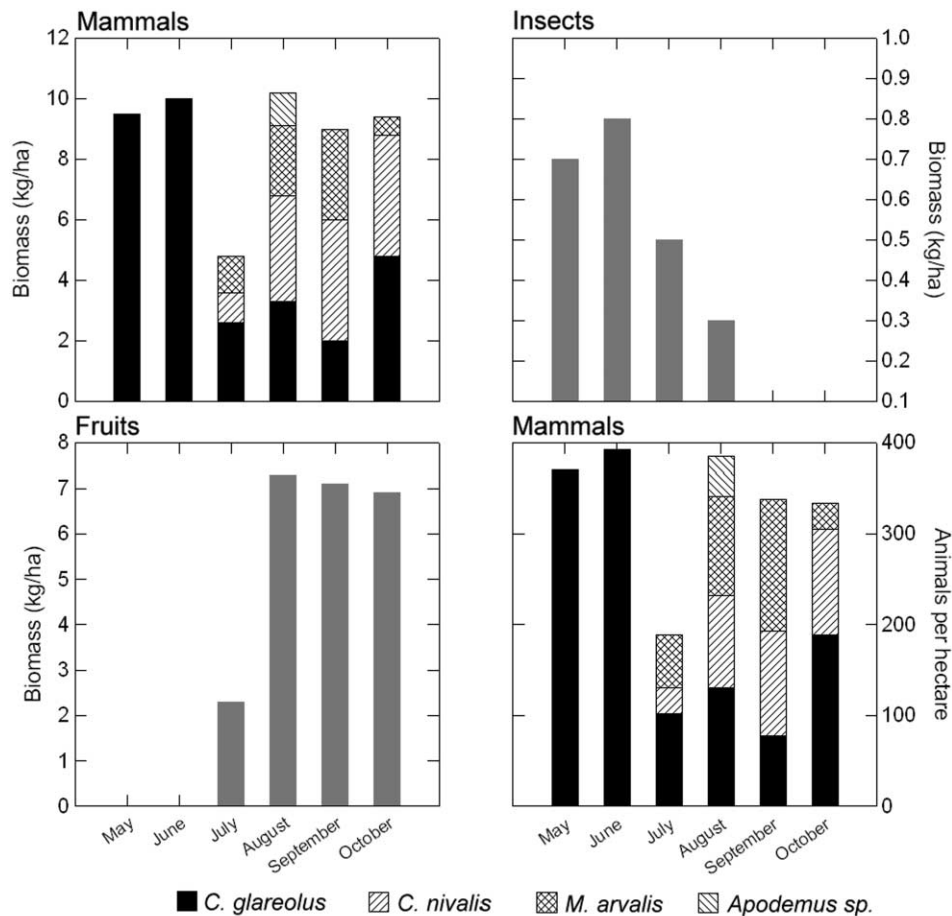

Figure 1. Seasonal variation in the availability of different food types of alpine stoat in the study area. Biomass (kg·ha^{-1}) of mammals, insects and fruits, and densities of different rodents species.
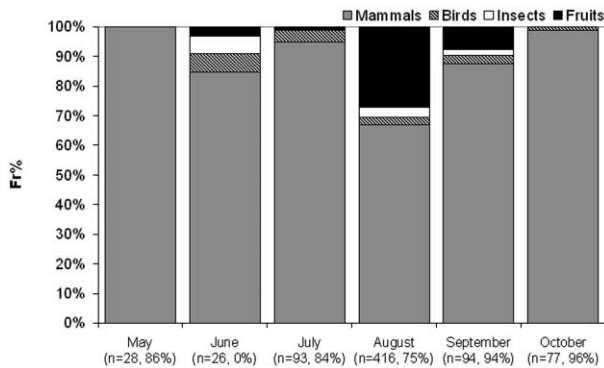
Figure 2. Seasonal variation of the main food types in stoat scats expressed as frequency of occurrence on the total number of scats collected per month (Fr%). Number of stoat scats recorded per month with % found near dens between parentheses.

Scat collection yielded a total of 734 samples, 486 for 1996 and 248 for 1997. In the same period, we collected only eight scats attributed to *Martes* sp. Most stoat scats (79 %) were found in latrines near burrows (*figure 2*), counting five to ten scats for each latrine. One out of seven scats of captured stoats found inside traps contained only *Juniperus communis* fruits.

We tested for a year effect (1996 vs. 1997) on the monthly frequencies (June to October) of: (1) food items availability; and (2) food items used, with a two sample Kolmogorov-Smirnov test [37]. None of the frequency distributions compared were significantly different (Kolmogorov-Smirnov test $n_1 = n_2 = 5$ for all tests; availability: mammals $D = 0.75$, $P = 0.12$; fruits $D = 0.25$, $P = 0.92$; insects $D = 0.52$, $P = 0.50$; use: mammals $D = 0.40$, $P = 0.82$; fruits $D = 0.66$, $P = 0.22$; insects $D = 0.50$, $P = 0.50$), allowing us to pool data over both years.

Food availability (biomass·m^{-2}) for the three principal food categories fluctuated seasonally (*figure 1*). A sharp decline in mammal density and biomass in July was followed by a marked increase in August (*figure 1*). Fruit biomass was high in August, September and October, remaining almost constant during this period (*figure 1*).

Mammals accounted for over 75 % (78.2 % in frequency and 80.7 % in volume) of the diet, followed by fruit (between 10 and 20 %, *table II*). Mammals were represented almost exclusively by rodents, except for *Sorex* sp. and alpine chamois (*Rupicapra rupicapra* L., 1758), the latter consumed occasionally as carrion. The only fruits eaten were juniper berries and bilberries, accounting for about 16 % of the trophic spectrum, both in frequency and volume (*table*

II). The relative frequency of occurrence of food items (Fr%, *figure 2*) varied significantly through the summer season ($G_{adj} = 135.3$, df = 15, $P < 0.001$, [37]). The relative frequency of occurrence of fruits in the diet increased in August and decreased sharply in September and October (*figure 2*), despite their available biomass remaining nearly constant during this period (*figure 1*). Consumption of small rodents was high in all months (*figure 2*). However, frequency of occurrence of mammals as prey decreased in August, about 1 month after rodent densities, and hence also biomass had decreased by > 50 % (*figures 1, 2*). Consequently, niche width changed markedly with month, it was very small in July, September and October (Bs = 0.04, 0.10 and 0.01, respectively), somewhat lager in June (Bs = 0.19), and largest in August (Bs = 0.30) when important amounts of fruits were eaten. Pearson's correlation coefficients between monthly frequencies of main food categories were significant only between fruits and mammals ($r = -0.94$, $n = 6$, $P = 0.005$; all other $P > 0.1$). Stoats used insects less than expected in all months (Ivlev's index E = –1 in July and October; E = –0.16 and –0.1 in August and September, respectively). Fruits were also used less than expected from July (E = –0.93) to September-October (E = –0.72 and –1, respectively). Only in August was the electivity index of fruits less strongly pronounced, although they were still used less than expected based on their relative availability

Table II. Food categories identified in stoat diet, represented as grand totals both in frequency over the total number of scats (Fr%, $n = 734$) and as estimated mean volume (Vm%).

Item	Fr%	Vm%
Mammals	78.22	80.74
Rupicapra rupicapra	0.12	0.02
Undetermined rodents	4.46	4.85
Microtus sp.	17.08	17.46
M. arvalis	2.85	3.11
Chionomys nivalis	35.89	38.41
Clethrionomys glareolus	5.32	5.74
Apodemus sp.	1.11	1.23
Marmota marmota	0.37	0.41
Eliomys quercinus	10.77	9.23
Sorex sp.	0.25	0.27
Birds	2.60	2.31
Insects	2.48	0.89
Fruits	16.71	16.06
Juniperus communis	12.00	11.95
Vaccinium uliginosum	4.71	4.11

Table III. Fresh weight (g), dry weight (g) and weight specific energy value (kJ·g^{-1} dry weight) of different food types of alpine stoats. Total energy intake after consumption of a single prey item and minimum number of prey items that need to be consumed to cover daily energy requirements are calculated.

Species	Fresh weight	Dry weight	Energy value	Energy/prey	Food items per day	
	(g)	(g)	(kJ·g^{-1})	(kJ)	Female	Male
Bank vole	25.60	9.78	23.5	229.8	1–2	2–3
Mice	25.90	10.06	23.3	234.4	1–2	2–3
Snow vole*	34.10	12.62	23.4	295.3	1–1.5	1.5–3
Juniper berries	0.17	0.16	23.2	3.7	73–124	131–226
Bilberries	0.17	0.03	18.3	0.5	540–918	972–1 674

* Extrapolated values.

(Ivlev's index E = –0.21; see also *figure 2*). For mammals, Ivlev's index was positive in all months (E ranging from 0.11 in August to 0.27 in October), indicating that they were the primary prey throughout spring–autumn (*figure 2*). The lowest value in August, suggesting a less pronounced selection for rodents, agreed with the largest index of food niche width in this month.

The majority of scats contained a single prey item (90.6 %), and some contained two different prey items (8.9 %), but very rarely three or four different items were found in a single scat (0.5 %). Since stoats can only eat about 10 g per meal [7], scats probably contain, in most cases, the remains of a single meal. Therefore, we analysed scat contents in detail on a monthly basis.

Interestingly, from May to July, 138 out of 147 scats (94 %) contained a single prey item, in majority (90 %) mammal remains. Only seven scats (5 %) had two prey items, six containing only mammals, one mammal and bird remains. In August, 374 out of 416 scats (90 %) contained a single prey item, and 40 (9.5 %) two prey items. In contrast with the previous months, only 274 (66 %) of single prey scats had mammal remains, and 88 (21 %) had only fruit remains. Thus in August, several stoat meals consisted of only juniper berries and bilberries. Moreover, in August, 17 out of 40 scats (43 %) with two prey items contained mammals, while 24 (60 %) contained fruits. This suggests that in August, fruits were frequently eaten shortly before or after consumption of a small meal, probably the remains of a cached rodent prey, to increase meal size and energy intake. In September-October, still 153 out of 171 scats (89 %) had a single food item, but 146 of these (85 %) contained only mammal remains, and only four (2 %) fruit remains. Of the eighteen scats with two prey items, 15 (9 %)

had only mammal remains and three (2 %) mammals and fruits. Thus most meals that consisted of more than one food type were composed of two different mammal prey.

We estimated daily energy consumption of stoats in two ways.

– Daily food intake of captive weasels (*M. nivalis*) at a free-access diet composed of rodents, varied from 0.35 to 0.6 g·g^{-1}·d^{-1} [17, 30]. Using mean body mass of adult male (155 g, *table I*) and adult female stoats in our study area (85 g, *table I*), we calculated an average daily food intake ranging between 30 and 51 g·d^{-1} for female stoats and between 54 and 93 g·d^{-1} for male stoats. This gave estimates of daily energy intake (*table III*) of 270 to 459 kJ·d^{-1} for females and 486 to 837 kJ·d^{-1} for males.

– Basal metabolic rate (BMR) estimates of female and male stoats were 3.91 and 5.91 kJ·h^{-1}, respectively [3], which extrapolated to 94 and 142 kJ·d^{-1}. Multiplying the BMR estimate by two, we obtained estimates of mean daily metabolic rate (MDMR) of 188 kJ for a female and 284 kJ for a male stoat. Hence, the MDMR estimate was only 70 (females) and 58 % (males) of the minimum values of estimates based on food consumption.

We therefore considered minimum estimates of energy intake based on daily food intake as the most realistic ones. In this case, female stoats needed to consume a single snow vole per day, or, when feeding on smaller rodents such as bank vole or mice (230–234 kJ per prey, *table III*), integrate their daily food consumption with fruits or insects. Male stoats had to eat two rodents per day and consume the remains of previously killed, cached prey, extra fruits or insects when bank voles or mice were eaten; or kill and consume a single snow vole and integrate their

diet with cached prey remains, or large amounts of fruits and/or insects (*table III*).

5. DISCUSSION

5.1. Stoat numbers and activity

During spring and summer, male stoats have large territories that can overlap strongly [11]. Female stoats, in contrast, generally use smaller territories and show a higher degree of intrasexual territoriality defending exclusive territories against other females [14, 34]. The sexual differences in spacing pattern can explain the higher number of male stoats caught during our study. Moreover, it has been shown [33] that residence time is significantly higher in females than in males and that stoat populations are composed mostly of visiting males and resident females. This was confirmed by the low recapture rate of male stoats (1 out of 5), indicating a high male stoat turnover rate, and by the movements of radiotracked males. This spacing pattern and our trapping data suggest that the collected scats belonged to at least nine different stoats that temporarily used the study area. Therefore the scats collected were considered a representative sample for analysis of the diet of the local stoat population.

Activity of radiotagged stoats consisted of active bouts of intensive prey searching in a small patch (foraging), and consuming (part of) the caught prey, interrupted by fast long distance movements to other patches or to a den. Mean length of these foraging bouts, searching for rodents, was about 2 h (118 min). Considering an average meal size of 10 g rodents, this corresponded to an energy intake of 90 kJ, thus a rate of energy intake of 45 kJ·h^{-1}. The remains of such a relatively large prey are probably brought to the den and consumed, after a resting phase, in a short period of time. In the latter case, rate of energy intake of consumption of the cached prey remains must be high, but impossible to estimate in wild stoats. When foraging on juniper berries and bilberries in late July-August, activity bouts of stoats lasted about 55 min. If we presume that stoats also consumed 10 g berries in a single meal (about sixty berries), equivalent to 165 kJ, rate of energy intake averaged at 180 kJ·h^{-1}. We did not apply a correction for the assimilation efficiency of different food types (metabolisable energy, see [33]), since we found no data on assimilation efficiency of fruits. Although we were unable to calculate foraging costs, they must have been lower for foraging on fruits than foraging on mammals, since stoats were more mobile, and thus consumed more energy, in the latter case. Therefore, our estimates of rate of energy intake in August suggest that foraging on fruits, especially to integrate the daily diet after capture of a rodent prey, is more profitable than continuing to search for other rodent prey and, probably, leaves more time available for behaviour related to reproductive activity of (male) stoats.

5.2. Prey availability and selection

The feeding habits of alpine stoats were similar to those determined for central and northern European stoat populations. In fact a strong dependence on voles (in our case snow vole *Chionomys nivalis*, bank vole, *Clethrionomys glareolus*, and *Microtus* sp.) was ascertained. Monthly estimates of vole densities showed that these small rodents were a predictable resource, and their constantly high frequency of occurrence in the diet indicated that they could be considered as the stoat's primary food resource (see *figure 1*). The main difference in the diet of alpine stoat compared to diet composition monitored in other studies was the remarkably high fruit consumption: 21 % of the scats found in August contained only fruit remains, and in 60 % of scats with more than one food type there were fruit remains, indicating a non-accidental occurrence of fruit in the diet. Many scats from late July-August undoubtedly belonged to male stoats, that during this period engaged in mate searching and mating behaviour. Because of low female densities, adult males were forced to cover large distances in search of a potential partner to mate with (Chiarenzi et al., unpubl. data). Thus, energy demands of males are likely to be higher in August than in other months and the profitability of alternative food items, with low foraging costs, will increase which could explain the frequent consumption of fruits.

The use of alternative food sources is a typical characteristic of generalist carnivores. In foxes (*Vulpes vulpes*), juniper berries are quite a substantial food resource, requiring low searching and handling times, but characterised by a low protein content [4, 5]. Moreover, the decrease in staple resource availability causes a shift in the diet towards a higher occurrence of alternative food items: for instance, when there is a decrease of water vole (*Arvicola terrestris*) populations, foxes increase fruit consumption [15]. A similar pattern has also been reported for the stone marten (*Martes foina*) with variation in the diet related to changes in small mammal availability [16]. In northern Europe and New Zealand, stoats shifted diet from small rodents to birds and lagomorphs [13, 25] when small mammals became rare. Remarkably, although rock ptarmigan, *Lagopus mutus*, and several species of small passerines were present in the study area, there was no shift of prey choice by stoats towards birds in any season (< 3 % frequency of occurrence, *table II*). Moreover, rock ptarmigan was never found in scats,

although in the nearby Stelvio National Park, stoat predation on brooding hens and eggs was documented [35]. These observations are consistent with optimal foraging theory [27]. If this mechanism of diet selection is also valid in the alpine stoat population we studied, we predict that consumption of the alternative prey, fruit, should increase when its profitability is high.

Rodent biomass in the study area decreased by more than 50 % from June to July, but fruit consumption increased only from late July-August onwards. Thus the diet of stoats indicated that animals did not respond to the decrease in estimated small rodent biomass by shifting diet immediately. They only increased fruit consumption when fruits were fully mature (end July-August). Moreover, in September and October, fruits were still abundant, but dried-out, and thus of little use to stoats. In this case, fruit abundance is constant through time but fruit availability as a palatable resource, thus its profitability, is high only during late July and August. Moreover, although total biomass of small rodents sharply decreased in July, densities and biomass of snow vole and *Microtus* increased. Hence, stoats probably shifted hunting effort concentrating on vole species other than bank voles and delayed a more drastic shift towards berries only when the latter were fully mature. In fact, compared with fruits, small mammals are an 'expensive' food source, their capture requiring a great effort by the predator (high costs) because small mammals may adopt anti-predatory strategies in addition to fleeing, such as disappearing amongst the vegetation and staying immobile, climbing or avoiding entering areas recently visited by a predator [19, 20].

5.3. Reliability of estimates of different prey species

The interpretation of our results strongly depends on the reliability of the estimates of monthly variation in the availability of total small rodent biomass, and of available biomass (densities) of the different vole species (see *figure 1*). We recognise that rodent trapping grids were small, increasing the possibility of having biased estimates of microtine densities, over-estimating real densities due to baited traps attracting also animals living off the grids [17, 21]. However, this bias should be persistent through time, and have no effect on monthly variation in estimated rodent biomass. We therefore feel that the seasonal changes in microtine biomass we measured reflected real changes in prey availability for the local stoat population. Interestingly, not only microtine biomass changed with time, but also the relative importance of different species. We only caught bank voles in May and June and started trapping the other species from July

onwards. This might have been caused by trapping bias with bank voles excluding snow voles and *Microtus* from traps. However, we are convinced this was not the case in our study for three reasons. First, snow voles are the largest species. Hence it seems unlikely it was excluded from entering baited traps by the smaller bank vole in May and June, even if the latter was abundant in this period. Second, *Microtus*, the smallest of the vole species, might have been excluded by bank voles through interspecific competition from baited traps in spring (May-June). However, high trapping success of *Microtus* during the rest of summer (July–October) despite relatively high bank vole densities (*figure 1*) makes it seem unlikely. Third, trap occupancy on our grids never exceeded 25 % (range monthly trapping success expressed as % captures on total number of trap days 5.8–21.3 %), suggesting that even when interspecific competition for traps would have been important, sufficient 'empty' traps remained for snow voles and *Microtus* to be captured also in May and June.

In conclusion, stoats seemed to show an unusual feeding strategy in our study area: although small mammal density was constant over the observed period (except for July), the consumption of this prey category decreased in favour of a higher fruit intake in August. It is our opinion that in this case, the exploitation of an alternative resource was independent of available rodent biomass but related to an increase in the profitability (maturing fruits) of the alternative 'prey'. Thus, alpine stoats seemed to behave as predicted by the optimal foraging theory.

REFERENCES

[1] Burnham K.P., Overton W.S., Estimation of the size of a closed population when capture probabilities vary among animals, Biometrika 65 (1978) 625–633.

[2] Burnham K.P., Overton W.S., Robust estimation of population size when capture probabilities vary among animals, Ecology 60 (1979) 927–936.

[3] Casey T.M., Casey K.K., Thermoregulation of arctic weasel, Physiol. Zool. 52 (1979) 153–164.

[4] Cavallini P., Lovari S., Environmental factors influencing the use of habitat in the red fox, *Vulpes vulpes*, J. Zool. (Lond.) 223 (1991) 323–339.

[5] Cavani C., Qualità della dieta della volpe (*Vulpes vulpes*) in un'area costiera mediterranea (Italia centrale), Hystrix, It. J. Mammal. 3 (1991) 63.

[6] Day M.G., Identification of hair and feather remains in the gut and faeces of stoats and weasels, J. Zool. (Lond.) 148 (1966) 201–217.

[7] Day M.G., Food habits of British stoat (*Mustela erminea*) and weasels (*Mustela nivalis*), J. Zool. (Lond.) 155 (1968) 485–497.

[8] Debrot S., Fluctuation de populations chez l'hermine (*Mustela erminea* L.), Mammalia 47 (1983) 323–332.

[9] Debrot S., Dynamique du renouvellement et structure d'age d'une population d'hermines (*Mustela erminea*), Terre Vie 39 (1984) 77–88.

[10] Debrot S., Fivaz G., Mermod C., Weber J.M., Atlas des poils de Mammiféres d'Europe, Institut de Zoologie de l'Université de Neuchatel Press, Neuchatel, 1982.

[11] Erlinge S., Spacing strategy in stoat *Mustela erminea*, Oikos 28 (1977) 32–42.

[12] Erlinge S., Movements and daily activity patterns of radiotracked male stoats, *Mustela erminea*, in: MacDonald D.W. (Ed.), A Handbook of Biotelemetry and Radiotracking, Pergamon Press, Oxford, 1980, pp. 703–710.

[13] Erlinge S., Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden, Oikos 36 (1981) 303–315.

[14] Erlinge S., Sandell M., Seasonal changes in the social organization of male stoats, *Mustela erminea*: an effect of shifts between two decisive resources, Oikos 47 (1986) 57–62.

[15] Ferrari N., Weber J.M., Influence of the abundance of food resources on feeding habits of the red fox, *Vulpes vulpes*, in western Switzerland, J. Zool. (Lond.) 236 (1995) 117–129.

[16] Genovesi P., Secchi M., Boitani L., Diet of stone martens: an example of ecological flexibility, J. Zool. (Lond.) 238 (1996) 545–555.

[17] Gillingham B.J., Meal size and feeding rate in the least weasel (*Mustela nivalis*), J. Mammal. 65 (1984) 517–519.

[18] Ivlev V.S., Experimental Ecology of the Feeding of Fishes, Yale University Press, New Haven, 1961.

[19] Jedrzejewski B., Jedrzejewski W., Antipredatory behaviour of bank voles and prey choise of weasels – enclosure experiments, Ann. Zool. Fenn. 27 (1990) 321–328.

[20] Jedrzejewski W., Jedrzejewska B., McNeish E., Hunting success of the weasel *Mustela nivalis* and escape tactics of forest rodents in Bialowieza National Park, Acta Theriol. 37 (1992) 319–328.

[21] Jedrzejewski W., Jedrzejewska B., Szymura L., Weasel population response, home range and predation on rodents in a deciduous forest in Poland, Ecology 76 (1995) 179–195.

[22] King C.M., A system for trapping and handling live weasels in field, J. Zool. (Lond.) 171 (1973) 458–464.

[23] King C.M., The relationships between beech (*Notophagus* sp. Seedfall and populations of mice (*Mus musculus*) and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forest, J. Anim. Ecol. 52 (1983) 141–166.

[24] King C.M., Edgar R.L., Techniques for trapping and tracking stoats (*M. erminea*); a review and a new system, N. Z. J. Zool. 4 (1977) 193–212.

[25] King C.M., Moors P.J., On co-existence, foraging strategy and biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain, Oecologia 39 (1979) 129–150.

[26] Korpimaki E., Norrdahl K., Rinta Jaskari T., Responses of stoats and least weasel to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? Oecologia 88 (1991) 552–561.

[27] Krebs J.R., Davies N.B., An Introduction to Behavioural Ecology, 3rd ed., Blackwell Scientific Publication, London, 1993.

[28] Krebs J.R., Erichsen J.T., Webber M.I., Charnov E.L., Optimal prey selection in the great tit, *Parus major*, Anim. Behav. 25 (1977) 30–38.

[29] Kruuk H., Parish T., Feeding specialization of the European Badger (*Meles meles*) in Scotland, J. Anim. Ecol. 50 (1981) 773–788.

[30] Moors P.J., Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (*Mustela nivalis* L.), Oecologia 27 (1977) 185–202.

[31] Mulder J.L., The stoat, *Mustela erminea*, in the Dutch dune region, its local extinction and a possible cause: the arrival of the fox, *Vulpes vulpes*, Lutra 33 (1990) 1–21.

[32] Poole K.G., Graf R.P., Winter diet of marten during a snowshoe hare decline, Can. J. Zool. 74 (1996) 456–466.

[33] Raymond M., Robitaille J.F., Lauzon P., Vaudry R., Prey-dependent profitability of foraging behaviour of male and female ermine, *Mustela erminea*, Oikos 58 (1990) 323–328.

[34] Sandell M., Movement patterns of male stoats *Mustela erminea* during the mating season differences in relation to social status, Oikos 47 (1986) 63–70.

[35] Scherini G.C., Tosi G., Ecologia e gestione faunistico-venatoria della Pernice bianca, Technical report, 1997.

[36] Sittler B., Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North East Greenland: preliminary results from a long-term study, Ann. Zool. Fenn. 32 (1995) 79–92.

[37] Sokal R.R., Rohlf F.J., Biometry, 3rd ed., W.H. Freeman & Co., New York, 1995.

[38] Tapper S.C., The diet of weasels, *Mustela nivalis* and stoats, *Mustela erminea* during early summer, in relation to predation on game birds, J. Zool. (Lond.) 179 (1976) 219–224.

[39] Tapper S.C., The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland, J. Anim. Ecol. 48 (1979) 603–617.

[40] Teerink B.J., Hair of West-European Mammals. Atlas and Identification Key, Cambridge University Press, Cambridge, 1991.

[41] Zielinski W.J., The influence of daily variation in foraging cost on the activity of small carnivores, Anim. Behav. 36 (1988) 239–249.

[42] Zielinski W.J., Weasels and martens - carnivores in northern latitudes, in: Halle S., Stenseth N.C. (Eds.), Activity Patterns in Small Mammals: An Ecological Approach, Ecological Studies, 141, Springer-Verlag, Berlin, 2000, pp. 95–118.