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Source: Wildlife Biology, 1(2) : 97-103

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1995.0015

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Hartman, G. 1995: Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. - Wildl. Biol. 1: 97-103.

On the basis of questionnaires to moose hunters the colonisation pattern of reintroduced beaver in the province of Värmland was mapped. The beaver spread rapidly within water drainage systems resulting initially in scattered colonisation and very low population densities in relation to range. Spread was slowed by watershed divides. Illustrating the shape of the expansion wave front by plotting the relative increase of the population and range against time, shows a very flat front characterised by long dispersal distances.

Key words: pattern of spread , beaver, reintroduction, Sweden

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Received 27 December 1994, accepted 18 May 1995

Associate Editor: Heikki Henttonen

Reintroducing exterminated species to areas within their former ranges is a conservational tool of increasing importance (Stanley Price 1989, Stuart 1991). Reintroduction programmes have not been numerous and most of them are fairly recent. To be able to predict the future development of reintroductions, it is important to study earlier cases and events with similar processes, such as deliberate or accidental introductions of non-native species and spontaneous invasions.

Organisms spreading into uninhabited areas is a phenomenon that has received much attention in spite of the relative scarcity of good data sets. The general picture of a spreading population is that of a rolling wave where the distribution increases linearly with time. There have been many attempts to model the process of spread of organisms (e.g. Skellam 1951, Okubo 1980, Hengeveld 1989, Kareiva 1990, van den Bosch et al. 1990, Holmes et al. 1994). Most models are based on the assumption that movements of individuals are indistinguishable from diffusion on a given geographical scale. Thus, the adequacy of a particular model can only be evaluated relevant to the purposes at hand, and to particular scales of investigation (Andow et al. 1990, Gardner et al. 1991, Hengeveld 1989, Johnson et al. 1992, Kareiva 1990).

Several models take special factors affecting the process into consideration, such as topographic irregularities (Andow et al. 1990, Gardner et al. 1991), finite velocity and non-random movement (Holmes 1993), Allee effects (Lewis & Kareiva 1993), and density-dependent movements (Namba 1980). The main goal has almost always been to predict the wave velocity. This has been criticised, however, because the trend of the radial equivalent on time does not reveal much about the processes by which populations spread. It may allow rejection of extreme hypotheses, but it does not differentiate between a number of very different processes (Caughley 1977). Several authors have emphasised the importance of the shape of the wave front, which is much determined by the frequency of long distance dispersers (e.g. Mollison 1986, Hengeveld 1989, Holmes et al. 1994, Gardner et al. 1991). Some have also warned about the danger in neglecting the tip of the tail of the dispersal distribution, since even a small frequency of long distance dispersers may be of importance (Andow et al. 1990, van den Bosch et al. 1992, Porter & Dooley 1993, Goldwasser et al. 1994). Thus, there is a need for more information on shapes of expansion wave fronts and the underlying factors determining these shapes.

The last well-documented observations of European beaver *Castor fiber* from the original Swedish population date back to the 1870s (Ekman 1910). By the time authorities banned beaver hunting in 1873, it was already too

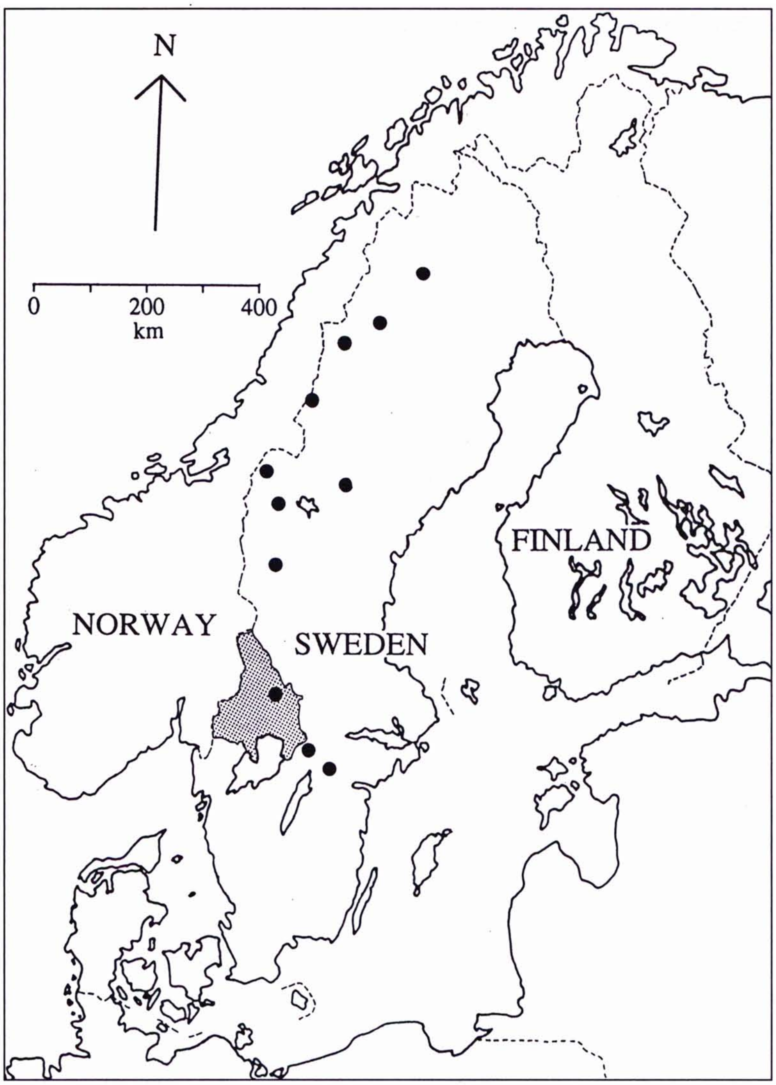

Figure 1. The 11 beaver reintroduction sites in Sweden where reproduction was observed (dots), 1922-1939, and indication of the study area in the province of Värmland (shaded).

late. The cause of extermination was apparently overexploitation because of the high prices of pelts and castoreum. By the beginning of this century, only a small remnant of the Scandinavian beaver population remained in southern Norway. In 1922, a pair of beavers were purchased from Norway and released in the province of Jämtland in central Sweden. About 80 Norwegian beavers were released at 19 different sites in Sweden between 1922 and 1939. Reproduction was observed at 11 of these sites (Fries 1940, Fig.1). Since then beavers have spread, and are still spreading, over large parts of the country, aided partially by translocations. In 1992, the population size was estimated at about 100,000 individuals (Hartman 1995).

The aim of this study was to describe the pattern of spread of a reintroduced beaver population in the province of Värmland in southwestern Sweden, and to discuss the results in a general context with special reference to the shape of expansion fronts and its importance for introductions.

Study area

The province of Värmland comprises an area of about 17,600 km^2 (see Fig. 3). Boreal forest covers about 75% of the area. Altitudes vary from 40 to 690 m, but only 23% of the area is higher than 200 m above sea level. The area can be divided into nine major water drainage systems which mainly flow in a north/southerly direction (see Fig. 3). The last beavers of the original population in Värmland were probably killed during the 1830s (Ekman 1910). In 1925, two beaver pairs were imported from southern Norway and reintroduced to the eastern parts of the province. This first introduction was followed by another (2 pairs) at the same site in 1927. Other introductions at a site 40 km southeast of the first site took place in 1928 (1 pair) and 1930 (1 pair), but these introductions probably were unsuccessful (Fries 1940). In 1960, 10 animals were translocated from the eastern parts of the province to a site approximately 45 km west of the expansion front (see Fig. 3).

Methods

The administration of moose hunting in Sweden is based on a system of license areas that consist of the land of one or several landowners or part of a larger property where hunting rights are rented by a hunting team. These hunting teams usually rent the same land year after year and often include the landowners. In 1987, I performed a beaver survey based on questionnaires sent to hunters in 426 moose license areas. One of the questions asked in the questionnaire was when beavers first settled in the hunting area. The accuracy of the answer depends mainly on the memory of the observer. As public interest in the species has been high since the first introduction and as the occurrence of beaver in new areas is often discussed and has frequently been reported in newspapers, this is an event likely to be remembered by local landowners and hunters. I received answers to the questionnaires from 322 areas covering 9,127 km^2 ($\overline{x}$ = 28.3 km^2). I studied the pattern of spread by marking colonisation for each year on computorised maps run in sequence. To determine the shape of an expansion wave front, when determined more by life history traits than by topography, one has to look within water drainage systems. I did this by plotting the relative increase in the population and in the range against time (referred to as p.r-plots). In the plots I used a population size index (the number of areas colonised in a certain year as a proportion of the number colonised by 1987), and a relative measure of range (the maximum distance between the two colonised areas furthest apart in a certain year as a proportion of the same measure in 1987). As I wanted to document the slope of the front, range expansion was simplified and viewed as if the spread was primarily one-dimensional. I did this by drawing a line through the middle of a water drainage system in its longitudinal direction, projecting the positions of colonised areas perpendicular to the line, and measuring distances between projection points (Fig. 2). If all dispersers settle in the first empty area they encounter (steep wave front), the plotted lines of population size and range against time will track each other closely. If, however, the wave front is flat, the range index will initially increase faster than the population index, and the longer the tail of the front, the larger a gap between the lines should be expected.

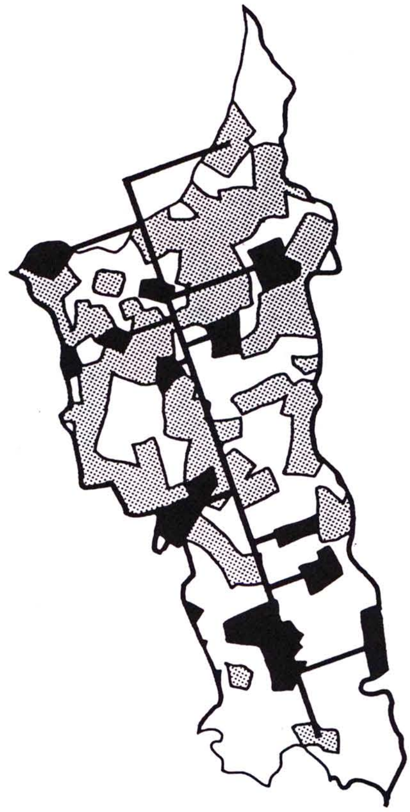

Figure 2. Schematic view of how the locations of colonised areas (black) were projected on a line representing the total range at the time of the latest survey (1987), within a water drainage system. The distance between the two projection points furthest apart, relative to the total length of the line, was used as a relative index of population range. Non-colonised areas included in the study are shaded. The map shows the situation in the water drainage system of Byälven in 1970.

Results

In 1945, 20 years after the first introduction, beavers were found 122 km northwest and 38 km southeast of the release point (Fig. 3a). This was also the first year, when beavers were observed west of the Klarälven drainage system (area A).

By 1950 the range had expanded even further northwest, and was now 306 km. Expansions in other directions were more limited, and the population was distributed in a very patchy way (Fig. 3b).

In 1960, the range covered most of the eastern drainage systems and the southern front had moved to 155 km south of the release point (Fig. 3c). At this time a considerable filling in of gaps in the distribution had occurred. The western front, however, had hardly moved at all and remained approximately 100 km west of the release point. This means that the yearly spread had been ca 3 km since 1925. In1960, 10 beavers were translocated to area B (see star in Fig. 3c). The most striking change in the following decade was the resulting rapid spread of beavers in area B, probably due to the above-mentioned translocation.

In 1967, a beaver colony was found in the northwestern corner of area B; thus the yearly spread in area B was 19.7 km. This means that beavers in area B dispersed much faster than beavers in area A, where maximum dispersal rates were 12-13 km/year.

In 1970, the distribution pattern in area B was very patchy, similar to that observed earlier in the eastern parts of the province. By 1970, colonised areas could be found in almost the entire province, except for the southern parts

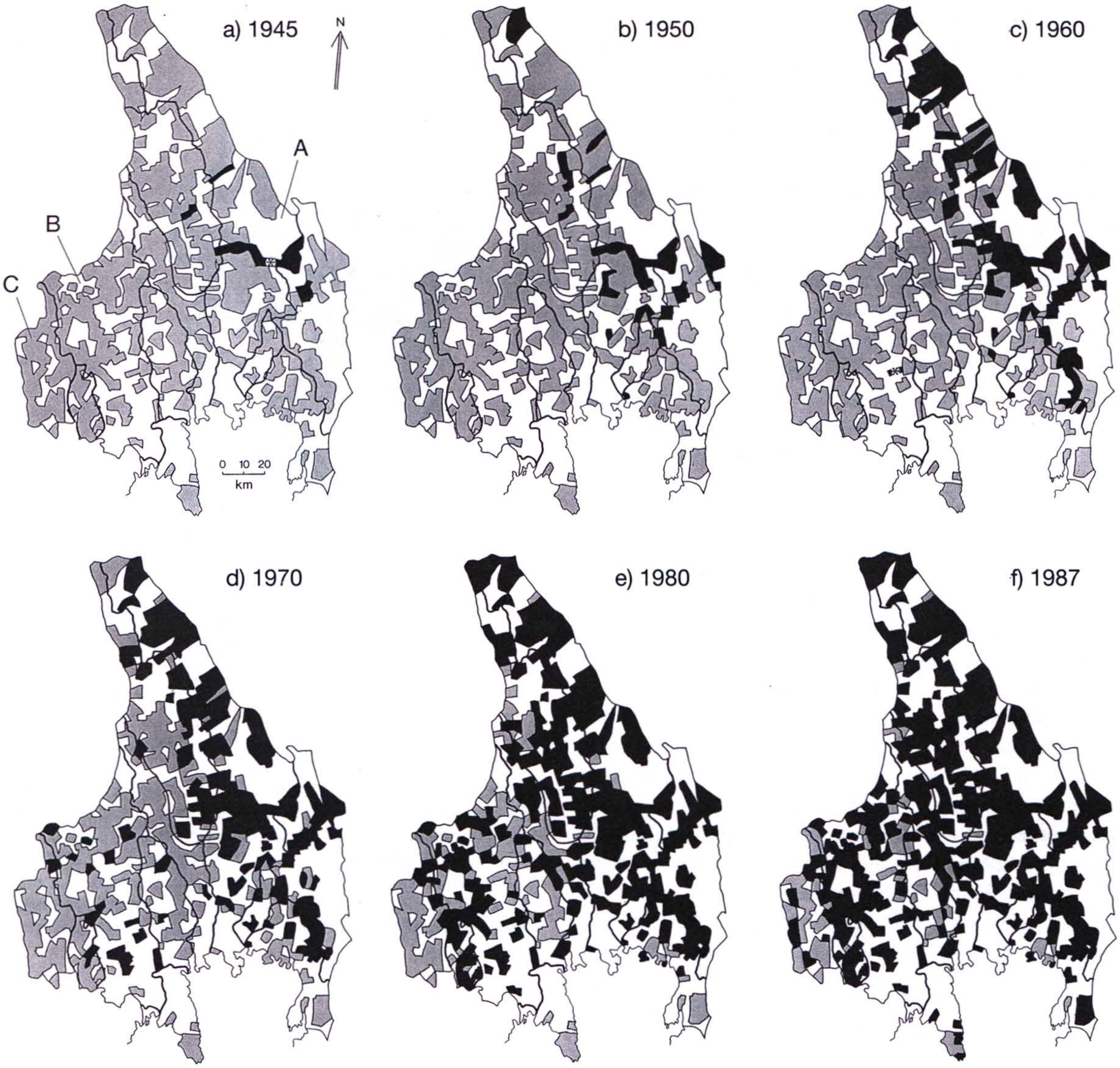

Figure 3. Pattern of spread of beavers colonising the province of Värmland, 1945-1987 (a-f). Non-colonised areas included in the study are shaded, colonised areas are black. Watershed divides are indicated as solid lines. Stars in a) and c) indicate introduction sites. Water drainage systems: Klarälven (A), Byälven (B), and Upperudsälven (C).

along the shores of Lake Vänern, and area C in the southwestern corner (Fig. 3d).

During 1970-1980 distribution became more continuous (Fig. 3e,f). A sharp front along the watershed divide formed the border of area C. This last hindrance to dispersal was passed in the mid-1980s, and by 1987, when the survey was performed, the beaver population range covered the whole province. There were, however, great differences in population density reflecting differences in time passed since colonisation (Hartman 1994).

Drawing p.r.-plots of the two water drainage systems with the largest number of reporting areas (A and B) showed that the relative increase in range was considerably faster than the relative increase in number of colonised areas (Fig. 4), thus indicating a flat expansion front. The whole province has been surveyed on five occasions after the reintroduction (Faxén 1939, Lundberg et al. 1965, Weinberg 1971, Lavsund 1979, Hartman 1994). A comparison of the relative population increase in the whole province with the relative increase in number of occupied areas, showed that the p.r.-plots using number of occupied areas as an index for population size underestimated the difference between population and range increase (Fig. 5).

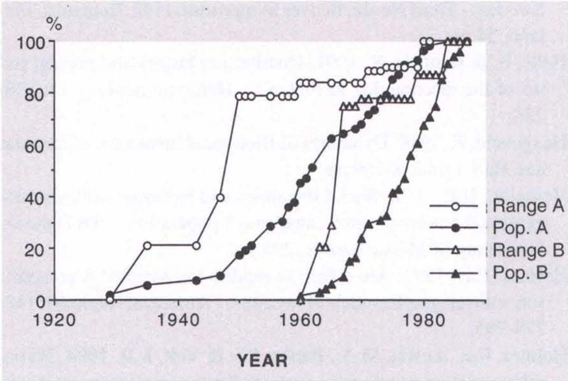

Figure 4. Relative increases of beaver population ranges (A and B) and number of colonised moose hunting license areas (pop. A and B) in the water drainage systems of Klarälven (A), and Byälven (B).

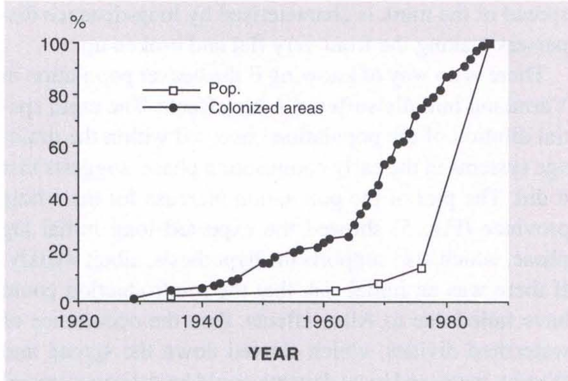

Figure 5. Relative increases in numbers of beaver-colonised moose hunting license areas (100% = 322) and numbers of beavers (100% = 15,000) in the province of Värmland, 1925-1987.

Discussion

In spite of the well-documented ability of beavers *Castor fiber* and *C. canadensis* to travel over land (Berghofer 1961, Wilsson 1971, Hodgdon 1978, Smith & Peterson 1988) the velocity of dispersal within and between drainage systems differs. Watershed divides were by no means absolute dispersal barriers, but they slowed the spread in certain directions and thereby had a considerable influence on the pattern of spread. The colonisation maps and p.r.-plots revealed a pattern with a flat wave front formed by long distance dispersers obviously passing large areas of suitable habitat before settling down. German and Polish reports of beavers moving long distances in the early colonisation phase after reintroduction also exist (Zuppke 1989, Zurowski & Kaspercyk 1988). The prevalence of long distance dispersers in expansion fronts has likewise been recorded in other species, for example, nine-banded armadillo *Dasypus novemcinctus* (Humphrey 1974), raccoon dog *Nyctereutes procyonoides* (Helle & Kauhala 1991) and shiny cowbird *Molothrus bonariensis* (Post et al. 1993).

It seems reasonable to assume that in most species, dispersal behaviour is adapted to finding vacant territories and mates within a relatively stable species range, rather than invading vast areas of suitable habitat, unoccupied by conspecifics even though so-called super-tramp species (Diamond 1975) exploiting temporary habitats, form an exception. This means that dispersal patterns may be different between more normal situations and an expansion front. If dispersers at the wave front search not only for an unoccupied site but also for a mate, they might keep moving further away from the core population. This might explain the long dispersal distances of beavers in the early stages of the colonisation of Värmland. Many areas that were passed in these early stages of colonisation later reached high population densities. This indicates that dispersing beavers passed them, not because they lacked suitable habitats, but for some other reason, e.g. because they lacked mates.

The risk of undercrowding effects, sometimes referred to as Allee effects (Allee 1938), has sometimes been mentioned in connection with introductions (Williamsson 1989, May 1991) and has been suggested as the reason why many attempts have failed (Hopper & Roush 1993). High dispersal rates from the reintroduction site were considered to be a major cause behind the problems with reintroducing beaver in Bavaria (Reicholf 1977). Even if an introduction is successful, population development might be limited by Allee effects in the expansion front (Hopper & Roush 1993). Caughley (1970) found no evidence of an Allee effect in the expansion front of Himalayan thar *Hemitragus jemlahicus* in New Zealand. His explanation was that, as dispersal in Himalayan thar is sex-biased, females dispersed into areas with a sufficient density of males. This situation is not likely to occur in a beaver population because dispersal distances are only weakly biased towards males (Berghofer 1961, Leege 1968).

Long-distance dispersal and flat wave fronts are by nomeans a general pattern in introductions. A p.r.-plot of the development of the reintroduced sea otter *Enhydra lutris* on the North American west coast (Lubina & Levin 1988) shows a radically different pattern with lines lying close to each other. In the case of the sea otter, the relative population increase was even faster than the relative increase in range, thus indicating a very steep wave front. Another illustrating example of how the pattern of spread of two different species may differ, is the invasions of American mink *Mustela vison* and coypu *Myocastor coypus* in England (Usher 1986). The coypu has a closed wave front leaving almost no suitable habitat behind it, whereas the spread of the mink is characterised by long-distance dispersers making the front very flat and broken up.

There is no way of knowing if the beaver population in Värmland initially suffered Allee effects. The rapid spatial dilution of the population observed within the drainage systems in the early colonisation phase, suggests that it did. The plot of the population increase for the whole province (Fig. 5) showed the expected long initial lag phase, which also supports the hypothesis, albeit weakly. If there was an initial risk that the reintroduction could have failed due to Allee effects, then the occurrence of watershed divides, which slowed down the spread and thereby increased local density, could have been a crucial factor.

Acknowledgements - I thank the hunters in Värmland for supplying me with the necessary information on beaver colonisation. I also want to thank Erik Lindström, Jon Swenson, Allan Carlsson and Lennart Hansson for valuable comments on the manuscript and Christina Hultgren for locating the watershed divides. The Swedish Environmental Protection Board funded the project.

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