

# Behaviour, dynamics and ecological impact of small mustelids

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Academic dissertation

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Huis vaan ni ollaan tohtoria!

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## Contributions

The following table indicates the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV	V
Original idea	IH, PaH	PaH, HH	PaH, JS, PeH, HH	PaH	PaH, HH
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Analyses	PaH, TK, IH	PaH	JS, PaH	PaH, EK	PaH
Manuscript preparation	PaH, IH	PaH, HH	PaH, JS, PeH, HH	PaH, EK	PaH, HH

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# Behaviour, dynamics and ecological impact of small mustelids

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- II. Hellstedt, P. & Henttonen, H. Influence of altered predator community on vole population fluctuations in Finnish Lapland. Manuscript.
- III. Hellstedt, P., Sundell, J., Helle, P., & Henttonen, H. Large-scale spatial and temporal patterns in population dynamics of the stoat (*Mustela erminea*) and the least weasel (*M. nivalis*) in Finland. Submitted manuscript.
- IV. Hellstedt, P. & Kallio, E. R. 2005. Survival and behaviour of captive-born weasels released in nature. *Journal of Zoology* 266: 37-44.
- V. Hellstedt, P. & Henttonen, H. Home ranges, habitat choice and activity of stoats (*Mustela erminea*) in relation to sex and dominance status during the snowless seasons in subarctic area. *Journal of Zoology*, accepted.

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## Introduction

Weasel (*Mustela nivalis*) and stoat (*M. erminea*) are two closely related mustelid species. Both are small in size, and the subspecies *M. nivalis nivalis*, the least weasel, is the smallest mammalian predator in the world. Even though the maximum lifespans of weasels and stoats may be relatively long (3-9 years), only a small proportion of individuals reaches more than one year of age (King 1989 and references therein). As with many other mustelid species, the stoat and the weasel exhibit marked sexual size dimorphism: males are always bigger than females. The sexual size dimorphism has been suggested to reduce competition between the sexes (Dayan and Simberloff 1994). In the Fennoscandian populations, there is a negative correlation between the average body sizes of stoats and weasels and latitude (Erlinge 1987). This is in contrast to the general expectation based on Bergmann's rule, according to which body sizes increase northwards.

Shape and size of stoats and weasels are adaptations to hunting voles in their subterranean holes (Andersson and Erlinge 1977). The main prey species of the least weasel in southern Fennoscandia are the field vole (*Microtus agrestis*) and other voles in the genus *Microtus* (Korpimäki *et al.* 1991, Hanski and Henttonen 1996). In the northern limits of the Fennoscandian conifer forest, weasels use *Microtus*-voles as well as the ecologically similar grey-sided vole (*Clethrionomys rufocanus*; Hanski and Henttonen 1996). Voles are also the main prey of stoats in most parts of Fennoscandia, but in southern Fennoscandia the main prey is the water

vole (*Arvicola terrestris*). The stoat is clearly larger than the weasel and it may more readily use alternative prey species, and therefore the stoat is thought to be a more generalist predator than the weasel (e.g. Hanski *et al.* 1991). A most notable difference between the two species is in their breeding biology. Stoat has delayed implantation, whereas weasel has direct implantation. This gives the weasel an opportunity to respond to changes in prey abundances more rapidly than the stoat (King and Moors 1979). Essential biological information on the two species is summarized in Table 1.

### Home ranges and territoriality

Both the stoat and the weasel are solitary species. The sizes of their home ranges depend on the geographic locality and season (King 1989, Chapter V). Male stoat home ranges may vary from 15.5 to 733 ha (Erlinge and Sandell 1986, Robitaille and Raymond 1995) and female ranges from 4.6 to 100 ha (Robitaille and Raymond 1995, Miller *et al.* 2001). In Poland the home ranges of male common weasels varied depending on rodent density from 11 - 37 ha in high-density years to 117 - 216 ha in low-density years (Jedrzejewski *et al.* 1995), while the least weasel home ranges varied from 0.2 to 10 ha (Nyholm 1959, Polder 1968, Chapter I). The main factor affecting the home range size is the availability of prey, especially during the non-breeding season (Erlinge and Sandell 1986, Klemola *et al.* 1999). During the non-breeding season both species are usually territorial, but during the breeding season territory borders break down as generally all

mature males start to search for receptive females (Erlinge 1974, Moors 1974, Erlinge 1977, Erlinge and Sandell 1986, Sandell 1986). In the non-breeding season, dominant males spend their time in areas

where vole density is highest (Erlinge 1977) or in areas where hunting requires less effort for other reasons (Edwards *et al.* 2001).

**Table 1.** Characteristics of the stoat and the least weasel.

Characters	Stoat <i>Mustela erminea</i>	Least weasel <i>Mustela nivalis nivalis</i>
Average size		
Male	244 g <sup>(7)</sup>	49 g <sup>(5)</sup> -54 g <sup>(1)</sup>
Female	103 g <sup>(7)</sup>	34 g <sup>(5)</sup> -35 g <sup>(1)</sup>
Implantation	Delayed implantation	Direct implantation
Gestation	220-380 days <sup>(4)</sup>	34-36 days <sup>(4)</sup>
Mean litter size	6-9 <sup>(4)</sup>	4.1-12 <sup>(6)</sup>
Mortality rate	1 <sup>st</sup> year: 83% in New Zealand <sup>(4)</sup> ; 3-6 months: 40-54% in Sweden <sup>(3)</sup>	1 <sup>st</sup> year: 80% in males, 75% in females in Britain ( <i>M. n. vulgaris</i> ) <sup>(2)</sup>
Maximal lifespan (years)	9 <sup>(4)</sup>	3 <sup>(2)</sup>

<sup>(1)</sup> Stolt (1979), <sup>(2)</sup> King (1980), <sup>(3)</sup> Erlinge (1983), <sup>(4)</sup> King (1989) and references therein, <sup>(5)</sup> Siivonen and Sulkava (1999), <sup>(6)</sup> Sundell (2003a) and references therein, <sup>(7)</sup> Hellstedt and Henttonen (Chapter V).

### Competition and co-existence

Even though the stoat and the weasel are similar in appearance, they have considerable differences in breeding habits, prey, habitats and body size (King and Moors 1979). These differences are consistent with the principle of limiting similarity (MacArthur and Levins 1967): two ecologically similar competing species cannot live in sympatry, which may lead to co-evolutionary character displacement. The weasel and the stoat have most likely diverged in their body size and related habits because of interspecific competition (Dayan and Simberloff 1994).

Stoats and weasels compete with each other for largely the same prey species.

Weasels, being smaller in size, usually avoid areas where stoats live (Erlinge and Sandell 1988, Oksanen *et al.* 1992, Oksanen and Henttonen 1996). The two species may however co-exist in heterogenous landscapes with refuges for the weasel (King and Moors 1979, King 1989, Aunapuu and Oksanen 2003). McDonald (2002) found dietary niche differences between British stoats and weasels: the stoats mostly preyed on rabbits (*Oryctolagus cuniculus*) and hares, whereas the weasels used more of voles. In northern Fennoscandia, competition between the stoat and the weasel has been shown to result in dissimilar habitat use: stoats use areas of higher productivity than weasels (Oksanen *et al.* 1992).



## Breeding

The stoat and the weasel have different reproductive biology. Stoats have delayed implantation but in weasels the embryo is implanted immediately after fertilization. Delayed implantation has been suggested to be a monophyletic trait in mustelids (Lindén *et al.* 2003). Female stoats come on heat soon after giving birth but fertilized eggs start to develop only after the following winter when the amount of light increases (King 1989). Because of delayed implantation, stoats cannot have more than one litter per year. In Fennoscandia, least weasel may breed also in winter if prey abundance is high. Common weasels in England have a long breeding season, and when voles are abundant weasels may have two litters per summer (King 1989). Furthermore, during times of abundant prey young female weasels may mature and have their own offspring during their first summer (King 1989). For all these reasons the breeding potential of the weasel is greater than that of the stoat, and hence weasel population densities may respond more rapidly to changes in food availability.

## Food

The hunting behaviour of small mustelids is characterized as ‘random search’ (King 1989). In Fennoscandia, as in most parts of their ranges, the diets of the stoat and the weasel vary (King 1989 and references therein). For instance, in southern Sweden male stoats prefer hares, water voles and *Apodemus*-mice (Erlinge 1975), whereas male weasels use mostly voles. But when voles are scarce, male weasels use young rabbits, water voles and *Apodemus*-mice. In both species, females prefer field voles and female weasels also bank voles (*Clethrionomys glareolus*) (Erlinge 1975).

In the north the weasel is highly specialized on *Microtus*-voles (Korpimäki *et al.* 1991, Korpimäki 1993). During the winter, in the northern parts of Fennoscandia, food resources are often limiting, and stoats and weasels are forced to use the same prey species (Korpimäki *et al.* 1991, Aunapuu and Oksanen 2003).

## The ecological impact of small mustelids in vertebrate communities

The weasel and the stoat are prey items for many raptors and owls as well as for larger mammalian predators, like the red fox (*Vulpes vulpes*) (Powell 1973). Small mustelids are active only when necessary, and they do not normally move in open places, apparently to avoid predation (Buckingham 1979, Korpimäki and Norrdahl 1989b, Aunapuu 2004). However, predation is not the main factor regulating stoat and weasel population densities – that factor is their own prey.

The stoat and the weasel are predators, that strongly influence the dynamics of the small mammal communities (including voles, lemmings, mice and shrews). Many small and medium-sized mammal species in the northern hemisphere have been observed to show regular multiannual fluctuations (e.g. Kalela 1962, Krebs and Myers 1974, Angelstam *et al.* 1985, Hansson and Henttonen 1985, Keith 1990, Hanski *et al.* 1991, Stenseth 1999, Klemola *et al.* 2002). Since Elton (1924) noticed extraordinary vole population fluctuations in Fennoscandia, the researchers have been interested in ‘vole cycles’ (Stenseth *et al.* 1998, Hanski *et al.* 2001, Korpimäki *et al.* 2005). Especially *Microtus* and *Clethrionomys* voles but also Norway lemming (*Lemmus lemmus*) populations have been much studied and long-term time series on their abundances

## Box 1

**The predator-prey hypothesis**

Vole cycles have been of substantial interest to scientists since Charles Elton's research on northern rodents (Elton 1924, 1942). A multitude of hypotheses have been suggested to explain these cycles: Batzli (1992) counted 22 hypotheses explaining the regular fluctuations of vole population numbers. In northern Fennoscandia the multiannual cycles used to be regular and more or less synchronous between different species. Cycles had large amplitude: the abundance between peak and low densities varied 50 to 100-fold (Siivonen 1954, Hansson and Henttonen 1985, Henttonen *et al.* 1987, Hanski *et al.* 1991, Korpimäki *et al.* 1991, Klemola *et al.* 2002). In southern Fennoscandia, there are no regular cycles but the vole populations fluctuate only seasonally (Hansson and Henttonen 1988). The main hypothesis to describe Fennoscandian vole cycles is the specialist predator hypothesis (Henttonen *et al.* 1987, Korpimäki *et al.* 1991, Hanski *et al.* 1993, Norrdahl 1995, Klemola *et al.* 2000), according to this predation by highly specialized mammalian predators, the least weasel (*Mustela nivalis nivalis*) and the stoat (*M. erminea*), drives the cycles due to delayed numerical response of the predators. This delayed numerical response to changes in vole population numbers (Korpimäki *et al.* 1991) delays their recovery from the low phase and allows vole population increase without pressure from the predators (Korpimäki *et al.* 1991, Norrdahl 1995). Least weasel uses voles (especially field voles, *Microtus agrestis*) even when vole density is low (Korpimäki *et al.* 1991). Stoat, as a bigger predator may more easily start hunting alternative prey. However, in the north, the stoat behaviour resembles that of a specialist predator due to lack of alternative prey species (Erlinge 1975, Korpimäki *et al.* 1991, Aunapuu and Oksanen 2003). Generalist predators as well as nomadic avian predators may switch between prey species or hunting areas, and therefore they tend to stabilize prey dynamics (Andersson and Erlinge 1977, Erlinge *et al.* 1984).

have been collected (Henttonen *et al.* 1987, Hanski *et al.* 1991). In northern Fennoscandia, the vole cycle used to have a regular 4-5 year interval (but see below). The cycle length becomes shorter with decreasing latitude, so that in southern Finland the cycle length is 3-4 years and in southern Sweden multiannual cycles are replaced by annual fluctuations (Erlinge *et al.* 1983, Hansson and Henttonen 1985, Hanski *et al.* 1991). Populations of predators using voles tend to fluctuate accordingly, though often with a delay in relation to vole dynamics (e.g. Norrdahl 1995).

The most popular hypothesis explaining the Fennoscandian vole cycles is the

predation hypotheses (e.g. Hanski *et al.* 2001). This involves the classification of vole predators into three categories: 1) generalist predators, which may switch between prey species depending on their abundances (Erlinge *et al.* 1984), 2) nomadic avian specialist predators, which may migrate to areas where the vole densities are currently high (Korpimäki *et al.* 1991), and 3) resident specialist predators, primarily the weasel and the stoat. Generalists as well as the nomadic avian predators tend to stabilize cycles, but resident specialists promote regular fluctuations (Erlinge *et al.* 1984, Korpimäki 1985, Norrdahl 1995, Hanski *et al.* 2001, Box 1). The population size of a specialist mammalian predator strongly

depends on the numbers of prey, but changes in vole population sizes influence weasel and stoat numbers with a time lag (Erlinge 1974, Korpimäki *et al.* 1991). Delayed predator dynamics is due to their numerical response, and specifically due to their slower rate of reproduction than in the voles (Korpimäki *et al.* 1991). When the vole populations are abundant, small mustelids may cache food (Oksanen 1983). They may kill more voles than needed, and thereby the strength of their impact on vole populations becomes amplified.

It has been suggested that in addition to the direct effect of predators on the prey populations, there are also significant indirect effects (Gorman 1984, Ylönen 1989, Lima and Dill 1990, Norrdahl and Korpimäki 2000, Ylönen 2001). Ylönen (1989) proposed the breeding suppression hypothesis (BSH), which suggests that the rate of reproduction by voles becomes reduced in the presence of weasels. Studies of the indirect effects are mostly done in the laboratory, and these studies are difficult to apply to natural populations

## Box 2

### Long-term declining trend in the Fennoscandian vole populations

In the past, the Fennoscandian voles had regular 3 to 5 year cycles in numbers. Along with weakening regularity of cyclicity in recent decades, a long-term declining trend in the overall numbers has been reported from different parts of Fennoscandia (Henttonen 2000, Christensen and Hörnfeldt 2003, Hörnfeldt 2004). The declining trend is notable especially in the 'key species', *Microtus*-voles, grey-sided vole (*Clethrionomys rufocanus*) and bank vole (*C. glareolus*: in Umeå, but not in Pallasjärvi), which previously exhibited most regular oscillations. No decline has been observed in some other small rodent species, such as red vole (*C. rutilus*) in subarctic birch forests (Chapter II) and bank vole in boreal Finnish Lapland (Henttonen 2000). The following factors have been suggested to explain the decline in the numbers and amplitude of oscillations (summarized from Hörnfeldt 2004):

- 1) Destructive sampling hypothesis (DSH). According to DSH the reported decline is an artefact created by permanent snap-trapping sampling plots. This is not a very likely hypothesis: evidently the trap-indices are comparable in permanent plots and in new plots (Christensen and Hörnfeldt 2003).
- 2) Natural long-term fluctuation pattern hypothesis (NFPH). Long-term natural trends are possible, but there is no positive evidence for this due to lack of long time-series.
- 3) Habitat fragmentation hypothesis (HFH). Intensive forestry, clear-cuts and reforested cultivated areas have fragmented the vole habitats (Östlund *et al.* 1997, Hansson 1999). Fragmented habitat affects vole abundances but, according to Hörnfeldt (2004), this is unlikely to explain the decline of vole populations.
- 4) Adverse winter hypothesis (AWH). Reduced snow-cover and earlier snowmelt may lead to increased predation risk for voles. In Norway, the mortality risk for root/tundra vole (*Microtus oeconomus*) was greater during mild than cold winters (Aars and Ims 2002). Mild winters may also increase disease and parasite risk.

Continues on next page

- 5) Predation increase hypothesis (PIH). Hörnfeldt (2004) suggests that decreased numbers of red fox (*Vulpes vulpes*) reduce the predation risk on small mustelids. This is supposed to lead to faster numerical response in mustelids and therefore to increase mustelid predation on voles. However, according to many earlier studies great abundance of small mustelids is the factor that maintains vole cycles (Erlinge *et al.* 1983, Henttonen *et al.* 1987, Korpimäki *et al.* 1991, Hanski *et al.* 1991, 1993, Norrdahl 1995, Norrdahl and Korpimäki 1995, Korpimäki and Krebs 1996). The invading new generalist predator, the American mink (*Mustela vison*), or increased predation by avian predators due to reduced snow cover may have decreased vole abundances and stabilized dynamics (Hörnfeldt *et al.* 1990, Oksanen *et al.* 2001).
- 6) Food/shelter decrease hypothesis (FSDH). Bilberry (*Vaccinium myrtillus*) is an important food item for grey-sided voles (Kalela 1957). Bilberry stands also provide shelters to grey-sided voles against predators (Löfgren 1995). Outbreaks of the moth *Operophtera brumata* and parasitic fungus (*Valdensia heterodoxa*) or warmer winters (temperature around 0°C during mid-winter) may destroy bilberry stands over large areas.
- 7) Food-quality decrease hypothesis (FQDH). This hypothesis has connections to the FSD-hypothesis (above). Environmental pollution (contamination by heavy metals or imbalance of mineral elements) alters the quality of food. These changes may decrease the survival rate or reproductive capacity of voles.
- 8) Environmental stress/disease hypothesis (ESDH). Previously unknown Ljungan virus has been reported to cause diabetes in bank voles (Niklasson *et al.* 2003). The virus has also been isolated from some other vole species such as grey-sided vole, field vole (*Microtus agrestis*) and Norway lemming (*Lemmus lemmus*). Imbalance of mineral elements due to pollution (FQDH above) may weaken the immune system of voles and therefore they may have become more sensitive to diseases and stress.

(Mappes *et al.* 1998, Norrdahl and Korpimäki 1995).

Regular, high amplitude multiannual vole cycles have changed in many areas in Fennoscandia since the 1980s (see Box 2). More stable or irregular small mammal fluctuations have been reported from e.g. the northern taiga forest: Pallasjärvi in 1982 (Henttonen *et al.* 1987, Hanski and Henttonen 1996), Umeå in the mid-1980s (Hörnfeldt 2004), birch forest/tundra in Kilpisjärvi in 1990 (Henttonen and Wallgren 2001), and boreal taiga in southern Finland (Sundell 2003b). The change in the pattern vole dynamics may

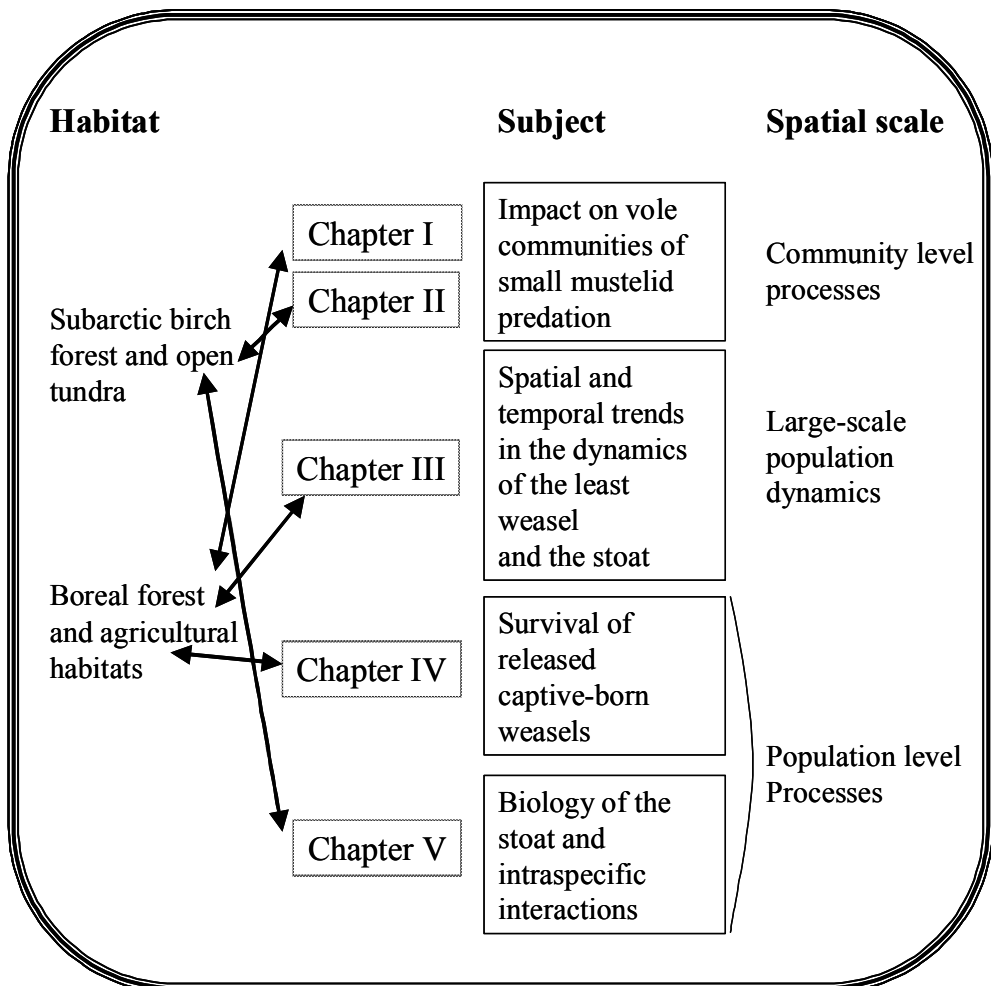
be due to changes in the relative numbers of different kinds of predators. In northern Fennoscandia, the weasels used to be the numerically dominant resident specialist predators (Kaikusalo 1982, Henttonen and Wallgren 2001), but more recently the stoat populations have increased relative to weasel populations (Chapter II).

### Outline of this thesis

In this thesis I have studied the impact of the stoat and the least weasel on their prey populations, their population dynamics, behaviour and habitat use (Fig. 1).

Chapters **I** and **II** are focused on the ecological effects of small mustelids on the dynamics of voles. Chapter **III**, based on snow track counts, investigates large-scale temporal and spatial dynamics of the stoat and the weasel. Chapter **IV** deals with survival of captive-born weasels following their release in the field. Finally, stoat behaviour and differences between sexes are discussed in more detail in Chapter **V**.

Indirect effects of predator presence on vole breeding and behaviour, and ultimately on vole population dynamics, have been studied during the last decades (Gorman 1984, Ylönen 1989, Heikkilä *et al.* 1993, Koskela and Ylönen 1995, Mappes *et al.* 1998, Carlsen *et al.* 1999, Korpimäki *et al.* 1996, Norrdahl and Korpimäki 2000, Pusenius and Ostfeld 2000, Ylönen 2001, Fuelling and Halle 2004). Here we tested with a novel method in the field whether long-term



**Figure 1.** Relationship between the Chapters. On the left are the habitats where data were collected, next the five Chapters and the topics of the Chapters. On the right is shown the spatial scale of the each study.

presence of the weasel has any behavioural or demographic effects on the field vole (**I**).

Regular and synchronous small mammal fluctuations used to be characteristic for northern Fennoscandia, but since the 1980's the vole cycles have been replaced by more stable dynamics. It has been suggested that a possible reason for this shift is a change in the species composition in the predator guild. Here, we studied the dynamics of small mustelids in the entire Finland (**III**) and more specifically how changes in the relative abundance of stoat and weasel affect the vole populations in northern Lapland (**II**).

Introductions and re-introductions from captive-bred colonies is one possible way to restore rare animal populations (Kleiman 1989, Griffith *et al.* 1989). But captive-bred animals, especially predators, have often problems in adapting to natural

conditions (Kleiman 1989). Predators may have certain times in their development when they learn important skills for survival, which makes the adaptation to nature more challenging. We studied how captive-bred least weasels survived and how they behaved following their release to nature (**IV**).

Size differences between the two sexes in small mustelids are supposedly caused by the avoidance of intersex competition (Brown and Lasiewski 1972, Dayan and Simberloff 1994) or by difference between male and female reproductive strategies (Erlinge 1979, Moors 1980, Sandell 1989). The male and female stoats are specialized to use different prey species, and during the non-breeding season male and female territories do not generally overlap (**V**). Habitat use may be different between the sexes but may also differ between males with different dominance status (**V**).

## Material and methods

### Study areas

Material for this thesis was obtained from several localities across Finland (Fig. 2). A captive-bred colony of least weasels was maintained at the Lammi Biological Station (61°03'N, 25°05'E) (Chapters **I**, **IV**), where the indirect effects of predator presence (**I**) and some of the release experiments (**IV**) were conducted. Other release sites were located at Punkaharju area (61°47'N, 29°17'E) and in the Päijänne area (61°42'N, 25°35'E). Habitat

choice and home range studies in stoats (**V**) and the effects of changes in the carnivore guild (**II**) were performed in Kilpisjärvi (69°03'N, 20°45'E). The data for studying the large-scale spatial and temporal dynamics of the stoat and the least weasel come from c. 1500 wildlife snow tracking triangles (collected by the Finnish Game and Fisheries Research Institute), and covers the entire Finland (**III**). The southern study areas were mostly fragmented landscapes with managed coniferous forest and agricultural

areas. The Kilpisjärvi habitats were mountain birch forest and open tundra at higher altitudes (700 m above sea level).

### Field experiment on predation risk (I)

Two grids constructed of plastic drainpipe were placed on two meadows at the Lammi Biological Station. Each grid covered 2400 m<sup>2</sup> with each parallel line of pipes at 10 m distance from each other. The drainpipe was 80 mm in diameter and contained small holes. One least weasel was released into the grid of pipe, and the experimental grid was connected to a cage for the weasel. The weasel was fed dead chickens in different parts of the grid. A vole trapping area was located in and around each grid so that in the middle of parallel pipes there was a trap, and the trapping area extended 15 m beyond the outer limits of the grid. The purpose of the experiment was to investigate the presence of the weasel in the experimental grid on

the behaviour and demography of local voles.

### Captive-born weasels

The survival of captive-born least weasels was studied in Chapter IV, but one of the weasels was also used in the experiment on indirect effects in Chapter I. The least weasels were from the colony in the Lammi Biological Station (see Sundell 2003a). In captivity, the least weasels lived in 0.5 m<sup>2</sup> cages, but they spent 10-20 days in larger enclosures out of doors before being released to the nature. The captive-born least weasels used in the experiments were 12 to 40 weeks old.

### Vole, weasel and stoat trappings

We made vole trappings in studies reported in Chapters I and II using the CMR-method (capture-mark-recapture, Myllymäki 1977). We used Ugglan

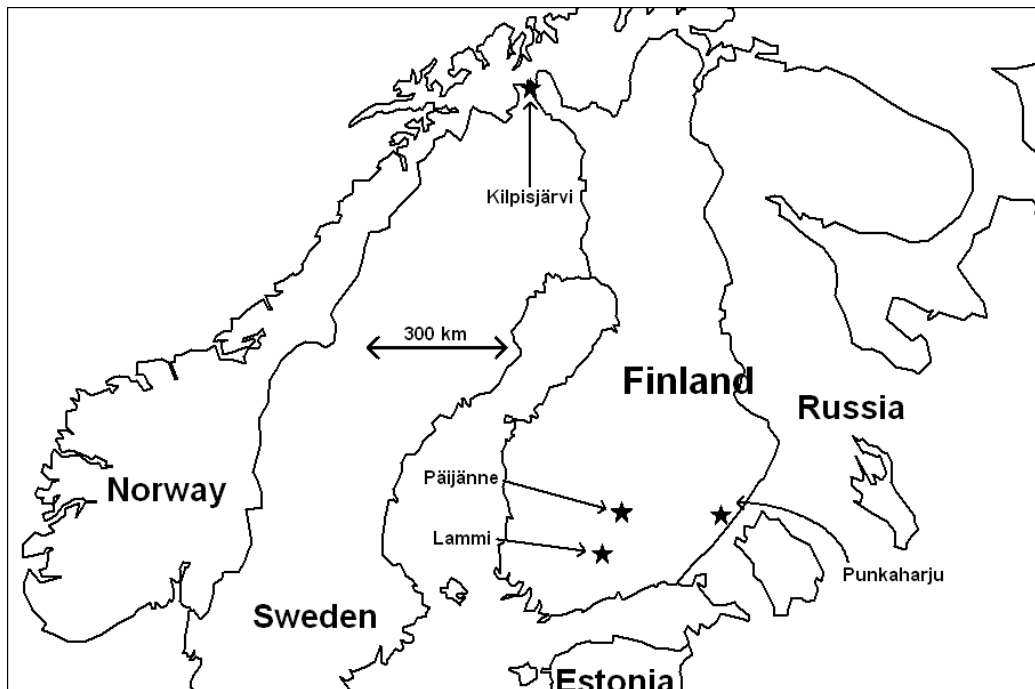


Figure 2. Study localities in Finland.

Special-traps or Ugglan lemmel-traps (Grahnb, Hillerstorp, Sweden) with oat as a bait. In the study in Chapter I we placed traps in the middle of each grid cell. The size of each trapping area was 6300 m<sup>2</sup> and the traps were located within each 100 m<sup>2</sup>, with the outermost traps laid 15 m outside the edge of the grid (altogether 80 traps/area). Nine trapping periods, each 2-4 days in length, were performed from late April to mid-July. In Chapter II there were three experimental trapping areas and three control areas. Each trapping area was 3.61 ha in size and each trapping session lasted for 4 days. Altogether 100 traps in each area were rotated between trapping points in every 24 h so that the actual distance between the traps at any one time was 20 m (see Henttonen *et al.* 1987, Yoccoz *et al.* 2001).

Least weasels were trapped mainly using Ugglan special or Ugglan lemmel live-traps (Chapter IV). Stoats were trapped (Chapter V) using wooden 'Erlinge'-model live traps with piece of reindeer liver as a bait.

### **Weasel, stoat and vole radio-tracking**

We studied weasel activity, visibility, habitat use and avoidance of predation using radio-tracking. In addition, radio-tracking was used to study the survival of captive-born least weasels of different ages, and differences in their survival in different seasons (Chapter IV). Radio-tracking was used in Chapter I as a control method, to verify that the least weasel inside the experimental grid moved around the entire grid area. In Chapter I we radio-tracked mature female field voles to estimate their home range sizes and movement activity.

Captive-born released weasels, wild-caught and released weasels, stoats and female voles were fitted with a 2 or 4.2 g TW-4 transmitter collar with one or two batteries (Biotrack, Dorset, United Kingdom). Every observation of a tagged animal was marked on a map. The locations of stationary animals were estimated by taking bearings from two or three directions at the distance of 15-25 m from the animal. When the animals were moving around the route taken was marked on a map.

Home ranges of weasels (Chapter IV) and stoats (Chapter V) were analysed using the Ranges V program (Kenward and Hodder 1996) and survival rate of released least weasels (Chapter IV) using the Mayfield-method (Bart and Robson 1982). The habitat use of stoats (Chapter V) was characterized with a compositional analysis (Aebischer *et al.* 1993).

### **Snow tracking**

The data in Chapter III were collected using the Finnish wildlife snow tracking monitoring system, the wildlife triangle method (Lindén *et al.* 1996). We analysed data involving the 12 km wildlife triangles for the years from 1989 to 2003, with the sample size varying from 400 to 1043 triangles per year. The data have been collected by the Finnish Game and Fisheries Research Institute, and the actual field work has been done by volunteers. Part of the data in Chapter II came from snow-tracking records. Snow tracks were counted six times, once or twice a year in 1998-2004. The snow track index for each species gives the number of tracks crossing the inventory route per 10 km in 24 h.



## Scat analyses

We collected stoat and least weasel scats (Chapter II) in Kilpisjärvi in 1998-1999. Scats were collected from stoat traps, along the snow tracks, and from the

resting and nestings spots of small mustelids located during radio-tracking. Scats were analysed under dissecting microscope or using the cross-section method.

## Main results and discussion

### Indirect effects of least weasel presence on field vole behaviour and dynamics (I)

Field vole numbers in the different functional groups (mature females, males and immature), home range sizes and mature female vole's movement activity were studied in the control and experimental grids. In the experimental grid weasel was present but had no access to voles. The purpose was to study whether the presence of the weasel had any indirect effect on the behaviour or demography of field voles and on their population dynamics. There were no statistically significant differences in the behaviour between the experimental and control grids. Furthermore, there were no differences in maturation age or reproduction of female voles. In the beginning of the experiment the vole population growth rate was faster in the control grid than in the experimental grid, but this difference disappeared after a few weeks.

Many previous studies have found physiological or behavioural effects in voles of the presence of predators (Gorman 1984, Ylönen 1989, Heikkilä *et al.* 1993, Koskela and Ylönen 1995,

Korpimäki *et al.* 1996, Pusenius and Ostfeld 2000, Fuelling and Halle 2004). Most of these studies were conducted in laboratory. The studies that have been conducted in the field have shown no effect of weasel odour on field voles (Korpimäki *et al.* 1994, Chapter I). In our experiment, weasel presence had no effect on field voles either at the individual or at the population level. However, our experiment was done in the summer during the peak breeding season. A modified version of the breeding suppression hypothesis by Norrdahl and Korpimäki (2000) assumes that the indirect effects may be present only during the autumn and spring.

### Impact of stoats on the dynamics of the rodent community in Finnish Lapland (II)

Snow track lines were counted six times in Kilpisjärvi in the years 1998-2004. Stoat tracks were clearly more numerous than the tracks of any other predatory mammal, including the least weasel. The results show that stoats change their habitat between autumn and mid-winter. In the autumn they spend more time in productive habitats, while in mid-winter stoats move to poorer habitats, consisting

of birch forest. Least weasel and red fox tracks declined from autumn to mid-winter. Vole trappings and a feeding experiment conducted in summer 1998 showed a clear change in the most numerous vole species. The numbers of red-backed vole increased 4-6 times from June to September, whereas the grey-sided vole, *Microtus*-vole and lemming numbers remained at a low level. We examined 54 stoat scats. Rodents were the most used prey both in the winter (79%) and in the summer (57%). *Clethrionomys*-voles appear to be the main prey item of stoats. The results of the faecal analysis and vole trappings indicate that the less agile and bigger species (*Microtus*-voles, lemming and grey-sided vole) are the primary prey of stoat. We did not observe high-amplitude fluctuations in the numbers of weasel as Kaikusalo (1982) reported, and stoat was the constantly most numerous species in the study area. Comparing the relative abundances of the vole species in the 1960s and 1970s and at present also shows a difference. The previously dominant species, the grey-sided vole, is now permanently uncommon while the subordinate species, the red vole (*Clethrionomys rutilus*), is now the numerically dominant species. Apparently, the red vole cannot maintain regular predator-prey cycles driven by small mustelids (Hanski and Henttonen 1996). We thus propose that changes in small mammal population dynamics from regular cycles to more stable dynamics are associated with changes in the relative abundances of the mammalian predators. However, the actual causal mechanisms remain poorly understood.

### Large-scale dynamics of stoat and least weasel (III)

According to the predator-prey hypothesis about voles and their predators (Hansson and Henttonen 1985, Henttonen *et al.* 1987, Hanski and Henttonen 1996), regular vole fluctuations are caused by specialist mammalian predators, the stoat and the weasel, which are dependent on voles as their main prey. Using the wildlife triangle data covering most of Finland, we examined the large-scale and long-term dynamics of the stoat and the least weasel, including the spatial synchrony in their dynamics.

The relative densities of the two mustelids were as expected: stoat is more abundant in the north and weasel in the south. Numbers of weasels and especially stoats decreased in every part of Finland between 1989 and 2003. Our results show that both the least weasel and stoat populations exhibit largely periodic fluctuations at the scale of Finland. We found similar amplitudes and cycle lengths for the mustelids, than found for voles (Chapter III). The geographical trend in the weasel cycle length was however unexpected. In the north, vole cycles used to be 4 to 5 years long, and much longer than at lower latitudes, but the average weasel cycle length was shorter in the north than in the south. Notably, in southern Lapland both mustelids had apparent 7 year cycles in many areas. This result might be expected in short time series if the true cycle length varies between 3 and 4 years and the amplitude is not high, giving rise to a spurious 7 year cycle.

For the weasel the S-index, which indicates the strength of cyclicity, showed an opposite trend (Chapter III) than

expected. For the vole populations S-indices increase northwards (Henttonen *et al.* 1985), but in the weasel there was no such trend or the trend was slightly decreasing. There is however one methodological issue that may bias snow tracking results. Especially the least weasel hunts regularly under the snow (Henttonen 1987). As the snow cover lasts longer and is thicker in the north, it is likely that weasels spend more time in the subnivean space in the north (Korpimäki and Norrdahl 1989a, b), which might lead to low numbers of tracks recorded in the north as well as to the unexpectedly low S-indices in the north. The stoat is considerably larger in body size, and therefore likely to move longer distances and spend more time on the snow surface than the least weasel. The differences in the activity and behaviour between the two species in snow-covered terrain may explain the generally lower track counts for the weasel (Jedrzejewski *et al.* 2000).

The weasel and stoat populations were in synchrony over long distances. Large-scale synchrony is apparent even if there is variation in the length of cycles as well as in their regularity in different parts of the country.

#### **Survival of captive-born released least weasels (IV)**

We studied the activity, visibility, habitat use and avoidance of predation by released weasels. The behaviour of captive-born weasels was markedly different than that of wild-born ones. Captive-born weasels were more often visible on top of the vegetation and were generally less wary than wild-born weasels. Captive-born weasels appeared to have problems in hunting and avoiding predation. Raptors, various mammalian

predators, and starvation killed many of them during the period of observation. The probability of death was generally higher among the captive-born than wild-born weasels.

According to our results the age of the released weasels as well as the season contributed to their survival. Relatively young weasels (12 to 18 weeks old) survived better than older animals (20 to 40 weeks). The normal weaning age is 8 to 9 weeks in the least weasel, suggesting that the older animals have grown too accustomed to cage conditions. Weasels, as all predators, must be able to search and kill their food, and it has been suggested that they have a period in their development when they learn these important skills (Miller *et al.* 1990, Vargas and Andersson 1999, our results). The survival of individuals that were released during autumn or winter (September to March) was particularly low. Even though in the autumn the vole density is usually high (Erlinge *et al.* 1984), weasels survived better if they were released during the summer. The weasels that were released in summer were younger, which might explain their higher survival. However, we cannot exclude an alternative explanation: the higher mortality rate in the autumn may result from competition. In the autumn, the numbers of wild least weasels are probably higher than in the summer, and therefore the numbers of vacant territories are low. Released weasels are thus forced to search larger areas for places to stay, which increases their activity and visibility, increasing in turn their risk to predation.

### **Behavioural differences among stoats depending on their sex and dominance status (V)**

In Finnish Lapland, the stoat home range sizes and habitat choice differ among individuals depending on their sex and dominance status. Both sexes move and are active in the same areas during the breeding season, but after that the home ranges generally do not overlap. Female stoats start to avoid males after cessation of their heat. Male home range size did not vary between the seasons, but habitat selection changed. Following the breeding and mating season, female stoats stay in the most productive habitats (high density of *Microtus*-voles), whereas males move to lower quality birch forest and open tundra habitats.

We found no differences in the daily activity between male and female stoats. However, during the non-breeding season stoats were more active than during the breeding season. In northern Lapland, the size difference between the sexes is bigger than at lower latitudes. This might be due to stronger intersex competition and differences in the preferred prey species. The habitat choice of stoats is influenced by their dominance status. Subdominant males spend their time in open tundra or in birch forest, whereas dominant males occur in the same areas where females are found. We found overlap in the home ranges of individuals of different dominance status during the breeding season but also during the non-breeding season. This may be caused by males in the lower levels of the hierarchy trying to use more productive areas (territories of dominant males) when possible.

### **Conclusions**

In this thesis, I have studied the behaviour and ecological impact of small mustelids on their prey species. In nature it is often hard to distinguish between the factors affecting the prey populations directly versus indirectly. Weasel presence seems not to have a strong indirect effect on field vole individuals or populations (I). However, our experiment was conducted during the main breeding season, when delaying reproduction would be very costly to voles; the results might be different during other seasons (Norrdahl and Korpimäki 2000).

During the breeding season stoats are active in habitats where the main prey species are common: meadows, riverbanks and gardens (V). Female stoats stay in these high-productivity habitats also following the breeding season, but males in northern Lapland change their habitat more readily to birch forest and open tundra (II, V).

Reintroductions of captive-born animals often fail (Kleiman 1989). We considered several factors that might help improve the survival of released mustelids (IV): released individuals should be in their normal dispersal age and they should have enough time to practise hunting. Human contacts with released animals should be minimized. Additionally, competition with wild-born individuals and the amount and availability of prey used affect the success of introduction.

Changes in the predator guild may affect the dynamics of the prey community (II). Both small mustelids have exhibited decreasing temporal trend in Finland in the past decades (III). Slight changes in the relative numbers of different predators

may lead to large-scale consequences. In the northernmost Lapland the most numerous vole species in the 1970's and the 1980's was the grey-sided vole, which ecologically resembles Fennoscandian *Microtus*-voles (Henttonen and Wallgren 2001). The vole cycles have now largely disappeared in northern Lapland, which

may be due to relatively large stoat populations keeping the grey-sided vole populations at low level, and thus preventing the least weasel – grey-sided vole dynamics leading to regular cycles. However, it is not clear what allows the stoat populations to remain at high or relatively high density.

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