



Master thesis
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The use of tracking tunnels to monitor the activity of small mammals in habitats associated with the northern wheatear (*Oenanthe oenanthe*)

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Abstract

Nest predation is the main cause of nest mortality among birds and is thought to be the main reason for breeding failure amongst northern wheatears (*Oenanthe oenanthe*) in Swedish farmland habitats. Previous studies suggest that small mammalian predators and snakes are important nest predators for wheatears. However, other factors behind nest predation among wheatears have not been thoroughly studied. Here I used ink tracking tunnels (with a piece of meat as bait) to monitor the activity of small mammals in relation to landscape elements (such as linear, forest edge, open area, tall vegetation and stone piles) and land-use types (pastures, crop fields and ungrazed grasslands) in wheatear breeding territories.

I also investigated whether the activity of the mammals changed over time using four survey periods (each period represents the time when collecting tracks from tunnels). The two first survey periods took place during the peak of incubation for wheatears and the last two during the peak of nestling provisioning. Footprint tracks from the tunnels revealed that small mammals (shrews, mice, rats, weasels, stoats and cats), birds, lizards, insects and amphibians visited the tunnels.

The activity of small mammals increased over time so that the highest tracking rates occurred when wheatears were feeding nestlings. The proportion of tunnels with tracks varied according to landscape features, with the highest percentage of tracks found in forest edges (35.5 %) and the lowest in stone piles (17.6 %). However, in stone piles the proportion of tunnels with tracks of small mammals was dependent on land-use type. Whereas mammal prints were generally rare in stone piles located in pastures (12 % of all mammal tracks in pasture) they were much more frequent in crop fields (33 % of all mammal tracks in crop): possibly because stone piles offer the only available predator refuge in crop fields.

The increase of mammal activity between the four survey periods differed between land-use categories with a greater increase in grasslands than in pastures and crop fields. Tunnels with tracks of mammals were positively correlated with the amount of local shrub coverage and tall vegetation. No connection was found between proportion of mammal tracks and breeding success for the northern wheatear.

This study suggests that there are temporal and spatial variation in small mammal activity and demonstrates the value of using tracking tunnels in a Swedish farmland landscape to increase the knowledge of predator movements. However, further studies with long-term data on small mammal activity are needed for to draw conclusions about mammal activity and breeding success for the northern wheatear.

Keywords

Predation; weasel; rodent; wheatear; landscape elements; tracking tunnels.

Introduction

Nest predation is the predominant cause of nest mortality and a major cause of reproductive failure amongst avian species (Ricklefs, 1969) and may therefore be of great importance to habitat selection and spatial distribution (Martin, 1988), life-history evolution (Martin, 1995) and prey behaviour of species (Lima & Dill, 1990). Nest predation risk may vary with type of habitat and habitat elements (e.g. high risk at forest-field edges; Andrén, 1995), species of nest predators and their abundance (Söderström, Pärt, & Rydén, 1998), types of nests (concealed or open) and nest position (ground or in trees). Nest predation risk is often greater for open nests on the ground than for nests off the ground (e.g., Loiselle & Hoppes, 1983; Wilcove, 1985). The

identification of nest predators can often be difficult since in many cases the nest is empty and there is no evidence of what took the eggs or chicks, and since most studies concerning nest predation has been on artificial nests (e.g Söderström et al., 1998; Pärt & Wretenberg, 2002; Roos, 2002).

Ground nesting species are often vulnerable to mammal predation, especially cavity nesting species and bird species that have cryptic concealed nests (Moorhouse et al, 2003). Small mammalian nest predators such as mice and mustelids are very hard to observe because of their cryptic behaviour. Thus, investigating such predators at the landscape scale requires large-scale studies that are labour-intensive and expensive. The studies can also be invasive and disturb the normal behaviours of the predators with the risk of altering predation risk (Connors et al., 2005). This has led to the development of non-invasive methods as, for example, the tracking tunnel technique (King & Edgar, 1977) which provides information on the presence and relative abundance of small mammal species (Blackwell, Potter, & McLennan, 2002; Glennon, Porter, & Demers, 2002; Whisson, Engeman, & Collins, 2005; Gillies & Williams, unpublished A). The method is harmless to animals and cause almost no disturbance since it is a run-through tunnel with free access. The tunnel contains two pieces of paper on either side of an ink tray and some form of bait to attract target species. An animal walking through the tunnel will pick up ink on its feet and leave footprints on the papers. However, there are some limitations of using tracking tunnels; there is a need for a good reference collection for analyzing footprints, which can be time consuming to collect; also no individual data is collected why absolute density and home range area of target species cannot be estimated (Palma & Gurgel-Goncalves, 2007). Therefore, to avoid biases when using tracking tunnels, it is important to only compare abundances within similar habitats, since the habitat type, sample size and study species influences the relative density indices (Blackwell et al., 2002). Because tracking tunnels measure mammal activity at ground level, they may be particularly suited to study the predation risk for ground nesting birds.

Northern wheatears (*Oenanthe oenanthe*) are insectivorous ground-foraging birds which are commonly found in open farmland habitats where they usually nest in cavities under stones or within stone walls. In Sweden, this species has declined during the last two decades (Wretenberg, Lindström, Svensson, Thierfelder, & Pärt, 2006). Previous studies show that the population growth rate of this species is very sensitive to habitat structure within the territories of breeding pairs (i.e. short vs. tall field layer height), as field layer height is closely related to reproductive success and survival (Arlt, Forslund, Jeppson, & Pärt, 2008). The main causes of this habitat-specific variation in demography are nest predation and food availability (Pärt, 2001; Low, Arlt, Eggers, & Pärt, in press). It is thought that snakes (e.g. adder *Vipera berus*) and ground-living mammals, such as stoat (*Mustela erminea*), weasel (*M. nivalis*), red fox (*Vulpes vulpes*), badger (*Meles meles*) and domestic cat (*Felis catus*), are the main nest predators and the predominant cause of nest failure amongst wheatears (Pärt, 2001; Pärt & Wretenberg, 2002).

It has been estimated that weasels and snakes are responsible for up to 65 percent of depredations on wheatear nests (Pärt & Wretenberg, 2002); therefore understanding weasel movements within wheatear territories may provide information on the relationship between landscape variables and nest predation risk. Weasels seldom move more than 5 meters from linear habitats (MacDonald, Tew, & Todd, 2004) and are more likely to use areas with high vegetation coverage, which are associated with a higher abundance of voles which are their main prey (Erlinge, 1974; Brandt & Lambin, 2007; Zub, Sönnichsen, & Szafránska, 2008). Rodents may play an important role as nest predators (Pärt & Wretenberg, 2002), but their effect on wheatears is largely unknown (but see Pärt & Wretenberg, 2002). However, rodent activity and abundance may also affect the activity and abundance of their predators since it is more likely to find a predator in areas where its main prey is found. Avian nest predators are not considered to be a significant cause of nest failures of breeding wheatears because the majority of nests

are inside cavities in stone piles or stone walls, and thus are inaccessible to predatory birds. Thus, in any study system where predation is thought to play a key role for demographic rates, such as for the northern wheatear, it is important to quantify the abundance and location of predators and their prey in relation to the study species in question.

Based on existing knowledge of how weasels use different habitat elements (see above), the observation that most depredations occur in habitats with tall and dense field layers and less in grazed pasture land with short or sparse vegetation (Pärt, 2001) and the fact that the most risky territories are generally depredated first (Martin, Scott, & Menge, 2000), I formulated three objectives: (1) Is there temporal variation in small mammal activity (as determined by footprint tracking rates) during the breeding period of the northern wheatear which could account for periods of higher predation risk? (2) Does landscape composition affect the likelihood of detecting small mammals (i.e. footprint tracks), and can this landscape variation account for areas of higher predation risk for nesting northern wheatears? (3) Is there a link between small mammal activity and breeding success for the northern wheatear?

Method

Study area

The study area (60 km²) is a heterogeneous agricultural landscape situated southeast of Uppsala in southern central Sweden (59°50' N, 17°50' E). The northern wheatear population inhabiting this area has been intensively studied since 1993 (e.g. Pärt, 2001; Arlt & Pärt, 2007; Arlt et al., 2008) thus giving long-term data on nest failure and habitat choice amongst northern wheatears.

Wheatears are territorial, and each territory within the study area can be categorised as belonging to one of the following six habitat types characterised by different land-use: (1) farmyards including bare ground, mowed

lawns and gardens, (2) pastures grazed by cattle or sheep, (3) pastures grazed by horses, (4) spring-sown crop fields, (5) autumn-sown crop fields, and (6) ungrazed pastures and other unmanaged grassland habitats. The first three habitat types were generally characterised by a field layer kept permanently shorter than 5 cm and grouped together as short field layer habitat. The latter three habitat types were characterised by a field layer which was often short at the time of territory establishment, but grew to 15 cm or more during late incubation and nestling care, and grouped together as tall field layer habitat (see also Pärt, 2001; Arlt & Pärt, 2007; Arlt et al., 2008).

Previous analyses suggests that nest predation rate varies both within and between short and tall field layer habitats and based on this knowledge I categorized territory land-use as pasture (pastures grazed by cattle, sheep or horses, low risk), crop field (spring-sown and autumn-sown crop fields, intermediate-high risk) and grassland (ungrazed pastures and other unmanaged grassland habitats, high risk; Arlt et al., 2008).

These habitat differences in nest predation risk may be explained by a corresponding difference in predator abundance or activity during the nesting period. Because of this, the current study was conducted in 2008 between May 21 and June 18, which is the main period of incubation and nestling rearing in breeding wheatears, when birds were most vulnerable to nest predation.

Tracking tunnels

In this study I used tracking tunnels (FEETures Tracking System, Connovation®), to detect the presence of small mammals. The system consists of a plastic tunnel (50x10x10cm) which is anchored to the ground. The floor of the tunnel contains a patch of non-drying ink (in the middle) on which the animal steps and two tracking papers (one at each end) which record the footprints or marks on the tracking papers (fig. 1).

Previous studies (e.g. Blackwell et al., 2002; Glennon et al., 2002; Whisson et al., 2005; Gillies & Williams, unpublished A) have shown that

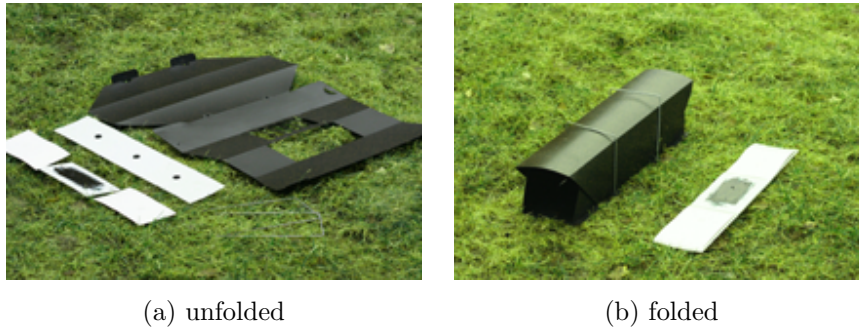


Figure 1: a) The tunnel unfolded and the ink patch and tracking papers are separated from the plastic tray. b) The tunnel folded together and attached to the ground with two metal wires. The ink patch and tracking papers are attached to the plastic tray.

tracking tunnels can be used to study activity and relative abundance of small mammals, and I therefore make the assumption that an increase in tracks shows an increase in activity and relative abundance.

Because animals may need time to adjust to new items in their environment it is recommended to place out the tunnels at least three weeks before the first survey session (Gillies & Williams, unpublished A); however, due to lack of time I placed out the tunnels only two weeks before the first survey. A total of 520 tunnels were placed in 52 wheatear territories (i.e. 10 tunnels in each territory) which were actively selected for this study based on land use (i.e. pasture, crop or grassland) and the long-term breeding success (breeding success per attempt being defined as at least 1 chick fledged) for wheatears in each territory (i.e. high numbers of failures versus high proportion of breeding success). The proportions of each were chosen to approximate a balanced experimental design, with the territories being selected from across the entire study area of 229 territories to limit the possible impact of local factors.

Within each territory I placed two tunnels in each of five landscape elements (linear edge – such as a fence line or ditch; forest edge; open – often under small isolated bushes; stone pile; and tall vegetation) with a minimum

distance of 20 meters between each tunnel.

In order to study the effect of temporal variation in small mammal activity during the wheatear nesting period, I divided the study into two main time periods; the first during the peak of incubation (May 21-27) and the second during the peak of nestling provisioning (June 11-17). Each period consisted of six tracking nights with the bait and papers being replaced after the third night. The decision to have three tracking nights before each check is based upon the directions given by Gillies and Williams (unpublished A) and thus I baited the tunnels three days before each check.

For each 3-day tracking period the central ink patch was inked or refreshed with new ink, clean tracking papers were inserted and 4-5 cm³ of fresh pork meat placed in the middle of the ink patch. Meat was used as bait because I was primarily interested in predatory mammals which might pose a threat to nesting wheatears (i.e. fox, cat, stoat, weasel and rat). For each check of a tunnel I noted: (1) whether the bait had been taken, (2) if the tracking papers were marked with ink and (3) if there was something unusual around the tunnel at the time (e.g. tunnel displaced, predator faeces). Papers with tracks were marked with tunnel number and date and removed for later analysis.

During the last check of the second period, the immediate area surrounding each tunnel within a 5 meters radius was carefully described. Within this area the proportion of the area covered by shrubs and tall vegetation was estimated. Also, the closest linear element was noted (fence line, ditch, road verge, forest edge) and the distance to it was estimated if shorter than 15 meters; if longer, the distance was noted as >15 meters.

Footprint identification

To enable footprint identification of the tracks recorded on the tracking papers, I developed a reference collection of footprints in conjunction with printed references (Ratz, 1997; Gillies & Williams, unpublished B, and expert knowledge (L. Hansson, personal communication)).

First, I live-trapped small mammals during five trapping nights where six traps were placed in tall grass vegetation and four traps were placed in forest habitat. Six mice (wood mice and yellow-necked mice) and three bank voles were trapped and released into a triple-length tracking tunnel with ink patch and papers; each animal left a series of tracks that I could use as guidelines.

Second, I used dead specimens of shrews, wood mice, yellow-necked mice and weasels from which I gathered footprints by using the same ink and papers as used in the study, by gently pressing their inked paws against the paper.

Third, I installed a movement-activated camera in one tunnel and filmed the small mammals visiting the tunnel; from this I could match prints to individuals that visited the tunnel. Fourth, I opportunistically recorded footprints from household pets (rats and cats) and amphibians using the same technique as with dead specimens.

Categorizing tracks

Tracks were initially separated into six categories: mammals, birds, lizards, amphibians, insects or unknown (see Table 1; Appendix 1). Mammal tracks were further subdivided into nine categories (1-9) based on the size and character of the prints. Cat/ fox tracks could be easily distinguished from rodent prints; however, cats and foxes did not always leave a clear footprint when removing bait. In cases when bait was removed and only recorded as an ink drag mark across the tracking paper, these were definitively classified as cat/ fox where a fur imprint accompanied the drag mark (Appendix 1j).

Other mammalian prints (shrews, mice voles and small mustelids) were classified according to size by using a series of eight circular templates – ranging in diameter from 4.5 to 17.5 mm – with each subsequent size increasing in diameter by 20% from the previous. The template was used by overlaying it on a print of the hind foot and selecting the size category which completely encircled the central pad and the three front toes, or the print of a front foot and selecting the size category which completely encircled the central pad

and all four toes (Fig. 2).

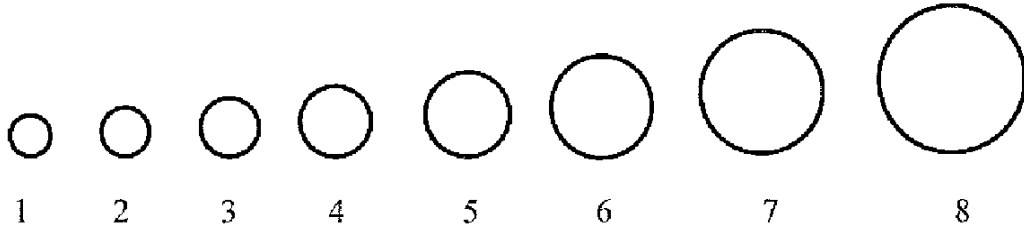


Figure 2: Template used for categorizing tracks.

On many occasions the bait was removed with no tracks and sometimes the tracking papers were dragged out from the tunnels without any marks. To determine the cause of these removals, I used a tunnel with a movement-activated camera which was placed in areas where these trackless removals were common. The film showed that mainly magpies (*Pica pica*) were responsible for removals by dragging out papers or when the bait had been taken without a print or when there was a print of a beak. Therefore, when the bait was missing without any prints, I classified these as magpie predation.

Data analysis

Because magpies often removed bait from tunnels within hours of their placement, this had strong implications for analysis: i.e. they were effectively unbaited and could not be used for many analyses. To account for magpie predation I omitted all tunnels where the bait was removed and no tracks left for all test except for some analyses concerning distribution of small mammals (random or not) and of temporal variation in activity. Territories with >1 magpie predated tunnels (out of ten) were removed from analyses testing differences in track rates between the different habitat elements (i.e. linear, forest edge, open area, tall vegetation and stone piles). For tests based on the level of territories, (i.e. the proportion of tunnels with prints within a territory), I omitted territories with >5 tunnels being depredated by magpies.

For tracked tunnels I did not differentiate between tunnels with a single or multiple tracks, because it was often impossible to determine whether the multiple tracks were created by one individual tracking multiple times or multiple similar-sized individuals tracking once. When analyses were at the territory scale, and proportions of tunnels tracked per territory were compared, I used arc-sin transformed proportions. When analyses were at the individual tunnel scale, I recorded the tunnel as tracked or not and so analyses were based on logistic regression of binomial data (i.e. 0 or 1). Such logit-link binomial general linear models (GLM) generally included interactions between survey periods, landscape elements and/ or land-use category where non-significant interactions ($p > 0.05$) were removed from the final model.

Based on preliminary analyses, I pooled within-territory habitat element data into three categories: (1) linear (linear elements such as ditches, road verges and forest edges), (2) open (open area and stone pile) and (3) patch with tall vegetation.

Breeding success for wheatears was transformed into proportions of successful breeding attempts per area. Mammal activity was analysed as weighted proportions. All tunnels (not magpie predated or destroyed ones) in an area were weighted with the size class of the tracks from the tunnels.

Results

Tracking frequency and footprint identification

Tracks were identified as small mammals (shrews, mice, voles, rats, weasels, stoats and cats) ranging from size class 1-9, birds, lizards, insects and amphibians (Table 1; Appendix 1). The size classes 1-2 is most likely to correspond to shrews, size classes 3-6 to mice and voles and size classes 7-9 with rats, mustelids, cats and foxes. Birds were identified from footprints in the tunnels, or from the bait being taken with no prints on the tracking paper (most probably magpies; see methods).

The number of tunnels tracked by mammals in each territory did not

significantly differ from an expected Poisson distribution for any of the four survey periods (G-tests, expected vs. observed; all P -values >0.1). However, this was not the case for bait theft by magpies, with these birds tending to take bait from fewer or more tunnels than expected (G-tests, expected vs. observed; all P -values <0.01) – suggesting that if magpies find one tunnel, they are attracted to others in the local area.

Temporal variation

Samples were taken at four different periods, the first two during the peak of incubation for the northern wheatear and the third and fourth during the peak of nestling provisioning. The probability of a tunnel having tracks from a mammal significantly increased during the time of the season (logistic regression, $X^2 = 165.3$, $P < 0.001$; Figure 3). This temporal increase occurred regardless of whether tracks were found in the first time period or not (ANCOVA: $F = 1.67$, $df = 1$, $P = 0.20$; Figure 3). There was no difference in the proportion of tracks from different mammal size classes (i.e. they all tended to increase at the same rate) between the four time periods (Kruskal-Wallis test, $H(3, N=349) = 0.938$, $P = 0.82$).

Table 1: Percentage of tunnels with animal tracks for the four survey periods. Numbers do not necessarily add to 100% because a small number of tunnels had tracks from more than one species or size class. The majority of size 9 mammal tracks were from cats, but may include a small number of stoats or foxes. Sample sizes change between time periods because some were removed, lost or destroyed.

| | Survey period | | | |
|--|----------------------|-------------|-------------|-------------|
| | 1 (n = 510) | 2 (n = 515) | 3 (n = 491) | 4 (n = 487) |
| No tracks | 82.9 | 61.6 | 28.5 | 20.1 |
| Small mammal tracks | <hr/> | | | |
| size 1 | 0 | 0.4 | 4.5 | 5.3 |
| size 2 | 0.6 | 1.4 | 2.9 | 3.5 |
| size 3 | 0.8 | 2.3 | 3.7 | 4.5 |
| size 4 | 2.2 | 3.7 | 5.5 | 8.4 |
| size 5 | 2.7 | 3.3 | 5.5 | 4.1 |
| size 6 | 1.2 | 1 | 0.2 | 0.8 |
| size 7 | 0.2 | 0.2 | 0.6 | 1 |
| size 8 | 0 | 0 | 0.2 | 0.2 |
| size 9 (cat) | 0.8 | 4.3 | 9.6 | 14.8 |
| Total small mammal (Σ size 1-9 above) | (8.5) | (16.6) | (32.7) | (42.6) |
| Magpie | 10 | 17.9 | 37.5 | 35.7 |
| Other bird | 0.2 | 0 | 4.3 | 4.9 |
| Lizard | 0.8 | 3 | 2.9 | 3.9 |
| Insect | 0.2 | 0.4 | 1.2 | 4.7 |
| Amphibian | 0 | 0 | 0.6 | 0.6 |
| Unknown | 0 | 0.8 | 1.6 | 2.9 |

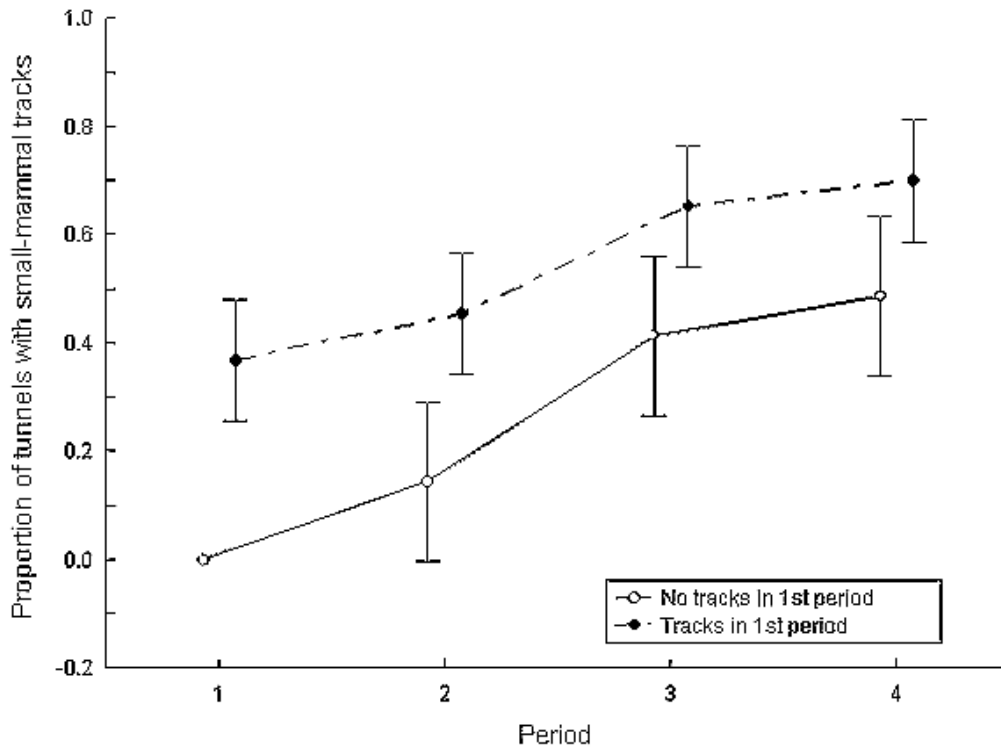


Figure 3: The proportion of tunnels with tracks of small mammals for four survey periods in relation to whether there are tracks in the first survey period or not.

Habitat relationships

The landscape element with the highest percentage of tunnels with mammal tracks was forest edge (35.5 %; averaged across all four periods), as compared to stone piles which had the lowest percentage of tunnels with mammal tracks (17.6%; Table 2).

Table 2: Proportion of tracks in linear (L), stone pile (S), forest edge (F), tall vegetation (V) and open (O) landscape elements as averaged across all four periods. Numbers do not necessarily add to 100% because a small number of tunnels had tracks from more than one species or size class. The majority of size 9 mammal tracks were from cats, but may include a small number of stoats or foxes. Sample sizes change between time periods because some were removed, lost or destroyed.

| | Habitat category | | | | |
|--|-------------------------|-----------|-----------|-----------|-----------|
| | L (n=715) | S (n=258) | F (n=339) | V (n=132) | O (n=516) |
| No tracks | 50.1 | 45.0 | 44.8 | 47.7 | 56.0 |
| Small mammal tracks: | | | | | |
| size 1 | 3.9 | 0.8 | 2.7 | 3.0 | 1.4 |
| size 2 | 2.9 | 1.6 | 1.5 | 1.5 | 1.7 |
| size 3 | 2.2 | 1.6 | 6.5 | 3.8 | 1.9 |
| size 4 | 4.3 | 4.3 | 8.0 | 3.8 | 4.7 |
| size 5 | 2.8 | 2.7 | 6.2 | 4.5 | 4.7 |
| size 6 | 0.42 | 1.2 | 1.2 | 0.8 | 1.0 |
| size 7 | 0.0 | 0.4 | 0.3 | 0.0 | 1.6 |
| size 8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.39 |
| size 9 | 7.33 | 5.0 | 9.1 | 9.1 | 3.56 |
| Total small mammal tracks (Σ size 1-9 above) | (23.85) | (17.6) | (35.5) | (26.5) | (20.95) |
| Magpie | 25.3 | 33.3 | 23.6 | 24.2 | 23.3 |
| Other bird | 2.1 | 2.7 | 3.5 | 0.0 | 2.3 |
| Lizard | 3.5 | 2.3 | 1.5 | 2.3 | 0.39 |
| Insect | 1.5 | 1.2 | 2.4 | 3.0 | 1.0 |
| Amphibian | 0.0 | 0.8 | 0.6 | 0.8 | 0.19 |
| Unknown | 2.62 | 3.9 | 1.5 | 2.3 | 1.73 |

However, the likelihood of a tunnel having tracks was not a simple relationship with landscape elements, but was modified by an interaction with land-use (i.e. pasture, crop or ungrazed grassland). The proportion of small mammal tracks was not significantly different between land-use categories (GLM: land-use $X^2 = 4.5$, $df = 2$, $P = 0.10$); but the use of landscape elements by mammals differed between land-use categories, as shown by the significant interaction term (Table 3).

Table 3: Final model of interactions between the three factors land-use category, landscape elements and time period.

| Final model | | | |
|-----------------------------|--------------------|---------|----------|
| | Degrees of freedom | Wald | <i>P</i> |
| Intercept | 1 | 226.014 | <0.001 |
| Landscape elements*Land-use | 8 | 24.9505 | 0.002 |
| Land-use*Period | 2 | 7.7080 | 0.021 |
| Landscape elements | 4 | 4.7300 | 0.316 |
| Land-use | 2 | 4.5649 | 0.102 |
| Period | 1 | 122.389 | <0.001 |

Much of this interaction effect can be seen in the different use of stone piles relative to other landscape elements for the pastures versus crops (Figure 4).

Although the likelihood of tracking a mammal increased sequentially for each of the four survey periods ($X^2 = 122$, $df = 3$, $P < 0.001$), there was a significant interaction between land-use category and time period (Table 3). The proportion of mammal tracks in crop and pasture habitats appeared to increase in a similar way whilst grassland habitats showed a disproportionate increase between the second and third survey periods (Figure 5).

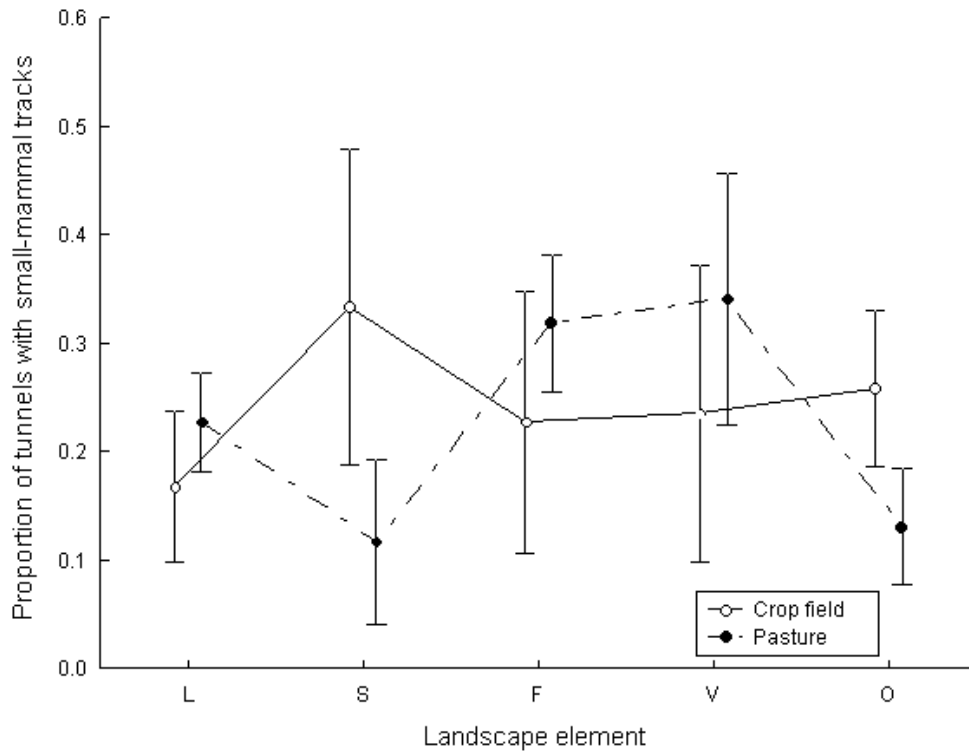


Figure 4: The proportion of tunnels with tracks of small mammals in linear (L), stone pile (S), forest edge (F), tall vegetation (V) and open (O) landscape elements in relation to land-use category (pasture or crop field).

Habitat variables

The coverage of shrubs and tall grass (>15 cm) was estimated in a circle with a radius of five meters around each tunnel as well as the distance to the closest linear element. Small mammal tracks were significantly higher in areas with greater local shrub coverage (Table 4) and also with greater local tall vegetation coverage (Table 4). The distance to the closest linear element did not appear to affect the likelihood of a tunnel having tracks of a mammal (Table 4).

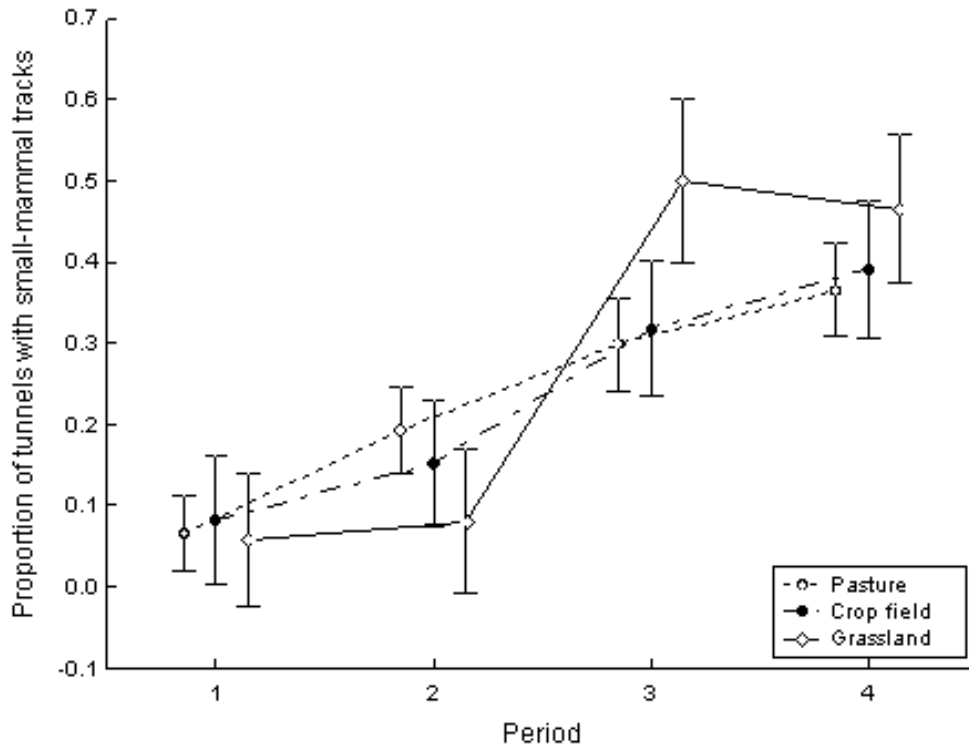


Figure 5: The proportion of tunnels with tracks of small mammals for four survey periods in relation to land-use category (pasture, crop field and grassland).

Table 4: Final model of effects of coverage of shrubs, tall vegetation and closest linear element on small mammal tracks.

| Final model | | | |
|------------------------|--------------------|----------|----------|
| | Degrees of freedom | Wald | <i>P</i> |
| Intercept | 1 | 101.8856 | <0.001 |
| Coverage shrubs | 1 | 29.2581 | <0.001 |
| Coverage tall veg | 1 | 13.0237 | <0.001 |
| Closest linear element | 1 | 1.4077 | 0.235 |

Small mammal activity and breeding success for wheatears

There was no significant correlation between proportion of tunnels with mammal tracks and proportion of long-term breeding success for each territory (Pearson correlation, $r^2 = 0.002$, $P = 0.72$) or between proportion of tunnels with mammal tracks and breeding success for these territories in 2008 (t-test, t-value = -1.34, df = 29, $P = 0.19$).

Discussion

Nest predation is an important factor determining nesting success in northern wheatears (Pärt, 2001; Low et al., in press); therefore an understanding of the activity patterns of small predatory mammals in wheatear habitat is likely to help explain habitat-specific differences in nest predation risk. Thus, this study was designed to look for relationships between habitat features and mammal activity within a well-studied wheatear population and to determine the following: (1) temporal variation in small mammal activity as it relates to the timing of nesting in the northern wheatear, (2) if there is evidence that mammals prefer specific landscape elements or habitat features within the agricultural environment in which wheatears breed, and (3) if there is a link between mammal activity and breeding success for the northern wheatear.

Temporal variation in small mammal activity

Often, the most risky breeding sites are depredated first (Martin et al., 2000), which is why one could expect nest predation rates to decline with time in the season for wheatears. However, data on nest predation on wheatears suggest no such temporal patterns (T. Pärt, unpublished results). Thus, it is possible that the risk of nest predation actually increases over the course of the breeding season and these two factors cancel each other out. My results showed that mammal activity increased during the course of the study, with the same proportional increases for prints from the different mammal size

classes. If tracking probability relates to the relative abundance and activity of mammals this could mean that there is a higher nest predation risk during the peak of nestling provisioning (surveys 3 & 4) than during the peak of incubation (surveys 1 & 2). However, any correlation between nest predation risk and mammal activity for these periods is complicated by other factors which might affect nest predation risk. Studies suggest that nest predation from small mammals is an incidental process rather than an active search (Vickery, Hunter, & Wells, 1992; Schmidt, Goheen, & Naumann, 2001) and may therefore increase with an increased activity of predators. For weasels, olfaction and vision are of equivalent importance in hunting (Zielinski, Halle, & Stenseth, 2000) and parental activity of wheatears may therefore also affect the predation risk between these two time periods. An incubating female is less active than during the nestling provisioning period; northern wheatear adults feed their nestlings 500 times per day (Low, Eggers, Arlt, & Pärt, 2008) and it has been shown that nest predation risk increases with increasing parental activity when taking the nest site effects into account (Martin et al., 2000).

Variation in small mammal activity relative to land-use and habitat elements

Mammals were more likely to track tunnels placed in linear elements or on forest edges (27.6 %) than those placed in small isolated habitat elements (e.g. stone piles, shrubs) or in the open (19.8 %), corroborating the general view that mammals use these edges as movement pathways (see MacDonald et al., 2004). However, such small-scale landscape structures interacted with larger-scale habitat types in determining the likelihood of a tunnel having tracks; there was a higher activity in stone piles in crop fields than stone piles in pastures. A potential explanation is that stone piles may become relatively more important as predator refuges in land-use types with almost no other potential refuges. For example, there are predominantly two rodent species that live in crop fields: field voles (*Microtus agrestis*) and yellow-

necked mice, which both prefer a cover of vegetation and if this is missing they will use stone piles as protection instead (Jensen, 2004).

Between the second and third survey period, there was a disproportionate increase in mammal activity in grassland as compared to crop field and pasture. One explanation for this increase could be that the vegetation has grown taller and denser towards the third survey period and thus the availability of food and shelter has increased for rodents and the area can support more individuals. One might expect that if the activity of rodents increase in the area then also the activity of small mammal predators will increase since there is a relationship between increasing abundance of mammal predators and increasing abundance of its main prey (Erlinge, 1974; Brandt & Lambin, 2007; Zub et al., 2008). The same increase in activity was not observed for crop fields and pastures which could be explained by the less dense vegetation layer found in these areas. It has been shown that ungrazed grasslands may act as sink habitats for wheatears (Arlt et al., 2008) and thus further studies of the activity of small mammals in grasslands would be valuable.

Small mammal activity and breeding success

There was no significant correlation between the proportion of mammal tracks and breeding success for the northern wheatear when considering both long-term breeding success and success in 2008. Instead, the data from 2008 suggests that there were a higher proportion of mammal tracks in territories where wheatears succeeded than where they failed. The lack of significance between proportion of mammal tracks for specific territories and long-term breeding success for those territories is difficult to interpret because the tracking data does not account for changes in land-use between years and its possible relationship with mammal activity and breeding success. When considering the lack of significance for the correlation between the proportion of mammal tracks and breeding success in 2008 this could be due to a low sample size. If this had been increased it might have revealed a different pattern.

The use of tracking tunnels to estimate activity of small mammals

Studies have shown that the probability of nest predation may increase with increasing activity of small mammals (e.g. Cain, Smallwood, Morrison, & Loffland, 2006) and it might therefore be possible to estimate nest predation risk from the occurrence of tracks from small mammals in tracking tunnels. It is likely that when activity of potential predators increase, the likelihood of detecting a nest also increases (either randomly or by active search for nests; see above). This study suggests that tracking tunnels are a viable way for studying the activity of small animals in Swedish farmland habitats. However, the method was not free from problems.

First, magpie ‘predation’ had a huge impact on the data collected for this study. My results suggest that once magpies have detected and removed the bait from one tunnel, they will actively seek more tunnels within their territory. Tunnels predated by magpies increased over time with almost the same proportions in all five landscape elements: possibly slightly higher in stone piles (tunnels were very visible in these areas). Magpies stole the bait from the tracking tunnels in one of two ways; either by pulling out the sheet holding the tracking papers and ink patch or by entering the tunnel. My videos from the movement-activated cameras showed that if the sheet was properly attached to the tunnel the magpies could not pull it out and were forced to enter the tunnel, but still the bait was taken without leaving any prints. As magpies cannot depredate real wheatear nests because these are not possible to reach, magpie predation only reduces the sample of tunnels available for tracking other animals. One solution to this problem might be placing a wire across the middle of the entrance to the tunnel and properly attaching the tracking paper holding sheet. However, magpies are curious and can easily solve problems in new situations (Prior, Schwarz, & Guenterkuen, 2008); thus, magpies might introduce us to new problems in the future. Of course, any modification to the tunnels would have to be carefully considered so that it did not affect the ability of species of interest (e.g. cats) from accessing

the tunnel and leaving prints.

Second, grazing animals (cows, sheep and horses) sometimes moved or destroyed the tunnels despite that I tried to place tunnels under bushes or stones in pastures. Consequently the sample of tunnels were sometimes reduced in pastures, especially intensively grazed pastures. Therefore I used proportions instead of absolute numbers when analysing the data. Third, it was not always possible to determine which kind of animal or animals had passed through the tunnel (approximately 1 %), because the tracking papers were sometimes saturated by tracks. One solution could be to have tunnels open for less than three tracking nights; however, this would have to be balanced against the lower number of tunnels encountered and tracks recorded. However, this was a minor problem as in most cases the tracks suggested very small mammals.

Species identification based on ink tracks

When building the reference key for species identification from ink prints, I used a number of sources: (1) live-trapped animals and opportunistic captures, (2) pet animals, and (3) dead specimens. From this and from an understanding of the basic anatomy of many species, I was able to definitely identify animals in broad categories (i.e. insect, snail, amphibian, lizard, small bird, rodent and cat; see Appendix 1); however, from prints obtained by live-trapping and dead specimens it was obvious that differentiating between many of the rodent species and between small mustelids was difficult. This is in contrast to New Zealand where much tracking tunnel work has been undertaken, because they have a very limited number of rodent species, and the mustelids (i.e. weasel and stoat) are much larger than those found in Sweden (L. Hansson, personal communication). This allows tracks to be identified in New Zealand studies with much greater certainty than can be here, which is why I decided to use an objective classification scheme for these types of prints: the circle templates (Figure 3). As this work progresses, the footprint reference key can be refined to improve the species specificity; how-

ever, using live-trapped and pet animals may be a better alternative than dead specimens since the tracks from the dead specimens are affected by how hard the feet are pressed against the paper, how stiff the dead animal is and the possibility that the dead animal shrink when getting dried out.

Conclusions

Predation risk could be an important factor behind the decline of the Swedish northern wheatear population. There was temporal variation in small mammal activity between the four survey periods of this study which indicates that there could be a higher nest predation risk during nestling provisioning than during incubation for the northern wheatear. Habitats such as ungrazed grasslands showed a greater increase in mammal activity than pastures and crops fields suggesting that grassland could be high-risk habitats for wheatears. Within-territory differences were found in how mammals used stone piles, showing a higher activity in stone piles in crop fields than in pastures. Variation was also found in mammal activity between high and low coverage of vegetation; activity increased with increasing percentage of coverage. No link was found between proportion of mammal tracks and breeding success in a territory. By increasing the amount of data over a period of years it would be possible to study the correlation between breeding success amongst wheatears and the predation risk that small mammals constitute over time and in different habitats.

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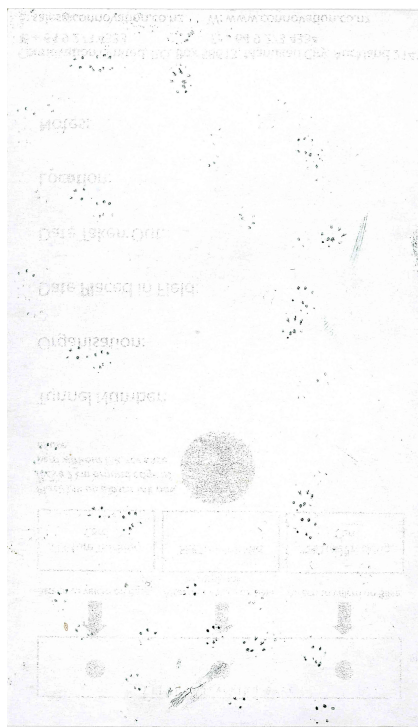
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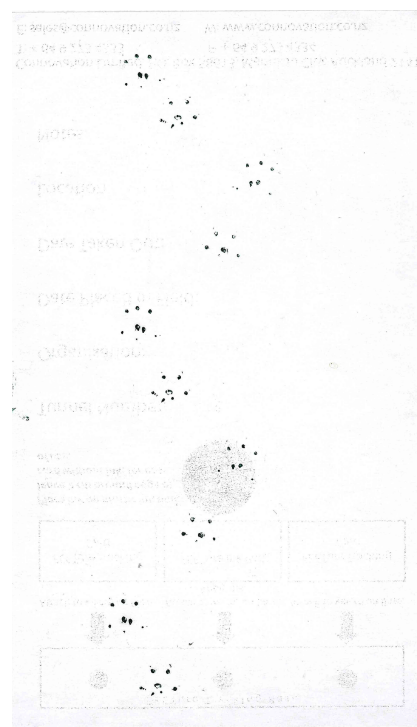
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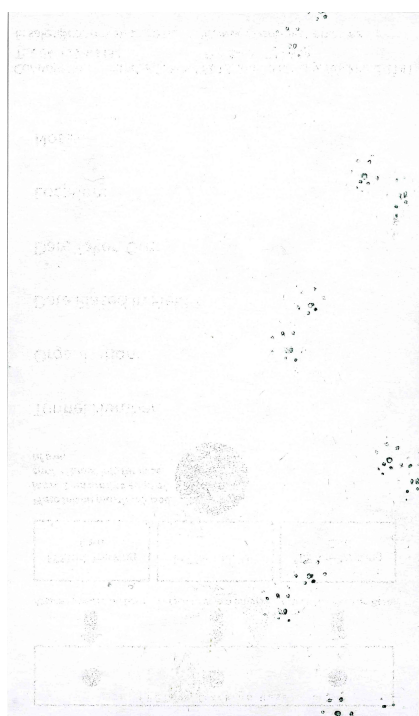
Appendix 1. Examples of tracks collected from ink tracking tunnels in this study



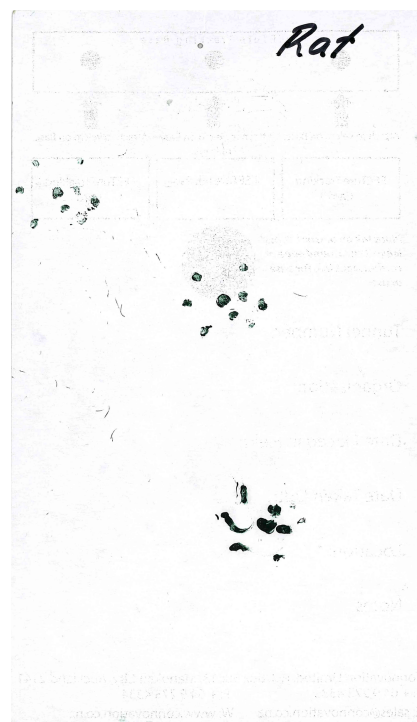
(a) Shrew



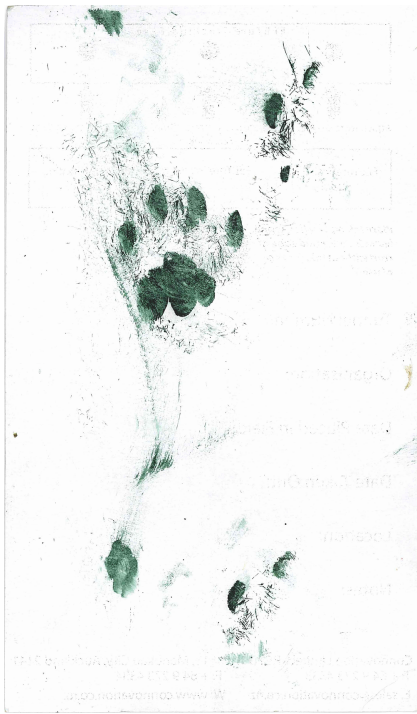
(b) Wood mouse



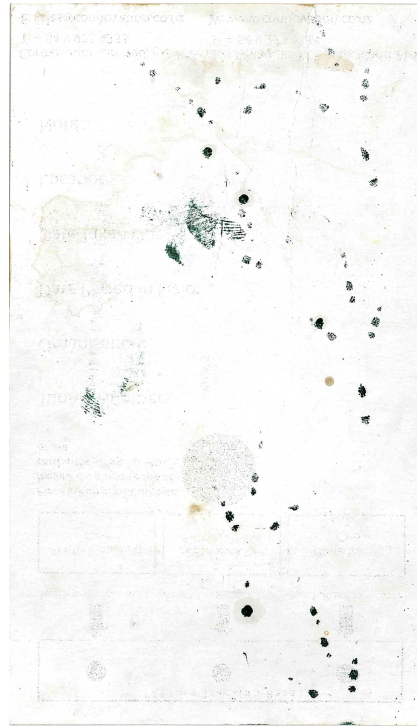
(c) Vole



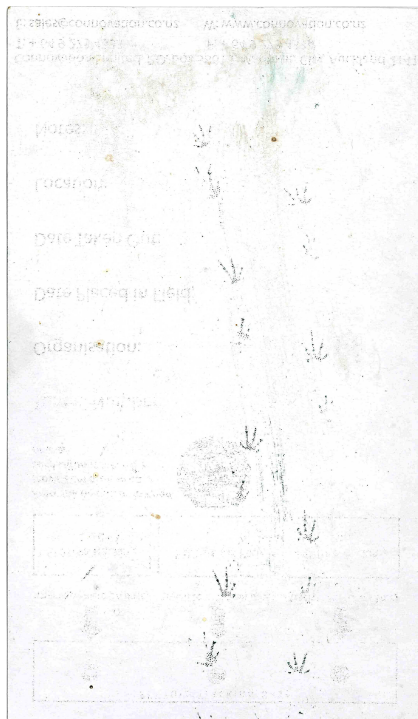
(d) Rat



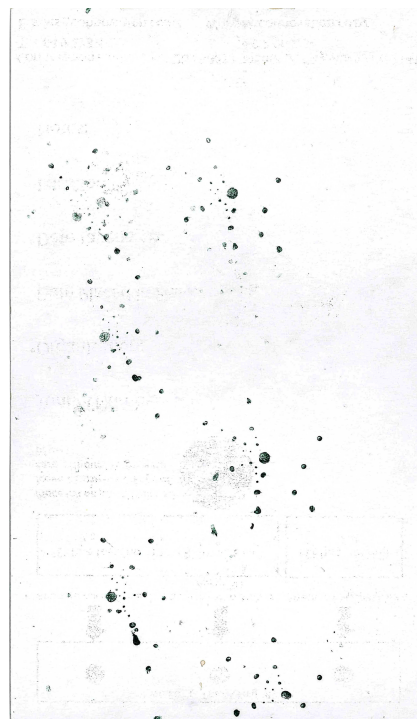
(e) Cat



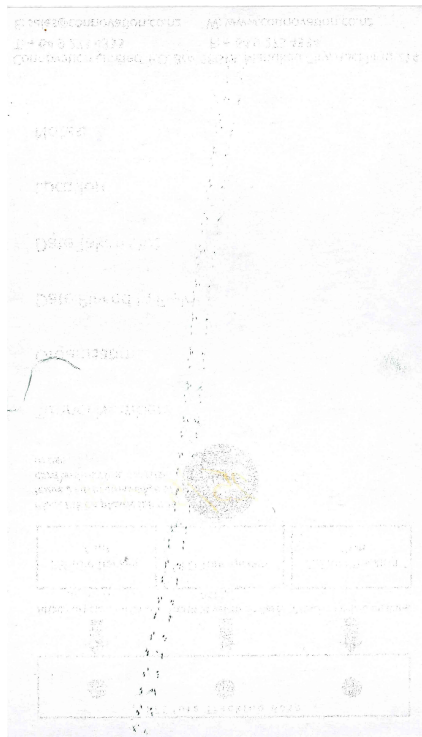
(f) Bird



(g) Lizard



(h) Amphibian



(i) Insect



(j) Drag mark