Irruptive population development of European beaver (*Castor fiber*) in southwest Sweden

Göran Hartman

Department of Conservation Biology, Swedish University of Agricultural Sciences, P.O. Box 7002, 750 07 Uppsala, Sweden, e-mail: Goran.Hartman@nvb.slu.se

Abstract: European beavers (*Castor fiber*) have been reintroduced to many areas within their former range. The resulting populations are still in a phase of population growth and range expansion. From a management point of view it is of interest to understand the pattern of population development that these populations are, or will be, exhibiting. Based on data from two surveys of a province in southwestern Sweden, I have earlier proposed that reintroduced beaver populations may exhibit an irruptive pattern of development, possibly as a result of overutilization of resources and lack of predators. The aim of this study was to see if a repeated study, twelve years after the previous, would support or question the proposed pattern of population development. Data from three surveys of the same province were used. The overall population density for the total area had increased from 0.10 colonies/km^2 in 1976, to 0.19 in 1987, and to 0.21 in 1999. However, when population density of local areas with time passed since colonisation was related, a peak in density (mean: 0,34 colonies/km^2) after 25 years was revealed. Dividing the data into groups, areas colonised more or less than 25 years ago, and beaver population density decreased or increased since the previous survey (1987), showed that a negative change in population density was significantly more common in areas colonised more than 25 years ago. The results support the proposed pattern of population irruption in the studied beaver population.

Keywords: Castor fiber, reintroduction, population irruption.

Introduction

The European beaver (*Castor fiber* L., 1758) was historically found from England in the west across the whole Eurasian continent, and from the Mediterranean Sea in the south to the tundras in the north. Mainly due to overhunting, the beavers disappeared from most of Eurasia and at the beginning of the 20th century only eight remnant populations with a total of about 1200 beavers were left. The reintroduction of a Norwegian beaver pair to Sweden in 1922 was the first of a large, and still increasing, number of reintroductions and translocations to many areas within the beavers' former range in Eurasia (Nolet & Rosell 1998).

The resulting populations are still in a phase of population growth and range expansion. From a management point of view, whether it is a question of conservation, hunting, or reduction of damage, it is of great interest to understand the pattern of population development that these populations are, or will be, exhibiting. The main conceptual model of a successful reintroduction would be that the population development is in line with the classic sigmoid growth curve. If, on the other hand, the population would be limited by its food resources and the population itself influences the standing crop of available food, the eventual development would be a population irruption (Caughley 1970, Caughley 1976).

Being the result of the oldest reintroduction of beavers, the Swedish population may give insight into long-term development of reintroduced beaver populations. By comparing survey results, eleven years apart, from the two Swedish provinces of Värmland and Västernorrland, with beaver populations dating back to the 1920s, I have earlier proposed that these populations showed patterns of development similar to what could be predicted by the Riney-Caughley model for irruptive ungulate populations (Riney 1964, Caughley 1970, Caughley 1976, Hartman 1994). The aim of this study was to see if a repeated study of the Värmland-population, twelve years after the previous, would support or question the proposed pattern of population development.

Materials and methods

In 1976, Lavsund (1979) performed a beaver survey in the province of Värmland, based on questionnaires sent to moose-hunting license areas. The administration of moose hunting in Sweden is based on a system of license areas that consist of land of one or several landowners or are part of larger property where hunting is rented by a hunting team. The information used in this article is based on answers to the following questions in these questionnaires: 1. What is the size of your area? 2. What year was the first beaver settlement observed in the area? 3. Give a rough estimate of how many occupied beaver settlements there are in the area. 4. How many beavers were shot last year?

A description of how to define an active settlement was enclosed with the questionnaire. I conducted similar surveys in 1987 (Hartman 1994) and 1999. Pearson correlation and Chi-square tests were used to analyse the data.

Study area

The province of Värmland is situated in south-western Sweden. It has an area of approximately 17,600 km^2. Roughly 75% is covered by boreal forest. Altitudes vary from 40 to 690 m, but only 23% of the area is higher than 200 m. The last beavers of the original population 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 reintroduction was followed by another two pairs at the same site in 1927. Other introductions at a site 40 km south-east of the first site, took place in 1928 (one pair) and 1930 (one pair), but no offspring was observed (Fries 1940). In 1961/1962 the population was estimated at about 1000 individuals, and in 1976 at 7500-9500 individuals (Lavsund 1979).

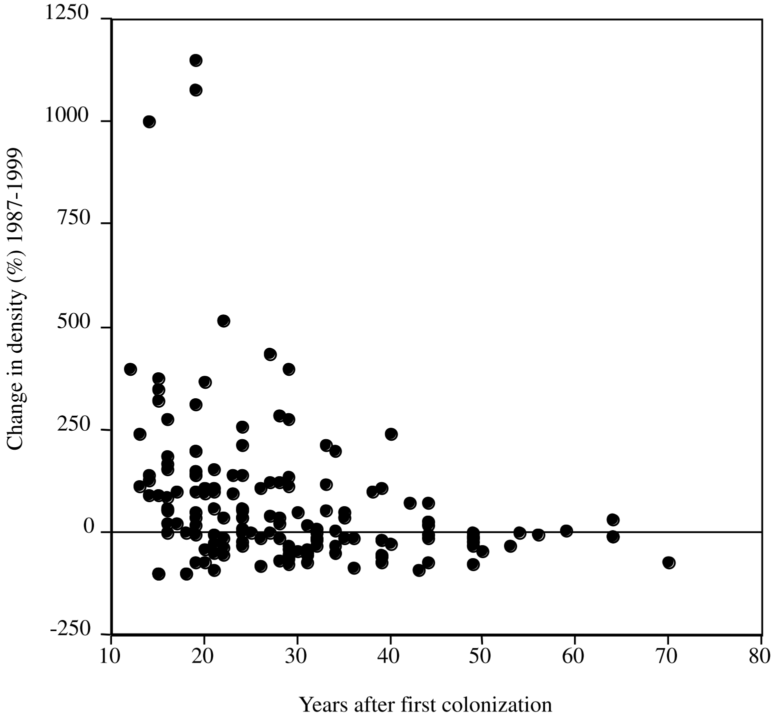
Results

Questionnaires were sent to 315 moose-hunting areas in 1976, to 426 areas in 1987, and to 475 in 1999 (table 1). The percent of hunting areas not yet colonized by beavers decreased from 45% in 1976, to 17% in 1987, to 6% in 1999. Expressed as percent uncolonized area this yields 35% in 1976, 17% in 1987, and 3.5% in 1999. This, in addition to the fact that answers were often incomplete, is the reason why *n*-values vary between analyses. The overall percent of areas with negative population development had increased from 23% during the period 1976-1987, to 40% during the period 1987-1999.

According to an estimate calculated as the sum of all found colonies divided by the sum of all surveyed areas, the beaver population density of the whole province increased from 0.10 colonies/km^2 in 1976 (n=192), to 0.19 colonies/km^2 in 1987 (n=356), and then levelled at 0.21 colonies/km^2 in 1999 (n=248).

Using areas that provided data both in 1987 and 1999, and plotting relative changes in density between the two surveys against year of colonization, shows a rapid increase in roughly the first 25 years after colonization, but then a levelling out or decrease (figure 1). By dividing the data into groups, areas colonized more or less than 25 years ago, and beaver population density decreased or increased since the previous survey, and after excluding areas colonized between surveys, a negative change in population density was shown to be significantly more common in areas colonized more than 25 years ago. During the period 1987-1999, 24% of the areas showed a decrease in density in the more recently colonized group, and 58% in the >25 year group (n=155, *Chi-Square*=18.0, P=0,0001). The same type of plot, using data collected 23 years apart in time

Figure 1. Relative changes in local beaver population densities in the province of Värmland during a twelve-year period, related to time since colonization (*n*=155).



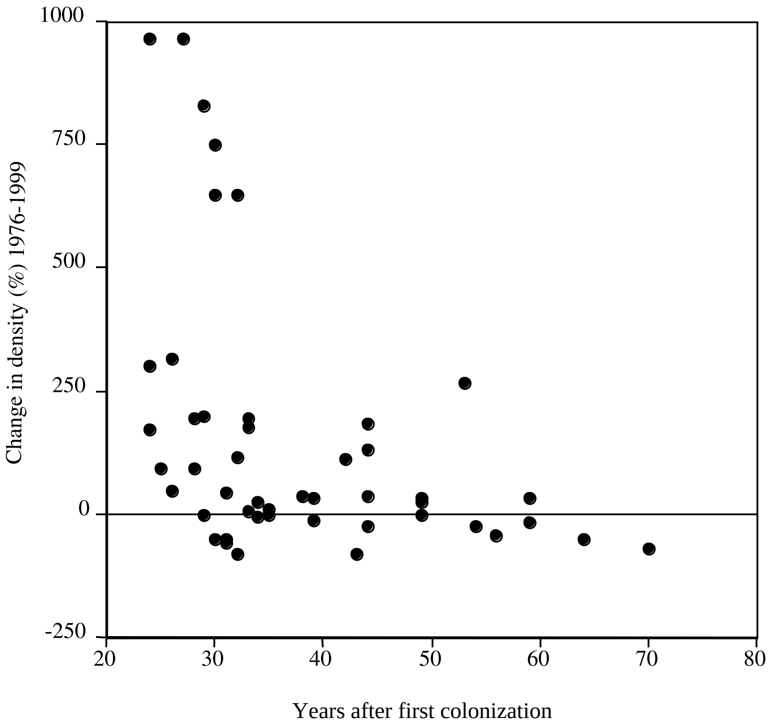


Figure 2. Relative changes in local beaver population densities in the province of Värmland during a 23-year period, related to time since colonization (*n*=47).

Table 1. The response to questionnaires sent to moose-hunting areas in 1976, 1987, and 1999, and the area of moose-hunting areas involved.

Year	Number sent	Number of answers	Total area (km^2)	Mean area (km^2)	SD	Min. (km^2)	Max. (km^2)
1976	315	192	6,533	36	36	5	38
1987	426	356	10,359	29	29	4	313
1999	475	248	6,632	27	26	2	240

(1976 and 1999), yields a similar pattern (figure 2, *n*=47). In this case 19% of the 37 more recently colonized areas showed a decrease in density, while this was found in 50% of the 10 in the >25 year group. However, low expected frequencies preclude further statistical analysis here.

As expected, the magnitude of change in population density between surveys (1987-1999) is negatively correlated to the size of survey areas (*n*=155, *r*=-0.172, *P*=0,03). By pooling data from all three surveys, and excluding areas without beavers and areas colonized less than one year ago, and by grouping the data by time since colonization into five-year periods, and plotting the average densities against period, a peak in density 25 years after colonization was found (figure 3, *n*=574).

Mean hunting pressure in 1999 was rather low (0.51 animals/colony, *sd*=0.44). Hunting pressure was not significantly correlated to current population density (*n*=179, *r*=0.01, *P*=0.22) or change in population density between 1987 and 1999 (*n*=122, *r*=0.38, *P*=0.68). There was, however, a negative correlation between time since colonization and hunting pressure (*n*=169, *r*=-0.22, *P*=0.003).

Discussion

Temporal variability in size of the entire population should be less than temporal variability in population size within local populations, provided that factors that affect population size on a large spatial scale, e.g. weather, are less important than local ecological factors. Hence, local rapid population increase will be compensated for by equally rapid population decrease in another local population. This is the reason why there is a negative correlation between the magnitude of change over time and the size of surveyed areas. It also explains why the total density has increased between the surveys in spite of an increased percent of local areas with negative population development. The time of the observed density peak (after 25 years) is, consequently, also related to the average size of moose-hunting areas in the province, and the large range of sizes of these areas will make the results less distinct.

The results of this study correspond to my previous study of the beaver population in Värmland (Hartman 1994) and support the conclusion that it exhibits dynamics of an irruptive nature. Hunting has not likely affected the pattern of population development, considering the low hunting pressure and the fact that it seems to decrease in time since colonization, possibly indicating a decreasing interest in beaver hunting in time. Predation can also be eliminated as an important factor because the first wolves (*Canis lupus*) did not reappear in Värmland until the beginning of the 1980s. A rough estimate of the current wolve population is 50 individuals.

The most plausible explanation to the observed pattern of population development is that food availability decreases over time. The decrease will be because local beaver populations have come to a point where they utilize food resources faster than they are renewed. This is the most common explanation to population irruptions. It has been shown that food availability determines local population dynamics in beavers (Fryxell 2001). If overutilization is the sole factor, the reduction in food abundance is reversible. It might, however, also be that beavers by consuming favoured tree species induce a change in succession towards less palat-

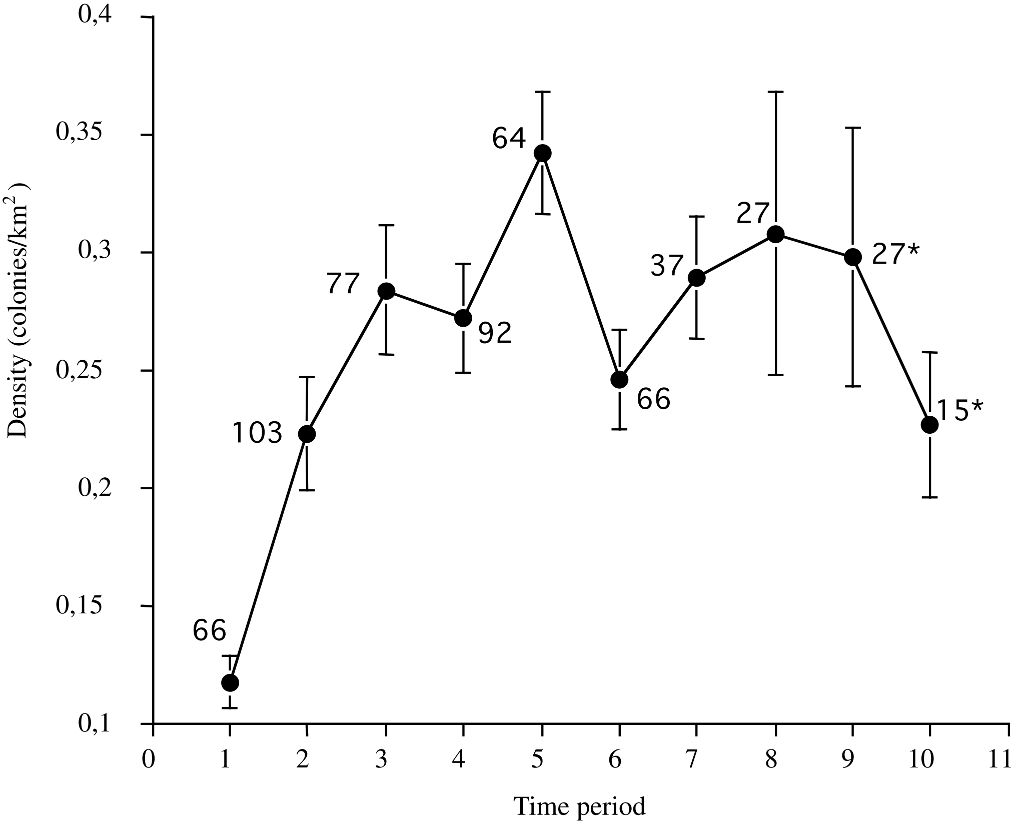


Figure 3. Average density of local beaver populations in relation to time since colonization (*n*= 574). 'Time' is divided into five-year periods. Data from three surveys (1976, 1987, 1999) of the province of Värmland are pooled. Periods 9 and 10, marked *, are not five-year periods but denote 41-50 and 51-70 years since colonization. Vertical bars show standard errors. Numbers are *n*-values.

able species (Fryxell 2001). If this is the case, major disturbance, e.g. forest fire, will be necessary to restore degraded areas. These factors are of course not mutually exclusive so a combination of overutilization and induced succession may be the underlying cause. Similar patterns of population irruption in American beaver (*Castor canadensis*) populations have been found in North America (Busher & Lyons 1999). Notable in their study is that the Prescott peninsula population peaked after 30 years and the size of the study area is 50 km^2, which is very similar to what is presented in this study. Busher & Lyons (1999) suggest that grazing by white-tailed deer (*Odocoileus virginianus*) will inhibit regeneration of woody species, which might be an additional explanatory factor to the observed decline in beavers. The abundance of moose (*Alces alces*) in Värmland (more than 9,000 were shot in 2002) might accordingly have an affect on beaver food abundance.

There are two management consequences of the results of this study. First, monitoring of an introduced beaver population has to be performed at a geographical scale small enough to detect the different phases of population development in the irruptive process. Second, if management authorities wish to reduce the phase in which densities peak, and for example the strong impact beavers have on their surroundings, hunting should be allowed during the rapid increase phase when the population is able to sustain a higher harvest rate than during the post-irruptive decline. From a strictly conservational point of view there might also be a reason to try to level the population development, considering that demographic instability may jeopardize the survival of local populations.

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Samenvatting

Explosieve populatieontwikkling van Europese bever (*Castor fiber*) in zuidwest Zweden

De Europese bever (*Castor fiber*) is in grote delen van zijn vroegere verspreidingsgebied geherintroduceerd. De populaties die het gevolg zijn van deze uitzettingen, vertonen nog steeds groei en areaaluitbreiding. Gezien vanuit het beheer van deze populaties, is het belangrijk de achterliggende processen van de populatieontwikkeling te begrijpen. Eerdere studies in 1987, in het zuidwesten van Zweden, leidden tot de voorspelling dat de beverpopulaties een explosieve groei zouden vertonen. De verwachting was dat dit samenhing met overexploitatie van het gebied, alsmede met het ontbreken van predatoren. Om te zien of de eerdere voorspellingen ondersteund worden door de huidige ontwikkelingen, is het onderzoek twaalf jaar later, in 1999, herhaald met gegevens uit hetzelfde gebied. De dichtheid over het hele onderzoeksgebied bleek te zijn toegenomen van 0,10 kolonies/km^2 in 1976, tot 0,19 in 1987 en 0,21 in 1999. Er zijn echter grote lokale verschillen. Het beeld is daarom anders wanneer dichtheden van lokale populaties in de loop der jaren worden uitgezet: na 25 jaar blijkt een maximum bereikt te worden van 0,34 kolonies/km^2. Negatieve populatiegroei sinds 1987 kwam vaker voor bij populaties die meer dan 25 jaar geleden waren gekoloniseerd. De resultaten van het onderzoek ondersteunen het eerder voorspelde model van explosieve populatiegroei.

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