

Summertime activity patterns of common weasels *Mustela nivalis vulgaris* under differing prey abundances in grassland habitats

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Weasels *Mustela nivalis* Linnaeus, 1766 in Kielder Forest, UK showed a diurnal rhythm of activity in summer and we argue that this is the prevailing rhythm found in weasels under natural conditions. Climatic conditions influenced weasel activity with weasels decreasing activity under rainy conditions, but we found no influence of month or weasel weight. In certain habitat types levels of weasel activity increased with increasing field vole *Microtus agrestis* density. This result stands in contrast to results from studies carried out in the laboratory and may reflect a greater proportion of time spent in reproductive activity and intra-specific interactions in areas where vole density, and hence conspecific density is high.

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Introduction

Mammals divide their time budgets between activities such as foraging, mate acquisition, resting and predator avoidance. If for example food becomes harder to earn, overall activity might increase as a result of animals increasing the time spent foraging and reducing the time spent resting. Being highly specialised on hunting small rodents, weasels *Mustela nivalis* Linnaeus, 1766 are a good species to investigate how time budgets of a predator vary with prey availability. This knowledge would also be helpful to gain more detailed results from methods where measurements of mustelid activity are used for inferring mustelid abundance. Little is known about activity patterns of weasels and existing information is

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contradicting. Some studies reported that weasels show a diurnal rhythm of activity, whereas others reported a nocturnal one. Little information is available on the factors that might influence the patterns and duration of weasel activity.

Several factors have been shown to influence mustelid activity such as differing foraging costs (eg Zielinski 1988, Samson and Raymond 1995, Zalewski 2000), climatic conditions (eg Robitaille and Baron 1987, Jędrzejewski *et al.* 2000), age and condition (eg Zielinski *et al.* 1983) and prey behaviour and density. The information on the latter is, however, limited and somewhat contradictory. Sundell *et al.* (2000) observed that least weasel activity was highest at vole densities of 8 voles per ha and declined at densities of 12 voles per ha, probably because hunting became more efficient. This was consistent with Price's (1971) and Zielinski's (1988) observations that captive weasels increased their total activity in response to food deprivation. In contrast, there was little detectable influence of rodent densities ranging from 8 up to 300 voles per ha on the activity of common weasels radio-tracked in a deciduous forest (Jędrzejewski *et al.* 2000).

Weasels and stoats have been found to be diurnal in most studies (King 1975, Samson and Raymond 1995, Sundell *et al.* 2000, Jędrzejewski *et al.* 2000, Macdonald *et al.* 2004), although Zielinski (1988) reported that captive weasels were most active at night while others observed seasonal shifts in stoat activity (Erlinge 1980, Debrot *et al.* 1985). Erlinge (1980) also reported a shift by stoats towards more diurnal activity in summer, coinciding with the onset of mating behaviour. Jędrzejewski *et al.* (2000) proposed that the diurnal activity rhythm of weasels is caused by a higher predation risk during the night due to a higher abundance of nocturnal predators. As no quantitative link has been established between variation in predation risk and weasel activity rhythms, the evidence must be considered as tentative. On the other hand, Zielinski (1988) argued that the nocturnal activity of weasels is linked to the largely nocturnal behaviour of forest-dwelling *Clethrionomys* voles and mice. Accordingly, weasels preying on mostly diurnal voles may be less nocturnal.

The aims of this study were to investigate how different field vole, *Microtus agrestis*, densities influence weasel activity and to gain more information on other factors that may influence weasel activity rhythms. We expected weasels to spend more time being active and have longer activity periods with decreasing vole density.

Study area

The study was carried out in Kielder Forest (55°13'N, 2°33'W), Northumberland, UK, a large man-made coniferous forest managed for commercial timber production. The dominating tree species are Sitka spruce *Picea sitchensis*, Norway spruce *Picea abies* and Larch *Larix* spec. The area is managed by rotational clear felling which leaves large clear fell patches of varying ages with many clear-fells dominated by grasses, mainly *Deschampsia cespitosa*, *Agrostis tenuis* and *Juncus effuses*, 3 years after felling onwards. The dominant rodent species is the field vole *Microtus agrestis*, but bank voles *Clethrionomys glareolus* and wood mice *Apodemus sylvaticus* also occur. The most abundant

predators are red foxes *Vulpes vulpes*, common buzzards *Buteo buteo* and tawny owls *Strix aluco*. Vole density varies widely between clear fell patches (Lambin *et al.* 1998, 2000).

Material and methods

Live trapping, handling and radio-tracking of weasels

We selected clear cuts where felling had taken place more than 5 years ago and which were dominated by *Deschampsia caespitosa* and *Juncus effusus*. Weasels were live-trapped using wooden flip-door boxes, built following King (1973) and baited with fish, saw-dust soiled with vole urine, straw and in addition pieces of carrot for rodents caught incidentally. Traps were spaced evenly throughout the study area with a distance of about 50 m between traps. Where possible traps were placed in vole runs or close to linear features such as ditches, stone walls or fences. Clear-fells, where weasel trapping was carried out, varied between 10 and 50 ha in size. Traps were checked daily. Animals other than weasels were released and weasels were returned to the laboratory for handling. Date, site and trap number were recorded for each weasel and all other vertebrates caught. Weasels were anaesthetized in the laboratory with 1–2 ml Halothane. Under anaesthesia, a skin biopsy and a hair sample were taken and a PIT-tag injected underneath the skin of the neck. Body length and weight were measured and tooth wear recorded as a relative age indicator. Weasels were sexed from external appearance. Radio collars (Biotrack, Dorset, UK) weighting between 3.5 and 4.5 g (about 4% of the weasels' body weight) were fitted around the weasels' neck. Weasels were then kept in a holding tank, given a dead field vole and released 12–24 hours later, after they had eaten the vole. Signal range of the radio transmitter was between 100 and 400 m depending on terrain and vegetation. Weasels were usually followed at a 10–30 m distance. Following weasels at such close distance had no obvious impact on their behaviour. Weasels were followed continuously and fixes were recorded at 15-minute intervals using a GPS Garmin 12. Weasels were tracked until either the transmitter failed or contact was lost. The location error, as indicated by the GPS, ranged around 10 m. Habitat type for each location was recorded by visually scoring grass cover (including sedges) in a 5 m radius around the weasel. Habitats were classified into 5 types depending on how much grass they provided. These types were as follows: Type 1: 0–20%, Type 2: 21–40%, Type 3: 41–60%, Type 4: 61–80%, Type 5: 81–100% grass cover. For each fix we also recorded whether a weasel was active or inactive during the last 15 minutes. Activity was defined as locomotory activity in that weasels were considered to be active if they had changed location at least once during the time interval. We recorded the weather as four categories: sunny, cloudy, drizzly and rainy.

In total, we radio-tracked nine male common weasels, one of which was tracked in June 2001 and 8 of which were tracked between April and September 2002. While tracking these nine weasels, we obtained a total of 2331 fixes over 59 days. Tracking was curtailed by premature radio failure for at least 4 of these weasels. Details on each weasel's capture dates, radio-tracking periods and biometrics are given in Table 1.

Measuring field vole density

To gain an estimate of field vole density within a clear fell patch, we followed the grass-clipping-based method described by Lambin *et al.* (2000). We searched 25 randomly placed quadrats (25 × 25 cm) for the presence or absence of fresh grass clippings, which are the most reliable signs of field vole presence. Vole signs were recorded within the optimal field vole habitat (corresponding to habitat types 4 and 5 above) of a clear fell patch. This vole sign index (VSI) was then converted into numbers of voles per ha using a calibration method based on live-trapping data and explaining 67–72% of the variance in vole densities (Lambin *et al.* 2000). Vole density estimates were obtained every month on each site except for the site where weasel no. 8 was tracked. In the analyses below, we used the field vole density estimate that was closest to the period at which weasels were tracked to a maximum interval of four weeks.

Table 1. Summary of biometrics, tracking period, vole density and fate of male weasels radio-tracked in this study. Weasel no 7a and 7b refer to the same individual tracked during two different time periods.

Weasel ID	Weight (g)	Body length (mm)	Period tracked	Days tracked	Vole density (voles / ha)	Fate
1	110	272	26.6.–12.7.2002	17	151	disappeared
2	158	268	19.7.–23.7.2002	5	193	radio failure
3	114	255	19.8.–26.8.2002	7	123	probable radio failure
4	97	242	11.9.–27.9.2002	11	161	radio failure
5	102	273	7.8.–13.8.2002	7	66	radio failure
6	106	233	29.4.–5.5.2002	4	81	disappeared
7a	135	238	25.7.–26.7.2002	2	38	collar slipped off
7b	120	261	6.9.–7.9.2002	2	94	died
8	58	200	18.9.–24.9.2002	8	151	taken by raptor
9	116	280	20.6.–27.6.2001	6	128	disappeared

Data analysis

For analysis of daily activity fixes were pooled by hour with the hour 01:00 including fixes taken at 00:15, 00:30, 00:45 and 01:00. The percentage of fixes whilst active during each hour tracked was plotted against time (Fig. 1).

To calculate the mean duration of activity bouts we only included periods when weasels were inactive for at least 15 minutes before and after active bouts. For the analyses of the duration of activity during the day and the mean number of activity bouts, only days with a minimum of 10 hours of radio tracking were included.

Activity data were tested for serial autocorrelation and re-sampled by omitting every second data point until no significant ($p < 0.05$) autocorrelation was found. Since the response variable was binary [active (1) or non active (0)], logistic models with a logit link and a binomial error term were fitted in a step down stepwise fashion until all remaining covariates were significant. We first included all variables considered as “sampling noise” (month, time of day and weasel weight) in the model and then removed non-significant variables stepwise. We chose the model with the smallest Akaike’s information criterion (AIC) as the best model. If the difference in the AIC between models was smaller than 2, we selected the most parsimonious model. We then added all biologically relevant explanatory variables to this “sampling noise model” and again excluded non-significant variables in a stepwise fashion. Explanatory variables considered were vole density, habitat type and weather. Time of day was included as Hour² to allow for a quadratic relationship between activity and time of day in the model. The model with the smallest AIC value differing from any other models’ AIC by at least 2 was then considered as the best model, as recommended by Anderson *et al.* (2000). One weasel tracked in 2002 could not be included in the analyses of factors influencing weasel activity, as it lacked data on habitat and weather.

Results

Patterns of weasel activity

Male weasel activity, pooled over all individuals, increased in the morning and abruptly ceased in the evening after 22:00 hrs. Only in one weasel (no. 5) did we observe three occasions of extended activity after sunset, each lasting for about one

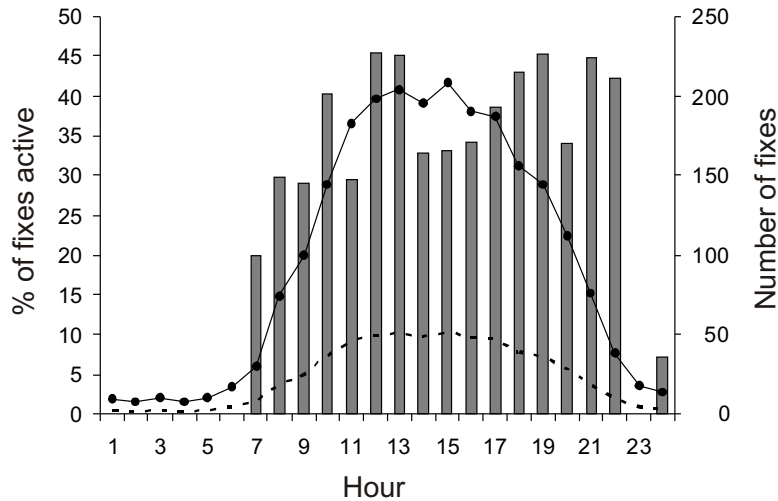


Fig. 1. Weasel activity in Kielder Forest. Bars show the percentage of 15-minute intervals at which weasels were found to be active plotted by hour of the day. The dotted line represents expected number of fixes active if activity was evenly spread over the day. Points connected by a solid line represent the sample size of periods gained per given hour. Hour 0 includes fixes at 23:15, 23:30, 23:45 and 00:00.

hour. Activity was evenly distributed throughout the daylight period (Fig. 1). There was a slight decrease in activity in the early afternoon between 13:00 hrs and 16:00 hrs and in the early evening between 19:00 hrs and 20:00 hrs. The observed activity differed, however, from what would be expected under an even distribution over the 24 hour-day ($\chi^2 = 198.2$, $df = 23$, $p < 0.01$). The distribution of the proportion of beginnings of activity bouts per fixes inactive and endings per fixes active shows that only few bouts started after 21:00 hrs, in contrast to many ending at that time (Fig. 2). Neither beginnings nor endings were evenly distributed over the day ($\chi^2 = 114.9$, $df = 23$, $p < 0.01$ and $\chi^2 = 105.6$, $df = 23$, $p < 0.01$).

Three weasels were tracked during the hours of darkness on one occasion each. They were inactive at all but one fix ($n = 94$ fixes during three nights) when one weasel just slightly changed its location by ca 20 m before becoming inactive again. In contrast there was only one out of all 59 days of radio tracking during daylight when a weasel was totally inactive.

On most days weasels had several short activity bouts (mean: 3.7 bouts, $SD = 1.9$, range: 1–7, $n = 20$) separated by short periods of inactivity. Activity bouts lasted on average 1.2 hours (0.25–6.25 hr, $SD: 1.01$, $n = 112$) and inactivity periods, separating activity bouts during the day, 1.3 hours (0.25–6 hr, $SD = 1.15$, $n = 89$). Out of 21 days including data from 7 weasels (the other three were only tracked for less than 10 hours per day), we calculated a mean of 4.84 hours (0.25–8.5 hr, $SD = 2.32$, $n = 21$) spent active per day.

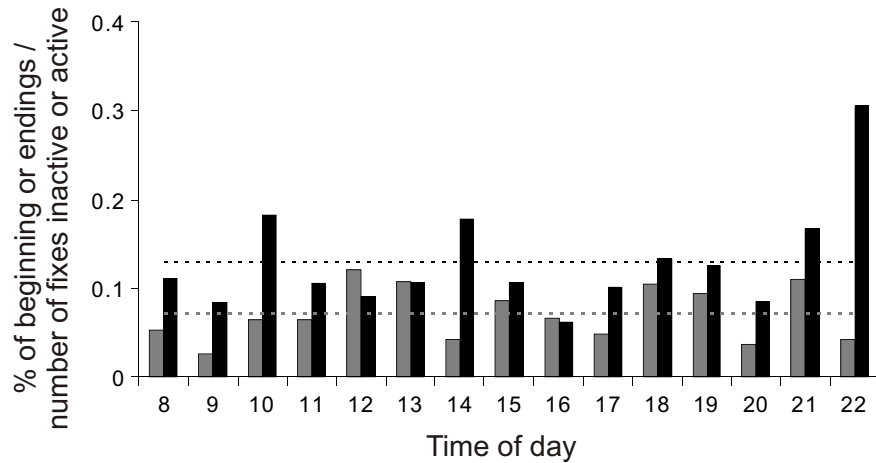


Fig. 2. Shown are the beginnings of weasel activity bouts as percentage of fixes where weasels were found inactive (light bars) and endings of activity bouts as percentage of fixes where weasels were found active (dark bars). Light and dark spotted lines represent expected values for beginnings and endings of activity periods for an even distribution respectively.

Factors influencing weasel activity

We found a statistically significant positive autocorrelation for a 15 minute lag (regression coefficient = 3.18, SE = 0.16, $df = 1$, $p < 0.01$) but no statistically significant correlation for a 30 minute lag (regression: coefficient = 0.346, SE = 0.20, $df = 1$, $p = 0.08$). We therefore re-sampled the data set and excluded every second data point for the subsequent analysis.

Of the variables initially entered in the model predicting weasel activity, weight was not retained (Table 2). Month and hour were retained in the initial model including only noise variables but their contribution became non-significant when biologically relevant explanatory variables were entered (Table 2). The overall model was significant ($\chi^2 = 122.82$, $df = 13$, $p < 0.01$) and explained 63.4% of the variance in the data. It included prey density, habitat type, weather as well as the interaction between habitat and vole density (Table 2). Surprisingly, the relationship between absolute prey density and the weasel activity level was positive (Table 3, Fig. 3) with male weasel activity increasing with vole density faster in habitat with intermediate grass cover (habitat 3 and 4) than in the habitat with the highest and lowest grass cover (habitat 5 and 2). The coefficient of the effect of vole density in the habitat with the least grass cover (habitat 1) could not be computed due to few data for this habitat. The overall influence of weather on weasel activity mostly reflected the fact that weasels spent most time active under sunny conditions and least time active under rainy conditions (Table 3, Fig. 4).

Table 2. AIC values for the different models including noise variables and fixed factors. Δ AIC gives the difference of the each models' AIC to the AIC value of the best model.

Model	DF	AIC	Δ AIC
Month, Hour ²	2	1538.9	0
Month	1	1539.8	0.9
Month, Weight	2	1540.1	1.2
Hour ²	1	1542.5	3.6
Hour ² , Weight	2	1544.5	5.6
Weight	1	1545.6	6.8
Month, Hour ² , Weight	3	1559.2	20.3
Month, Hour ² , weather, vole density, habitat, habitat \times vole density	13	1333.1	0
Month, Hour ² , weather, vole density, habitat	10	1362.1	29.0
Month, Hour ² , vole density, habitat	7	1371.2	38.1
Month, Hour ² , weather, habitat	9	1380.5	47.4
Month, Hour ² , habitat	6	1386.6	53.5
Month, Hour ² , weather, vole density	7	1514.5	181.4
Month, Hour ² , vole density	3	1524.9	191.8
Month, Hour ² , weather	6	1531.6	198.4

Table 3. Results of logistic regression testing factors influencing weasel activity. Habitat 5 and rainy weather are reference points included in the intercept of the model. Coefficients and interaction terms for the other levels of habitat and weather variables denote the amount by which they deviate from the reference levels.

Variable	B	SE	df	<i>p</i> -value	Exp (B)
Intercept	-1.6630	0.6830	1	0.02	
Month	-0.0544	0.0626	1	0.39	0.9470
Hour2	0.0011	0.007	1	0.10	1.0011
Vole density	0.0062	0.0026	1	0.02	1.0063
Habitat			4	0.00	
Habitat 1	6.6846	7.0072	1	0.34	800.0293
Habitat 2	3.7650	0.9047	1	0.00	43.1644
Habitat 3	0.3451	0.7065	1	0.63	1.4122
Habitat 4	-0.9505	0.5788	1	0.10	0.3866
Weather			3	0.00	
Weather sunny	0.7386	0.3183	1	0.02	2.0930
Weather cloudy	0.3491	0.2773	1	0.21	1.4177
Weather drizzly	-0.8515	0.4496	1	0.06	0.4268
Vole density	0.0062	0.0026	1	0.02	1.0063
Habitat \times vole density			3	0.00	
Habitat 2 \times vole density	-0.0289	0.0065	1	0.00	0.9715
Habitat 3 \times vole density	0.0041	0.0050	1	0.41	1.0042
Habitat 4 \times vole density	0.0109	0.0042	1	0.01	1.0109

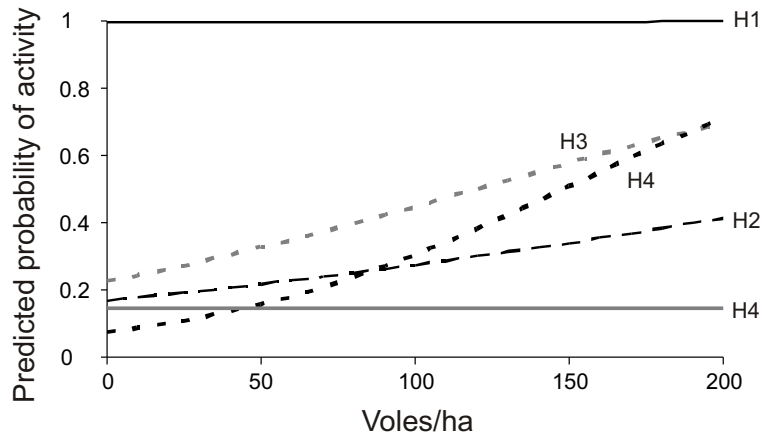


Fig. 3. Weasel activity in relation to field vole density in differing habitat types as predicted from logistic regression model (habitat type: 1 – dark solid line, 2 – dark broken line, 3 – light dotted line, 4 – dark dotted line, 5 – light solid line). The interaction for vole density and habitat 1 could not be computed but was still included without considering an interaction term.

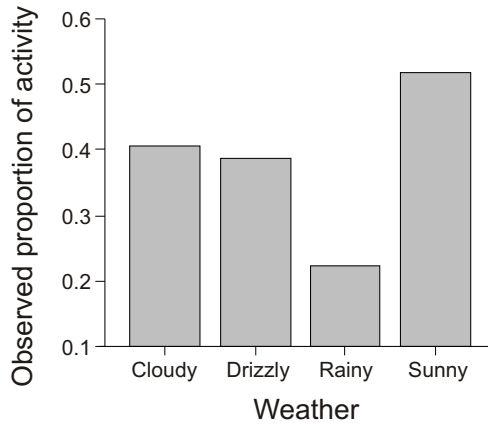


Fig. 4. Proportion of 15 min intervals at which weasels were found to be active plotted by weather conditions.

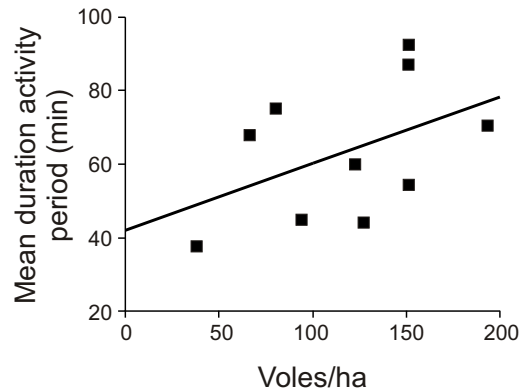


Fig. 5. Mean duration of weasel activity bouts by field voles per ha.

There was no significant relationship between vole density and the mean duration of activity periods ($F_{1,8} = 2.170$, $p = 0.179$, $R^2 = 0.21$), however, the slope estimate suggests a tendency for activity periods to become longer with increasing vole density (slope = $0.18 + 0.12$) (Fig. 5).

Discussion

Male weasels had a diurnal pattern of activity during a summer of high vole density in Kielder Forest, with mobility abruptly decreasing in the evening. The apparent increase in activity after 20:00 hrs, however, is probably an artefact of tracking being interrupted at 20:00 if weasels had ceased to be active, such that samples from 21:00 hrs and 22:00 hrs tended to be biased towards times of weasel activity. In this respect, random sampling would probably have shown a more gradual decrease towards total inactivity at 22:00 hrs. This is further suggested by the fact that only few bouts were started after 21:00 hrs in contrast to many ending after this time. Our observation that weasel activity was quite evenly distributed throughout the daylight period is in line with findings by Jędrzejewski *et al.* (2000) and Sundell *et al.* (2000). This pattern typically observed in weasels and stoats (eg Pounds 1981, Jędrzejewski *et al.* 1995) is usually explained as reflecting the high metabolic costs and the small capacity of the digestive tract in weasels, requiring frequent feeding (Gillingham 1984, Samson and Raymond 1995). The interval of 2.5 hr between beginnings of successive activity periods in this study is indeed similar to the mean of 2.5–3 hr between meals reported by Gillingham (1984). This suggests that activity bouts in fact do indicate foraging activity.

The trade-off between food intake and predation risk ought to influence when foraging is most profitable and so affect the timing of activity. The available evidence for weasels is inconclusive on this and may reflect variation in sampling techniques. In all studies carried out on small mustelid daily activity patterns in the field, weasels and stoats preferred the light phase (Table 4), at least during the summer (King 1975, Erlinge 1980, Pounds 1981, Jędrzejewski *et al.* 2000, Macdonald *et al.* 2004). In contrast, they preferred the dark phase in all studies carried out in captivity even when under equally profitable foraging conditions (Price 1971, Kavanau and Ramos 1975, Zielinski 1988). However, when Zielinski (1988) experimentally manipulated the energy cost of food gain, weasels extended the duration of activity towards the initially non-preferred phases, when food could be earned more easily. Zielinski (1988) suggested that weasels are nocturnal so as to adjust their activity rhythms to that of their prey. However, only *Apodemus* mice are mainly nocturnal (Wójcik and Wołk 1985, Corbet and Harris 1991). Bank voles and *Microtus* voles can be active day and night (Corbet and Harris 1991, Halle and Lehmann 1992). Field voles in cyclic populations in Sweden were mostly diurnal during vole density peaks and nocturnal during population declines (Halle and Lehmann 1992). Weasels, however, need not be strictly constrained to hunting only when voles are active, as they can enter the burrow of small rodents and find them in their nests when they are inactive (Erlinge 1974, Samson and Raymond 1995). The fact that captive weasels in Price's (1971) and Zielinski's (1988) studies were supplied with live mice released into small weasel cages and cat food, respectively, may have lifted the constraint of visibility, such that other factors such as predator avoidance then influenced weasel activity.

Table 4. Overview of existing studies on small mustelid activity.

Species	Months	Habitat	Method	Preferred light phase	Author
<i>Mustela frenata</i>		Indoor chambers	Observation	Dark	Kavanau and Ramos 1975
<i>Mustela nivalis</i>		Indoor chambers	Observation	Dark	Zielinski 1988
<i>M. nivalis</i>		Indoor chambers	Observation	Dark	Price 1971
<i>M. nivalis</i>	September–June	Deciduous woodland	Trapping	Light	King 1975
<i>M. nivalis nivalis</i>	October–November	Outdoor enclosures	Radio-tracking	Light	Sundell <i>et al.</i> 2000
<i>M. nivalis</i>	All months	Deciduous woodland	Radio-tracking	Light	Jędrzejewski <i>et al.</i> 2000
<i>M. nivalis</i>	January–November	Arable farmland	Radio-tracking	Light	Macdonald <i>et al.</i> 2004
<i>M. nivalis</i>	Winter months	Farmland	Radio-tracking	Light	Pounds 1981
<i>M. erminea</i>	February–May	Marsh	Radio-tracking	Light in summer, dark in winter	Erlinge 1980
<i>M. erminea</i>	All months	Field	Trapping	Light in summer, dark in winter	Debrot <i>et al.</i> 1985
<i>M. erminea</i>	May to August	Mixture of woodland, farmland and logging areas	Radio-tracking	Light	Samson and Raymond 1995

We only radio-tracked male weasels during the mating season. Hence we were unable to detect variation that would be related to mate searching by males. Reproductive behaviour probably plays a major role in the activity patterns we found, in that males utilise much available time and energy for reproductive activities. Activity patterns outside the mating season may vary considerably. The detected influence of weather on activity is consistent with thermoregulatory constraints. Weasels may reduce activity in rainy conditions so as to avoid the cost of a wet fur combined with cool temperatures. Sunny conditions probably further reduced heat loss as temperatures in our study never reached 35°C, below which Brown and Lasiewski (1972) found the metabolism of weasels to be inversely related to ambient temperature.

More efficient hunting at high prey density is likely to result in shorter hunting sessions and, if the activity of weasels is mainly determined by hunting behaviour, would result in shorter activity periods and shorter total activity. Comparisons between habitats and experimental studies shed light on this issue. Price (1971) and Zielinski (1988) indeed both described weasels increasing their total activity under food deprivation. Price (1971) argues that this is an adaptive behaviour in weasels as energy demands are high and energy reserves are not available.

Consistent with this suggestion, least weasels in large grass-covered outdoor enclosures hunted voles more successfully at vole densities of 16 voles per ha than at 8 voles per ha and duration of activity bouts tended to decrease at lower vole density (Sundell *et al.* 2000). From a comparison of two studies on common weasel activity it appears that weasels on the clear cuts in Kielder Forest met their food requirements with less effort than weasels in the forest in Białowieża forest in Eastern Poland. The duration of weasel activity periods in Kielder Forest was slightly shorter than found in Białowieża with 1.2 h and 1.8 h respectively (Jędrzejewski *et al.* 2000). The same was true for the duration of short inactivity bouts that lasted on average 1.3 h in Kielder Forest in contrast to 2.0 h in Białowieża (Jędrzejewski *et al.* 2000). The shorter activity periods might be explained by more efficient hunting in Kielder Forest, where weasels mainly fed on abundant field voles. *Microtus* voles are less agile than *Apodemus* mice, which also respond with freezing behaviour as an escape technique more often than *Microtus* voles, resulting in weasels having difficulties to locate them (Erlinge 1975). The most abundant rodent species in Białowieża are bank voles *Clethrionomys glareolus* and yellow-necked mice *Apodemus flavicollis* and weasels were observed feeding on both species (Jędrzejewski *et al.* 2000). Weasels in Kielder Forest primarily feed on *Microtus* with 78% of scats with prey remains ($n = 116$) containing remains of *Microtus agrestis* (X. Lambin *et al.*, unpubl.). Less efficient hunting by weasels in Białowieża could therefore be due to feeding on *Apodemus* mice to a larger extent in contrast to *Microtus* voles in Kielder Forest. However, our data represent estimates over the summer only, whereas the estimates of weasel activity in Białowieża include data from all seasons. It remains possible that the differences in the duration of activity periods are related to seasonal differences in activity.

Despite the above difference between weasels in Kielder Forest and Białowieża (Jędrzejewski *et al.* 2000), it is striking that in neither study was there any influence of prey density on the length of activity periods, despite marked variation in prey density in both studies. This suggests that the length of activity periods might not be a good indicator of hunting efficiency and might be influenced by other factors. Weasels may not immediately cease activity after catching a field vole, but continue hunting, as was indeed found by Sundell *et al.* (2000), or devote time to other behaviour.

It is probably too simplistic to assume that weasel activity consists mostly of hunting behaviour and that the time weasels have to invest for hunting determines the overall time spent active. They might spend less time hunting under higher prey density but allocate the saved time to other behaviour such as searching for mates. This is further suggested by the fact that, against our expectations, we detected an increase in weasel total activity with vole density in three habitats. This may be linked to an increase in time allocated to intra-specific interactions that would otherwise have been spent resting. Our observation of 3 intra-specific aggressive interactions between weasels in areas where vole densities exceeded 120

voles/ha, suggests that one such activity might be the defence of home ranges. Our observation that weasel activity increased with higher vole densities seemingly contradicts Graham's (2002) conclusion that the best calibration relationship between the number of weasel caught and the number of weasel tracks recorded in tracking tunnels indicated, that less weasel tracks predicted the same number of weasels caught at high vole density. However, new analyses based on a much increased sample size failed to detect any influence of vole density on the same calibration (J. Fairbairn *et al.*, in prep.).

We have shown that weather and habitat influenced weasel activity in Kielder Forest. Vole density did not influence weasel activity as expected if weasel were food limited. However, higher weasel density in areas of high prey availability might have caused weasels to spend more time in other activities, resulting in an overall increase in weasel activity. So far there is no specific information on how weasel activity varies with weasel density. From our results it appears that weasels activity may increase with higher weasel density. To what extent weasel activity might be influenced by predation risk remains to be studied.

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