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# Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe

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ABSTRACT

Large carnivores, such as wolves and lynx, are strictly protected by law in most European countries. However, they are still vulnerable due to habitat loss and illegal hunting. The Bohemian Forest Ecosystem lynx population is exemplary as a reintroduced carnivore population in Central Europe. The population expanded rapidly after the reintroduction (phase I) but then declined and stagnated at a low population size (phase II). There is some evidence that illegal hunting might have caused this development, but reliable data on the intensity of illegal hunting is lacking, and hence long-term consequences for the population cannot be assessed. We used a spatially-explicit individual-based dispersal and population model to inversely fit mortality probabilities to long-term monitoring data; the model integrated both chance observations and telemetry data, and discriminated between baseline mortality, road mortality and added unknown mortality. During phase I, the estimated added unknown mortality ranged between 3 and 4%, with an extinction rate < 5%; during phase II, the estimated added unknown mortality reached 15–20%, which would prevent animals from colonizing new habitat patches. The probability of extinction in phase II ranged between 13 and 74%, thereby reaching a tipping point at which the additional unknown mortality of a few animals could drive the population to extinction. However, when we considered the national parks as fully protected, the extinction probability dropped to < 1%. Based on our results, we conclude that the added unknown mortality is most likely explained by illegal hunting and therefore the highest priority for the conservation of the lynx population in the Bohemian Forest Ecosystem should be the prevention of illegal hunting in national parks and their immediate surroundings.

## 1. Introduction

In the last centuries, large carnivores were systematically hunted and persecuted. These factors, in conjunction with habitat destruction (deforestation) and overhunting of their wild prey, led to a worldwide decline of their populations (Mech, 1995; Breitenmoser, 1998). At the turn of the 20th century, pressure on natural systems was reduced by industrial processes. In the subsequent years, forest and ungulate species were protected and either recovered naturally or by means of planting or reintroduction. In the 1960s and 1970s, when biodiversity reached the political agenda, conservationists and governments began rallying to support new policies to protect the last populations of large carnivores and even started their reintroduction in areas where they were once extirpated (Treves and Karanth, 2003). Nowadays, large carnivores are strictly protected or managed by quotas in many countries of the world, and great efforts are undertaken to protect and conserve their recovering populations (Ripple et al., 2014). These efforts led to successful conservation measures for some species, e.g. wolf (*Canis lupus*) (Boitani and Mech, 2009), puma (*Felis concolor*) (Hornocker and Negri, 2010) and Eurasian lynx (*Lynx lynx*) (Molinari-Jobin et al., 2010), while other species still face strong population declines, e.g. lion (*Panthera leo*) (Ray et al., 2005, Bauer et al., 2015) and tiger (*Panthera tigris*) (Seidensticker, 2010).

Although the recovery of large carnivores in North America and

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Europe is undeniable, these populations and those across the world are often small and isolated and are vulnerable due to destruction of their habitats, persecution, diseases and genetic deterioration (Butler et al., 2004; Enserink and Vogel, 2006; Kaczensky et al., 2012; Kenney et al., 2014). Large carnivores are particularly vulnerable because they need large home ranges, occur in low densities, and have slow life histories (Woodroffe and Ginsberg, 1998; Crooks, 2002; Cardillo et al., 2005).

Despite full protection of large carnivores, persecution is still one of the major causes of death (Woodroffe, 2000; Andrén et al., 2006; Chapron et al., 2008; Liberg et al., 2012; Gangaas et al., 2013). In developed countries, most large carnivores are killed because of conflicts with human interests (Liberg et al., 2012). However, even if illegal hunting of these carnivores is not tolerated by the public and is punishable by law, its impact on the population is difficult to assess because poachers try to conceal their activities (Gavin et al., 2010). In addition, law enforcement, even with existing political will, is difficult in large forested areas, which cannot be completely controlled by wildlife rangers and police. The chance of solving such criminal cases is low in much of Europe, where hunting rights belong to landowners and where there are no publicly employed game wardens or dedicated police officers (Apollonio et al., 2010). Scientific assessment of illegal hunting is difficult because radio transmitters, which can be used to evaluate causes of mortality, are invasive and costly, especially when large numbers of individuals need to be collared. Furthermore, these collars are often destroyed by poachers, so that the cause of death remains unknown (Goodrich et al., 2008). Liberg et al. (2012) defined this unobserved source of mortality as “cryptic poaching” and used a hierarchical state–space model combined with multiple sources of data to estimate the effect of illegal hunting relative to other sources of mortality. The authors showed that the growth of the wolf population has been significantly slowed down, with total illegal hunting rates estimated to be around 15%, or 50% of the total mortality.

A similar phenomenon was observed in the lynx population of the Bohemian Forest Ecosystem, the area in which the first Eurasian lynx in Central Europe were reintroduced. The initial clandestine reintroduction of around 5 to 10 individuals between 1970 and 1974 failed, with illegal hunting believed to be the main cause (Festetics, 1980). Lynx were again reintroduced between 1982 and 1989; 18 lynx were relocated by Czech authorities from the Carpathian Mountains to the Bohemian Forest Ecosystem (Cerveny et al., 1996). After their release, the population grew to an estimated 60–69 individuals and expanded to a range from Austria in the south to the Fichtelgebirge, Germany, in the north by the end of the 1990s (Wölfl et al., 2001; Cervený et al., 2002). Since then, the population has declined, shrunk in spatial extent and stagnated at a low level (Chapron et al., 2014; Wölfl et al., 2015). Current analyses indicate that the local lynx population occupies only a small part of the potential habitat (Magg et al., 2016); the current lynx population is strongly connected to the protected areas along the German–Czech border where the animals were introduced (Müller et al., 2014). No major causes of death of individuals of the population, such as disease (based on observations of collared lynx) or elevated road mortality have been observed and is there is no shortage of prey (Heurich et al., 2015). Several cases of illegal hunting in the Bohemian Forest Ecosystem have been proven in recent years, especially in the period before the Czech Republic joined the European Union in 2004, when illegal hunting of lynx became a serious crime. We thus hypothesize that illegal hunting is the most important driver of lynx population dynamics in the region.

Models are suitable tools for estimating unknown quantities by inversely fitting unknown parameters to ecological processes, while known parameters inform the model fit in a pattern-oriented way (Grimm et al., 2005). We applied the spatially-explicit lynx population viability model developed by Kramer-Schadt et al. (2005) to 33 years of population monitoring. We integrated chance observations, such as road kills, illegal hunting events, telemetry and camera trapping data. Other chance events, such as the discovery of kill sites of lynx or tracks, were used to define the spatial extent of the lynx population. The model is especially useful because it was specifically designed for lynx in fragmented landscapes; the model spatially-explicitly accounts for mortality causes during dispersal (e.g. road mortality) and for habitat configuration, while projecting the population trend and spatial spread of the entire population. Our aim was (1) to derive illegal hunting rates by comparing the simulation results with monitoring data, while discriminating road mortality and natural mortality (e.g. disease and injury) and (2) to analyse population survival under different illegal hunting probabilities. We present two spatial illegal-hunting scenarios, where the illegal-hunting probability in the national parks was either zero or similar to that of the national park surroundings.

## 2. Material and methods

### 2.1. Study area

The Bohemian Forest Ecosystem is located in the border region between the Czech Republic, Germany and Austria. The forested low mountain range represents one of Central Europe's largest strictly protected ecosystems and includes the Bavarian Forest National Park (243 $km^2$) and the Bohemian Šumava National Park (681 $km^2$), which are surrounded by the Bavarian Forest Natural Park (3007 $km^2$) and the Bohemian Forest Protected Landscape Area (1000 $km^2$). Human population densities are comparatively low and vary between < 2 inhabitants per $km^2$ in the national parks and 30–70 inhabitants per $km^2$ in the nearby regions (Heurich et al., 2015). The study area ranges from the northern extensions of the Franconian Forest and the Erzgebirge in the north to the beginning of the Limestone Alps and the Berchtesgaden Alps in the south, and from Vienna, Austria in the east to Würzburg, Germany in the west. The total study area comprises an area of ~218,000 $km^2$ (Fig. 1).

### 2.2. Model components

To disentangle different sources of mortality and ultimately assess rates of illegal hunting, we used the existing population model of Kramer-Schadt et al. (2005), which consists of three modules: 1) a habitat suitability model (Schadt et al., 2002), which together with 2) spatial models of road mortality and illegal hunting risk forms the basis of the spatially explicit individual-based dispersal model (Kramer-Schadt et al., 2004), and 3) a demographic component (Kramer-Schadt et al., 2005). For model parameters see Table 1.

This dynamic model considers the fate of individual lynx from birth until death and accounts for spatially-explicit processes, namely movement of dispersers within a heterogeneous landscape comprising breeding habitat, dispersal habitat, avoided matrix habitat and barriers. We accounted for per step mortality probabilities that occur randomly (baseline mortality) when crossing linear infrastructure (road mortality) or when illegally hunted Illegal hunting is spatially explicit and is dependent on whether or not the individual's location is inside the national parks (see scenario 2, illegal hunting-free zone). Specifically, depending on the status (resident/disperser), the location of the animal and hence the underlying maps with their respective values (i.e. illegal hunting risk map and road risk map), the animal has a certain probability of dying described by a multinomial distribution, i.e. there is no preference in any mortality event trials. We then recorded the fate and cause of death of each simulated lynx. We can then compare the number of simulated dead lynx per year with the numbers of road casualties and illegal hunting that we compiled (Table 2). The mortality risk values for the baseline mortality per model step were parameterized in previous publications to reflect known values, i.e. baseline mortality is about 10% for residents, which increases to 24% when road mortality and illegal hunting are included (Breitenmoser-Würsten et al., 2007); these values were confirmed by our survival analysis based on telemetry data from the study area (see below). We did not accept