

SOCIAL ORGANIZATION IN EUROPEAN SMALL MUSTELIDS

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ABSTRACT – A review of the social organization in the weasel (*Mustela nivalis*) and stoat (*M. erminea*) is made, based mainly on my earlier mark-recapture studies on weasels and stoats and radio-tracking studies on stoats. During the non-breeding season, from September to April, the small mustelids are organized in a territorial pattern; individuals of the same sex exploit exclusive areas. The extensive male territories often include one or several female ranges. The territories are probably delineated mainly by scent marking. During the breeding season the males increase their movement activity and extend their ranges. The territorial systems break down and male ranges generally overlap considerably. Depending on their social status, males adopt different strategies, i.e. roaming or staying, in their attempts to obtain as many matings as possible. Prey abundance and distribution are considered to be the decisive factors determining female spacing behaviour throughout the year. The great amount of food required by females when rearing young makes it rewarding to defend and use restricted areas exclusively. In males there is a seasonal change in social organization resulting from a shift in decisive resources; i.e. priority is placed on procuring receptive females during the breeding and food during the non-breeding season.

Key words: *Mustela nivalis*, *M. erminea*, Territorial pattern, Marking behaviour, Mating system.

RIASSUNTO – *Organizzazione sociale nei piccoli mustelidi europei.* – L'autore presenta un'analisi dell'organizzazione sociale della donnola (*Mustela nivalis*) e dell'ermellino (*M. erminea*), basata soprattutto sui suoi studi effettuati mediante i metodi di marcamento-ricattura per entrambe le specie e di radio-telemetria per l'ermellino. Durante la stagione non riproduttiva, da settembre ad aprile, i piccoli mustelidi sono organizzati secondo un modello territoriale: individui dello stesso sesso utilizzano aree esclusive. Gli ampi territori dei maschi spesso includono quello di una o più femmine. Probabilmente i territori sono delimitati principalmente con marcamenti odorosi (feci). Durante la stagione riproduttiva i maschi incrementano i loro movimenti e estendono le loro aree vitali. Il sistema territoriale non viene più mantenuto e le aree vitali dei maschi generalmente si sovrappongono notevolmente. In relazione al loro stato sociale, i maschi adottano differenti strategie: cioè, vagano o restano nella loro area vitale nel tentativo di avere più accoppiamenti possibile. La distribuzione e l'abbondanza delle prede sono considerati i fattori prioritari che determinano il comportamento spaziale delle femmine nell'arco dell'anno. L'elevata richiesta di cibo da parte delle femmine durante l'allevamento della prole si traduce nella difesa ed uso esclusivo di aree limitate. L'organizzazione sociale dei maschi varia stagionalmente in relazione al cambiamento delle risorse di "vitale importanza": durante la stagione riproduttiva diventa prioritario procurarsi femmine recettive, mentre durante quella non riproduttiva diventa fondamentale il cibo.

Parole chiave: *Mustela nivalis*, *M. erminea*, Modelli territoriali, Marcamento, Sistemi riproduttivi.

INTRODUCTION

The small mustelids that will be considered are the weasel (*Mustela nivalis*) and the stoat (*M. erminea*). Their social behaviour can be best understood from the viewpoint of the individual animals' spacing behaviour. This in turn is largely determined by the distribution and abundance of decisive resources (e.g. Krebs and Davies, 1991). Since resources can vary locally and seasonally, one would expect a great flexibility and variation in social organization.

Small mustelids are solitary animals. This solitary behaviour can be ascribed to their foraging behaviour; i.e. they are extremely carnivorous and hunt warm-blooded animals. Small rodents are their main prey (Erlinge, 1975 and 1981). The body shape and hunting behaviour of small mustelids are well adapted to the size and habits of their prey. They track and kill their prey individually and kill in excess of their immediate needs if given the opportunity. Surplus prey are stored in order to meet future needs. The advantage of solitary living is obvious: they need not fight over or share captured prey with conspecifics. Group-living would not provide any increased protection against predators or increase deficiency of catching prey, which probably explains why small mustelids are not gregarious. One of the most important decisions to be made by an individual is whether or not a decisive resource should be defended by territorial behaviour. Theoretically this decision should depend on a cost-benefit assessment, i.e. whether or not it is energetically feasible to defend an exclusive area.

Food is probably the decisive resource for females. When rearing young, females are expected to be territorial. At that time females require a great amount of food. Thus they should benefit by monopolizing available prey in the area surrounding nest-site. Defence of that area also reduces the risk of infanticide by conspecifics.

Also, outside the breeding season, a territorial organization among females is expected, if territory defence is not too costly.

A territorial organization is also expected in males during the non-breeding season. Due to the great difference in body size between males and females (males often weigh twice as much as females) the two sexes could differ in diet and hunting behaviour making coexistence between the sexes easier. Males should be most likely to have intra-sexual territorial systems with larger ranges.

To test these ideas I have summarized current information on the weasel (*M. nivalis*) and the stoat (*M. erminea*) mainly obtained from my own studies.

Social organization was examined primarily by mark-recapture. At first capture the individuals were marked with stamps on the edge of their ears, in different positions and combinations (Fig. 1). Additional detailed information on the stoat's social organization was obtained by telemetry. The animals were fitted with radio-collars, that were ca. 4-5 % of their body weight, i.e. 6 g for females and 10 g for males (Fig. i). Battery life was about a week at the beginning of the study (Erlinge, 1977a) but by 1986 it was about four weeks (Erlinge and Sandell, 1986). The animals were generally tracked continuously. Social dominance interactions and scent marking behaviour were studied in enclosed areas with simulated natural habitats (Erlinge, 1977b).

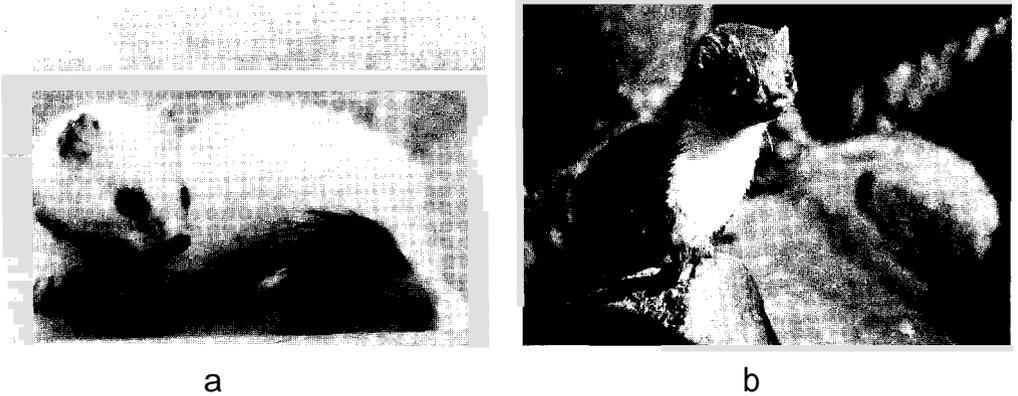


Fig. 1 – A male stoat (a) in its winter coat and with a radio collar on. The method used for marking individuals by stamping the edge of the ear is shown. A male weasel (b).

MARKING BEHAVIOUR

The territories are defended primarily through scent marking. The stoat and weasel show two kinds of marking behaviour: anal drag and body rubbing (Fig. 2). During anal dragging scent material from the anal glands is deposited on stones and other bare places by depressing the anal region while moving slowly forwards and backwards. During body rubbing, the sides, belly and other parts of the body are rubbed against the environment, and in the process contacted vegetation, runways walls and tunnels, etc., are scented. Both males and females display the two types of marking behaviour. Anal drag is probably used primarily for individual recognition; the scent has a chemical composition that seems to be specific for each individual (Erlinge et al., 1982). Body rubbing occurs predominantly in connection with agonistic interactions and appears to convey a threatening message. Both kinds of scent are probably used in territorial defence. Dominant individuals mark much more frequently than do subordinate individuals. Scent marking is considered to be important in allowing assessment of the asymmetry in a conflict, such as one between a territory owner and an intruder.

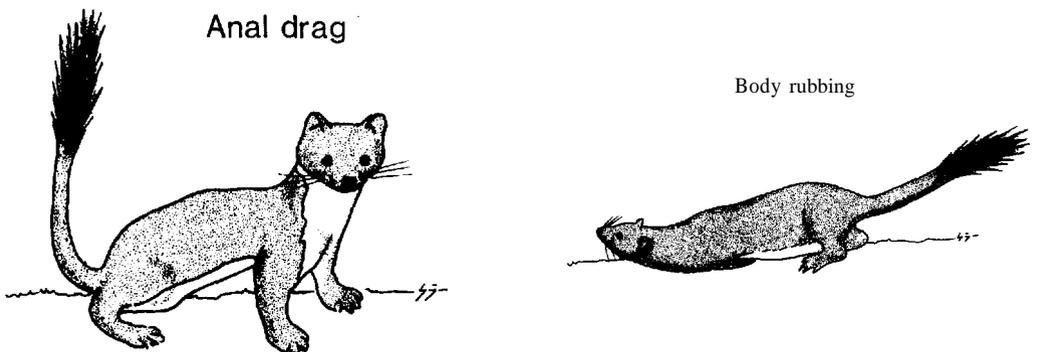


Fig. 2 – Two types of scent marking behaviour in stoats, anal drag and body rubbing. (drawings by G. Goransson).

TERRITORIAL PATTERN IN NON BREEDING SEASON

During the non-breeding season, from September to April, individuals of the same sex were distributed in a territorial pattern. In one marsh area three male stoats were repeatedly trapped in autumn 1973, each of them in separate areas. In November, December and January they were followed during periods with a snow cover so that their home ranges could be determined based on their tracks (Fig. 3). The males covered well defined areas of about 8-13 ha (male 17, which was a large adult, occupied the largest range). Between two of the male ranges there was a narrow zone of overlap. Three females were established in the same area (Fig. 3). They exploited smaller areas within or adjacent to the males' ranges, well separated and without any contact with each other. In some of the other examined areas radio-tracked females occupied exclusive home ranges adjacent to each other according to a territorial pattern (see Figs. 3 and 4, in Erlinge, 1977a).

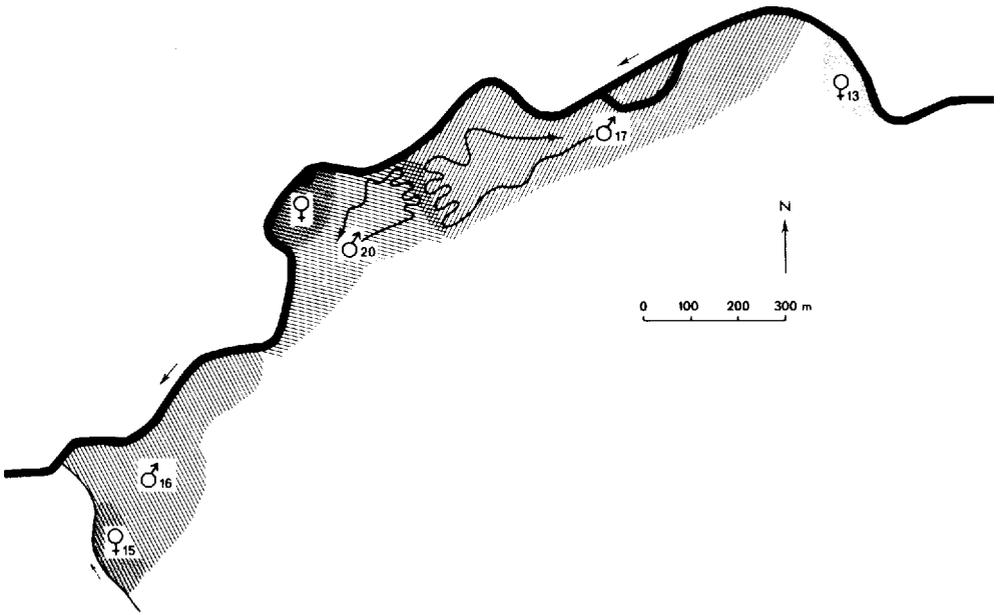


Fig. 3 - Distribution of three male and three female stoats in autumn and winter 1973-74 (from Erlinge, 1977a).

A similar distribution pattern was found in the weasel (Erlinge, 1974). In an examined woodland area some adult males established home ranges within which other individuals of the same sex were excluded (Fig. 4). The ranges were in a spruce plantation on an abandoned field and in a clear-cut area. Both habitats contained high densities of small rodents (field voles and bank voles). A male range had one female range within or adjacent to his own. That the established males were confined to definite areas was confirmed by replacement experiments (Fig. 5). When male A was placed outside its range, it immediately returned, as did male B. When released at the same site they took off in opposite directions and returned to their respective home ranges (Fig. 5). Removal experiments revealed the territorial

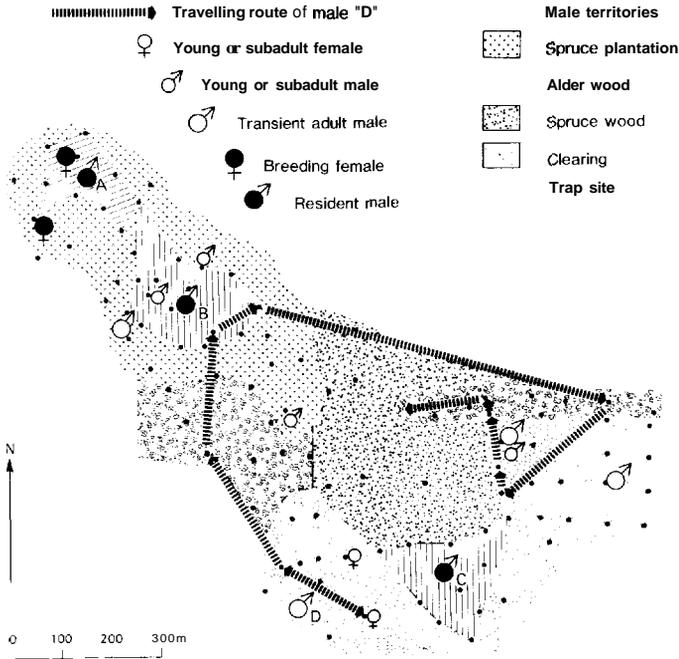


Fig. 4 – Distribution of weasels in a woodland area in autumn 1972. Established males' territories are marked out along with the sites of which other captured animals were trapped (from Erlinge, 1974).

significance of the males' ranges (Fig. 6). In one case, two males had adjacent ranges in September. Early in October male K extended his range while the range of male A shrunk. The dominance relationship between the two males was tested in a cage experiment (about 1.5 m²) with two compartments. When the two males caught sight of each other, male K tried to attack and made sharp, threatening sounds, and when the door separating the two males was opened, male K attacked A, who fled out of the cage pursued by K. Obviously male K dominated the other male. To confirm the influence of K's dominance on A, K was removed. Male A then extended his range to cover central parts of K's earlier range (Fig. 6).

In addition to established adult males, juvenile males were also trapped. They generally occurred outside the resident males' ranges (Fig. 4). One tracked male covered a large area between the established males' ranges.

To sum up: the data obtained confirm the predictions made in the introduction. The social organization among small mustelids during the non-breeding season is characterized by intra-sexual territoriality among both males and females. The extensive male territories often include one or several female ranges.

DISTRIBUTION PATTERN IN BREEDING SEASON

During the breeding season, males extended their movements and their territorial system breaks down. Male weasel A illustrated the change in spacing

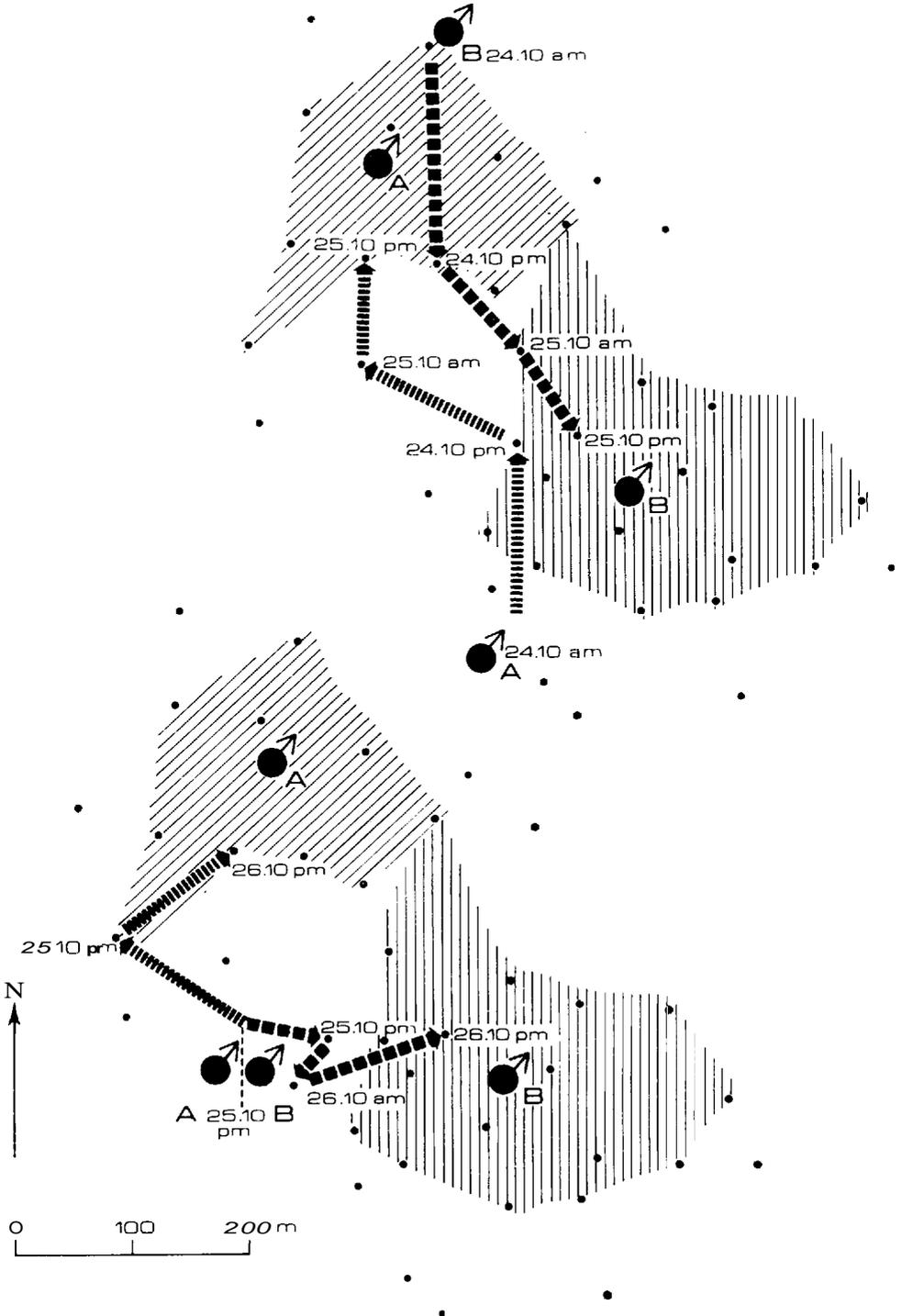


Fig. 5 - Replacement experiment with two resident males, A and B. Their returns are indicated by broken lines. Dots denote trap sites. Capture dates are given (from Erlinge, 1974).

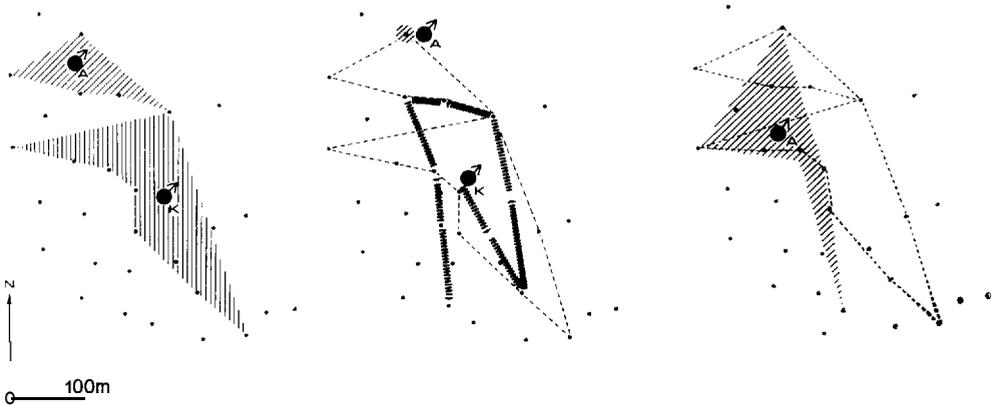


Fig. 6 - Removal experiment with male weasels. To the left: the territories of **A** and **K** (striped areas) in late summer and autumn 1973. In the middle: the situation in October. The patrol route of male **K** during a 5-day period is shown. To the right: the area occupied by **A** (striped area) after the removal of **K**. The territories in early autumn are denoted by broken lines. Dots indicate trap sites (from Erlinge, 1974).

behaviour (Fig. 7). Throughout autumn and winter it confined its activity to a restricted area in the spruce plantation. Towards the end of March it left its winter territory and moved to a clear-cut area about 1 km away where it had contact with two females. It returned to its winter range after a month but paid another visit to the clear-cut area in May. Movements of another male were recorded in the same clear-cut area (Fig. 7 below). It visited ranges of the females, but the two males avoided close contacts. Thus, extended movements and overlapping ranges characterize the spacing behaviour of male weasels during the breeding season,

The same pattern was found in male stoats. A second-year male established itself in a marsh area early in September and was recaptured throughout autumn and winter in an area of about 11 ha. In October, its movements were traced continuously by radio-tracking (Fig. 8). A young male was trapped in the periphery of the resident male's territory. In an encounter test the young male showed submissive behaviour in presence of the adult male. In spring and summer the male greatly extended its range so that it eventually included two other marsh areas (Fig. 8). Each of the marsh areas was occupied by one or two female stoats and also other males visited these areas.

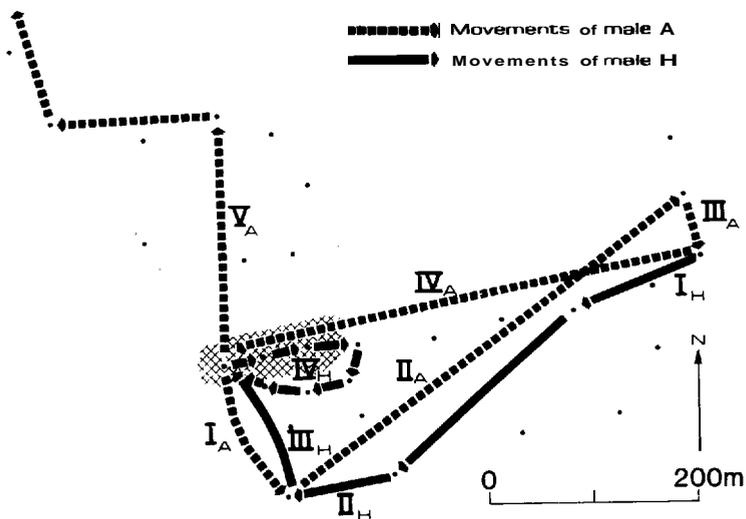
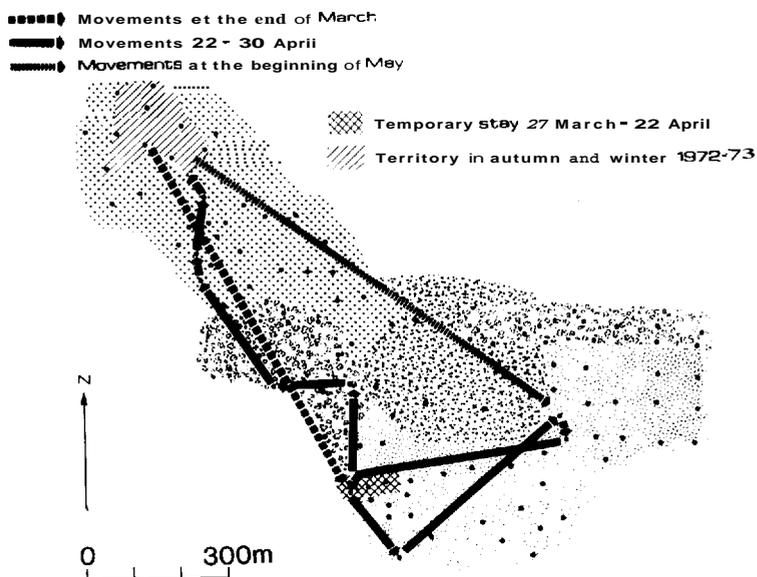


Fig. 7 - Movements and stays of male A in spring 1973 (above). Movements of male A connected with a visit of another male H (below). The sequence of events are indicated by Roman numerals. The area occupied by male A before the intrusion of male H, is indicated by cross-hatching. The habitats are designed as in Fig. 3 (from Erlinge, 1974).

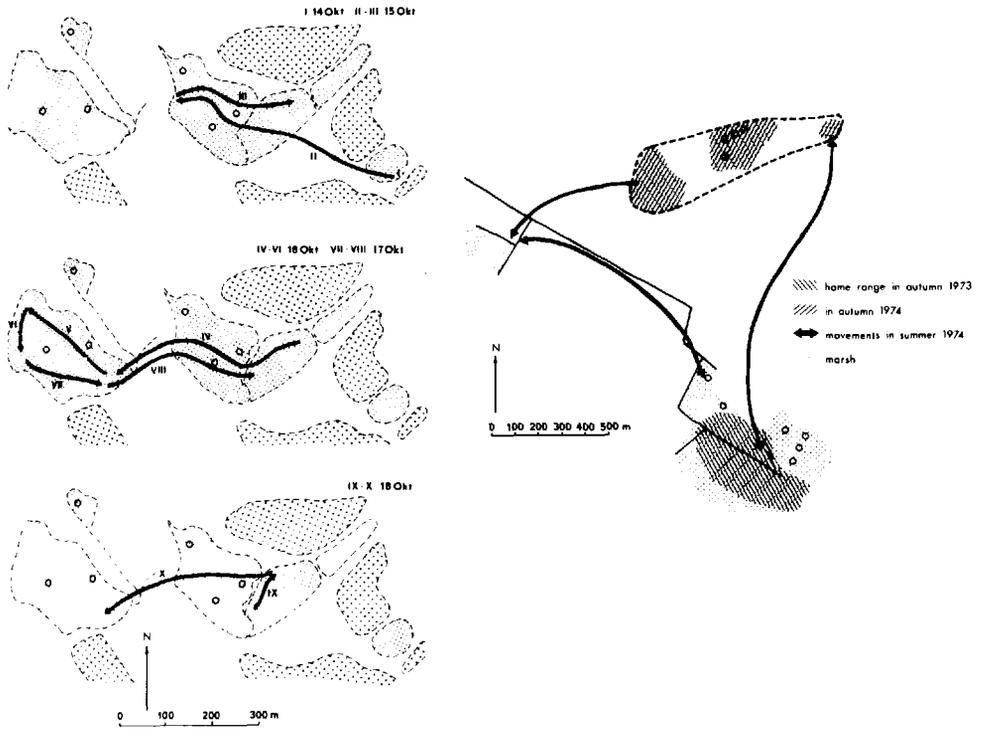


Fig. 8 – Movements of a resident male stoat radio-tracked in October 1974 (to the left). The male's range comprised three smaller marshes (dotted areas) separated by open fields. The increased movements of this male in spring and summer are shown to the right (from Erlinge, 1977c).

FACTORS AFFECTING SPACING BEHAVIOUR

How should this change in male spacing behaviour be interpreted? Why do males change their behaviour? During the non-breeding season, in autumn and winter, survival is the small mustelids' sole interest. Thus, food and foraging conditions, i.e. foraging and avoiding predation are decisive factors. Conversely, during the breeding season, females may be the decisive resource for males. The small mustelids have, in fact, a promiscuous mating system, and males do not provide any parental care (Erlinge, 1979). Mating opportunities presumably are decisive for males. To maximize their mating success, they adopt different strategies which differ depending on their social status (Erlinge and Sandell, 1986). Young and first-year males are subordinate to older males (Erlinge, 1977b) and were observed to adopt a staying strategy (Fig. 9), remaining in areas close to breeding females. Older males adopt a roaming strategy, moving extensively in their attempts to mate with as many females as possible (Fig. 8). In the stoat,

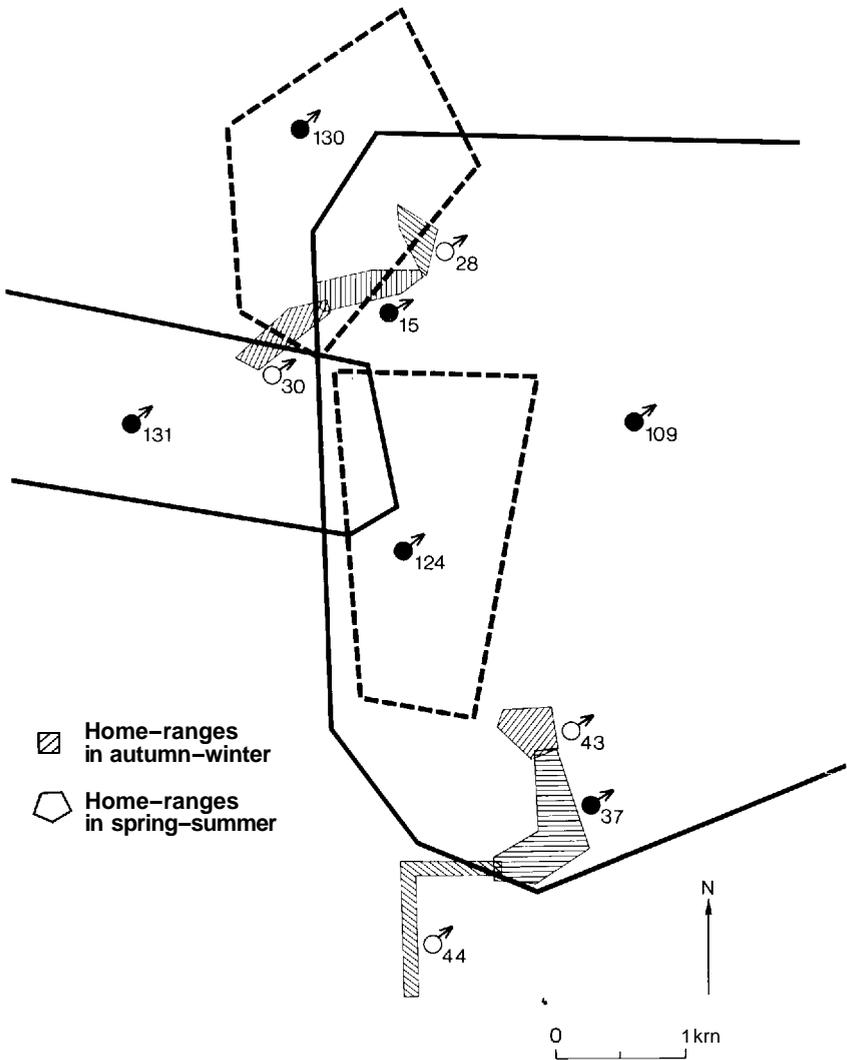


Fig. 9 – The two patterns of spacing in male stoats: territorial in autumn and winter (hatched areas) and non-territorial in spring and summer (open, delineated areas). For males 109 and 131, only about half of the recorded ranges are shown on the figure. Data based on radio-tracking. Open symbols denote juvenile males and filled symbols represent adults (from Erlinge & Sandell, 1986).

females come into oestrous shortly after parturition in April or May. The young females are extremely precocious and sometimes become receptive even before leaving the nest, but some young females do not mate until July and August. The extended mating season, with asynchronous females in oestrous, the overdispersed distribution of females and their low density promote a spacing behaviour in males with extensive, overlapping home ranges. The roaming strategy works especially well for dominant males: once having localized an unmated female, a dominant male can stay nearby it for a number of days in order to keep other males away and mate with the female and its female offspring. A dominant male can even repel a subordinate male and take over an unmated

female. A good way for a subordinate younger male to achieve matings would probably be to stay close to a female and hopefully mate with it before a dominant male appears.

CONCLUSION

The social organization during the breeding season can be summarized as follows: in females, prey abundance and distribution are the decisive factors determining their spacing strategy. At low prey density females can adopt nomadic habits and carry their young between different places. The area around the temporary nest sites is vigorously defended. At high prey density, a territorial pattern similar to that in autumn and winter is expected.

For males, receptive females are the decisive resource. At low female densities, male ranges overlap extensively and the males adopt staying or roaming strategies depending on their dominance rank. At a high female density, male ranges can be more restricted and the distribution pattern might to be more of a territorial system. In Lockie's pioneering mark-recapture study on weasels in an area of high vole density the males also retained a territorial system during the breeding season although the ranges overlapped a bit more (Lockie, 1966)

REFERENCES

- ERLINGE, S. 1974. Distribution, territoriality and numbers of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos*, 25: 308-314.
- ERLINGE, S. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos*, 26: 378-384.
- ERLINGE, S. 1977a. Spacing strategy in stoat *Mustela erminea*. *Oikos*, 28: 32-42.
- ERLINGE, S. 1977b. Agonistic behaviour and dominance in stoats (*Mustela erminea* L.). *Z. Tierpsychol.*, 44: 375-388.
- ERLINGE, S. 1977c. Home range utilization and movements of the stoat *Mustela erminea*. XIII Int. Congr. Game Biol. (Atlanta), 31-42.
- ERLINGE, S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos*, 33: 233-245.
- ERLINGE, S. 1981. Food preference, optimal diet and reproductive output in stoat *Mustela erminea* in Sweden. *Oikos*, 36: 303-315.
- ERLINGE, S., SANDELL, M. & C. BRINCK. 1982. Scent marking and its territorial significance in stoats, *Mustela erminea*. *Anim. Behav.* 30: 811-818.
- ERLINGE, S. & M. SANDELL. 1986. Seasonal changes in the social organization of male stoats, *Mustela erminea*: an effect of shifts between two decisive resources. *Oikos*, 47: 57-62.
- KREBS, J.R. & N.B. DAVIES. 1991. Behavioural ecology. An evolutionary Approach. Blackwell, London, Third edition, 428 pp.
- LOCKIE, J.D. 1966. Territory in small carnivores. *Symp. Zool. Soc. Lond.*, 18: 143-165.