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Original Investigation

Spatial and temporal circumstances affecting the population growth of beavers

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ABSTRACT

Understanding the spreading patterns of an invading or expanding species is necessary for ecological theory and conservation. The return of the Eurasian beaver throughout Europe is considered one of the biggest conservation success stories. In general, the process of the spreading beaver population has been described in detail, however several aspects regarding the principles of colonisation have not been mentioned. We propose that the process of colonisation should follow Skellam's model for the case of first occupation by a pioneer beaver during the establishment of population growth.

We retrospectively reconstructed the continuous colonisation of Eurasian beavers in six catchments in Western Bohemia in the Czech Republic. The extracted data from published resources were analysed to reveal (in detail) the progress of the colonisation front, in addition to considering current population densities in the catchments. All of the catchments were settled from one possible source, but were reached by pioneer beavers regardless of the distance or the considered source of the spread. However, an increased distance from the source of spread delayed the start of rapid population growth. The barrier effect among the divides of the watershed was not substantial because beavers regularly crossed the divides. The progress of the colonisation front followed Skellam's diffusion model as densities spread from sites with higher values into areas with lower values. The model did not, however, accurately predict the pattern of the first pioneer occupancy.

Introduction

The patterns of how species spread are still of great interest in both spatial ecology and conservation practice. Future scenarios regarding the spread of species (e.g., invading or newly expanding species) may be predicted based on either simulations of mechanistic models or extrapolations from previously observed patterns (Liebhold and Tobin, 2008). Therefore, the descriptions of general dispersal mechanisms in various environments (especially in human made landscapes) have become increasingly important in spatial ecology. Linearly-spreading species fit the principles established for species spreading in two-dimensional (Euclidian) environments (Skellam, 1951; Gilbert and Liebhold, 2010); however, Barták et al. (2013) showed discrepancies when the models are used in spatially inappropriate situations. Lubina and Levin (1988) published one of the first approaches on how to measure the spread of a species in a one-dimensional space (i.e., a linear branching river system). They also described the illustration of the sea otter (*Enhydra lutris*) and how range expansion is influenced by the movements of individuals, population growth, and temporal and spatial variation in environmental factors through their effects on growth and spread. The sea otter was thought to be extinct in early 1900s, however a small population was discovered which had increased and expanded its range to reoccupy areas from which it had been extirpated. The expansion front of sea otter was very steep, as is the case with the coypu (*Myocaster coypus*) in the British Isles (Usher 1986). Whereas another mammal species had a different process of expanding: first pioneers spread over long distances with a gradual colonisation front, e.g. the American mink (*Mustela vision*) (Usher 1986) or the raccoon dog (Helle et Kauhala, 1991).

Both extant beavers (*Castor* fiber and *C. canadensis*) are examples of semiaquatic mammals which mainly require the use of a linear platform for spreading (i.e., most often dispersal trips follow the waterlines), but many authors (e.g., Hartman, 1994; Halley et al., 2012) have documented trips among catchment basins. In the past, the distribution of Eurasian beavers covered nearly all of Europe (Veron, 1992), but in the beginning of the 20th century beavers were close to extirpation (Heidecke, 1984). Nevertheless,

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beavers have recently established several large populations across Europe and Asia (Halley et al., 2012), and their numbers are still growing. For example, after complete eradication, the population in Central Europe has since been restored, which is primarily due to reintroduction programmes conducted in Germany, Austria, Poland and the Czech Republic between 1967 and 1996 (Nolet and Rosell, 1998). To date, the spread of beavers in Europe is still an ongoing process, and one might expect that over the next few decades beavers will colonise their former distribution area in Europe. However, increasing conflicts among beaver conservation and human-made landscape utilisation (Parker and Rosell, 2003) raise interest in the detailed patterns of beavers' expansion and increases the necessity to acquire and predict future spreading scenarios. Hartman (1994, 1995) published a general model for the spread of beavers by describing the rapidity of the colonisation front and the development of the population density during decades of population establishment. However, a detailed study of the colonisation of a small area may provide more accurate data regarding the principles of how several established populations are colonised from one source.

Both beaver species have similar morphologic and behavioural characteristics (Novak, 1987; Wilsson, 1971), and most ecological articles adopt similar characteristics across both species. Beavers are crepuscular and nocturnal, herbivorous, territorial and social rodents (Wilsson, 1971). Established territories are defended by members of beaver families which consist of an adult parental pair and several generations of offspring (Heidecke, 1984). Due to the incoming litter, two-year-old subadults are usually ousted from the natal family to disperse (Hodgdon and Lancia, 1983; Hartman, 1997). Typical dispersal behaviour begins at the end of winter (when the ice melts) and ends in the early summer, however dispersals have been documented in autumn as well (Hartman, 1997). During dispersal, beavers search for new unoccupied sites or try to mate within already settled sites (Svendsen, 1989). Usually, individuals use permanent waterways during dispersal (Leege, 1968), but they are able to temporarily conquer terrestrial areas as well (Hartman, 1995). The dispersal distances of beavers can range from a few kilometres to tens of kilometres from their parental territory. Saveljev et al. (2002) determined that beavers dispersed in Tuva at an average distance of 3.9 km, although dispersals have been documented at over 80 km from the natal territory (Zurowski and Kasperczyk, 1990; Fustec et al., 2001). Sun et al. (2000) showed that North American beavers primarily settle down near their parental territories (up to 5 km); meaning distances of dispersal are influenced by sex: males generally colonise sites closer to the parental territory than females.

The growth of beaver populations follows a general logistic pattern, even for unexploited populations (Hartman, 1994) and even with predation pressure (Balodis, 1990). The initial slow phase is driven by sparsely distributed pioneer individuals (mostly subadults) with low probability of mating (Barták et al., 2013); however as opportunities for mating increase (i.e., the chances of encountering an unpaired floater of the opposite sex), new territories are established and the population density increases. The process of population establishment accelerates with the rapid phase of population growth until the saturation point is reached (Hartman, 1994). According to Nolet and Rosell (1994), the initial colonisation of unoccupied areas follows the quality of the habitats, and that habitats of the highest quality are settled first. As the population density within a colonised area increases, the opportunities to establish new territories decreases, meaning beavers then settle in less suitable (suboptimal) sites or they spread over the current distribution range (Nolet and Rosell, 1994; Fustec et al., 2001).

We focused on two different causes for the continuous population growth, namely (1) the importance of episodic occupation of the area and (2) how continuous growth allows approaching dense population. The targeted population in Western Bohemia is most likely to have one colonisation centre in the Regensburg area of the Danube in Bavaria (our estimation is based on Schaper, 1976 and Zahner, 1997). We used published data of various sources (Červený et al., 2000; Šafář, 2002; Schwab, 2009; Vorel et al., 2012) to reconstruct the beavers' initial colonisation of the six different catchments by an ongoing spreading front leading from Bavaria into Bohemia. Due to the different positioning and size of the studied catchments, we described principles of population establishment: beginning by initial occupation and finishing in its current status in winter 2011/2012. We questioned if the distance of the catchment to the source of the spread might correlate with (a) the time of the first colonisation, (b) the beginning of rapid population growth or (c) its current population density. In particular, we studied whether the first occupation, or any other reason occurred in the beginning of rapid population establishment. Our expectation was that the closer and smaller catchments would be colonised earlier and we would observe an earlier and higher rate of population growth with a higher final population density.

Material and methods

Study sites

The colonisation process was studied at six sites in Western Bohemia in the south-western part of the Czech Republic (Fig. 1). Our sites were located within catchments of the following rivers: Mže (MZE), Radbuza (RAD), Úhlava (UHL) and Berounka (BER). Additionally, we focused on the Czech portions of the catchments of the following streams: Kouba (Chamb in German; KOU) and Kateřinský (Pfreimd in German; KAT); however, to complete the integral catchment in this case, we also used small parts of streams in Germany and all of the Czech streams (i.e., Nivní and Hraniční streams are included in KAT with its confluences in Germany; Myslívský and Rybniční streams are included in KOU with its confluences in Germany). In general, the landscape of all of the catchments is composed of a mosaic of hilly coniferous forests, agricultural areas and small ponds with a low density of urban areas. The upper parts consist of mostly coniferous forest and the low-lying parts are rather agricultural with mixed or deciduous forests. The riparian stands are not well developed and are primarily composed of alders (*Alnus* spp.), willows (*Salix* spp.), poplars (*Populus* spp.), maples (*Acer* spp.), birches (*Betula* spp.), and occasionally spruces (*Picea* spp.). All six sites had a similar landscape mosaic with similar habitat quality and human exploitation.

The beavers in Western Bohemia originate from the Bavarian reintroduction programme performed from 1967 to 1991 (Zahner, 1997), where releases occurred in the Danube and Isar Rivers (Schwab and Schmidbauer, 2003). Since 1980, the continuous colonisation process of established Bavarian populations have extended the beaver populations into western Bohemia (Šafář, 2002; Vorel et al., 2012). Thus, possible directions of spread occurred along the rivers belonging to the Danube basin: Naab, Pfreimd, Regen and Chamb. In Western Bohemia, beavers made frequent dam systems on tiny streams, whereas on wider rivers, settlements exhibit rare building activity and are generally without dams. Large carnivores (Eurasian lynx *Lynx lynx* and Grey wolf *Canis lupus*) sporadically populate the border areas (Schadt et al., 2002). Red foxes (*Vulpes vulpes*) usually occupy these regions, but no recent evidence has been shown to suggest that they prey on beavers. In the Czech Republic, beavers are a protected species with a year-round ban on hunting (i.e., the population growth is unexploited).