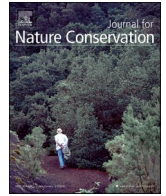


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Hunting harvest data in Sweden indicate precipitous decline in the native mountain hare subspecies *Lepus timidus sylvaticus* (heath hare)

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ABSTRACT

Brown hare (*Lepus europaeus*) seems to outcompete mountain hare (*L. timidus*) wherever the two species co-occur, but few studies have validated or even addressed this issue. In southern Sweden, the distribution of non-native brown hare overlaps with that of the mountain hare subspecies heath hare (*L. t. sylvaticus*), possibly the only mammalian subspecies unique to Sweden. In any competitive interaction, at least one species is negatively affected. If outcompetition occurs, then population trends over geographical areas where both species occur should be correlated. In order to assess this, we analysed Swedish hunting harvest data on brown hare and mountain hare for correlations on different spatial scales. We also assessed the relative importance of red fox (*Vulpes vulpes*) for hare populations by incorporating hunting harvest data for red fox in the analysis. A decline in hunting harvest was observed for both hare species throughout Sweden, while harvest of foxes increased. The harvest decline in mountain hare was generally larger than that in brown hare, particularly in the southern half of Sweden where heath hare is the dominant mountain hare subspecies. Observed patterns in the hunting harvest data for southern Sweden indicate an alarming declining trend for heath hare subspecies, with an obvious risk of extinction. In combination with continued research efforts, we suggest an adaptive management programme to preserve and restore the heath hare subspecies in its current range, through a network of 'reservoir islands' with supplementary translocation of heath hare. Developing and implementing an educational public outreach programme aimed at local hunting and naturalist associations can also help facilitate heath hare conservation.

1. Introduction

The composition, distribution, and abundance of Europe's fauna has always fluctuated over time. Over the past few centuries, however, increased human activity and disturbance have drastically altered the amplitude and frequency of these natural variations (Dirzo et al., 2014). For example, the introduction of non-native species to the Eurasian continent has negatively influenced a range of native taxa (e.g. Vahlenkamp et al., 1998; Carlsson et al., 2010; Keller et al., 2011; Barbar & Lambertucci, 2018). Simultaneously, large-scale changes in climate and land use have altered trophic interactions and ecosystem organisation (Scheffer et al., 2001). Such anthropogenic disturbances can lead to alternative stable states within ecosystems that are often difficult to reverse and may hinder the conservation and management of

endangered species (Scheffer et al., 2001; Groffman, 2006).

The mountain hare (*Lepus timidus*) is native to Sweden, and its distribution ranges across the Scandinavian Peninsula and northern Eurasia. In southern Sweden, the local mountain hare comprises a defined subspecies, the heath hare (*Lepus timidus sylvaticus* Nilsson 1831) (Angerbjörn & Flux, 1995). The heath hare has a grey winter pelage that is specifically adapted to the milder southern Swedish climate (Bergengren, 1969; Lindström, 1980; Angerbjörn & Flux, 1995; Suchentrunk et al., 1999; Thulin, 2003; Winiger, 2014), as opposed to the white winter pelage featured by the nominate mountain hare subspecies (*Lepus timidus timidus* Linnaeus 1758). The heath hare also occurs in southernmost Norway and reportedly in western Estonia (Bergengren, 1969).

The non-native brown hare (*Lepus europaeus*) was introduced to southern Sweden during the late 19th century and subsequently spread

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northwards over the next century (Thulin, 2003; Jansson & Pehrson, 2007). As the brown hare spread north, a successive decline in mountain hare density and distribution was observed (Lönnberg, 1908). This stepwise reduction in time and space was most apparent in Skåne County in the southernmost tip of Sweden, where the heath hare population was functionally replaced by brown hare by the end of the 20th century (Thulin, 2003). Currently, mountain hare and brown hare distribution overlap across the southern half of Sweden, which comprises the entire known range of the heath hare subspecies (cf. Bergengren, 1969). This distributional overlap is a conservation concern, since brown hare may outcompete mountain hare where the two species coexist (Lind, 1963; Levänen, 2019).

There is substantial niche overlap between the brown hare and several European subspecies of mountain hare (Carvaggi et al., 2017). The highly adaptable brown hare has a relatively broad niche compared with mountain hare and there are indications of complete niche replacement by the brown hare in several regions across Europe, including southernmost Sweden (Thulin, 2003; Carvaggi et al., 2017). In addition, hybridisation and interspecific gene flow between brown hare and different mountain hare subspecies have been confirmed in the wild in Sweden (Thulin et al., 1997), Iberia (Alves et al., 2003), Denmark (Fredsted, 2006), Russia (Thulin, Fang, & Averianov, 2006), Switzerland (Zachos et al., 2010), Ireland (Hughes et al., 2011) and Finland (Levänen, 2019), although not in Scotland where the species distributions also overlap (Balharry et al., 1994). Importantly, this gene flow appears to be mainly unidirectional (e.g. Wirtz, 1999), with mountain hare females hybridising with brown hare males (Thulin & Tegelström, 2002). This interspecific gene transfer may facilitate northward adaptation of the brown hare (Thulin, 2003).

The potential for non-native brown hares to outcompete the heath hare subspecies is concerning, especially in Sweden where it is a vivid cultural symbol and a popular game species. A shift to an alternative stable state, where brown hare abundance exceeds heath hare abundance, has already occurred in the southern-most tip of Sweden (Thulin, 2003). There is potential for this switch to occur also in other parts of Sweden, given time and functional conditions. Consequently, documenting and evaluating hare population trends across Sweden is important to determine the status of the heath hare population and devise effective management strategies for both mountain hare and brown hare.

Red fox (*Vulpes vulpes*) is an efficient predator of hares (Marcström et al., 1989; Hewson, 1991; Angerbjörn & Flux, 1995). Assessments of red fox scat content in winter and spring indicate that up to 94% (range 34–94%) of the fox diet in the central Swedish archipelago is based on mountain hare (Angerbjörn, 1989). Similarly, Kauhala et al. (1998) report for a Finnish study area that the frequency of hare remnants in red fox scat in summer varies between 57 and 59%. Both these studies show that hares, regardless of species, are a main prey for the red fox, and thus it is possible that hare populations are regulated by red fox predation. The relative importance of red fox predation on mountain hares and brown hares in sympatry is uncertain, however.

In this study, hunting harvest data for Sweden were used to assess population trends in mountain hare, brown hare and their main predator in southern Sweden (red fox), in order to determine whether the heath hare, possibly the only mammalian subspecies unique to Sweden, is in danger of extirpation. Possible causes of decline and potential loss of the heath hare subspecies were considered and target areas for conservation efforts and management strategies were identified.

2. Methods

2.1. Study area

The study was conducted in Sweden, where the vegetation cover is primarily comprised of managed boreal forests dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), interspersed with

lakes, bogs, rivers and managed agricultural land. The Scandinavian mountain range, and its associated high-elevation habitat, runs north to south along the western border between Sweden and Norway. Weather, climate and human density also vary along a latitudinal gradient across Sweden, with temperature increasing from north to south and snow accumulation increasing from south to north. Human population density is highest along the eastern coast and in southern and south-eastern Sweden, which contain large urban areas and a larger proportion of agricultural land.

The current range of mountain hare is across almost all of Sweden except for the southernmost tip, where it has become locally extinct (Thulin, 2003). As mentioned, the heath hare subspecies *L. t. sylvaticus* occurs only in southern Sweden, parts of southern Norway and possibly in Estonia (cf. Bergengren, 1969). The distribution of the heath hare overlaps with that of the northern hare subspecies *L. t. timidus* in a contact zone through southern Norway, south-central Sweden and western Estonia (Carvaggi et al., 2017). The range of the brown hare is currently limited to the southern half of Sweden (below latitude 61°N).

Red fox is common across all of Sweden, but occurs in higher densities in the southern half of the country. Other mammalian predators in the area are Eurasian lynx (*Lynx lynx*), for which the range extends across most of Sweden, wolverine (*Gulo gulo*), which occurs primarily in the northern half of the country, grey wolf (*Canis lupus*), the range of which is restricted to south-central Sweden (Chapron et al., 2014), pine marten (*Martes martes*), which also has a range across all of Sweden (Helldin, 2000) and the American mink (*Neovison vison*) (Carlsson et al., 2010).

2.2. Hunting harvest data

Hunting harvest data were acquired from the Swedish Association for Hunting and Wildlife Management (www.viltdata.se) and compiled at Swedish county (Sw. "län") level. Hunting harvest data are voluntarily reported and consist of the number of harvested individuals (here mountain hare, brown hare and red fox) during one hunting season, i.e. from 1 July to 30 June. Note that hunting harvest statistics do not differentiate between mountain hare subspecies *Lepus timidus timidus* and the heath hare (*L. t. sylvaticus*), so we inferred heath hare status based on the expected range of its population across Sweden (Bergengren, 1969; Carvaggi et al., 2017). The hunting harvest data available covered the hunting season from 1960/1961 (hereafter 1960) until 2017/2018 (2017). We used the number of harvested individuals per km² as a proxy for mountain hare, brown hare and red fox density. Harvest data are reasonably reliable proxies for animal abundance, and are particularly useful in the absence of alternative long-term data (e.g. Ueno et al., 2014).

Since trends in mountain hare, brown hare and red fox harvest varied dramatically by county, we split Sweden into four different study regions based on the relative occurrence of hare species and subspecies (Fig. 1). We excluded the island of Gotland in the Baltic Sea, as it may be considered a special case because of the geographical separation from mainland Sweden. We categorised the four regions based on data patterns, current knowledge of brown hare, mountain hare *L. t. timidus* and heath hare *L. t. sylvaticus* distributions, and general variation in the landscape. In the northern region (A), the nominate subspecies of the mountain hare *L. t. timidus* dominates, with only a few recent documentations of brown hare (Jansson & Pehrson, 2007). Region (A) is predominantly boreal habitat and comprises almost two-thirds of Sweden (Helldin, 2000). The region south of the boreal habitat border, i.e. southern Sweden, was divided into three regions (B-D). The eastern region (B) is characterised by both urban and agricultural land use. The brown hare has been the dominant hare species there since 1960 and both subspecies of mountain hare, *L. t. timidus* and *L. t. sylvaticus*, also occur. The southwestern region (C) is generally patchier and more forested, but the current hare species composition is similar to that in region B. However, the mountain hare subspecies *L. t. timidus* and *L. t.*

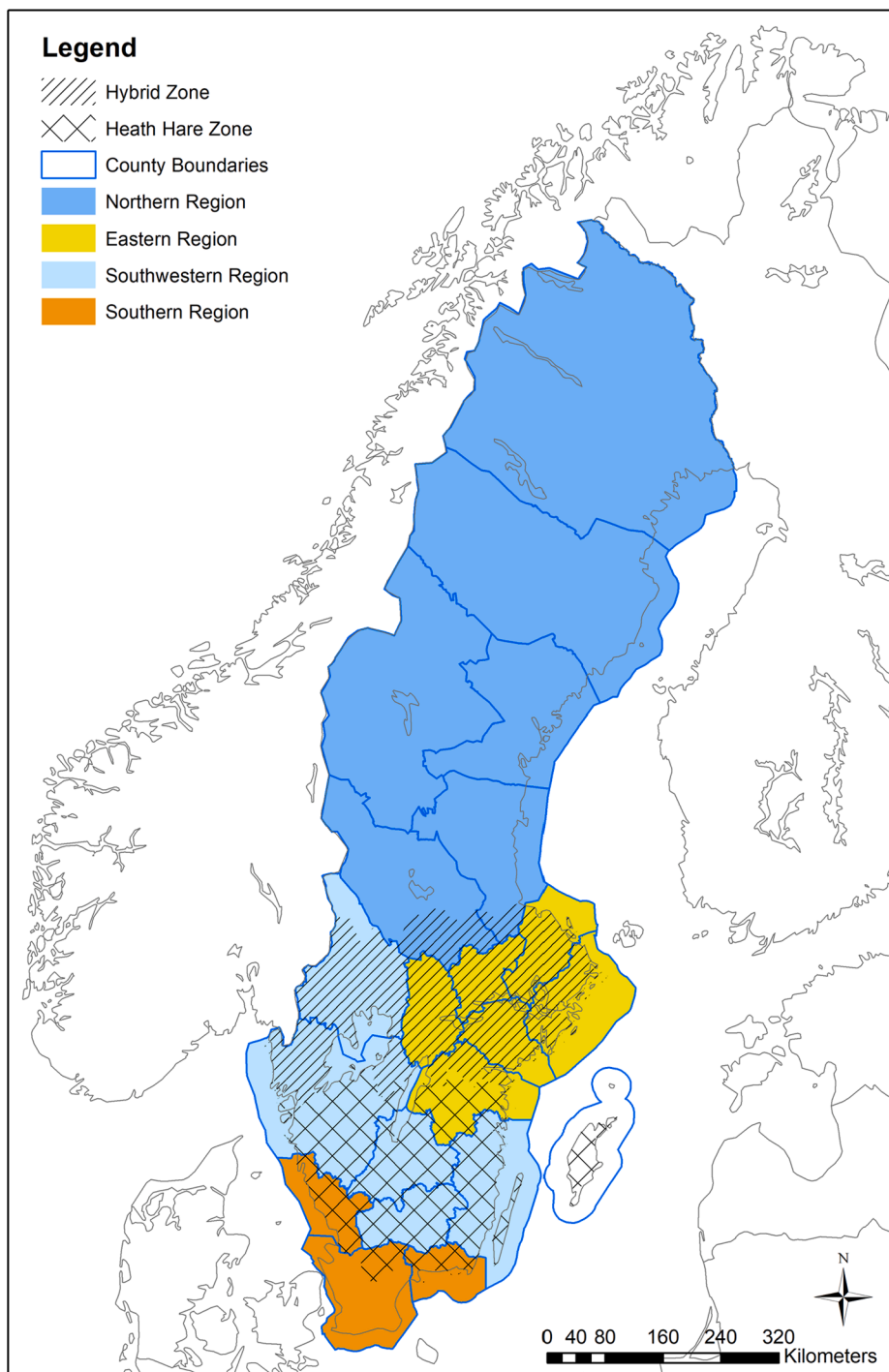


Fig. 1. Study areas in Sweden (regions A-D) divided into regional subsets based on data patterns, current knowledge of brown hare (*Lepus europaeus*), mountain hare *L. t. timidus* and heath hare *L. t. sylvaticus* distributions, and general variation in the landscape. The northern region A (blue) is predominantly boreal habitat where the mountain hare *L. t. timidus* dominates. The eastern region B (yellow) is an agricultural and urban area where the brown hare has been the dominant hare species since 1960, but both subspecies of mountain hare (*L. t. timidus* and *L. t. sylvaticus*) also occur. The southwestern region C (light blue) is patchier and more heavily forested than B. Species composition in C is similar to B, although the mountain hare subspecies *L. t. timidus* and *L. t. sylvaticus* were more abundant than the brown hare in the 1960 s, and the heath hare *L. t. sylvaticus* was likely more abundant than *L. t. timidus* (cf. Bergengren 1969). The southern region D (orange) is predominantly agricultural and urban landscape where the brown hare has been the dominant species for over 100 years. County (Sw. 'län') boundaries are outlined in blue. The distribution of heath hare *L. t. sylvaticus* (cross-hatched area) and the overlapping distribution (hybrid zone) of both mountain hare subspecies *L. t. sylvaticus* and *L. t. timidus* (diagonal hatched area) depicted is after Bergengren (1969; Fig. 20 in that paper). Hunting harvest data from the island of Gotland in the Baltic Sea (no fill) were not included in the regional subsets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sylvaticus were more abundant than the brown hare in region C the 1960 s and the heath hare *L. t. sylvaticus* likely dominated the majority of the area (Bergengren, 1969). The southern region (D) is predominantly an agricultural and urban landscape and the brown hare has been the dominant hare species in this region for almost 100 years (Thulin, 2003), with rare and local occurrence of mountain hare, primarily the heath hare *L. t. sylvaticus*.

2.3. Statistics

To assess trends in abundances based on hunting harvest data on hares and red fox over time, we plotted general trends in hunting harvest

(per km²) of mountain hare, brown hare and red fox for each region (A-D) between 1960 and 2017, using the *loess* function in the *ggplot2* package (Wickham, 2016). We also estimated the numbers of mountain and brown hare harvested per km² between 1960 and 2017 in regions B and C, to assess trends in the relative abundance of each species in these primary regions of concern. We used descriptive analysis techniques because we were interested in documenting the population status of the species relative to each other.

3. Results

3.1. Species abundance

The analysis showed that the abundance (i.e. hunting harvest) of both brown and mountain hares declined across almost all of Sweden between 1960 and 2017 (Figs. 2 & 3). However, the percentage decrease in the mountain hare population was generally greater than that in the brown hare (Fig. 3). Mountain hare population decline was greatest in the southern half of Sweden, particularly in the southwestern region (C) (Fig. 2), where the heath hare *L. t. sylvaticus* is the dominant mountain hare subspecies (Fig. 1). Between 1960 and 2017, mountain hare

abundance increased in only one county in northern Sweden (region A), where only the nominate subspecies *L. t. timidus* occurs (Figs. 1 & 3). Interestingly, red fox abundance in that county was low and actually decreased over the study period (Fig. 4). Brown hare abundance increased in two counties, one in the southwestern region C and one in the northern region A (Fig. 3). Brown hare dominated in the southern study area (region D) and the population fluctuated independently of the very low to non-existent heath hare population. In the northern study area (region A), mountain hare remained the dominant species up to 2017 and, apart from one county, its population cycle displayed the same trend in fluctuations over time as the rest of Sweden (Fig. 3).

The abundance of red fox decreased across most of Sweden between

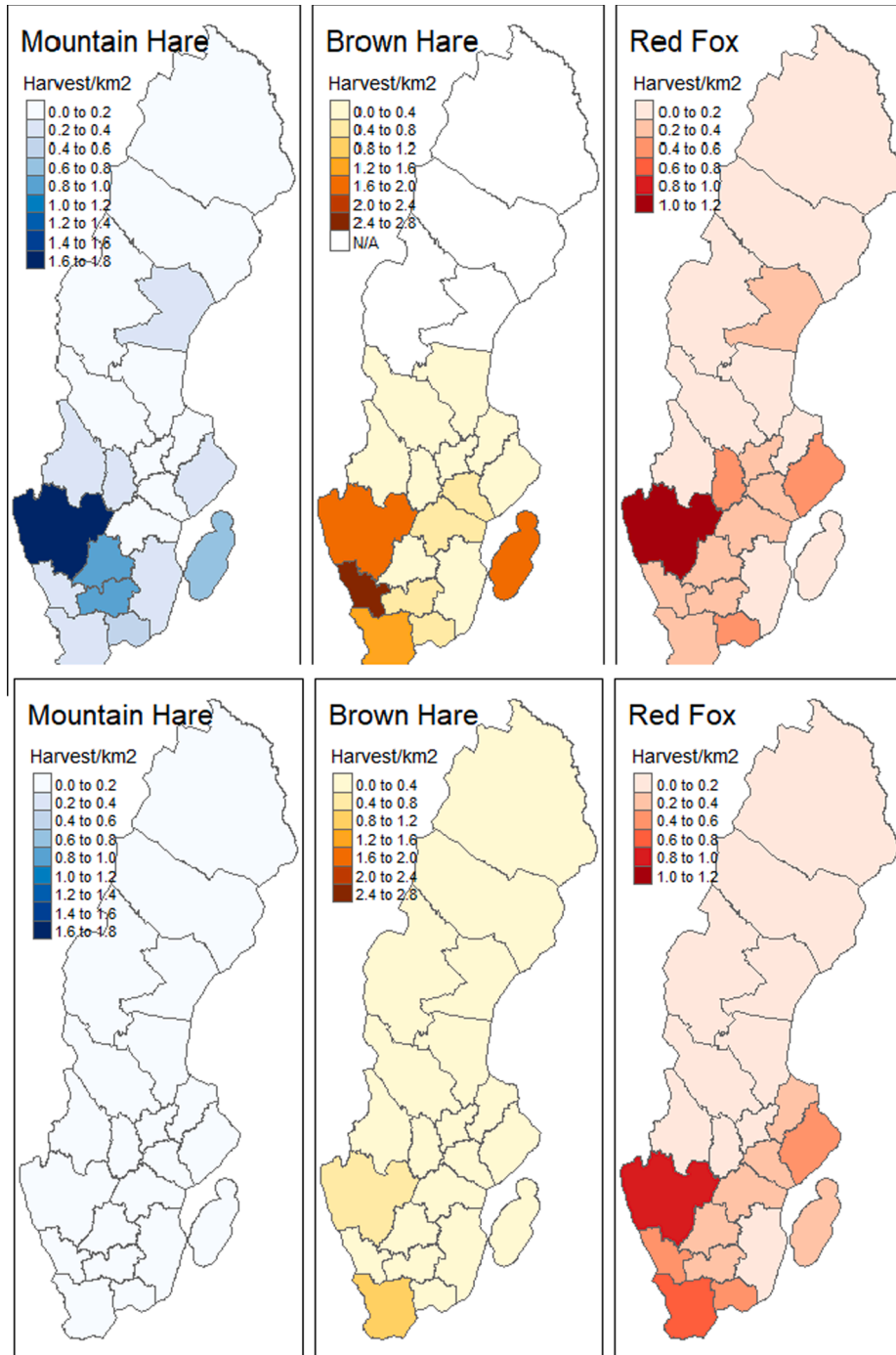


Fig. 2. Numbers of mountain hare, brown hare and red fox harvested per km² by county ('län') in Sweden in 1960 (top panel) and in 2017 (bottom panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

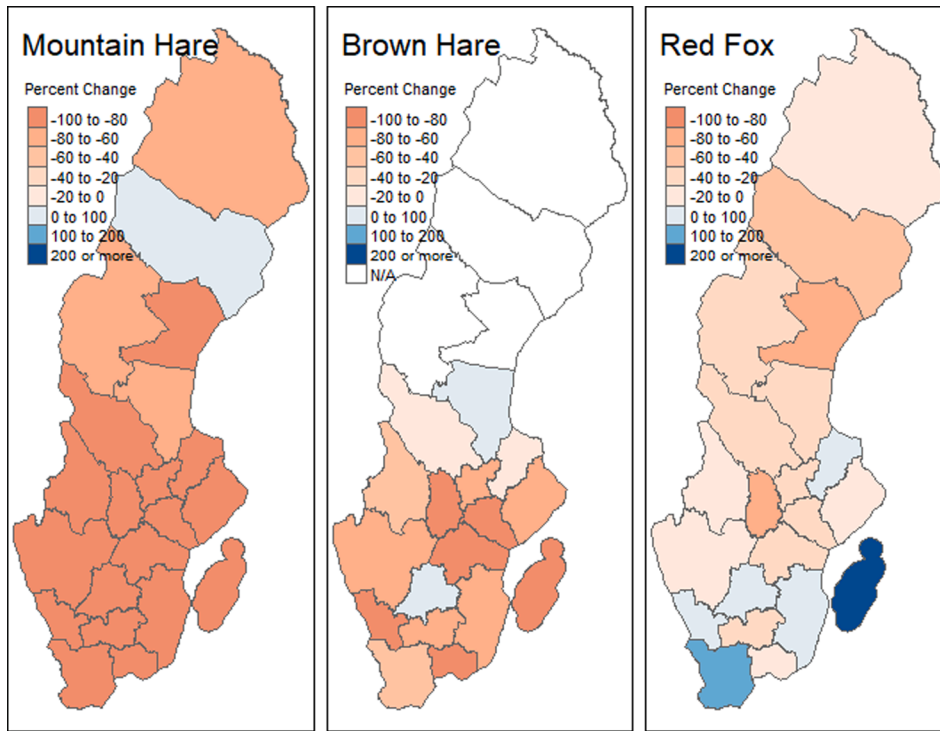


Fig. 3. Percentage change in mountain hare, brown hare and red fox harvested (per km²) by county (‘län’) between 1960 and 2017 (red values denote a negative change, blue values a positive change). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

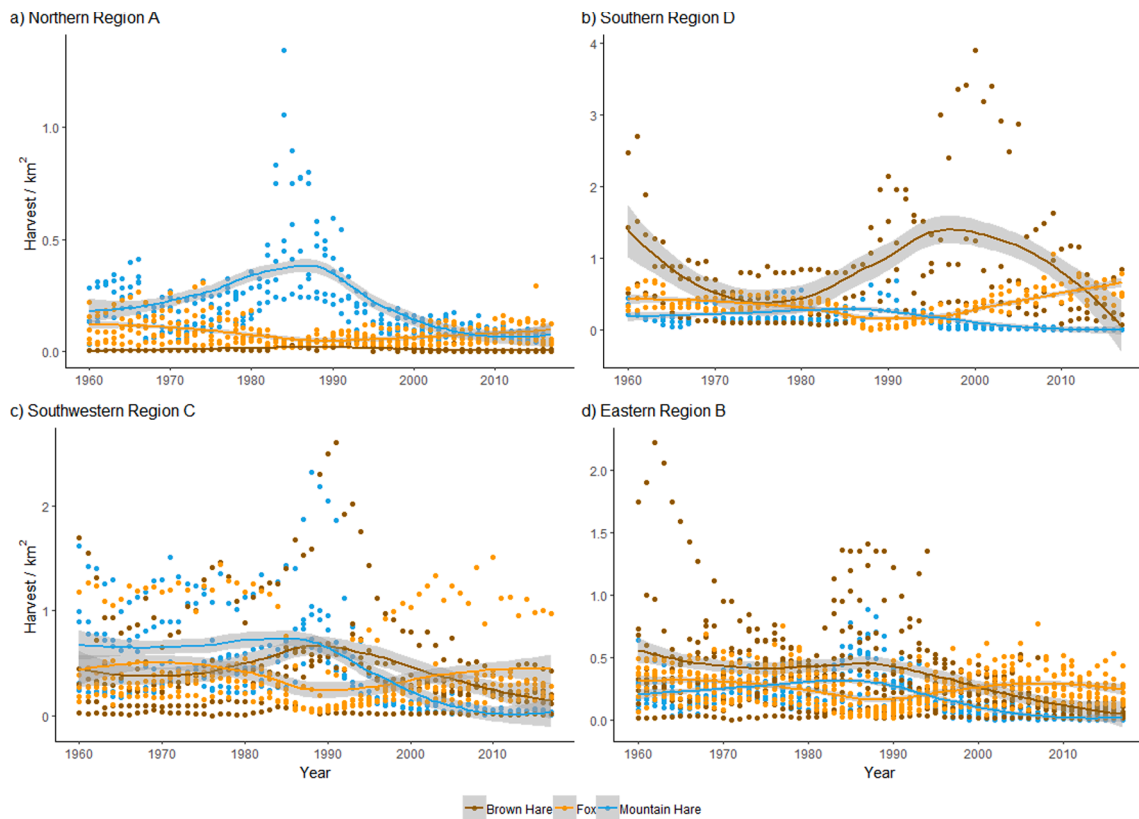


Fig. 4. Temporal trends in hunting harvest (per km²) of mountain hare (blue), brown hare (brown) and red fox (orange) between 1960 and 2017 within a) the northern Swedish region A, b) the southern region D, c) the southwestern region C and d) the eastern region B (regions defined based on landscape characteristics and occurrence, see Fig. 1). Lines are smoothed curves based on the raw data points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1960 and 2017, with the exception of five counties in the southern half of Sweden (regions B-D) that showed a marked increase (Fig. 3). The red fox population in Sweden showed signs of crashing during the 1980–1990 s (Fig. 4), due to an outbreak of sarcoptic mange (Lindström et al., 1994). Across all of Sweden, mountain and brown hare populations seemed to respond positively to the crash in the red fox population, with both hare populations increasing when the red fox population declined and subsequently decreasing as red fox numbers rebounded.

3.2. Harvest trends

General trends in mountain and brown hare hunting harvest between 1960 and 2017 suggested that in the study period, the southwestern region C likely underwent a stable state shift whereby brown hare became the dominant hare species (Fig. 4). Mountain hare harvest was greater than brown hare harvest in the beginning of the study period, but that pattern reversed during the 1990 s. Interestingly, this switch coincided with the red fox population crash. Importantly, the heath hare *L. t. sylvaticus* is the dominant mountain hare subspecies in this region (Bergengren, 1969) (see Fig. 1).

In the eastern region B, mountain and brown hare harvest data closely tracked each other (Fig. 4). The brown hare was already more abundant in the hunting harvest data than the mountain hare subspecies *L. t. timidus* and *L. t. sylvaticus* at the beginning of the study period, suggesting that the switch to the alternative stable state, with brown hare dominating, occurred prior to the study period. The pattern observed in region B may represent the new alternative stable state to which region C has shifted. In region B the heath hare *L. t. sylvaticus* was frequent, but not as historically dominant as in region C (Bergengren, 1969) (Fig. 1).

4. Discussion

4.1. Interspecific competition

Analysis of Swedish hunting harvest data 1960–2017 indicated that the overlapping hare populations in Sweden have undergone a shift to an alternative stable state. In the study period, brown hare harvest surpassed mountain hare harvest in every area in which the species currently co-occur and then stabilised. Importantly, the heath hare subspecies *L. t. sylvaticus* range completely overlaps with brown hare distribution in Sweden, implying that heath hare populations have experienced a decline across their range. The shift obviously took place before our study period in regions B and D. However, we were able to observe the shift in the southwestern region C (Fig. 4). This shift is likely due, at least in part, to the ability of the non-native brown hare to outcompete the native mountain hare subspecies *L. t. timidus* and *L. t. sylvaticus* in areas where they co-exist.

Patterns of interspecific competition among hares were first noted by Lönnberg (1908) in an assessment of changes in distribution that followed introduction and subsequent establishment of brown hare populations in Skåne County in southern Sweden. Thulin (2003) reviewed the distribution pattern and population history of the two species in Europe, indicating a postglacial pan-European process similar to that observed in Skåne County. The nature of competition is largely unknown. In a study of hare lay selection in two areas where the species were allopatric and sympatric, respectively, Lind (1963) observed that mountain hares co-occurring with brown hares more frequently avoided lays in open areas (i.e. brown hare habitat), indicating competitive exclusion in action. In a more recent study, Levänen (2019) concluded that asymmetric crossbreeding has negatively impacted the mountain hare population, while the brown hare population has potentially benefited from the introgression of locally adapted alleles. When modelling climate and habitat preferences and scenarios for the two species in all of Europe, Carvaggi et al. (2017) concluded that the situation for several subspecies of mountain hare is distressing.

It should be noted that supplemental release of mountain hares, in particular the nominate subspecies *L. t. timidus*, was relatively common and unregulated until restricted by Swedish law in 2003. Thulin (2000) found that over a five-year period, 22 breeders released 3167 mountain hares, of which about two-thirds were released in areas where brown and mountain hare occur in sympatry (i.e. southern and central Sweden). However, experimental release of mountain hares generally results in low survival of captive-bred hares (Lemnell & Lindlöf, 1982), suggesting a low probability of successful reproduction and subsequent admixture with locally existing populations of heath hare.

4.2. Predation impact

Interestingly, the shift to brown hare dominance in the hunting harvest data from southwestern Sweden (region C) coincided with a crash in the population of red fox, a primary predator of both hare species in that area. Although consumption varies based on the availability of alternative prey, hares can comprise a large proportion of red fox food biomass (Kauhala et al., 1998). The observed pattern in our data suggests the possibility that reduced predation pressure facilitated release in the brown hare population, with brown hare then able to outcompete and exclude the local mountain hare subspecies. This new stable state persisted even after the fox population rebounded (Fig. 4), resulting in a new equilibrium in region C whereby hare populations tracked each other, but brown hare dominated. This equilibrium was observed over the entire study period in the eastern region B (Fig. 4).

The decline in mountain hare subspecies could be further explained by predation: i) if red fox preferentially preys on mountain hare or ii) if red fox abundance, and subsequent predation pressure, is boosted by the presence of brown hare. Unfortunately, investigations of red fox dietary composition in Scandinavia have generally not distinguished between specific hare species, (e.g. Lindström, 1982; Angerbjörn, 1989; Kauhala et al., 1998), making it difficult to assess red fox preference for brown versus mountain hare. However, a climate change-induced mismatch in the timing of seasons and the development of seasonal coat colour camouflage could lead to increased detection, vulnerability and preference for fox predation on mountain hare over brown hare (e.g. Mills et al., 2013). Apparent competition could also explain the switch in hare abundances across Sweden (Holt, 1977). For example, a recent study found that presence of non-native eastern cottontail (*Sylvilagus floridanus*) increased fox predation pressure on native brown hare, suggesting apparent competition between the two species (Cerri et al., 2017). However, Thulin (2003) concluded that mountain hare has the capacity to survive periods of intensive predation and is often an alternative prey for red fox only when the vole (*Microtus* spp.) population density is low (Lindström et al., 1987; Marcström et al., 1989).

4.3. Causative factors

It is not clear whether the decrease in mountain hares during the 1990 s was caused by a predatory release in the brown hare population, or merely correlated. The decline in mountain hare subspecies abundance is likely also related to multiple other changes that occurred in Sweden during that decade (e.g. changes in climate and weather, land use and species assemblages). Shifting climate pattern can alter predator–prey interactions, resulting in alternative stable states and the extinction of prey species (Tyson & Lutscher, 2016). Interspecific competition with ungulate species may also have caused a broad decline in hare numbers over the past century, a period in which multiple ungulate species have shown dramatic resurgence in Sweden (Thulin & Röcklinsberg, 2020). Several of these ungulate species are likely to compete with hare for forage. For example, the populations of both moose (*Alces alces*) and roe deer (*Capreolus capreolus*) have rebounded from near extirpation in the early 19th century and moose density in Sweden is now one of the highest in the world (Lavsund et al., 2003), while the roe deer population is currently estimated at several hundred

thousand (Kardell, 2016). The wild boar (*Sus scrofa*) was re-introduced in the 1970 s and is now one of the most common ungulates in Sweden, with approximately 450,000 individuals if following the principle that the population size equals three times the annual hunting harvest (cf. H. Thurfjell, pers. comm. 2018). A large abundance of ungulates could lead to competition for high quality forage (Belovsky, 1984; Ranglack et al., 2015). In interactions with conspecifics such as the brown hare, ungulates could also facilitate apparent competition, i.e. keep predator populations high, resulting in increased predation on hares. Conversely, high-density ungulate populations could have a buffering effect if predators direct their attention to ungulates instead of hares. Grazing from ungulates could also boost the energy content of the forage, as recently shown in a study of horses kept year-around on pastures without supplementary feeding (Ringmark et al., 2019).

Increased predation pressure from other carnivores could potentially exacerbate declines in hares as a whole. Multiple carnivore species in Sweden have recovered over recent decades and many of these utilise hares as prey (Table 1). The grey wolf, wolverine, and lynx have increased in numbers and distribution across various parts of Sweden since the latter half of the 20th century (Chapron et al., 2014), and all these species occasionally prey on hares, albeit infrequently (Müller, 2006; Odden et al., 2006; Mattisson et al., 2016). For example, lynx in Scandinavia primarily preys on roe deer and reindeer, but also hunts hares, particularly in the summer months (Odden et al., 2006). The pine marten and non-native American mink, which was introduced to Sweden in the 1920 s, also frequently prey on hares (Helldin, 1999; Carlsson et al., 2010). However, interactions between carnivores can have varying effects on each other, depending on species assemblages and densities (Ritchie & Johnson, 2009). For example, both wolves and lynx suppress mesopredator populations, including the red fox, thereby buffering red fox prey from predation (Elmhagen & Rushton, 2007). Interestingly, the strength of mesopredator suppression and release is also mitigated by bottom-up processes, such as landscape productivity and the fluctuation of rodent cycles (Elmhagen & Rushton, 2007). Another important factor to consider is diseases and parasites, which

Table 1

Compilation of results from investigations in Fennoscandia (Sweden, Finland, Norway) on the proportion (%) of predation by different predator species on brown hare (*Lepus europaeus*) and mountain hare (*L. timidus*) by frequency of occurrence (FO) or biomass consumed (BM), time of year (period) and method of data collection, and source of the data.

Predator	<i>Lepus</i> sp.	Proportion (%)	Period	Method	Data source
<i>V. vulpes</i>	<i>L. timidus</i>	<1–20 FO	Autumn	Scat	Lindström (1982)
<i>V. vulpes</i>	<i>L. timidus</i>	38–94 BM	Winter/spring	Scat	Angerbjörn (1989)
<i>V. vulpes</i>	<i>Lepus</i> sp.	57–59 FO	Summer	Scat	Kauhala et al. (1998)
<i>M. martes</i>	<i>Lepus</i> sp.	8.15 BM	Winter	Scat	Helldin (1999)
<i>L. lynx</i>	<i>Lepus</i> sp.	79.5 FO	Winter	Stomach	Pulliaainen (1981)
<i>L. lynx</i>	<i>L. timidus</i>	15.7–22.9 FO	Winter/spring	Tracking/scat	Odden et al. (2006)
<i>G. gulo</i>	<i>L. timidus</i>	12.7–15.6 FO	Denning	Scat	Koskela et al. (2013)
<i>C. lupus</i>	<i>Lepus</i> sp.	1.9 FO	Year	Scat	Müller (2006)
<i>A. gentilis</i>	<i>L. timidus</i>	69.6 BM	Winter	Tracking	(Tornberg and Colpaert, 2001)
<i>B. buteo</i>	<i>Lepus</i> sp.	17.8 BM	Breeding	Pellet	Reif et al. (2001)
<i>A. chrysaetos</i>	<i>L. timidus</i>	5.6 FO	Breeding	Pellet	Nyström et al. (2006)

may affect the two hare species unequally (Thulin, 2003).

Habitat degradation, monoculture and reforestation could also affect both hare species in the intensively managed anthropogenic Swedish landscape. The past 100 years have been detrimental to Sweden's biodiversity, particularly for species bound to grazed and managed pastures and meadows (Cousins et al., 2015; Sandström et al., 2015; SLU Artdatabanken, 2020). Although grazed pastures intuitively seem to be unsuitable habitat for a boreal species such as the mountain hare, it is likely that the diverse flora of pastures heterogeneously integrated within a forest-dominated landscape provides opportunities for mountain hare. In Ireland, for example, the mountain hare inhabits open agricultural landscape, indicating that this landscape form at least provides no particular restraints. Intensive forestry has led to emaciated, spruce-dominated forests (Lindbladh et al., 2014), with little undergrowth to provide forage and protection for herbivores in general, and perhaps hares in particular. Mountain hare habitat quality, in the form of dense understorey vegetation, is valuable for forage availability and for mitigating predation pressure (Hiltunen et al., 2004).

Hunting harvest data have been used previously to evaluate trends in hare populations in Sweden (Newey et al., 2007; Carlson et al., 2010). Other methods for population monitoring are available (Williams et al., 2002), but none has the temporal coverage of harvest data. It must be noted, however, that hunting harvest statistics are not a perfect proxy for abundance (e.g. Ranta et al., 2008), particularly if hare hunting patterns have shifted during the study period (Winterhalder, 1980). For example, it is possible that concern for the mountain hare population caused a gradual shift in hunter preference from mountain hare to brown hare, with this bias resulting in underestimation of mountain hare abundance. The willingness of hunters to report their harvest may also influence the reliability of the data (Aubry, Guillemin, & Boyce, 2019), for example if non-reporting hunters have a lower harvest or if reporting hunters overestimate their harvest (Wright, 1978).

Hunter behaviour and hunting preferences may also influence harvest data. During the past century, hunting objectives in Sweden have shifted from a focus on small and medium-sized species such as hares, rabbits, game fowl and mesopredators to large ungulates, geese and large carnivores. The reason for this shift in focus is large-scale comeback of larger species of birds (e.g. geese) and mammals (e.g. ungulates) (cf. Thulin & Röcklinsberg, 2020), while many small species have suffered from landscape impoverishment (as outlined above). With changing game availability, the focus of hunters' efforts naturally shifts. With respect to hares, this shift is indicated by a decrease in the number of registered hounds for breeds specified for hare (and/or fox) hunting (Winiger, 2014).

Finally, climate change needs to be considered when evaluating the interspecific relationship and population development of brown hare and the two Scandinavian subspecies of mountain hare. A warmer climate should in principle favour the heath hare over the northern hare mountain hare subspecies, but instead it seems that the non-native brown hare is exploiting this change.

Regardless of the underlying mechanism, a novel equilibrium or stable state has interesting conservation and management implications, especially if it leads e.g. to an extinction vortex in which the heath hare *L. t. sylvaticus* gradually disappears. Such a pattern might be indicated by the ongoing comparatively declining trend in eastern and southwestern parts of Sweden (regions B and C), where heath hare has historically been the dominant subspecies (sensu Bergengren, 1969) (see Fig. 1). If the pattern in the extreme south (region D) is an indicator of the future of regions B and C, then the Swedish heath hare population is currently at great risk.

4.4. Conclusions and management suggestions

We believe that the patterns seen for the southern half of Sweden indicate an alarming situation for heath hare subspecies *L. t. sylvaticus* and obvious potential for regional extinction, such as already

documented in most of Skåne County in southernmost Sweden. Thus more research is required to determine with accuracy the population status of the heath hare and identify underlying mechanisms behind the dramatic decline observed in hunting harvest data 1960–2017. For example, future studies should quantify actual mountain hare subspecies abundance in regions of concern (i.e. B and C) in order to determine heath hare population status more accurately. A better understanding of predator preference and impact on the hare population, particularly with respect to local carnivore assemblages, would help guide future management decisions. A clear understanding of the implications of interspecific introgression from mountain hare to brown hare would also be of great value, for example regarding the potential for adaptation through hybridisation and introgression (cf. Thulin, 2003; Levänen, 2019). In addition, it is important to explore the ecology, status and distribution of heath hare, as existing knowledge is mainly based on a study by Bergengren in 1969. Determining the role of large-scale landscape shifts and anthropogenic climate change can help guide the future conservation of the heath hare subspecies. The potential shortcomings of hunting harvest data, as described above, may warrant a human dimension survey of whether decreasing hunting effort follows a decline in mountain hare density, or vice versa.

In combination with continued research efforts, we suggest an adaptive management programme that focuses on preservation of the heath hare subspecies in its current range and specifically in areas where: i) brown hare abundance is currently low or can be efficiently managed, b) both wolf and lynx are present and can potentially suppress red fox populations, and therefore predation on hares, and c) historical climatic habitat preferences are projected to match future climate change scenarios. In such areas, we suggest establishment of a network of heath hare ‘reservoir islands’ that are managed to facilitate local heath hare population increase and eventual stability. Translocations between these reservoirs and supplemental release of wild heath hares in areas as described above may expedite population increase. Habitat improvements adapted to heath hare preferences can add to the long-term sustainability of the reservoir network. Developing and implementing an educational public outreach programme aimed at local hunting and environmental protection associations could further facilitate heath hare conservation. Finally, we suggest establishment of a Scandinavian monitoring system for hares (both species) based on a combination of hunting harvest data, pellet inventories with DNA-based species assessment and camera images retained from the ongoing ScandCam project (<https://viltkamera.nina.no/>). The utilisation of independent data in such a system would enable qualitative assessment of population development and avoid the shortcomings of using hunting harvest data alone.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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