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The ecology of weasels (*Mustela nivalis*) on mixed farmland in southern England

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As part of a programme of research into the effects of cereal farming on wildlife, we investigated habitat use by weasels (*Mustela nivalis*) on mixed farmland. Three female and seven male weasels were radio-tracked. Weasels on arable land were exclusively diurnally active, perhaps in response to higher predation risk at night. Females and sub-adult male weasels had smaller ranges than did adult males, but all ranges were unusually large, probably as a result of low prey densities. Weasels rarely traveled more than 5 m from linear habitats, which were composed mainly of woodland edge and hedge with ditch. These habitats were relatively rich in small mammals. Heavier males had lower densities of linear habitats in their ranges than did lighter males, but larger absolute amounts of woodland edge. The proportion of linear habitat used by male weasels decreased with an increase in percentage and density of woodland edge available within their range. In contrast to females, males rarely entered the woodland. Differences between males and females in habitat use may be due to differences in their size-related ability to exploit small rodent prey.

Key words: weasel, *Mustela nivalis*, farmland ecology, home range, movement patterns.

Introduction

As part of a wider programme of research centering on wildlife in the cereal ecosystem (Macdonald et al., 1993), we studied the ecology of the weasel (*Mustela nivalis* L., 1766) on farmland in Oxfordshire. Previous studies of weasels living in Oxfordshire woodland (King, 1971, 1975; Hayward, 1983) showed that they made use of adjoining arable land, and in some areas weasels used farmland almost exclusively (Pounds, 1981; Moors, 1975).

Small rodents are a major part of weasel diet (Day, 1968; Tapper, 1979; King, 1980, 1991), and prey availability is an important determinant of weasel density and habitat use. In woodland, densities of wood mice (*Apodemus sylvaticus* L., 1758) are usually up to 40 ha^{-1} (Flowerdew, 1991), and in Oxfordshire the combined density of wood mice and bank voles (*Clethrionomys glareo-*

lus Schreber, 1780) in woodland ranges from 10–52 ha^{-1} (Southern & Lowe, 1982). Densities of wood mice on farmland tend to be lower: Green (1979) recorded densities of 8.4–17.5 ha^{-1} in summer and 0.5 ha^{-1} in winter, and on three arable fields within our study area Tew (1991) found mean annual density of 2.57 ha^{-1}. Furthermore, densities of wood mice vary through the crop cycle as cover and food increase in open fields during spring and summer and then decrease after harvest (Todd et al., 2000) Differences between woodland and farmland in prey availability and protection from predators might be reflected in differences in the ecology of weasels in these two broad environments.

We were interested to know whether weasels were influenced by farming practices through their use of different components of the cereal ecosystem, and if so, how they were influenced. Live-trapping, radio-tracking, data-logging and direct observations were used to estimate weasel densities and to study range size, activity patterns and hunting behaviour.

Material and methods

Weasels were studied on approximately 210 ha of arable farmland and woodland at Wytham, Oxfordshire, UK (OS Ref 47200 09700), 51°46′12″ N, 01°19′58″ E). Within the study area some arable fields had 5 m margins subjected to a variety of sowing and mowing regimes (Smith et al., 1993). Concurrent research on wood mouse ecology (Macdonald et al., 1993) was carried out on three contiguous arable fields totalling 13.4 ha within our study area. Stoats (*Mustela erminea* L., 1758), a potential competitor of weasels, were absent.

Weasels were live-trapped in custom-built marine plywood boxes of 410 × 100 × 95 mm, fitted with standard 130 mm Longworth trap tunnels. Traps were lined with cotton wool, baited with dead laboratory mice, and covered with a plastic bag as waterproofing. 30–40 traps were placed in suitable sites, and pre-baited for seven days. Thereafter they were set and subsequently checked at 12 h intervals. Trap success was best when entrances were marked with either rabbit puree or male weasel anal sac secretions. Successful traps were taken to a warm room where captured weasels were anaesthetised with 3–6 ml of inhalant Metofane (Methoxy fluorane) (C–vet Ltd, Bury St Edmunds, UK), administered on cotton wool placed within the trap. The animal's reaction throughout the procedure was observed through a Perspex plate in the trap. Anaesthesia was induced within 10 min in males weighing 125 g. Anaesthetised animals were given an individual ear-tag and fur-clip, weighed, sexed and radio-collared. Weasels were aged as adult or sub-adult on the basis of weight, wear on canine teeth, body length and time of year. Males normally attain adult weight of 106–131 g at 3–6 months, while females reach adult weight of 55–69 g at 3–4 months, although young born later in the year develop slower than those from earlier litters (King, 1989; East & Lockie, 1964, 1965).

Three female and seven male weasels (including three sub-adults) were successfully radio-tracked. Two types of radio-collars were used: Biotrack (Dorset, UK); and Holohil Systems Ltd (Ontario, Canada). Radio-collars for males weighed 4–4.5 g, while females' radio-collars weighed 2–3 g. Although Biotrack's radio-collars for males and both Holohil radio-collars had whip aerials, these were usually lost within hours; Holohil radio-collars also had a built-in collar-loop aerial. Without their whip aerials the radio-collars had a claimed maximum range of 250 m although in field conditions the normal range was ca. 50 m. Mariner model 57 receivers (Mariner Radar, Lowestoft, UK) were used with a hand-held 3 element Yagi antenna. Fixes were taken every 10 min. The tracked weasel was located initially by progressive triangulation (i.e. the tracker progressively homed-in on the weasel by quickly taking a succession of bearings from strategic locations) and thereafter the weasels, which rapidly habituated to the presence of the tracker, could readily be pinpointed to within 5 m as they were tracked continuously from a range of 5–50 m.

No radio-tracking data were collected for the first 24 h after a radio-collar was fitted in case movements were atypical. In total 5,091 fixes were obtained during 852 h over 103 days during 1991 and 1992. Data were obtained for males in 11 months (January–November), and for females in five months (May–October). Individuals were not tracked simultaneously. Each weasel was tracked for between 2–18 days (mean = 10.2 ± 5.5), or 10–130 h (mean = 84 ± 51.6). Radio-tracking was confined to daylight as data loggers (Grants Instruments, Cambridge, Ltd, Barrington, UK) left near known weasel nests indicated there was no nocturnal activity.

Home range areas were calculated as minimum convex polygons (MCP) and restricted polygons (RP) using the Wildtrak computer software (Todd, 1992). Linear strip (LS) home ranges were plotted and measured by hand where appropriate. LS ranges were defined as 10 m wide strips following landscape features used by weasels, plus additions for any open areas exploited.

Results

Body weights

Mean weight of four adult males was 111.3 g ± 12.9 (mean ± SD) (range = 100–128 g), mean weight of four subadult males was 90.8 g ± 3.8 (range = 86.5–96 g), and mean weight of five adult females was 58.4 g ± 9.6 (range = 48–69 g).

Table 1. Home ranges (ha) of weasels at Wytham, Oxford, calculated by three methods: minimum convex polygon (MCP); restricted polygon (RP); and linear strip (LS).

Ind.	MCP	RP	LS	H	Season
F1	27.9	13.5		120.5	Summer
F2	4.5			177	Summer
F3	29.2	13.1		102	Autumn
M1	116.4	59.9	7	130.2	Spring
M2	58.5			30	Summer
M3	192.6	108.5	9.2	57	Summer
M4 (s)	21.2	4.7		44	Summer
M5	85.5	77.2	7.7	106.5	Autumn
M6 (s)	21.6	15.5	2	10.5	Spring
M7 (s)	12.1	4.8	1.2	64.5	Autumn

Key: F – female, M – male, (s) – subadult; H – hours of radio-tracking data.

Range size

Range sizes were estimated for all radio-collared weasels (Tab. 1). For the three females (including breeding Female 2, which had a very small range within woodland rather than arable land), mean MCP range was 21 ± 14 ha. For the two non-breeding females alone mean MCP range was 28.6 ± 0.9 ha. Mean MCP range size for the three subadult males was 18.3 ± 5.4 ha, smaller (although not statistically significantly) than mean range sizes for females; however, subadult Male 6 was only tracked for 10 h over 2 days, and thus the estimate of his range is incomplete. The four adult male weasels had the largest mean MCP range size (113.3 ± 57.9 ha), which differed significantly from those of subadult males ($t = 3.27$, df = 3, $P = 0.047$) and those of adult females ($t = 3.09$, df = 3, $P = 0.05$). Daily MCP ranges varied widely: for males mean daily MCP range was 22.3 ± 34.4 ha (range = 0.03–83.1 ha, $n = 7$), while for females the mean was 58 ± 27 ha (range = 38–88.7 ha, $n = 3$). MCP methods overestimated areas exploited on farmland because weasels rarely moved more than 5 m from field boundaries or other linear habitats. RP measures of range size gave smaller values: 13.3 ± 0.3, 8.3 ± 6.2 and 81.9 ± 24.6 ha for non-breeding females ($n = 2$), subadult males ($n = 3$) and adult males ($n = 3$), respectively. However, mean LS ranges are probably most meaningful in this case. Mean LS ranges were 1.6 ± 0.6 ha for subadult males ($n = 2$) and 8.0 ± 1.1 ha for adult males ($n = 3$). Our samples were too small to categorise the analyses by season.

Range composition

Six major types of linear habitat were used by weasels: plain hedge, hedge with ditch, fence, drainage ditch, wood edge and riverbank. Linear habitat within the study area totalled 20,644 m, at a density of approximately 100 m ha^{-1}. The largest component of linear habitat in the study area was hedge with ditch (31.7%; Tab. 2) followed by riverbank (19.4%); fence made the smallest contribution (6%) to linear habitat within the landscape. Of the six available linear habitats, only hedge with ditch and woodland edge were present in every weasel MCP range (Tab. 2). Riverside habitats were present in only three ranges, and ditches in five.

Table 2. Composition of linear habitat (%) within the landscape (A) and within weasel MCP ranges (F1–3 and M1–7).

Ind.	H	HD	F	D	W	R	Total length (m)
A	13.3	31.7	6	14.5	15	19.4	20644
F1	11.3	58.2	2	0	28.5	0	2436
F2	0	19.5	0	0	80.5	0	899
F3	2	57	6.8	0	34.2	0	2647
M1	8.3	60.2	0.6	5.3	17.1	8.6	9171
M2	8.7	41.3	10.8	6.2	33	0	4533
M3	14.7	39.2	5.2	14	17.3	9.7	14638
M4 (s)	12.2	63.9	0	0	24	0	2267
M5	9.9	34.4	5.5	24.9	15.5	9.8	8626
M6 (s)	9	59.6	7.6	10	13.9	0	2835
M7 (s)	0	74.3	12.1	0	13.6	0	1475

Key: F – female, M – male, (s) – subadult. Habitat was classified as: H – hedge, HD – hedge with ditch, F – fence, D – drain or open ditch, W – woodland edge and R – riverbank.

Table 3. Percentage of linear habitats available within MCP ranges used by weasels.

Ind.	H	HD	F	D	W	R	Total length (m)
F1	11.6	65.7	0	0	22.8	80	1194
F2	0	25.4	0	0	74.6	0	688
F3	0	61.3	0	0	38.7	0	1870
M1	7.5	63.9	0.8	7.5	9.4	10.8	6421
M2	5.3	54.2	0	6.2	34.3	0	1559
M3	17.6	36.8	4.1	22.3	10.1	9.1	8931
M4 (s)	0	59.9	0	0	40.1	0	754
M5	9.5	33	4.5	27.2	12.9	12.8	6558
M6 (s)	4.4	62.2	0	14.9	18.6	0	1897
M7 (s)	0	88.3	0	0	11.7	0	1179

Key: F – female, M – male, (s) – subadult. Habitat was classified as: H – hedge, HD – hedge with ditch, F – fence, D – drain or open ditch, W – woodland edge and R – riverbank.

Hedge with ditch was the prevalent linear habitat in every range except that of Female 2, whose small range was completely within, or bordering, woodland. Because she was effectively a woodland weasel, Female 2 is not included in the remaining analyses.

Within MCP ranges, hedge with ditch contributed 34.4–74.3% (mean ± SD: 54.2 ± 13, $n = 9$) to linear habitats, while woodland edge contributed 13.6–34.2% (21.9 ± 8, $n = 9$). There were no significant differences between subadult males, adult males and adult females in the percentage of hedge with ditch, or woodland edge (Mann-Whitney U-test, *n.s.*), although this may have been due to small sample size. Within MCP ranges there was a significant positive correlation between MCP range size and total length of linear habitat ($r = 0.987$, df = 7, $P < 0.001$), length (m) of hedge with ditch ($r = 0.944$, df = 5, $P < 0.001$), density (m ha^{-1}) of hedge with ditch ($r = 0.697$, df = 7, $P < 0.05$) and length of woodland edge ($r = 0.951$, df = 7, $P < 0.001$). Range size did not correlate significantly with lengths or densities of any other habitats.

Body weight did not correlate with the density (m ha^{-1}) of MCP range of hedge with ditch, or with the amount of hedge with ditch as a percentage of linear habitat within MCP ranges. However, when females were excluded from the analysis, male body weight correlated inversely with both hedge with ditch density ($r = -924$, df = 5, $P < 0.01$) and hedge with ditch as percentage contribution of linear habitat ($r = -0.874$, df = 5, $P < 0.02$). Amongst males, hedge with ditch invariably made the greatest contribution to the total of linear habitats in each territory, but in the case of the three heaviest males (Males 2, 3 and 5) the proportion comprised of hedge with ditch was lower than for the four lighter males. This is linked to the fact that the absolute amounts of woodland edge increased with male body weight ($r = 0.842$, df = 5, $P < 0.01$). In effect, heavier males operated along woodland edge, whereas lighter males made more use of hedge with ditch. No other correlations between range size, body weight or habitat composition were statistically significant.

Use of linear habitats

Linear habitat use was measured as the percentage of linear habitat available within an MCP range along which a weasel was known to have traveled at least once (Tab. 3). The mean length of linear habitat used by the two non-pregnant females was 1532 m ± 478, while the mean length used by subadult males was 1277 m ± 577. However, the four adult males used, on average, over four times as much linear habitat, with a mean of 5867 m ± 3095. The length of linear habitat used increased significantly with MCP range size ($r = 0.987$, df = 7, $P < 0.001$) and with the length of linear habitat available ($r = 0.94$, df = 7, $P < 0.001$), but not with body weight.

Weasels used between 33% and 80% of the linear habitat available within their MCP ranges (means = 60% for two females, 60% for three subadult males, and 60.5% for five adult males; Tab. 3). There were no significant differences between percentages of linear habitat used by adult males, subadult males and females. Percentage of linear habitat used did not correlate significantly with MCP range size, body weight or amount of linear habitat available, using data for all animals, males alone, or adult males alone. The percentage of linear habitats used by subadult and adult males, however, decreased with an increase in both percentage and density (m ha^{-1}) of woodland edge

within their ranges ($r = -0.893$, df = 5, $P < 0.01$ for percentage woodland edge; $r = -0.857$, df = 5, $P < 0.02$ for density of woodland edge).

Hedge with ditch and woodland edge, important components of the linear habitat available for weasels, were also important components of linear habitat used by weasels (Tab. 3). Overall, 55% ± 19 of linear habitat used by weasels was hedge with ditch, and 27% ± 20 was woodland edge. There were no significant differences in the percentage contributions made by woodland edge or hedge with ditch to the linear habitats used by adult males, subadult males and females. Indeed four weasels (including the woodland weasel, Female 2) used hedge with ditch and woodland edge exclusively (Tab. 3), despite other linear habitats being available to three of them. Riverside and fence habitats were used only by the three males with the largest ranges, but while riverside habitat contributed a mean of 10.9% to the total linear habitat used, fences contributed only a mean of 3.1%. Fences were used only by weasels when travelling between other habitats.

Unlike females, males very rarely entered the woodland. Female 2 made particularly heavy use of woodland, which covered 40.7% (1.83 ha) of her MCP range. Females 1 and 3 had larger areas, but smaller percentages, of woodland within their MCP ranges: 6.3 ha (22.6%) and 8.4 ha (28.8%), respectively.

Spatial relationships

Successively tracked males occupied overlapping MCP home ranges. Male 5 occupied the north west of the study area in late autumn 1991, and 47.9% of his range was later occupied by 35.2% of Male 1's range, in spring 1992. Later, in summer 1992, Male 3 occupied almost the entire area, covering 99.6% of Male 1's range within a month. Subadult Males 6 and 7 covered smaller ranges, largely within those of adult males, and possibly concurrently so. 79.3% of Male 7's range formed 11.2% of Male 5's range when he was radio-tracked a month after Male 5's radio failed. Male 6's range fell wholly within that of Male 1, and it seems highly likely that they were active concurrently.

Occasionally more than one animal was collared at a time. Aggressive interactions between radio-tracked males and unknown individuals were heard on three occasions, and the corpse of an unknown male was found in July. The last time that Male 4 was detected, he was observed fighting with an unknown male in a barley stubble field. Although Males 1 and 6 carried radio-collars concurrently, they were never observed together, possibly because their ranges overlapped only slightly. Male 2, hunting along a hedge in late May, apparently encountered Female 1 at 19.00 h, asleep in a burrow. Radio signals indicated that she awoke, and that he remained close to her for 30 min before moving on.

Table 4. Activity budgets (% time observed) for weasels, obtained using constant data-logging and radio-tracking.

Ind.	Days obs.	Sleep a	Inactive b	Active	Travelling
F1	4	51.7	16.2	20	12.1
F2	2	6.9	17.5	63.5	12.1
F3	7	46.9	29.4	15.6	8.1
M1	8	55.1	24.3	10.7	9.9
M3	2	66.9	14.1	9	10
M5	8	65.2	23.8	6.6	4.4
M7	5	47.5	32.6	14.1	5.9

Key: a – recorded as time spent resting/asleep in nest; b – recorded as time spent inactive outside nest.

Behaviour

Activity budgets were recorded for seven weasels (four males and three females) over a total of 36 days for which data were complete (Tab. 4). On average weasels spent nearly half their time (48.6% ± 20) apparently sleeping or resting. Time out of the nest was spent mainly inactive (mean = 22.6% ± 6.9) or locally active (mean = 19.9% ± 19.7). Least time was spent travelling, on average 8.9% ± 2.9.

An exception to the general pattern of activity was breeding Female 2 which, over two days, spent only 6.9% of her time asleep, and spent 63.5% of her time active out of her nest. Most of her local activity was near a nest believed to contain her litter. There was a tendency for animals tracked during the autumn (Female 3 and Males 5 and 7) to spend less time travelling, and more time either asleep or inactive, out of the nest, than animals tracked during spring and summer.

Weasels were observed hunting along linear features such as hedge bottoms, field margins and tracks, as well as areas such as gardens, farm tips, and straw bales in a barn. Under cover, such as along a hedge bottom, weasels travelled at 3–5 km h^{-1}, increasing to approximately 10 km h^{-1} in the open.

Weasels were occasionally seen digging to capture wood mice; one individual was observed digging for nearly 30 min in a stubble field before flushing a wood mouse, which it eventually caught

in another burrow. On arable land, but not woodland, weasels frequently climbed in hedges and mature trees, and we observed one eating blackbird (*Turdus merula* L., 1758) eggs. Carrion was also taken – the remains of a mute swan (*Cygnus olor* Gmelin, 1789) were eaten over several days.

Discussion

MCP ranges of weasels on farmland at Wytham were up to 192 ha in area, far larger than those recorded by MOORS (1974) on a mixed arable and pasture farm with stone wall or fence boundaries, or recorded by POUNDS (1981) on arable land, rough grassland and sand dunes However, LS measures may be a better reflection of range use by the weasels at Wytham. LS ranges were much smaller than those calculated using MCPs and were more similar to other studies. KING (1975) found that female weasels in woodland at Wytham had ranges of 2–4 ha, while males had larger ranges of about 11.5 ha. Lower densities of prey in arable land may require weasels to have larger home ranges than weasels in woodland (LOCKIE, 1966; ERLINGE, 1974; HAYWARD, 1983), and in our study the one woodland weasel (Female 2) had the smallest range recorded (although this may also have been because she was rearing young).

Large adult males in farmland at Wytham had ranges 3–6.5 times larger than those of adult females. This difference parallels the results of MOORS (1974) and POUNDS (1981). Smaller female ranges have also been reported by KING (1975) and by ROBITAILLE & RAYMOND (1995). The three subadult males had small ranges largely contained within the ranges of adult males, although our data are insufficient to reveal seasonal trends. The apparent tendency for the entire or almost entire range to be usurped quickly by other males is in accord with other studies: KING (1975) found that neighbours or non-residents would quickly take over an empty territory.

Linear habitats, particularly hedge with ditch and woodland edge, were clearly important to farmland weasels. Hedgerow is one of the most prey-rich arable habitats available to hunting weasels (ARNOLD, 1983; TATTERSALL et al., 2001, 2002), and rodent nests are found, in, or close to, hedges with and without ditches, and along woodland edges. In summer, when the crop was up, bank voles and wood mice at Wytham ranged widely in the fields. After harvest, bank voles used hedgerows exclusively, but while wood mice predominantly used hedgerow, a few remained in the fields (TEW et al., 1994), mostly close to the field margin.

Larger male weasels had a lower density of linear habitat within their ranges than did smaller males, and hedge with ditch formed a smaller proportion of linear habitat available within their MCP ranges; these differences were not a result of range size. Differences in range size and composition between males and females, and between larger and smaller males, might have resulted because larger male weasels find it hard to enter small rodent burrows, and therefore have different foraging tactics to smaller weasels.

The diurnal activity pattern of weasels on Wytham farmland contrasted with the more usual arhythmic patterns of regularly spaced short activity periods throughout 24 hours (KING, 1991). Weasels may have restricted their nocturnal activity because the risks from nocturnal predators were greater than the risks from diurnal predators (LIMA & DILL, 1990). FENN & MACDONALD (1995) document a case of rats (*Rattus norvegicus* Berkenhout, 1769) at Wytham which were unusually diurnal in response to predation by nocturnal foxes. Nocturnal predators of weasels were present at Wytham: tawny owls (*Strix aluco* L., 1758) (SOUTHERN, 1954, 1969; KORPIMAKI & NORDAHL, 1989) regularly hunted the study area, and mammalian predators (LATHAM, 1952; GAUGHREN, 1950) such as foxes (*Vulpes vulpes* L., 1758) and cats (*Felis catus* L., 1758), were common. Furthermore, there was little evidence of diurnal predators; in 103 study days there were only six sightings of kestrel (*Falco tinnunculus* L., 1758) or sparrowhawk (*Accipiter nisus* L., 1758), both known to take weasels (KORPIMAKI & NORDAHL, 1989; SULKAVA, 1964). However, we found no evidence that weasel activity patterns changed through the seasons as vegetation cover, and presumably also the risks from predation, changed.

Alternatively, diurnal activity may have been an effective strategy for weasels hunting wood mice, which spend daylight hours in burrows where they are largely defenceless (KING, 1991), unable to use their effective climbing and freezing escape behaviour (ERLINGE, 1975).

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