Ann. Zool. Fennici 28:15–21
Helsinki 31 May 1991
ISSN 0003-455X

Muskrat (*Ondatra zibethica*) territoriality, and the impact of territorial choice on reproduction and predation risk

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Received 23 April 1990, accepted 17 January 1991

A muskrat population in northern Sweden was studied during one breeding season. The spatial distribution of muskrat houses was regular, indicating that the animals are territorial even at relatively low densities. Muskrats preferably constructed houses on elevated places, or on the edge of deeper water and in stands of *Phragmites*. The number of young produced per house was correlated with territorial quality. Predation by red fox occurred in houses situated in shallow water close to the shore. The few cases of predation by mink that were recorded seemingly occurred independently of water depth or distance to shore.

1. Introduction

At the beginning of the 20th century (1905) the muskrat (*Ondatra zibethica* (L.)), indigenous in North America, was introduced into central Europe. Around 1950 the muskrat invaded northern Sweden from Finland and is currently spreading southwards at a dispersal rate of approximately 3 km/year (Danell 1977).

This large microtine rodent is mainly herbivorous in Sweden and, depending on the environment, either constructs houses or digs burrows in banks (Marcström 1964).

Muskrats often exhibit territorial behaviour, especially during the breeding season and when population density is high (Willner et al. 1980, Perry 1982). The population density of muskrats recorded in Sweden is low compared with the highest densities reported from North America. From Iowa, winter muskrat densities of up to 86 animals/ha in cattail marshes and 25 animals/ha in less favourable habitats have been reported (Errington 1948). These figures are considerably higher than the 3–6 animals/ha reported from Sweden (Danell 1978).

The choice of house building site by muskrats is influenced by water depth and vegetation in the vicinity of the site (Danell 1978). During winter most of the muskrat's foraging activities take place within a radius of 15 metres of the house

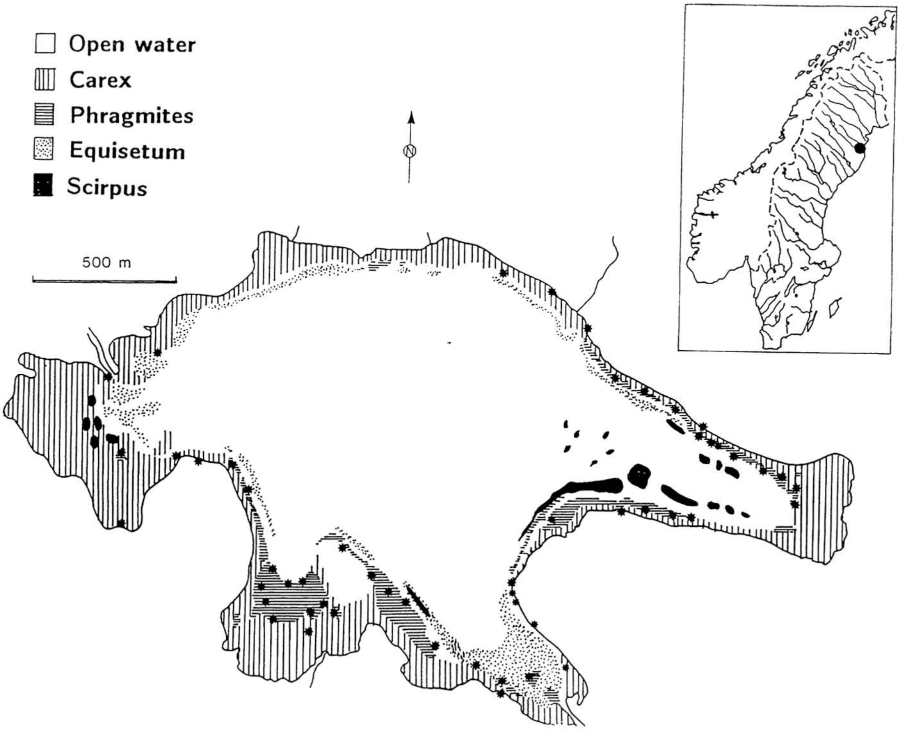

Fig. 1. Lake Ostträsket, situated in northern Sweden. Different habitat types are shown. The stars denote the location of individual houses.

(MacArthur 1978) and this indicates that the choice of house building site also determines other characteristics of the home range. Another factor which most likely influences the choice of house building site is that young muskrats are highly vulnerable to predation by red fox (*Vulpes vulpes* (L.)) and mink (*Mustela vison* (Schreb.))(Danell 1985).

In this paper I attempt to discover indications of territorial behaviour in muskrats during relatively low population densities. I show what kind of house building sites muskrats prefer and seek an ecological explanation for this choice. My main questions were:

1) Are muskrats territorial when population density is low?
2) What kinds of house building sites do muskrats prefer?
3) Is there a correlation between the choice of house building site and reproductive success?
4) To what degree is predation risk correlated with the choice of house building site?

2. Study area

Lake Ostträsket is situated in the coastal area of northern Sweden (65°55′N; 21°03′E) (Fig. 1), which belongs to the middle boreal vegetation zone (Ahti et al. 1968).

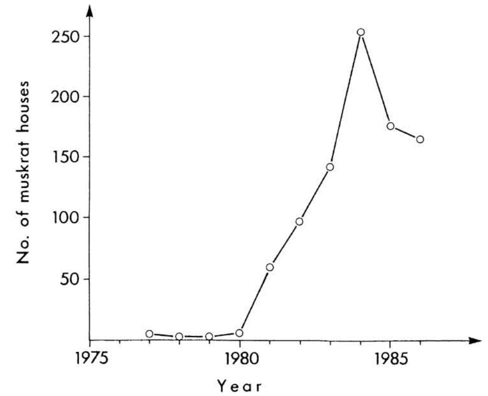

Fig. 2. Number of inhabited muskrat houses in late October to early December at Lake Oststräsket, northern Sweden.

At this latitude the lakes are ice-covered for 180–200 days per year, from late October until mid-May (Ångström 1974). The estimated mean annual temperature lies between 2 and 3° C and the mean annual precipitation is 400–500 mm (Ångström 1974). The growing period for plants (daily mean temperature > 3°C) lasts for 160–170 days (Ångström 1974).

The forests surrounding the lake consist mainly of Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* (L.)) and birches (*Betula* spp.). The macrophytic vegetation can be divided into four discernible belts (Fig. 1). The most landward belt mainly consists of sedges (*Carex rostrata* (Stokes) and *C. aquatilis* (Wahlenb.)). Beyond this, common reed (*Phragmites australis* (Cav.)) becomes the dominating species in large parts of the lake. This belt is succeeded outwards by stands of water horsetail (*Equisetum fluviatile* (L.)), and in deeper water scattered stands of bulrush (*Scirpus lacustris* (L.)) are present. Non dominant species such as *Potamogeton natans* (L.), *Nymphaea candida* (J. Presl.), *Nuphar* spp. and *Sparganium* spp. frequently occur in parts of the lake with clear water. Approximately 35% (80 ha) of the lake area (250 ha) can be utilized by muskrats (water depth less than 1.0 m).

Lake Oststräsket was colonized by the muskrat around 1975 (Danell 1985). In the first years following colonization the population density was low, then the population started to grow rapidly, and it peaked in 1984. During 1985 and 1986 the population density declined (K. Danell unpublished) (Fig. 2).

3. Methods

I conducted the field work at Lake Oststräsket during June, July and August 1986.

Old muskrat houses are destroyed every year by the spring flood. At the start of my investigation (June 1) 35 newly built houses were found (but no young had been born). In order to locate additional houses I surveyed the lake by canoe and on foot at ten-day intervals.

When a new house was found it was gently opened in order to determine if it was occupied or not. A small number of houses were excluded from the material, mainly those with a basal diameter of less than 0.7 m (these houses are most commonly used as a place to eat), but also four houses that were connected to a burrow system (however, these four houses were used in the calculations of spatial distribution). I used the following criteria for occupation: presence of young inside, perceptible warmth or presence of fresh food remnants. If the house was regarded as occupied, it was given a number, and its position was registered on detailed maps. If young muskrats were found in the house, their age was determined according to the length-age curve given by Errington (1939) and the litter size noted.

In order to examine what kind of territories muskrats prefer and the effect of house site characters on predation risk, I measured the following variables:

1) The water depth at 8 positions within a radius of 2 m from the house
2) The distance from the house to the shore,
3) The maximum water depth for a fox to pass when proceeding from the shore to the house, and
4) The distance from which the house could be seen by a fox (I placed my eyes at the same height as a fox).

To make it possible to determine to what degree muskrats have chosen high quality house building sites or not, 50 "imaginary houses" were randomly distributed (and marked with a stick) in parts of the lake which can be utilized by muskrats (water depth less then 1.0 m). These imaginary houses, which will be referred to as controls, were analysed according to the first 3 variables listed above.

Up to an age of approximately 14 days the young muskrats are blind, not very mobile, and unable to leave the house. During this time the young are highly vulnerable to attacks from red fox and therefore any signs of a fox digging in the house were recorded as predation attempts. Mink was abundant in the area, and signs of mink digging in a house were recorded.

4. Results

4.1. Spatial distribution of houses

I found a total of 51 houses in Lake Ostträsket. In order to test the hypothesis of random distribution of houses I used the nearest neighbour method (Clark & Evans 1954). The distribution deviated from being random towards regularity and this difference was statistically significant ($P<0.001$). The measure of area used in these calculations only included the parts of the lake with a water depth of less than 1.0 m, because muskrats will not build houses in deeper water.

The fact that muskrats prefered to build their houses in special parts of the lake (see 4.2, Density and habitat of houses) denotes that one of the conditions stipulated when using the nearest neighbour method, namely that any point (house) must have the same chance to occur in any part of the area chosen, is not fulfilled. In spite of this I used the original calculations because the circumstances discussed above reduced the area used for house building purposes so that the houses tend to show a more aggregated distribution. This makes it more difficult to detect any regular distribution pattern.

Table 1. The area covered by, and density of muskrat houses in each vegetation belt at Lake Ostträsket, northern Sweden. Only the parts of the lake with a water depth of less than 1 m were considered. The *Phragmites* belt was preferred for house building purposes (Chi-squared test; $P<0.001$).

Vegetation belt	Area (ha)	No. of houses	Density houses/ha
Carex	54.4	12	0.22
Phragmites	13.5	37	2.74
Equisetum	9.4	2	0.21
Scirpus	0.9	0	0
Total	78.2	51	Mean 0.65

4.2. Density and habitat of houses

The density of houses differed between the four vegetation belts. The *Phragmites* belt was preferred (Chi-squared test; $P<0.001$) (Table 1). In this belt the density was about ten times higher than in the *Carex* or *Equisetum* belts. No houses were found in the *Scirpus* belt. The total density of houses in the area which could be used by muskrats for house building purposes (water depth less than 1 m) was 0.65 houses/ha. By using the 8 values of water depth, measured within a 2 m radius of each house (plus controls), a mean water depth was calculated. Controls were situated in deeper water than houses (mean 38 and 27 cm respectively) (Mann-Whitney *U*-test; $P=0.0028$). I also checked if the variation between the 8 measurements was the same around houses and controls. The varia-

Table 2. Reproductive success of muskrats in houses situated in "good" and "bad" house building sites at Lake Ostträsket, northern Sweden. I considered houses (1) surrounded by more than 50 cm of water, (2) situated more than 35 m from the shore and (3) built in the *Phragmites* belt, as constructed in high quality house building sites. The number of young born per house differed between the categories of house building sites (Mann-Whitney *U*-tests, one sided; $P=0.027$).

Category	No. of houses	No. of young born per house (mean±*SD*)
Houses situated in "good" house-building sites	7	7.9 ± 4.0
Houses situated in "bad" house-building sites	9	3.9 ± 3.3

tion was greater around houses (coefficient of variation; Mann-Whitney *U*-tests; $P<0.0001$).

4.3. Reproduction

Young muskrats were found in 16 of the 47 houses. The total number of young was 90 and these came from 23 litters with a mean litter size of 3.9 (range 1–8). The higest number of young recorded in a house during the period June–August was 12, and these came from 3 successive litters.

4.4. Production of young in relation to quality of house building site

To test if the reproductive success of a muskrat couple was correlated with the quality of their house building site I divided the house building sites into two groups. At Lake Ostträsket a preferred house building site is situated:

1) In the *Phragmites* belt (far from the shore)
2) on an elevated place and
3) at the edge of deeper water.

Therefore, I have considered houses

1) surrounded by water, exeeding 50 cm in depth
2) situated more then 35 m from the shore and
3) constructed in the *Phragmites* belt as built in a high quality house building site.

The reproductive success was higher in these houses compared to the remaining houses (Mann-Whitney *U*-tests, one sided test; $P=0.027$) (Table 2).

4.5. Predation and relation to habitat choice

The recorded number of predation attempts by fox and mink were six and three respectively. In one of the mink attacks an adult muskrat had been killed. Because of the few cases of predation attempts recorded, no statistical calculations could be conducted on the material.

The risk of fox predation seems to be correlated with the choice of house building site. Houses situated close to the shore are more vulnerable to fox predation (Table 3). All six predation attempts by foxes were performed on the 31 houses situated within 40 m of the shore line. No attack was noted on the remaining 16 houses located further out. Moreover, 3 of the 5 houses situated in a water depth of less than 10 cm were visited by a fox. The distance from which a fox is able to detect a house by sight does not seem to affect the predation risk. This indicates that sight is not the only way for foxes to detect muskrat houses. The few mink predation attempts, on the other hand, seemingly occurred independently of water depth or distance from the shore.

Table 3. Frequencies of predation attempts by red fox and mink on muskrat litters at Lake Ostträsket, northern Sweden. Four variables, the vegetation belt in which the house was situated, the distance from the shore to the house, the maximum water depth for a fox to pass when proceeding to the house, and the distance from which a house could be detected by a fox, were used to investigate any relationship with predation risk. (Ca = *Carex*; Ph = *Phragmites*; Eq = *Equisetum*)

Number of houses	Vegetation belt			Distance of house from shore (m)					Water depth to house (cm)					Distance for house detection (m)				
	Ca	Ph	Eq	<20	–40	–60	–80	>80	<10	–20	–30	–40	>41	<5	–10	–20	30	>31
Total	9	36	2	15	16	6	6	4	5	8	3	11	20	16	9	6	7	9
Attacked by red fox	3	3	0	5	1	0	0	0	3	1	1	1	0	2	0	2	1	1
Attacked by mink	0	3	0	0	1	1	0	1	1	0	0	0	2	1	2	0	0	0

5. Discussion

The fact that the houses in my study exhibit a regular distribution indicates that muskrats are territorial even when population densities are relatively low compared to densities reported from North America (Errington 1948). It should be noted, however, that the population densities in Lake Ostträsket might be high in relation to the plant production in the lake. In fact the population peak in 1984 and the decline in 1985 and 1986 indicate that the lake's carrying capacity might have been exceeded in 1984. If so, we would expect to find territorial behaviour in this muskrat population even though the relative population density is low. The distribution pattern of houses was also investigated by Danell (1978). Although he expected to find a regular pattern during years with high densities, the houses in his material showed a random distribution pattern (only an indication of a regular pattern was found).

The analysis of water depth close to the house and variation between the measuring points indicates that muskrats build their houses on elevated places with access to deep water. Moreover, muskrats preferably constructed houses in the *Phragmites* belt and this may be due to the following factors. First, *Phragmites* forms strong floating mats, which can carry the weight of a muskrat house, and this makes it possible for muskrats to build houses in an area with rather deep water far from the shore. This minimizes the risk of attacks from non-flying predators (Pelikan et al. 1970). Second, if houses are built in deep water, this reduces the risk of freeze outs during winter (Aldous 1947). *Phragmites* is also used as a food resource by muskrats, although *Typha* spp., *Scirpus* and *Equisetum* are regarded as being more preferred as food by muskrats (Errington 1963, Pankakoski 1983). However, in Lake Ostträsket both the *Equisetum* and the *Scirpus* belts are mostly situated at water depths exceeding 1 m, and this makes it very difficult for muskrats to build houses in these parts of the lake. Moreover, the *Carex* belt is situated close to the shore, and it is therefore often left dry during summer droughts. This makes houses built in this area more vulnerable to non-flying predators.

The reproductive success in houses considered by me as built in high quality house building sites was higher than in the remaining houses. The explanation for this result might be that the muskrats building houses outside the high quality sites are young non-dominant animals with low reproductive potential. However, predation might also have reduced the numbers of young born in houses outside the high quality sites.

The number of recorded predation attempts are too low to permit any conclusive predictions regarding the foraging strategies by fox and mink. However, most of the houses subjected to fox predation were situated in shallow water close to the shore. This might be due to the reluctance of foxes to enter deeper water and these results could indicate that it might be a bad strategy to build houses in these places, especially in years with low vole abundance (see Danell 1985). Mink predation seemingly occurred independently of water depth or distance to shore. However, Proulx et al. (1987) found that water level also influenced the food preference of mink. In years with high water levels muskrat houses were more difficult to reach and the amount of muskrats taken by mink decreased. The importance of predator avoidance is also stressed in the work by Clough (1987).

To summarize, the regular distribution of muskrat houses indicate territoriality at a rather low population density. Furthermore, muskrats preferably constructed houses far from the shore in the *Phragmites* belt and the choice of house building site influenced the reproductive success of muskrats. The fact that most of the houses were built far from the shore might constitute a way of reducing predation risk. My data on predation indicate that this might be a good strategy.

Acknowledgements. I am grateful to K. Danell for helping me to plan this study, for making valuable comments on the manuscript, and for letting me use unpublished muskrat data. I also thank C. Otto, P. Lundberg and E. Pankakoski for valuable comments on the manuscript; S. Uvell and A. Salomonson for statistical advice. Financial support was given by the University of Umeå and the Swedish Natural Science Research Council (grant to K. Danell).

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