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Population biology of the weasel Mustela nivalis on British game estates

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The mean year-class ratio in 6 samples of weasels (total n = 477) ranged from 59% to 84% young, and mean age from 0.79 to 1.16 yr. There was no difference in age structure between samples from 5 game estates and 1 reserve. Mean annual mortality of weasels of both sexes and all ages was 75–90%. In 12 pregnant weasels the mean number of embryos, observed from April to June, was 5.6. There was a definite anoestrous season in winter. Records of the number of weasels killed on game estates show that weasels and stoats reacted differently to the first outbreak of myxomatosis in England in 1954; and that weasel populations are capable of enormous sudden increases (usually associated with "mouse years"). These increases are probably due largely to summer litters produced by precocious juveniles, and also to some adults breeding a second time (both possibilities confirmed from ovarian histology on this material). Traditional gamekeeping practice may influence the seasonal pattern of mortality of weasels (highest in spring) but its effects are probably short-lived.

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1. Introduction

Published studies of the population biology of *Mustela nivalis* are few, mainly because the two essential requisites, an accurate method of age-determination and unbiased samples, are difficult to supply. The age of weasels is difficult to determine (King 1980b), and in Britain, though large samples may be collected from co-operative gamekeepers, they are usually biased in several different ways.

The literature does not contain a single analysis of the dynamics of a wild population of *Mustela nivalis,* not even a first approximation, although the commercially valuable mustelids have received closer attention, especially in the USSR (see, for example, many of the papers on sable, marten and ermine translated in King, 1975c, 1980a). In Britain the population biology of weasels is of considerable interest to the game industry, though the lack of any population data hitherto has prevented rational assessment of the traditional methods usually employed for "vermin control". The present study sketches a first outline of this important missing information.

Published estimates of age ratios for *Mustela nivalis* are difficult to compare with present results because not all authors defined their terms and methods in sufficient detail. Since first-year weasels* comprise about threequarters of the population, the total number at any time will depend largely on the production and survival of young, and the proportion of young in the sample will depend on the season of collecting and the definition of the youngest age class(es). Lockie (1966), Hansson (1968), Fog (1969), Barbu (1968) and Stubbe (1969) all used different definitions of age. Comparing them all shows only that all authors except Barbu and Hansson found the young animals to be in the majority.

The distribution and abundance of weasels is clearly related to the local population of small rodents (Rubina 1960, Parovshchikov 1963, Heptner et al. 1967, Erlinge 1974, King 1975a), though there are few direct data on the influence of nutrition on productivity (Tapper 1979), and none on its effect on survival. Reproductive cycles and development have been described by Hill

* Throughout this paper, the name "weasel" refers only to *Mustela nivalis,* and "stoat" to *M. erminea.*

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(1939), Deanesley (1944), and Heidt (1970); and variations in fur, bounty or vermin records by Parovshchikov (1963), Jefferies and Pendlebury (1968), and Hewson (1972).

2. Material and methods

Five of the samples (455 weasels) were collected by gamekeepers on estates in England and Scotland (numbers 1, 2, 5, 6 and 7 on the map in King 1977). All were killed in Fenn traps, described by King and Edgar (1977), and were from populations regularly cropped by trapping. A small sample of 22 weasels from Wytham Woods, Berkshire, a reserve with no history of weasel-trapping before 1968, is considered separately: these animals were either caught in box traps or shot. Weasels which had been held in captivity or picked up dead were excluded.

Most carcases were stored frozen. Autopsy procedures included recording of measurements, food habits and *Skrjabingylus nasicola* (King 1977), and counting of embryos, and, for the first 171 specimens (samples 4, 5 and 6, plus the first 55 of sample 1) also fatness, moult pattern, weight of gonads and histology of ovaries. Placental scars were not visible (Heidt 1970). Skulls were cleaned by dermestid beetles. Demographic procedures followed, where possible, the advice of Caughley (1977).

As on most game estates, the keepers concentrated on trapping predators in spring, and hence the monthly distribution of the samples is very uneven: 46% of the weasels examined were caught during March, April and May. This sampling programme was not ideal for population analysis, but the resulting material can at least be regarded as typical of the annual weasel harvest on many British game estates.

All the game estates were mixed arable farmland at less than 500 m altitude: the largest sample came from North Farm, Sussex, the study area described by Potts and Vickerman (1974). Wytham is a largely deciduous woodland described in detail by Elton (1966). There were no estimates of weasel density on any of the game estates, but the resident population on a small part of Wytham was observed by livetrapping during 1968–70 (King 1975a).

The method of age-determination used is based on the progression of changes in the shape of the skull established from specimens of known age (King 1977, 1980b) Skulls were grouped first according to the month killed, and then into year-classes, divided at 1 June. Weasels in their first year are called "Young", and those in their second year "Adults". Adults past two years of age ("Old") may be distinguished by wear of the carnassial teeth, which is not significant before that age; but as this distinction is not precise it is used in only Tabs 1, 3 and 4. Mean age was estimated from a median birth date assumed to be 1 June, although the season of births, beginning in April, is variable in length according to environmental conditions. The few old animals were all given an arbitrary age of 30 months.

The weasel is a short-lived animal, but the age structures are expressed in year-class ratios, for practical reasons. The method of age determination has to work in chronological categories, because young weasels vary greatly in the age at which they reach reproductive maturity, according to when in the season they were born. The year classes can of course be subdivided by month, but if this is done, as in Tab. 4, the season at which the sample was collected determines the relative prominence of each monthly or quarterly class. A sample collected in summer (June–August) contains many juveniles and few sub-adults, and vice versa one collected in spring, though the same cohort of young, at different stages in their development, is represented in both. By comparing samples in year-classes, differences due to season of sampling are reduced. Further, as pointed out by Caughley (1977) and illustrated particularly well in weasels, differences between age classes spanning less than a year will relate more to season than to chronological age, so classes defined in years are not arbitrary; they are the only natural units of age.

Young weasels cannot be trapped before four weeks of age, when they first leave the nest, and are unlikely to enter traps before eight weeks, when they can kill for themselves (East and Lockie 1964). Hence, all figures derived from trapped samples refer to mortality from at least two months, not from birth. The samples are taken to represent the standing age distribution in the living population from independence (at about three months) onwards.

The problems of population biology can be approached at several levels of detail, depending on the precision of the answer required and the difficulty of extracting it (Caughley 1977). In the first instance, the simplest approach is to treat all individuals of a given sex or age group as if they were identical and to assume that the population statistics are representative and apply as an average over several years. This approach is the most appropriate one for a pilot study, and is the one used here.

3. Results

3.1. Sex ratio

The great excess of males in the samples (Tab. 1) was analysed previously by King (1975b), who considered it more likely to be a sampling error arising from the differences in the biology of males and females than a measure of the real sex ratio of the population. However, there were no seasonal variations in the relative number of males and females caught (Tab. 2); there was no significant difference between males and females in age structure as estimated from these trapped samples

Tab. 1. Age distributions of weasels from 5 game estates and 1 reserve.

	Game estates						Reserve
	Sussex	Oxon.	Northumb.	Wigtown.	Aberdeen	Estates Combined	Wytham
Males							
Young	130	32	28	24	56	270	7
Adult	27	7	11	6	10	61	6
Old	7	0	0	0	1	8	1
Total	164	39	39	30	67	339	14
	Difference in age structure between estates (males): $\chi^2 = 2.75$, 4 df (adult and old year classes combined), NS.				Mean age 0.86 yr		
Females							
Young	66	2	8	2	9	87	6
Adult	13	1	6	1	2	23	2
Old	5	0	1	0	0	6	0
Total	84	3	15	3	11	116	8
	Difference in age structure between estates (females): $\chi^2 = 4.82$, 4 df, NS.				Mean age 0.93 yr		
Total	248	42	54	33	78	455	22
		Difference in age structure *between sexes on the estates:* $\chi^2 = 1.05$, 1 df, NS.				Difference in age *structure between* estates and reserve (sexes pooled) $\chi^2 = 2.13$, 1 df, NS	
% males	66.1	92.9	72.2	90.9	85.9	74.5	63.6
Mean age (yr)	0.85	0.93	1.16	0.99	0.79	0.88	1.02
% young	79.0	81.0	66.7	78.8	83.3	78.5	59.1
Ha/kill trap	5.3	?	8.1	9.7	?	–	–
Collected	1968–72	1968–70	1968–70	1969–70	1970–72	1968–72	1968–70
Sample number (King 1977)	1	2	5	6	7	–	4

(Tab. 1); and sex ratio did not change with age (King 1975b). For the purposes of this paper I assume that both males and females have been sampled randomly, but at different levels, and so the results for the two sexes are presented separately below.

3.2. Age structure

In every sample most of the weasels examined were in the first yearclass (Tab. 1). The actual ages of the old (2 years+) animals is unknown, but the age structures suggest that very few of them were much past their third year. The differences in age structure within the game estates, and between the game estates together and the reserve, were not significant (Tab. 1).

The individual weasels examined lived on average about one year or less (the range of mean ages observed was 0.79–1.16 yr, mean 0.88 yr, in different samples, and 0.86 in males, 0.93 in females). However, the mean for the total population (including the pre-independence age classes, which was not sampled) was no doubt much less. The mean expectation of life at birth cannot be estimated if mortality before independence is unknown. Weasels in captivity may live up to ten years (Frank, pers. comm.).

The youngest weasels collected by gamekeepers were all over fifty days old, as all had completed their permanent dentition (East and Lockie 1964). This is probably not because younger weasels cannot be caught, but because the gamekeepers on the estates studied paid less attention to trapping in summer. In Wytham, one young male with deciduous canines still in place was caught in a live-trap in September 1969.

A change in the proportions of the year-classes with time may indicate differential vulnerability to trapping (for example, in sable, many more young are caught at the beginning of the season than at the end: Mel'nikov 1975. In the present material, the proportion of young, in all samples combined, fluctuated irregularly through the year, with no obvious decline with time since the season of births (Tab. 2). The mean annual mortality rates of the two year classes were similar, in both males and females (Tab. 3).

If regular trapping were having any effect upon the target population, e.g. by stimulating breeding or immigration, or reducing the mean lifespan, a higher

Tab. 2. Proportion of young and adult weasels and sex ratios through the year (Game estates combined).

	Age			Sex (from King 1975b)		
	Young	Total	%Young	n ♂♂	Total	%♂♂
Jun	15	29	51.7	13	17	76.5
Jul	32	43	74.4	10	17	58.8
Aug	18	23	78.3	7	10	70.0
Sep	11	11	100	9	9	100
Oct	18	22	81.8	14	18	77.8
Nov	32	36	88.9	27	35	77.2
Dec	34	36	94.4	28	38	73.7
Jan	24	32	75.0	17	33	51.5
Feb	18	21	85.7	16	20	80.0
Mar	82	100	82.0	78	100	78.0
Apr	54	69	78.3	53	71	74.7
May	36	45	80.0	28	38	73.7

trapping pressure (expressed as ha/trap) should be associated with a lower mean age. The trapping pressure was estimated for only three of the game estates, and, within the range observed, was not obviously related to variations between estates in mean age (Tab. 1). The mean age in the Wytham Reserve was 1.02 yr (n = 22), which was within the range of mean ages observed on the game estates. The significance of the differences between these figures was not tested because the actual ages were not known: the range of birth-dates (4–5 months) is about the same as the range of differences observed.

3.3. Seasonal (three-monthly) variations in mortality rate (q_x)

The mortality pattern of the weasels on the game estates showed a well-defined peak in the spring of each year (Fig. 1). However, although this suggests that the activities of gamekeepers may affect the seasonal distribution of mortality, it does not imply that they necessarily affect the annual level of mortality.

The q_x curve for most mammals is U-shaped; the initial drop is absent from Fig. 1 because q_x data derived from trapped samples take no account of mortality before independence. All the colums of Tab. 4 are

Tab. 4. Seasonal pattern of mortality in weasels on game estates.

	Capture date	f_x	l_x	d_x	q_x
Males					
First year	Jun–Aug (Summer)	339	1.00	0.14	0.14
	Sep–Nov (Autumn)	293	0.86	0.14	0.16
	Dec–Feb (Winter)	245	0.72	0.15	0.21
	Mar–May (Spring)	193	0.57	0.37	0.65
Second year	Jun–Aug	69	0.20	0.05	0.25
	Sep–Nov	50	0.15	0.02	0.13
	Dec–Feb	45	0.13	0.02	0.15
	Mar–May	38	0.11	0.09	0.82
Older (all seasons)		8	0.02		
Females					
First year	Jun–Aug	116	1.00	0.15	0.15
	Sep–Nov	99	0.85	0.09	0.11
	Dec–Feb	88	0.76	0.17	0.22
	Mar–May	69	0.59	0.34	0.58
Second year	Jun–Aug	29	0.25	0.08	0.32
	Sep–Nov	20	0.17	0	0
	Dec–Feb	20	0.17	0.04	0.24
	Mar–May	15	0.13	0.08	0.62
Older (all seasons)		6	0.05		

mathematically related, but q_x is the only one plotted, as it is the statistic least affected by errors of age-determination and sampling bias (Caughley 1977).

3.4. Natural mortality

There is little evidence from this study of the causes of natural mortality in weasels. Of eight weasels found in the pellets of tawny owls in Wytham (Southern, pers. comm.), five were female, two male and one undetermined; two were adult, two young and four undetermined. The nematode parasite *Skrjabingylus nasicola* causes considerable damage to the skulls of weasels, and 77–100% of skulls in the present samples were infested, but there was no evidence that infested weasels were smaller, lighter, leaner or died younger than uninfested ones (King 1977).

Tab. 3. General pattern of mean annual mortality rates of male and female weasels on game estates.

Age (yr)	Frequency f_x	Survival l_x	Mortality d_x	Mortality rate q_x	Survival rate p_x
Males					
0.25–1	339	1.00	0.80	0.80	0.20
1–2	69	0.20	0.18	0.90	0.10
2+	8	0.02			
Females					
0.25–1	116	1.00	0.75	0.75	0.25
1–2	29	0.25	0.20	0.80	0.20
2+	6	0.05			

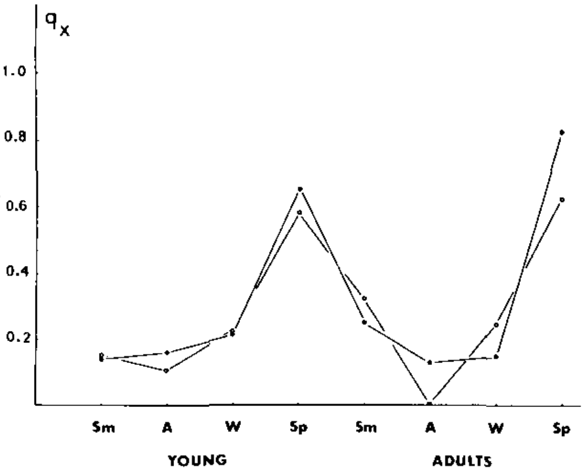

Fig. 1. Seasonal variation in mortality rate, q_x, in male (•) and female (o) weasels on game estates. Sm: summer, A: autumn, W: winter, Sp: spring.

3.5. Reproduction

3.5.1. Litter size

The mean number of embryos was 5.6 (Tab. 5). As found by Deanesly (1944) the corpora lutea in weasels persist for some time after parturition (in one pair of ovaries I sectioned, corpora lutea were still present in October, and in another pair, two generations of corpora lutea were found together in July); but the poor quality of the histological material made it impossible to count them.

3.5.2. Breeding season

Embryos were observed between April and June, and lactation between April and July with one (in the south of England) lactating in October (Tab. 5). The end of the season is difficult to determine, because few weasels were collected from mid-summer onwards, and in any case the length of the season probably varies from year to year. Tapper (1976) made a special effort to collect weasels in summer from North Farm, Sussex, and some of those he caught are included in this material. In July and August of 1971 and 1972, 19 females were collected, of which 5 were rotten. As the ovaries were not sectioned, the breeding condition of the remaining 14 could not be fully determined. From macroscopic signs, 2 of the 14 were lactating, and one was in oestrus, but none was visibly pregnant. At Wytham, the longest resident adult female, ♀ 18, was pregnant when live-trapped on 26 August 1969, but had apparently lost the litter by the time she was next captured three weeks later (King 1975a).

The non-fertile season was well marked. In 26 females collected between November and March inclusive, whose ovaries were sectioned, all but one were anoestrous (Tab. 6). The annual cycle of testis weight followed closely the description of Hill (1939).

Tab. 5. Records of weasel pregnancies and lactations.

Pregnancies Date	Sample area	Body wt (g)	No. of embryos
19 Apr 1953	Hampshire[1]	95	5
25 Apr 1958	Hampshire	60	6
26 Apr 1971	Sussex	63	5
27 Apr 1972	Aberdeen	55	6
during april 1969	Sussex	67	6
1 May 1969	Northumberland	77	7
10 May 1969	Northumberland	–	5
12 May 1969	Wytham	72	6
17 May 1962	Hampshire	66	6
21 May 1972	Sussex	78	4
during May 1969	Sussex	72	5
26 Jun 1958	Hampshire	82	6
		Mean	5.6

Lactations	Sample area	Dates
	Sussex	5 Apr 1971, 7 May 1971, 1 Jun 1971, 23 Jun 1972, 30 Jun 1971, 19 Jul 1971, 24 Jul 1972, 14 Oct 1971
	Northumberland	9 Jun 1969
	Hampshire	2 Jun 1949

1. Hampshire records from Blank (unpubl.).

3.5.3. Fertility and age

Tab. 6 shows the relationship between breeding condition, season and age in the 45 females whose ovaries were sectioned. All three young females caught before the end of the breeding season were fertile, though none had visible embryos. In 16 mature females caught after April, all except one were in breeding condition, and the only one caught in July was already fertilised for her second pregnancy; only five of these had visible embryos.

Tab. 6. Reproductive condition and age of 45 female weasels whose ovaries were sectioned.

A. Young ♀♀ caught before 31 Oct of their first year:	Fertile (in oestrus or with corpora lutea) 3. Infertile 0.
B. Females of all ages (mature and immature) caught 1 Nov–31 Mar inclusive:	Anoestrous 25 Oestrous 1 (12 Mar)
C. Females of all ages (all mature) caught after 1 Apr:	Anoestrous 1 (13 Apr) Oestrous 5 (16 Apr to 9 May) Between ovulation and lactation of first pregnancy of season 9 (28 Apr–9 Jun) Between ovulation and lactation of second pregnancy of season 1 (7 Jul) Infertile 0 Total 16

Tab. 7. Recent variations in the number of weasels killed per year on three of the game estates studied.

Year	Sussex (1200 ha)	Northumberland (4000 ha)	Wigtownshire (14000 ha)
1960	162	102	–
1961	345	69	308
1962	218	182	–
1963	192	141	151
1964	113	129	263
1965	55	209	295
1966	219	149	262
1967	246	136	–
1968	239	188	239
1969	258	162	227
1970	252	–	207
1971	254	–	183
1972	256	–	193

3.5.4. Uterus weights

Uteri were weighed complete with ovaries attached. The mean weight of 26 anoestrous uteri was 43 mg, range 24–76 mg: of 13 uteri, determined from ovarian sectioning and the appearance of the vulva to be pre- or post-oestrous, 137 mg, range 45–275 mg: of 5 uteri containing embryos, 2.17–6.68 g.

3.5.5. Population Fluctuations

The densities of weasels on the five game estates were not known, but they were certainly not stable from year to year. Records of the annual kill of weasels by gamekeepers, which are the crudest form of population estimate, were available from three of the estates for the years preceding the study (Tab. 7). They show that the "harvest" of weasels is unstable, frequently varying between years by a factor of 2 or 3. This instability means that data on mortality and reproduction based on specimens collected over several years provide only a general picture. Tapper (1979) describes the responses of a local weasel population to changes in its food supply.

4. Discussion

4.1. Age structure

The age structures observed correspond reasonably well with what would be expected in a small mammal capable of rapid reproduction, and with field observations. Few resident weasels hold their territories for more than one year (Erlinge 1974, King 1975a), and none has been known to live in the wild for more than three years (Lockie 1966). Because of the variable occurrence of summer litters, a theoretical age pyramid cannot be constructed for weasels to compare with that calculated for stoats by van Soest and van Bree (1970).

There was no difference between the age-structures of the weasels from the estates and the reserve, but none need be expected in these samples, for three reasons. Trapping need have no effect on age ratios if all ages are equally liable to be caught (Caughley 1974), or if the artificial mortality imposed by gamekeepers is insignificant; and in theoretical populations with similar patterns of age-dependent survival but different rates of increase, the age-ratios can be unrecognisably different (Caughley 1977). Hence, age-ratios cannot be interpreted without a knowledge of r.

4.2. Mortality and survival

The pronounced seasonal variation in mortality rate of weasels on game estates is probably a largely artificial consequence of the extra trapping effort traditionally made by gamekeepers in spring. However, weasels also change their behaviour with the onset of the breeding season in spring, and this may increase their "trappability" and also, on untrapped areas, increase the risk of death from factors other than traps. Several resident male weasels in the reserve died after drastic loss of weight at this season (King 1975a).

In the combined sample from the game estates, the survival of female weasels from independence to one year old was slightly higher (0.25) than that of males (0.20: Tab. 3), though the difference in the age distributions of the sexes was not statistically significant (Tab. 1). Gamekeepers invariably kill about three times more male weasels than females (King 1975b) which means that more females than males escape the trapping season and later die from natural causes. The small difference in these survival figures perhaps reflects the lower proportion of the female population vulnerable to the risk of being trapped. In contrast, live-trapping studies of undisturbed weasel populations have frequently recorded periods when females were apparently scarce or completely absent (Lockie 1966, Erlinge 1974, King 1975a, Moors pers. comm.). The difference could perhaps be due to the beneficial effects of cropping. Cropped populations often show improved condition and vigour; the effects of traditional weasel trapping, highly selective for males (Tab. 2) would benefit females the most, particularly as in weasels the non-breeding females are socially subordinate to males and inferior to them in hunting ability (Erlinge 1975).

4.3. Reproduction

Stubbe (1969) commented that the high proportion of young in samples of weasels implies high productivity in weasel populations; but immigration stimulated by constant cropping and selective trapping of young can result in an observed proportion of young far exceeding the possible productivity of a population. Hence, the productivity of the population sampled can be estimated only from fecundity data obtained from examining the females. In the present material, only 145 of the total of 535 weasels collected were females, of which only 8 were pregnant. Even when sampling is carefully controlled, female weasels are apparently particularly difficult to catch when pregnant (Deanesly 1944, Behnke 1966).

The only recorded count of corpora lutea in British weasels is that of Deanesly (1944), who found an average of 7.1 corpora lutea in 32 pregnant weasels examined. The mean number of embryos found in this study (5.6) was comparable to the 6.4 found by Deanesly. The mean number of young born, in 17 litters recorded in Britain, was 6.2 (range 4–8): if a further 22 litters from other parts of the species distribution are included, the mean is 5.0 (King 1975b). The limits of the anoestrous season in British weasels seem to be fairly definite (Deanesly 1944, Tab. 5, 6), in contrast to European *nivalis* (Stubbe 1969, Heptner et al. 1967) and American *rixosa* (= *nivalis*) (Hall 1951).

Adult female weasels are known to be capable of producing two litters a year (Heidt 1970), and young females born early in the season may themselves reproduce later in the summer (Deanesly 1944). Such extended breeding seasons are associated with years when small rodents are very abundant (Hensel 1881) and so also are records of very large litters, which may be up to at least fifteen young (Heptner et al. 1967, Fitzgerald in press). Second litters are possible in "lemming years" even in the short summers of the far north, as Frank (1974) reports that a captive female of the small boreal form *M. nivalis rixosa* regularly came into post-partum oestrus before the end of lactation, and could rear two litters in 5.5 months. However, monthly trapping records, showing two peaks in capture rate in April and July, do not infer that second litters are normal in Britain (Jefferies and Pendlebury 1968). The first peak is too early to represent dispersing young of the first litter (Tabs 5, 6) and may be more related to spring changes in behaviour and trappability mentioned above. In poor years, many adult weasels may fail to breed altogether (Tapper 1979).

4.4. Population fluctuations

The annual variation in the number of weasels killed on British game estates illustrated in Tab. 7 is comparable with figures published elsewhere: for example, for the ten years 1947–48 to 1956–57 inclusive, Anon (1960) reports the annual kill of weasels on 1336 ha in Hampshire as 82, 106, 185, 96, 84, 110, 46, 64, 53 and 68 respectively. Series of figures showing a similar range of variation can be found in the vermin books of almost any estate, and well back into last century (Middleton 1934).

Ocassionally, weasels are capable of sudden quite startling irruptions. The next figure in the above series, for 1957–58, is 348, a five-fold increase over that of the previous year. This is almost certainly due to the consequences of myxomatosis, which were demonstrated in records from all over the country (Jefferies and Pendlebury 1968, Hewson 1972, Appendix 1.) As the rabbits declined, followed by the stoats, the herb layer of the vegetation became luxuriant, and populations of small rodents reached peak levels (Fenner and Ratcliffe 1965, Hewson and Kolb 1973), followed by the weasels. Over much of the country the main result was a reversal of the previous ratio of stoats to weasels (Craster 1970, Hewson 1972). The increase in weasels was probably due mainly to the improvement in their

Appendix 1. Vermin records from Elveden estate, Norfolk (approx 9300 ha).

Year	Number of animals killed *M. nivalis*	*M. erminea*	rabbits	No. keepers and warreners employed	
1927	83	715	51563	35	
28	92	766	61571		Records not available
29	88	859	55986		
30	73	925	51777		
31	88	1013	57240		
32	56	825	48602		
33	59	459	58561		
34	168	419	54169		
35	56	422	52606		
36	73	439	51163		
37	75	596	48870		
38	85	655	43416	37	
39	90	643	42294	37	
40	34	434	31706	33	Keepers on War Service
41	7	409	20348	13	
42	10	438	15765	13	
43	11	569	13218	14	
44	10	517	22744	14	
45	4	495	40376	16	
46	3	855	47742	26	
47	14	624	50009	29	
48	8	568	53793	27	
49	20	735	47645	27	
50	17	647	27381	22	
51	18	603	23535	26	
52	11	645	19528	25	
53	17	727	19839	26	
54	35	825	8601	26	
55	22	257	401	19	First outbreak of myxomatosis
56	42	146	1864	19	
57	81	98	4968	19	
58	37	80	5016	20	
59	16	62	3037	19	
60	26	71	9001	23	
61	64	40	3962	23	
62	22	58	5105	22	
63	23	75	4864	19	
64	24	170	2607	15	
65	112	251	680	11	
66	72	257	849	11	
67	65	166	949	12	
68	104	138	1147	11	
69	89	164	1760	12	
70	55	225	1354	11	
71	123	270	2954	11	
72	88	168	3158	12	
73	77	249	4083	11	
74	124	348	8917	12	
75	74	318	14378	12	
76	55	448	15698	13	

food supplies, though the removal of interspecific competition from stoats may have helped (King and Moors 1979). Appendix 1 suggests that, at least over the last twenty years, the harvest of weasels on this estate has been higher than usual every three or four years.

The greatest value of vermin records is that they are an eloquent warning against any facile assumption of a stationary population in short-term or localised samples of weasels. Fur and bounty records in general are often unreliable, because the incentive to set traps changes with the density of the target population; but the figures provided by gamekeepers are probably less subject to this error, since setting traps is done in the course of other work (Hewson and Kolb 1973). It seems safe to assume that weasel populations are actually at least as unstable as these records suggest, and that the rate of increase is usually either positive or negative, but very seldom zero. This means that lifetables more accurate than the preliminary ones presented here can be constructed only by studying marked animals (Caughley 1977).

Sudden large population increases in weasels are often associated with years when small rodents are abundant (Swanson and Fryklund 1935, Lokemoen and Higgins 1972, McLean et al. 1974, Goszczynski 1977). This could readily be understood if the effect of extra food is merely to decrease the high mean annual mortality rate; but in weasels, improved survival can be augmented not only by an increase in fecundity, which occurs in other carnivores and may reasonably be expected, but also the capacity (unique among mustelids) of weasels to produce extra litters in good seasons.

4.5. Implications for the preservation of game

The flexible reproductive strategy of the weasel allows it to avoid surplus production in poor years, and to exploit *favourable circumstances very quickly*, despite the attentions of gamekeepers. This latent breeding capacity is certainly enough to account for large population peaks such as that of 1957–58 reported by Anon (1960) and others. In ideal conditions in Britain a single female weasel could theoretically produce in one season $12+(3 \times 6) = 30$ descendants; two litters of six young of equal sex ratio, with the three early-born young females each breeding later in the summer.

The actual rate of increase achieved in a given year depends of course on the interaction of productivity and mortality, but the general consequences of this breeding strategy on a game estate may be illustrated as follows.

In the present samples, between June and August the *newly independent young females had several times the* numbers and only half the mortality of the adult females (Tab 4). From Tab. 6 and Deanesly (1944) we may assume that both young and adult females are able to breed late in the season when conditions are favourable. Hence, the potential breeding stock in late summer contains many more females aged 3–4 months than 15 or more months of age, and it follows that, unless there is a gross increase in litter size with age, the greatest number of weasels comprising a peak population must have been produced by the early-born young females. The season of high mortality imposed by gamekeepers has largely passed by June (Fig. 1) and in any case affects mostly males; thus, the improved survival and precocity of the young females in summer ensures that the weasels killed in the spring trapping campaign can be more than replaced by autumn, certainly in years when rodents are abundant, and perhaps in most years. These preliminary results suggest that the traditional practice of weasel control on English game estates is probably effective only in the short term, if at all.

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