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Letter to the Editors

Range extensions of some boreal owl species: comments on snow cover, ice crusts, and climate change

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INTRODUCTION

Recent observations have documented that some boreal owl species in Europe have made unexpected eruptive movements and some have extended their distribution, among them the Great Grey owl (*Strix nebulosa*). Based on published data, it can be assumed that both the numbers and distribution have varied considerably in the past 120 years. In the Finnish population, for example, there has been a clear southward shift in range—from Lapland toward the central and eastern regions (Sulkava and Huhtala, 1997). In Sweden, the Great Grey owl is distributed throughout the boreal zone but is most frequently found in the northeasternmost parts of the country (Hipkiss et al., 2008). In 2010–2012, the species was found nesting in unprecedented numbers in southeastern Norway (Solheim, 2009, 2014a). Record-breaking numbers of breeding individuals were reported in Sweden and Norway in 2010 and 2011, followed by 4105 observations in 2012 as revealed by the National Species Archives in Sweden (Solheim, 2014b). In the first half of the last century, the species was known as a rare breeder only in northernmost Norway (i.e., in Pasvik, Finnmark) (Hagen, 1989; Sulkava and Huhtala, 1997). Today it is a regular breeder over a considerable part of the southeast forested area in the country (Solheim, 2014b). Other extensions have been noted as well. In 2007–2009, the species was found in Belarus near the Polish border, southwest of its

regular breeding grounds, and the species recently has been visiting many other areas (Ławicki et al., 2013). Rapid range extensions and population movements are so marked that they indicate a large-scale ecological change. Is it caused by climate change and global warming?

BOREAL OWLS

Species in a guild of overwintering boreal owls—that is, Tengmalms owl (*Aegolius funereus*), Hawk owl (*Surnia ulula*), Ural owl (*Strix uralensis*), and Great Grey owl (*Strix nebulosa*)—hunt during winter small rodents and soricine shrews mainly living in the subnivean air space below the snowcover. In winter ecological terms (Jones et al., 2001), they are supranivean raptors utilizing subnivean food resources. They are specialists on small mammals and hunt their prey on the surface or dive into the snow-cover catching prey based on auditory techniques. Hunting partly also on animals moving inside the snow carpet (i.e., intranivean prey) makes them highly vulnerable to changes in snow structure. How might these species be affected by climate change and global warming, and in what way can this change influence raptor range extensions for a species as *S. nebulosa*? Climate, weather, and snow may influence owls in several ways, and two critical conditions need to be evaluated. One is possible structural changes in the snow-cover, another is the food factor, that is, the production regime of small mammals.

GLOBAL WARMING

The interactions between snow and climate are extremely complex (Croisman and Davies, 2001; Armstrong and Brun, 2008), and consequences of the ongoing global climate change are predicted to be far-reaching (Gutman and Reissell, 2010). The United Nations Climate Working Groups have reported that the fastest changes will occur in the Arctic and Antarctica (Intergovernmental Panel on Climate Change, 2007, 2014). There is no longer any doubt from their research that the earth is warming up, and it is happening fast. The global average temperature has increased 0.74 °C between 1906 and 2005, the actual increase the last 30 years is ~0.2 °C per 10 years (Correll, 2007). Average temperature increase in the northern areas of Fennoscandia has been estimated to be 0.7 °C per 10 years—that is, almost the same as the global average. The longer north and east you come, the more evident is warming. It might even seem as if the change happened faster than expected from models (Mathiesen et al., 2007). Norwegian researchers are characterizing that climate change as creating a “warmer, wetter, and wilder” weather pattern (Alfsen et al., 2013), which in other words means higher temperatures, more rainy episodes, and stronger winds.

CLIMATE CHANGE AND SNOW

Boreal owl snow diving techniques are dependent on “loose” snow structures, hunting efficiency being vulnerable not only to low prey population, but also to hardness changes in the snow. Several of these owls are well known to be “irruptive species,” performing varying degree of nomadic behavior among winter seasons. They leave areas where the food supply runs out and settle to breed in areas where they find food (Hipkiss et al., 2008), often making long migrations to areas where food is available and snow condition suitable. Several abiotic processes can make significant changes to a snow cover, affecting owl hunting success. One important factor might be sudden melting periods or rain episodes followed by cold weather forming crusts. Repeated cycles of freezing and thawing—that is, the “frost seesaw effect” (sensu Solonen,

2006)—might through the winter create several ice layers being buried into the snow profile by new snowfalls (Marsh and Woo, 1984; Singh et al., 1999). The snow cover could also harden and be transformed by cold wind alone. The climate “wind pump” is tunneling cold air through the snowpack hardening it by “sintering,” the freezing of small ice bridges between crystals (Jones et al., 2001). Wind transformation of snow increases with longitude and altitude, a phenomenon highly evident with increasing elevations.

ALPINE MOUNTAIN AND ARCTIC SNOW

Wind might be the most significant abiotic factor that inserts extreme hardness to snow-covers in alpine and Arctic areas of Fennoscandia. To document how hard it might be, we presented a few measurements from the alpine mountain ecosystem Hardangervidda (1150–1350 m a.s.l.) in Norway. During seasonal field studies of wild reindeer (*Rangifer tarandus tarandus* L.), a ramsonde technique was used to measure the wind-hardened snow and a spring penetrometer to measure softer snow (Skogland, 1978). The reindeer scrape and dig during foraging with their winter-adapted foreleg cloves creating craters in the snow carpet. Hardness based on ramsonde measurements at the Finse location increased from 22 to 395 kg from early to late winter, hardness increased from 40 to 140 kg in uncratered areas and from 15 to 27 kg in cratered areas. Density increased from 0.20 to 0.37 g cm⁻³ in early winter to 0.40 to 0.55 g cm⁻³ in late winter prior to melt-off. Hardness measured with spring penetrometer increased from 200 to 400 g cm⁻² in early winter to 800 to 1000 g cm⁻² in late winter prior to melt-off in cratered areas. Wind-hardened snow in Fennoscandian mountains might thus develop extreme hardness over large areas often including several ice-crusts, impossible to penetrate even for large mammals. From earlier studies it is reported that small mammals avoid areas where the density of snow exceeds 150 kg m⁻³ (Spencer, 1984). In any snow-covered area, lemmings and other small mammal herbivores are totally dependent on the formation of a subnivean space, created either when heat from the ground melts a thin layer of the snow-cover leaving a small space between the ground and the snow, or by snow clinging up

in the ground vegetation. In alpine areas, the subnivean space is broken into a labyrinth of accessible and inaccessible patches by ice or dense snow tightly packed to the ground (Korslund, 2006).

ICE LAYERS IN TAIGA SNOW

Owl raptors in the northern forests are adapted to looser taiga snow, where also a subnivean space is more easily formed. Raptors like *S. nebulosa* might as mentioned dive down into the snow-carpet and catch small rodents and soricine shrews (Nero, 1969; Collins, 1980). However, it is presently unknown how vulnerable forest raptors are to slight increases in hardness both from formation of ice-crusts (the above-mentioned “frost seesaw effect”) and changes in wind regimes. Both phenomena might be expected of significance due to recent climate changes.

Terrestrial ice can form following thaw-freezing, rain on frozen ground (i.e., black icing), and in particular events with rain on snow (ROS) (Aars and Ims, 2002; Putkonen and Roe, 2003; Korslund, 2006; Grenfell and Putkonen, 2008; Bartsch et al., 2010; Hansen et al., 2011). Biotic effects of ROS are, however, understudied in most ecosystems. Basal ice might already establish in early winter and is probably caused by undrained water on the ground from rain and/or melted snow that freezes prior to the first permanent snow (Mast et al., 1998; Korslund, 2006). Basal ice (“ground ice”) might also build up, cover, and block up plants (Korslund, 2006; Hansen et al., 2010, 2011). How such icing events vary with climate is in general poorly documented (Rennert et al., 2009). In some parts of the southeastern lowland Norway, an ice-crust covered considerable areas in spring 2015 and locked up ground vegetation, being the last remains of a spring melting snow cover.

The frost seesaw effect might be more influential the colder and more continental an area is. The winter period is more stable in alpine and Arctic areas during cold and dry periods than in more southwestern and coastal areas, with more frequent fluxes from maritime influence. In forested areas further southwest in Scandinavia, milder climate conditions may in general induce a looser snowpack. This could induce irruptive southeast raptor movements. But climate effects are much more complicated. The second variable needed to be evaluated in raptor range extensions is the food factor.

CLIMATE CHANGE AND BOREAL OWLS

Both higher temperature and higher food abundance can separately lead to advancement of owl breeding (Hipkiss et al., 2008), and both timing of breeding and breeding success might be affected (Lehikoinen et al., 2011). Milder climate can improve body condition and winter survival of boreal owls because increasing temperature lowers their energy requirements and decreased snow depth may improve hunting success (Hipkiss et al., 2008). Conditions of breeding birds might be enhanced if the winter has been mild, allowing individuals to breed earlier. Studies of the performance of boreal forest owls confirm that it is to a substantial degree determined by weather conditions and not just by the abundance of their main prey (Lehikoinen et al., 2011). Interaction between food availability and climate on breeding has been studied, and increased snow depth might indicate delayed breeding of at least one large species, the Ural owl (Lehikoinen et al., 2011).

SMALL MAMMALS

A warmer climate pattern will in general shorten the snow-covered winter period at both seasonal ends, and such an extended snow-free period might affect general productivity. How will this affect small mammals? In more favorable snow areas, one possibility is that ice crusts in the snowpack directly restrict animals in the subnivean space to communicate with the surface. Gas concentrations under snow-cover can vary considerably in both space and time. A less efficient “wind pump” through a snow-cover might affect gas levels, or even induce changes in the flux of abiotic and biotic materials through the snowpack (Tranter and Jones, 2001). Below-cover gas levels might increase partly due to accumulated biological respiration from animals, and partly due to soil microbial activity (Aitchison, 2001; Tranter and Jones, 2001). A restricted gas exchange between ground layer and surface might influence the vegetation, or other elements of the subnivean environment as the gas levels increase.

When small mammal population densities are high, ventilation shafts or snow chimneys usually release the gas from under the snow (Tranter and Jones, 2001). By late winter, however, the subnivean

CO₂ concentration can rise under ice layers. Small mammals respond to increased CO₂ by avoiding areas where concentrations are high (Penny, 1977; Penny and Pruitt, 1984; Tranter and Jones, 2001). Today winter reproduction is well known for several lemming and vole species (Batzli et al., 1980; Stenseth and Ims, 1993). How gas level might affect the young of small herbivores born below snow in the subnivean space is presently unknown. However, it might add to restrictions of a population build-up during cyclic highs.

FOOD FACTOR CHANGES

Certain changes in the “normal” fluctuating population regime of small rodents in Fennoscandia have recently been reported. And there have been contradicting results from several field studies in vole and lemming cycling and abundance. The cycles of some species have decreased in amplitude or others have disappeared entirely. For example, lemming cycles have ceased to occur in some high-latitude locations (Kausrud et al., 2008; Gilg et al., 2009). Similarly, Hörnfeldt (2004) and Hörnfeldt et al. (2005) observed dramatic reductions in the amplitude and the 3–4 year population cycles previously seen in the grey-sided vole, *Myodes rufocanus*. A recent study reported that throughout Europe, 10 out of 12 populations of vole species showed at least a twofold decrease in the amplitude of their earlier population cycles. Climate warming is suggested to have caused the collapse of these vole population cycles throughout Europe and across different species (Cornulier et al., 2013). However, although changes continued to decrease in many areas, the vole cycling continued in some regions of Finland despite regional warming (Brommer et al., 2010).

“KICK-STARTING” OF LEMMING POPULATION GROWTH

Regular fluctuations of the lemming (*Lemmus lemmus* L.) populations seem to have changed over large areas in the northern parts of Scandinavia in recent years, and snow-structure might be of significance. One well documented case of a recent absence of outbreaks is that of a local Norwegian lemming population in alpine southern Norway,

where cyclic outbreaks at regular 3- to 4-year intervals prevailed until the past 15 years (Ims et al., 2008; Kausrud et al., 2008; Post et al., 2009). Population size amplitude, recent decline, and changing cycles of many small herbivores might be related to winter warming and hardness of the lowest snow layer (Kausrud et al., 2008). Changes in the weather patterns may in other words produce a “wrong” type of snow that has changed the population dynamics (Kausrud et al., 2008; Coulson and Malo, 2008).

A study of comparative population development between *L. lemmus* and *M. rufocanus* in Finnmark, northern Norway, revealed significant ecological differences between the two species (Ims et al., 2011). The Arctic lemming has evolved a population “kick-starter.” A steeper lemming population outbreak trajectory was caused by breeding and growth during winter, when nonbreeding vole populations consistently declined. The differently shaped lemming and vole outbreaks appear to result from a particular demographic tactic of lemmings evolving as an adaptation to the long and cold Arctic-alpine winters. The lemming outbreak amplitude increased with altitude and vole density, indicating that lemming outbreaks are jointly facilitated by low temperatures and apparent mutualism with voles mediated by shared predators. The combination of continued climatic warming and dampened vole cycles is expected to further decrease the frequency, amplitude, and geographical range of lemming outbreaks in tundra ecosystems (Ims et al., 2011). A more modest summer effect indicates that some additional mechanism also contributes, for instance, temperature-dependent quality of mosses (Tast, 1991; Ims et al., 2011).

WINTER “KICK-START” IN WOOD LEMMING?

A noteworthy connected event to the above discussion is a population high of unprecedented strength in the wood lemming (*Myopus schisticolor*) in the Norwegian southeastern lowland forests in 2014 (Mysterud, unpublished). During the 1960s, winter reproduction was detected in the wood lemming (Mysterud, 1966, 1968), and the author has had certain forested tracts in Akershus and Hedmark counties under wood lemming surveillance for more than 50 years. During this

period, there has never earlier been observed such a mass occurrence of wood lemmings. Maybe the “lemming of the forest” uses the same “kick-starter” adaptation in the form of winter breeding, and might benefit from climate change on snow structure in certain years? This might well be another factor in the puzzle of raptor range extensions.

FINAL STATEMENTS

Future increase in temperatures and global warming may affect the breeding of *S. nebulosa* and other boreal owls in several ways: by changes in their reproductive phenology, by directly affecting their winter hunting due to structural changes in the snow-cover, and indirectly through decrease of the food factor, that is, impacting the cycling of small herbivores. Predicted increases in temperature seem likely to exacerbate what is called the collapse of high-amplitude vole cycles decreasing small herbivore abundance. Milder winters with fluctuating periods of thaw and freezing, shortening of the snow period, and ice-bark formation on the ground change their abiotic environment. Voles and lemmings are denied optimal subnivean conditions to protect them from predators and adverse weather, probably decreasing their survival and leading to winter declines.

The hypothesis is that *S. nebulosa* and other boreal raptor species are dependent in their hunting not only of snow depth, but of hardness and ice structures in the snow carpet as well. The ice regime on and in the snow and on the ground may negatively impact populations of their main prey resources both through direct change of snow structure, and indirectly by lowering population regimes of small herbivores. However, the main cause underlying *S. nebulosa*'s distribution extension changes is presently unknown, and obviously deeper understanding of how climate change affects top trophic-level predators is vital. Therefore, studying survival and distribution in an apex predator, like the Great Grey owl, requires individual-based data from long-term studies and is complicated by the integration of climatic effects on prey species at lower trophic levels (Mikkola, 2014). Based on this paper, not only are field studies of raptor distribution extensions that take into account the food factor needed, but simultaneous snow-cover studies are very much needed as well. Among the most

important ecological winter factors might be “the frost seesaw,” that is, alternating thaw and freezing cycles and related ice formations blocking hunting and decreasing the food factor.

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