Seasonal Surplus Killing as Hunting Strategy of the Weasel Mustela nivalis — Test of a Hypothesis

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This paper questions the common explanation of surplus killing by small mustelids as an incidental response to superabundance of prey. Alternatively, we propose that surplus hunting in weasels is a regular seasonal (winter) strategy, a mean of: (1) balancing the cold-induced increase of energy need, (2) compensating the concurrent restriction in hunting activity, (3) constantly supplying a "buffer" cache against unpredictable winter conditions. We tested this prediction in seminatural conditions in nineteen experiments performed over three years with 8 nonreproductive weasels *Mustela nivalis* Linnaeus, 1766 and very high densities of rodents, mainly the bank voles *Clethrionomys glareolus* (Schreber, 1780). Each experiment lasted from 6 to 25 days. Within the temperature range from 20.4°C (in summer) to −7.3°C (in winter) the mean percentage of days on which the weasels hunted during each experiment decreased from 93 to 62%. The total daily consumption increased only slightly. In summer and autumn the daily kill rate oscillated around the daily energy needs. In late autumn and winter it exeeded daily energy needs, and vast storages of prey accumulated in weasels' nests. On days with the mean daily temperature above 5°C the weasels killed on average 1.8 voles per day (SD 1.3, range 0—5. Days with the temperature from 5°C to −5°C were the days when the most extensive surplus killing occurred. The kill rate was then 2.78 voles per day per weasel (SD 3.0, range 0—12). On frosty days (mean temperature below −5°C) the weasels drastically restricted their hunting activity (kill rate 0.57 voles per day, SD 1.1, range 0—3) and relied on previously stored food. When prey was constantly abundant the weasels used the caches very extensively, eating only parts of each prey, starting with the newly caught ones. In periods of simulated food shortage, the weasels could survive many days by relying exclusively on previously cached food. We concluded that surplus killing is a behaviour characteristic only of cold weather, and could not be stimulated in warm seasons even when prey were superabundant. The clear seasonal pattern and the great survival value of this behaviour in winter suggest that it is not a behavioural aberration but a genetically-based adaptation to severe and unpredictable winter conditions in the northern temperate zone.

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1. INTRODUCTION

Evidences of vastly excessive killings by different predators has recently intrigued ecologists, who have been used to think in terms of prudent predation. The seemingly wasteful behaviour, labelled "surplus

killing" was first interpreted as occasional malfunctions of killing instinct stimulated by an unusual superabundance of prey (Kruuk, 1972; Curio, 1976).

Lately, Oksanen (1983) and Oksanen, Oksanen & Fretwell (1985) have proposed a single explanation for both surplus killing and food caching, which are commonly observed in all small mammalian and avian predators. According to their model, surplus hunting is a deliberate strategy developed by the smallest, non-territorial members of a predator guild under the competitive pressure of larger, aggresive predators. Surplus killing is a way of gaining the maximum possible share of unpredictable or indefensible resources. Oksanen *et al.* (1985) assume that small predators kill in excess and cache the surplus of food during 'leisure' time and they predict that this behaviour is more likely under conditions of high abundance of prey and in cold or dry climates. Caches may be essential for survival when the time of shortage starts, but Oksanen *et al.* (1985) suppose that the cached food is mainly wasted. However, the basic assumption of their model, *i.e.* that surplus hunting and territoriality are mutually exclusive activities, does not fully apply to small mustelids, which are strictly territorial whenever prey (rodents) densities are adequate (Erlinge, 1974), but show no evidence of territoriality when food is scarce (King, 1975). Observations of food caching by mustelids are particularly frequent (see Ternovski, 1977; and Oksanen, 1983; for reviews).

In this paper we propose that surplus hunting in weasel *Mustela nivalis* Linnaeus, 1766 living in the northern temperate zone is a deliberate seasonal strategy, an adaptation to the severity and unpredictability of winter conditions.

2. THE PREDICTION

The seasonality of climate either directly or indirectly affects the behaviour of a weasel. First, low temperatures cause a drastic increase in its metabolic rate (Moors, 1977; Casey & Casey, 1979), so a cold weasel requires more food per unit time. Secondly, cold weather has a profound effect on the activity of weasels. Small mustelids are particularly susceptible to chilling, because they have an unfavorable surface-to-volume ratio, and their fur is a poor insulator (Brown & Lasiewski, 1972; Casey & Casey, 1979). Therefore, in winter, they spend less time foraging in the open air and more in exploring subnivean spaces (Kraft, 1966), they shorten their periods of daily activity (Sandell, 1985) and the lengths of daily movements (Robitaille & Baron, 1987), they reduce the number of

days spent hunting, and may stay hidden in the nest for several days (Ternovski, 1977; Richardson *et al.*, 1987).

Let N_h be the number of prey caught by a predator per unit of hunting time, so that:

$$N_h = C + S \qquad (1)$$

where C — consumption rate,

S — surplus of prey killed per unit of hunting time.

We assume that (under the condition of adequate food supply) the surplus killing and the amount of cached food is governed by time devoted to hunting. Therefore, in some period of time of duration D the storage should amount to:

$$D \times T_h \times S = D \times (1 - T_h) C \qquad (2)$$
$$T_h = D_h \times T_d \qquad (3)$$

where:

T_h — proportion (fraction) of time spent hunting within period D,

D_h — proportion (fraction) of days devoted to hunting,

T_d — proportion (fraction) of hours per day spent hunting.

Therefore S could be expressed as:

$$S = [(1 - T_h)/T_h]C \qquad (4)$$

The above mentioned data from literature provide evidence that T_h, the hunting time may be drastically lower in winter than in summer. Therefore, S should be much higher in winter than in warm seasons. Then

$$N_h = C + [(1 - T_h)/T_h]C \qquad (5)$$

that is

$$N_h = C/T_h \qquad (6)$$

This equation sets the rate of prey capture (N_h) at its lowest impassable limit under the unlikely condition that T_h does not change dramatically over short periods of time. However, the predator may constantly be subjected to sudden changes in external conditions, especially in winter. The animal which is then practically without any alternative food resources (such as insects, birds' eggs or earthworms), should maximize N_h within short periods of hunting rather than adjust it to a long-term balance of energy gain (*i.e.* we expect $N_h \gg C/T_h$ in winter time).

In summary we suppose that during warm seasons, the total number of prey caught per day depends only on the weasel's daily energy requirement — *i.e.* it stops hunting when it has filled its needs for the day. With the onset of cold, the weasel is forced to shorten its hunting

excursions but to hunt more prey, as it not only has to meet its current energy need in less time, but also to provide itself constantly with a "buffer" cache. To achieve this, it must increase its efficiency at finding/killing prey, and/or continue to hunt after it has caught enough for that day whenever hunting conditions remain favourable. Prey abundance is the prerequisite that weasels start hunting in surplus and store food in late autumn and winter. However, prey abundance *per se* can not trigger surplus killing during warm seasons.

3. TEST OF PREDICTION

We have tested the above hypothesis on 8 nonreproductive weasels (5 males and 3 females) hunting natural prey (bank voles) under conditions resembling their natural state as closely as possible. Both predators and prey were wild, live-trapped animals. Nineteen experiments (see schedule in Appendix 1) were carried out in an outdoor vivarium at the Mammals Research Institute, Polish Academy of Sciences, in Białowieża, eastern Poland in 1985—88. The vivarium was subdivided into enclosures of 50 m² (10×5 m) each. The natural rich soil remained in it. Ground cover consisted of dense vegetation in summer (*Aegopodium podagraria, Urtica dioica, Symphytum officinale*, and grasses up to 1 m high), deciduous litter in autumn, and deep snow (up to 54 cm) in winter. In each enclosure twenty-two 1 m-long logs were partially sunk into the ground to diversify the habitat, and a wooden two-chamber box with a removable roof was placed on the ground as a refuge for the weasels.

Bank voles *Clethrionomys glareolus* (Schreber, 1780) were the exclusive prey in 17 experiments, yellow-necked mice *Apodemus flavicollis* (Melchior, 1834), field striped mice *A. agrarius* (Pallas, 1771), and root voles *Microtus oeconomus* (Pallas, 1776) were also used. The rodents had been caught a few weeks before the experiments in which they were used. They were weighed and individually marked by toe-clipping plus either steel rings placed on the hind leg or steel eartags. From 14 to 51 voles (see Appendix 1) were released into each enclosure (50 m²) one week before the experiment. This corresponded to very high densities, of about 3000—8000 ind ha⁻¹. The reason such un-naturally high densities were used was that we wanted to give the weasels every opportunity to indulge in surplus killing if they "wanted" to. Food for rodents (oats, beet and carrot) was provided *ad lib*. One weasel was then introduced to the enclosure, usually at dusk. The experiments lasted from 6 to 25 days (see Appendix 1). Before and between successive experiments the weasels were kept in the vivarium and fed live rodents to avoid extravagant hunting activity during the first days of contact with live prey.

Records of each weasel's hunting performance were made by means of checking the number of prey caught and cached in the artificial nest box. Weasels nearly always carry their prey to cover (Oksanen, 1983) and consume them there. The weasels in our experiments did not swallow the steel rings or eartags but left them in the cache. The boxes were checked every morning until the last vole was killed. Each day, the addition of new prey items, and the total number of prey stored, were recorded. We did not observe the weasels nor measure the time of their activity. Due to natural (vegetation or snow) cover they were simply

not visible when they were hunting or exploring the area. Therefore the measures of hunting rate employed here were somewhat simplified. For each experiment we calculated:

(1) Percentage of days with hunting (D_h), defined as the percentage of days with new prey or remains found in the cache. We assumed that, when temperatures were not extreme, $T_h = D_h$.

(2) Average daily consumption (C), defined as the total number of voles eaten $\times$ mean body mass of voles $\times$ number of days^{-1}.

(3) Mean amount of prey caught per day with hunting (N_h), defined as the total number of voles killed $\times$ mean body mass of voles $\times$ number of days with hunting^{-1}.

Mean air temperature during each experiment was recorded by Białowieża Meteorological Station.

In two experiments the weasels used more than one caching place. The second one was usually an enlarged voles' chamber under a log. We discovered these caches some time after the weasels started to make them. For those experiments some measures could not have been calculated reliably (C, max storage, total number of voles killed during experiment) and were not considered. Two winter experiments ended when the weasels died of starvation. These were not incorporated into statistical analysis but are dealt with in Discussion.

4. RESULTS

The numbers of voles used in the experiments varied from 14 to 51, because they depended on the local and seasonal abundance of bank voles in our trapping source-area. We, therefore, checked whether the numbers of provided voles was likely to affect weasels' killing rate. The mean amount of prey (in grams) caught per weasel per day with hunting was plotted against the number of bank voles released to the enclosure in
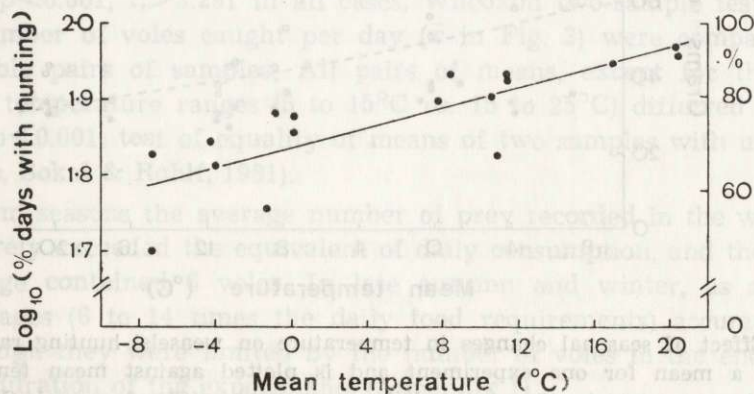

Fig. 1. Relationship between $\log_{10}$ percentage of days with hunting (D_h) and the mean temperature in enclosure experiments with weasels *Mustela nivalis* and small rodents, $Y = 1.837 + 0.0066X$, $R^2 = 0.66$ ($p < 0.025$, $F_s = 6.791$, d.f. = 1,15).

each experiment (N=17). The regression ($Y = 56.4 + 0.016X$, $R^2 = 0.0001$) was not significant ($F_s = 0.0131$, $p > 0.75$) and its slope did not differ from zero ($t_s = 0.0331$, $p > 0.9$). As only 0.01% of overall variability in weasels' killing rate might have been explained by the changes in prey abundance we neglected this factor.

Log-transformed data of percentage of days spent hunting in each experiment were plotted against mean temperature (Fig. 1). Within the observed temperature range (from 20.4°C in summer to −7.3°C in winter) the weasels reduced the mean proportion of days devoted to hunting from 93 to 62% (data read from the regression line) ($p \leq 0.025$, $G = 6.242$, d.f. = 1, G-test). Concurrently the mean daily consumption per weasel (expressed in grams of voles eaten per day) increased from 30.4 g to 35.8 g ($p = 0.5$, $G = 0.441$, d.f. = 1, G-test) (Fig. 2). No strong correlation between prey consumption and temperature could be expected here for the pooled sample. In laboratory trials performed by Moors (1977) the smaller weasels ate more per gram of body weight than larger ones, and the cold-induced increase in metabolic rate was different in male (large) and female (small) weasels. Nonetheless, we needed an estimate
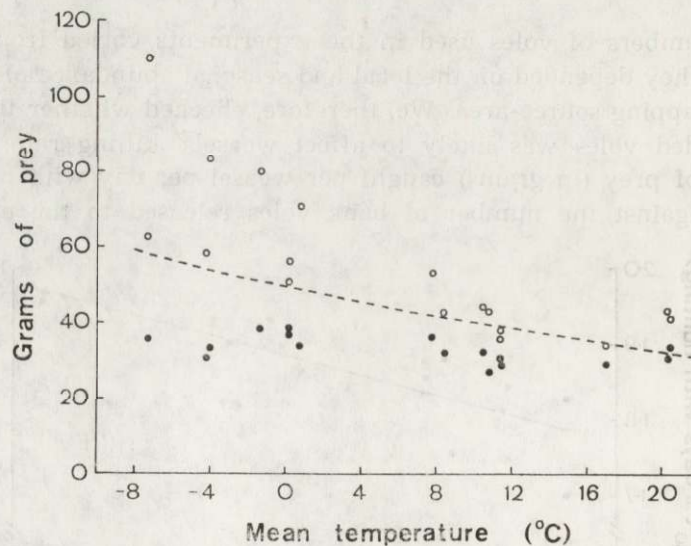

Fig. 2. Effect of seasonal changes in temperature on weasels' hunting rate. Every point is a mean for one experiment and is plotted against mean temperature during the experiment: (●) mean daily consumption (C) of weasel ($Y = 34.35 - 0.195X$, $R^2 = 0.26$, $p > 0.5$, $F_s = 0.447$, d.f. = 1,14). (○) mean amount of prey caught per day with hunting (N_h). Broken line designates the predicted killing rate (as $N_h = C/D_h$) calculated from regression equations for C and D_h (see Fig. 1).

of the daily consumption of food (C) in summer and in winter to compare with the number of days with hunting (D_h) in those seasons. From the two regression equations (Figs 1, 2) the predicted values of N_h (as equal to C/D_h) over the same temperature range were calculated (dotted line on Fig. 2). The real N_h values were close to the predicted ones in summer and early autumn, but in late autumn and winter the hunting rate became strikingly higher than predicted (Fig. 2, the deviations of summer *vs.* winter points from expected values: $p < 0.05$ $U_s = 58$, Wilcoxon two-sample test).

To show the weasel's hunting pattern in relation to ambient temperature we pooled all the experiments into four ranges of mean daily temperature and compared the percentages of days with a hunt success of 0, 1, 2, 3, ... n voles per day (Fig. 3). Vastly excessive killings (6—12 voles/day) were recorded only on days with the mean temperature from —5°C to 5°C (late autumn and winter). Then, 43% of all prey were caught on days when hunt success exceeded 5 voles. The mean number of voles killed per day (2.78) amounted to nearly 170% of weasel's daily consumption.

On frosty days (mean daily temperature below —5°C) the weasels drastically restricted their hunting activity. The kill rate per day (0.57 voles) covered only one-third of the daily energy needs of a weasel. The weasels survived cold days by relying on previously stored food.

In summer and early autumn (mean daily temperatures above 5°C) number of voles killed per day per weasel oscillated around the daily food consumption (Fig. 3). The distribution for the coolest range of temperature (—15.1 to —5°C) differed significantly from all other distributions ($p < 0.001$, $t_s > 3.291$ in all cases, Wilcoxon two-sample test). The mean number of voles caught per day ($\bar{x}$ in Fig. 3) were compared in all possible pairs of samples. All pairs of means, except for the two warmest temperature ranges (5 to 15°C *vs.* 15 to 25°C) differed significantly ($p < 0.001$, test of equality of means of two samples with unequal variances, Sokal & Rohlf, 1981).

In warm seasons the average number of prey recorded in the weasels' boxes rarely exceeded the equivalent of daily consumption, and the largest storage contained 6 voles. In late autumn and winter, as a rule, vast storages (6 to 14 times the daily food requirements) accumulated, even though they were limited by the number of voles in the enclosure and the duration of the experiments (Appendix 1).

The pattern of storage accumulation and diminution was alike in all weasels. Preferably the most recently caught voles were eaten first. If the daily kill exceeded the actual needs of a predator it usually gnawed

off and ate the parts (most often the heads and fore parts) of several prey and left the rest. Otherwise it lived on previously stored food. In several experiments we kept the weasels in the enclosures some days after the last vole was killed to check whether it would eat the stored material completely or not. In cold seasons the predator could survive many days relying exclusively on the cache. In warmer months the cached voles (if any) decayed quickly and were then usually ignored by weasels.
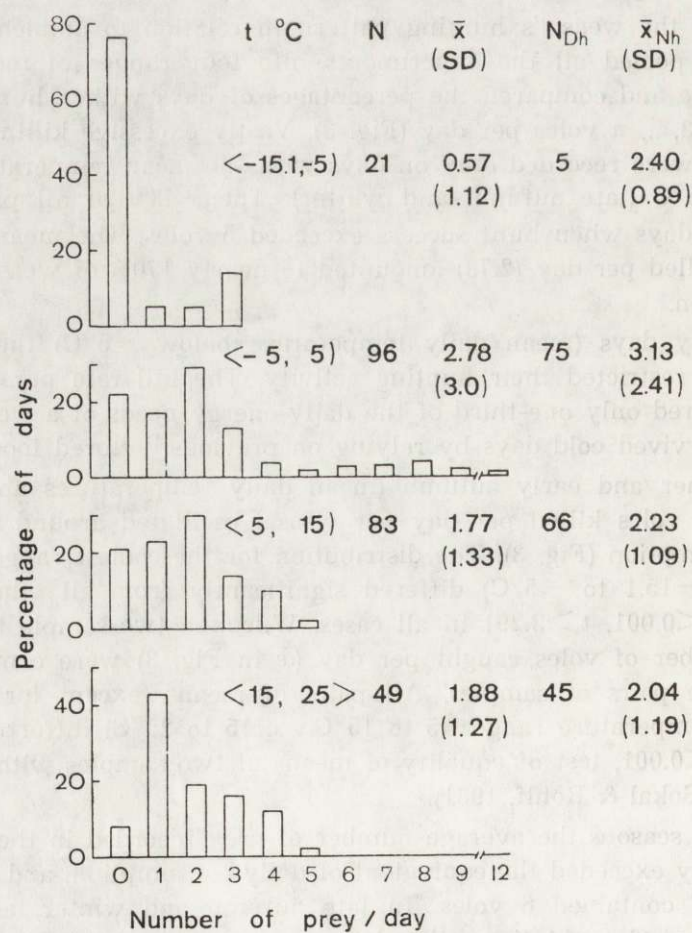

Fig. 3. Seasonal changes in weasels' hunting pattern. Data for 17 experiments were pooled and then grouped into four ranges of mean daily temperature (t°C). Bars are percentages of days with a given number of prey killed. N — number of days; $\bar{x}$ — mean number of voles killed per day per weasel; N_{Dh} —number of days on which the weasels hunted; $\bar{x}_{Nh}$ — mean number of voles killed per day with hunting.

5. DISCUSSION

In cold seasons the weasel has to balance two conflicting demands: a need for more food, and the need to reduce exposure to cold air during hunting. The predators compromise in several ways. First, they minimize the winter increase in energy needs by a series of physiological and (more important) behavioural adjustments to cold. These include loss of weight (Simms, 1979), reduction of activity, and insulation of the nest with prey fur (Banfield, 1974; McLean *et al.*, 1974; Debrot *et al.*, 1984). The weasels in our study used fur plucked from bank voles to line the inside of the nest. Second, the necessary reduction of a weasel's hunting time and the need for a "buffer" cache were balanced by an increase in number of voles caught per day with hunting. We suppose that in our experiments weasels' capture rate was not controlled by prey abundance or availability, since prey was superabundant in all seasons and there was no correlation between the number of voles provided by us and the mean amount of prey caught per day per weasel. This suggests that at high densities of prey weasels' hunting rates are governed intrisically by the rules of physiology (mainly thermoregulation) and not by intraspecific competition in the predatory guild as was suggested by Oksanen *et al.* (1985). Our results, however, proved the suggestion of Oksanen *et al.* (1985) that surplus killing is more likely to happen under circumstances *e.g.* in winter, that ensures the long retention of stored meat.

Two of our experiments that ended when the weasels died (Appendix 1) seem to support our argument. We did not supply the weasels with contingency storages in winter, in order not to alter their motivation for hunting. However, in these particular cases the sudden onset of hard frost (from —3 to —15°C and from —11 to —24°C, respectively) within first days of the trials found the weasels with almost empty larders. Both weasels barely managed to supply themselves with enough food at a price of spending much time outside and being exposed to extreme cold. By contrast with other winter trials of the same and other weasels, on these occasions they caught 1 or 2 voles per day, lost weight and finally died. Thus the huge abundance of highly vulnerable prey was not sufficient to provide these weasels with big storages quickly. These two experiments suggested that previously amassed food storages are necessary for weasels to survive periods of exceptional cold during winter. However, we could not disprove that these two would not die from cold even if their larder would have been full.

The common oppinion holds that mustelids are always prepared to kill well above their daily energy requirements. This behaviour, which is often labelled 'hen house syndrome', should not be identified with de-

scribed here seasonal surplus killing. 'Hen house syndrome' may easily be triggered by the constant presence of live prey within a sight of a predator and the small size of the 'hunting ground' (enclosure or cage). Ternovski (1977) has shown experimentally that weasels, stoats and polecats (*Mustela putorius*) introduced to enclosures (20—30 m²) with a large number of prey often exhibited extravagant activity, including the killing of greater numbers of prey during the first day than during any of the following days of the experiment. After 1 or 2 days the predators got used to the superabundance of prey and did not spend time and energy on continuous surplus killing. Erlinge *et al.* (1974) performed 16 enclosure experiments with *Mustela nivalis* in such a way that each animal was used only twice (one day at a time), so the sample was compiled of single days, records with 8 different weasels. The average number of prey (voles and mice) caught per 24 hrs reached 1.5 in females and 5.1 in males.

We contend that surplus killing and food storage are seasonal aspects of the weasel's hunting strategy that are of great adaptive value, since they increase its chance of survival in winter and determine its condition in spring, at the beginning of the reproduction period.

Recently it has been suggested that surplus killing by mammalian and avian predators may considerably extend their impact on rodent populations (King, 1985). It would be, therefore, desirable to specify how much surplus hunting by weasels increases the number of prey removed. It is not possible to do this accurately, but some suggestions can be made from thess experiments. The effect of surplus killing can effectively be ignored in summer. In winter, when prey are at low density, weasels will not be able to accumulate large caches; the prey killed will be eaten completely, and a high mortality of weasels is to be expected, especially when a scarcity of prey coincides with a hard winter. At high density of rodents in autumn and winter the weasel's opportunity for surplus hunting will be exploited freely. Vast caches will accumulate, and at least partially will be wasted because weasels tend to eat the freshly caught items first. Then, particularly when a mild winter coincides with abundant prey, the actual impact of weasels on rodent populations may be much higher than expected from calculating their food requirements.

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SEZONOWE NADMIERNE ZABIJANIE JAKO STRATEGIA POLOWANIA ŁASICY *MUSTELA NIVALIS* — TESTOWANIE HIPOTEZY

Streszczenie

Niniejsza praca kwestionuje powszechne tłumaczenie zjawiska nadmiernego zabijania przez małe łasicowate jako reakcję na przegęszczenie ofiar. Stawiamy hipotezę, że nadmierne zabijanie jest regularną sezonową (zimową) strategią łasic, sposobem: (1) bilansowania powodowanego zimnem wzrostu zapotrzebowania na pokarm, (2) kompensowania ograniczenia czasu polowania, (3) zapewnienia stałego zapasu pokarmu w czasie zimy.

Sprawdziliśmy tę hipotezę w półnaturalnych warunkach w czasie 19 eksperymentów przeprowadzonych w ciągu 3 lat z ośmioma nierozmnażającymi się łasicami *Mustela nivalis* Linnaeus, 1766 i gryzoniami, głównie nornicami rudymi *Clethrionomys glareolus* (Schreber, 1780), żyjącymi w warunkach bardzo wysokich zagęszczeń (Appendix 1).

Eksperymenty trwały od 6 do 25 dni. W zakresie temperatury od 20,4°C (latem) do —7,3°C (zimą) średni procent dni, w których łasice polowały w czasie eksperymentu zmalał od 93 do 62% (Ryc. 1). Dzienna konsumpcja łasic w tym zakresie temperatury wzrosła nieznacznie (Ryc. 2).

W dniach o średniej dziennej temperaturze powyżej 5°C łasice łowiły średnio 1.8 gryzoni na dzień (SD 1.3, zakres 0—5). Dni o średniej temperaturze od 5°C do —5°C były dniami najsilniej zaznaczonego nadmiernego polowania. Sukces łowiecki wynosił wówczas 2.78 gryzoni na dzień na łasicę (SD 3.0, zakres 0—12). W czasie mroźnych dni (średnia dzienna temperatura poniżej —5°C) łasice drastycznie ograniczały aktywność łowiecką, zabijając jedynie 0.57 gryzoni na dzień (SD 1.1, zakres 0—3) i przeżywając dzięki wcześniej zgromadzonym zapasom pokarmu (Ryc. 3).

Jeśli gryzonie były stale łatwo dostępne, łasice użytkowały zapasy bardzo ekstensywnie, zjadając jedynie części najświeższych ofiar. W symulowanych warunkach niedostatku żywych gryzoni późną jesienią i zimą łasice mogły przeżyć wiele dni żywiąc się zapasami pokarmu.

Nadmierne zabijanie przez łasice okazało się zachowaniem sezonowym, występującym jedynie późną jesienią i zimą. Latem natomiast u nierozmnażających się łasic nie mogło być wywołane nawet w warunkach bardzo obfitych zasobów potencjalnych ofiar. Jest to więc przypuszczalnie genetycznie uwarunkowana adaptacja łasic do surowych i nieprzewidywalnych warunków zimowych w północnej strefie umiarkowanej.

APPENDIX 1

Schedule of enclosure experiments on the seasonal variation in the hunting strategy of weasel *Mustela nivalis*. Bank voles *Clethrionomys glareolus* were prey in all experiments except of these marked * — in which also *Apodemus flavicollis*. *A. agrarius* and *Microtus oeconomus* were used; ** — experiments ended with deaths of predators. *** — mortality of voles from causes other than predation was high in this experiment, at least 6 voles died. N_h — mean number of prey caught per day with hunting.

Weasel sex, symbol	Body mass (g)	Beginning of experiment	N days	N rodents provided	N rodents killed by weasel	Max storage at any day as % of prey provided	N_h	Mean body mass of prey (g)	Mean temp °C
F C	60	04.12.85	17	42	all	69	3.23	22	0.8
	60	29.01.86	6	15	all	60	5.00	22	—7.3
	72	02.09.86	14	23	all	26	1.92	20	11.4
M B	147	24.09.85	15	29	all	14	2.42	18	10.5
	131	04.12.85	25	47	all	40	2.61	21.5	0.2
	130	29.01.86	6	15	14	64	3.50	18	—7.3
	140	19.06.86	9	14	10	14	1.28	26.5	17.0
	145	02.09.86	14	25	all	16	2.08	18	11.4
	137	08.01.87 **	13	25	all	12	2.00	19.5	—19.5
F A	73	24.09.85	18	28	all	14	2.33	18.5	10.8
	61	04.12.85	25	45	all	13	2.37	21.5	0.2
	61	29.01.86 **	15	16	?	?	?	23	—13.2
M 15	65	08.10.86	7	14	all	36	2.33	18.5	8.4
	67	12.12.86	20	44	all	61	3.14	18.5	—4.2
F 13	53	11.09.86 *	14	25	all	16	2.27	23	7.8
	48	12.12.86	17	44	all	66	4.00	21	—1.3
M 26	90	10.12.86 *	7	15	13	60	3.25	24.5	—1.3
M 126	84	23.06.88	21	42	all	14	2.21	19.5	20.4
M 136	117	23.06.88	14	51 ***	30	20	2.30	19	20.3