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Changed Arctic–alpine food web interactions under rapid climate warming: implication for ptarmigan research

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Ptarmigan are herbivorous birds that are year-round residents of alpine and arctic ecosystems − presently subjected to the most rapid climate warming on earth. Yet, compared to other bird taxa there has been little climate impact research on ptarmigan. Ptarmigan population dynamics, in particular in the sub/low-arctic, appears to be strongly influenced by complex interactions with a suite of functionally diverse predators in the food webs. We review evidence supporting that the strength of such predator–ptarmigan interactions has been altered, most likely due to climate change, having led to rapidly declining ptarmigan populations and in some places national red listing. Predation-mediated population declines are likely linked to dampened population cycles of keystone mammal herbivores (inducing increased apparent competition/reduced apparent mutualism), altitudinal/latitudinal expansions of boreal mesopredators and possibly mismatched ptarmigan plumage colour in spring and fall. Yet, other rapid food web mediated impacts are likely to act bottom–up, such as phenological mismatches with food plants and competitive interactions with other irrupting herbivores. We advocate that ptarmigan researchers should team up with specialists on other taxa in order to adopt a food web approach to their research. Coordinated action of research teams, to make comparative studies among ptarmigan species or populations imbedded in food webs of varying structure or ambient climate, may be rewarding in the age of rapid ongoing climate changes.

Climate change has profound effects on biodiversity in a range of habitats across the earth (Sala et al. 2000, Parmesan and Yohe 2003, Parmesan 2006, Miller-Rushing et al. 2010), including significant impacts on the distribution and abundance of bird species (Crick 2004, Gregory et al. 2009, Møller et al. 2010, Jenouvrier 2013). The rate of warming in regions at high altitudes and latitudes has been much higher than the global average (Brunetti et al. 2009, Ims et al. 2013a), and consequently some of the largest ecological impacts of climate warming have been observed in the Arctic (Post et al. 2009b). Furthermore, the continued warming projected to take place during this century in these regions are so extreme (Xu et al. 2013), that they can be expected to radically transform alpine and Arctic ecosystems (Ims et al. 2013a). In this paper, we focus on the likely implications of climate change for ptarmigan – a genus of birds of great ecological and societal importance in alpine and arctic regions.

Ptarmigan *Lagopus* spp. are among the most intensively studied birds worldwide (Storch 2007, Moss et al. 2010). The historic attractiveness of these herbivorous birds to research can be explained by their role as important upland game species (Aanes et al. 2002), both for recreation and subsistence (Barth 1877), and their fascinating population dynamics, often characterized by multiannual density cycles (Moss and Watson 2001). Willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus muta* have circumpolar distributions, whereas white-tailed ptarmigan *Lagopus leucura* are restricted to the western North America (Storch 2007, Potapov and Sale 2013). The willow ptarmigan, which is likely the Earths' most abundant tetranoid bird species, is continuously distributed in the low-arctic tundra and sub-arctic tundra–forest ecotone, while the rock and white-tailed ptarmigan are found in rocky habitats of high-arctic or high-alpine tundra (Storch 2007). The rock ptarmigan has the widest distribution range, spanning temperate alpine habitats in Europe and Japan to high-arctic regions in Greenland and Svalbard.

Despite being among the most studied bird species worldwide, studies concerning ptarmigan's sensitivity to climate change are limited (cf. Møller et al. 2010, Ims et al. 2013a), which is in stark contrast to the generally prominent position of bird studies in climate–ecological research (Guillemain et al. 2013, Jenouvrier 2013). In their extensive review of climate change effects on birds, Møller et al. (2010) included just a single citation of a ptarmigan study (Wang et al. 2002), while the same book has plenty of references to studies of arctic mammals. Knowledge gaps are not necessarily due to higher resilience of ptarmigan to climate change than other bird species. It is perhaps rather because most studies of ptarmigan has focused on aspects of ptarmigan

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biology that are less relevant in context of climate change, or because of a general bias among ornithologists to focus on aspects of climate change impacts (e.g. timing of migration) that are not that relevant for ptarmigan (but see Tape and Gustine 2014).

In our paper, we highlight aspects of the ecology of arctic and alpine ptarmigan that may render the birds vulnerable to climate change, which we propose should constitute the main focus in future research on these birds. Change in research focus may now be especially pressing as many species and populations of grouse have declined during the last decades, and some even close to extinction. Climate change has been forwarded as a potential cause of several of these declines (Thirgood et al. 2000, Wang et al. 2002, Ludwig et al. 2006, Storch 2007, Aldridge et al. 2008, Kausrud et al. 2008, Novoa et al. 2008, Lehikoinen et al. 2011, Revermann et al. 2012, Imperio et al. 2013), but empirical evidence remains missing. The tenet of our proposal is that climate sensitivity of ptarmigan is largely determined by a set of direct and indirect food web interactions that requires other approaches and emphasises than what has been mainstream in studies of songbirds and seabirds – the two taxa that predominate in the climate–ecological literature on birds (Møller et al. 2010). We start out with a short review of the ecological function of ptarmigan populations in alpine and arctic food webs. Next, we propose and discuss the most likely mechanisms by which ptarmigan are impacted by climate change. Finally, we propose how future research could be focussed to achieve a better understanding of climate impacts on ptarmigan populations.

Ptarmigan ecology in perspective of food web structure and dynamics

Ptarmigan are obligate herbivores and mainly year-round resident birds in alpine and arctic ecosystems, and are closely linked to sympatric herbivorous mammals (Ims and Fuglei 2005). In particular, ptarmigan belong to the same trophic guild as arctic rodents (voles and lemmings), hares *Lepus* spp. and reindeer *Rangifer tarandus*, in the sense that they share food plants, habitats and predators in most seasons. Hence, climate change impacts that involve either direct bottom–up or top–down trophic interactions may act similarly on the entire trophic guild, or that climate change may induce more complex indirect interactions between the guild members via apparent competition or mutualism (Abrams et al. 1998). Arctic and alpine food webs differ much, however, depending on biogeography and bio-climate (Ims et al. 2013a). High-arctic rock ptarmigan populations are embedded in very simple food webs with relatively few herbivores or trophic links (in particular islands such as Iceland, Svalbard and Franz Josef Land; Fig. 1a), whereas continental willow ptarmigan populations are generally placed in more complex food webs (e.g. the Varanger peninsula; Fig. 1b). Notice also that migratory populations of willow ptarmigan (Tape and Gustine 2014) may be placed in somewhat different food webs (low-arctic versus sub-arctic) in different seasons.

The geographically contrasting food web contexts of different ptarmigan populations is associated with patterns of contrasting population dynamics (Moss and Watson 2001). We propose that in food webs with profound trophic interaction cycles involving keystone mammal herbivores (sensu Ims and Fuglei 2005), ptarmigan population dynamics becomes entrained to the dominant interaction cycle. The prime example of this is the 3–5-year "northern cycles" (sensu Elton 1942) with voles and lemmings as the engine (Krebs 2011, 2013). The rodent cycle is a community-level process in boreal and arctic ecosystems that underlies the synchronous cyclic dynamics of small to medium-sized vertebrates, especially in Eurasia (Elton 1942, Hörnfeldt et al. 1986, Hansson and Henttonen 1988, Gauthier et al. 2004, Ims and Fuglei 2005, Gilg and Yoccoz 2010, Krebs 2011). The snowshoe hare *Lepus americanus* possesses an equivalent keystone role in boreal and sub-arctic ecosystems of North America, causing a 10-year cycle in many vertebrate species, including forest grouse and ptarmigan (Martin et al. 2001, Krebs et al. 2014). Hence, different ptarmigan populations tend to exhibit highly contrasting dynamics depending on the complexity of terrestrial food webs. Some ptarmigan populations are embedded in food webs with no keystone mammal herbivores that could drive such community-wide dynamics. A lack of competitors characterizes the endemic high-arctic Svalbard rock ptarmigan *Lagopus muta hyperborea* and rock ptarmigan populations in the European Alps (Fig. 1b). These ptarmigan populations usually occur at low densities (e.g. 3–5 pairs per km^2 in Svalbard) and with relatively little temporal variability (Bossert 1995, Nopp-Mayr and Zohmann 2007, Zohmann and Wöss 2007, Pedersen et al. 2012). In contrast, sub- and low-arctic willow ptarmigan populations, embedded in more complex food webs with key-stone mammal herbivores and several different guilds of predators (Fig. 1a), usually exhibit highly violent and complex population dynamics (Lindén and Pedersen 1997, Moss and Watson 2001).

With regards to the key ecological factors that regulate ptarmigan populations, there has been highly conflicting views, and to some extent strong controversy (Moss and Watson 2001). Again, this ongoing debate may be attributed to the fact that ptarmigan populations are studied in very different food webs resulting from contrasting climate and management regimes. For instance, the most extensively studied *Lagopus* populations are found in the moorlands of northern England and Scotland, subjected to intensive ecosystem management directed towards the goal of maximizing production of red grouse *Lagopus lagopus scotica*. Strong control of predators is considered to be crucial for successful red grouse management, causing populations to reach such high densities (max 115 pairs km^{-2}; Hudson and Rands 1988), where aggressive interactions during territoriality or high parasite loads act as strong population regulatory mechanisms (Mougeot et al. 2005). Hence, the case of the red grouse, and how it has been managed for centuries, is an implicit recognition of the often important role of predators as determinants of ptarmigan population dynamics (Fletcher et al. 2010).

Enemy – victim interactions: the importance of different predator guilds

Predation has also been highlighted as a key factor underlying the dynamics of ptarmigan populations in several

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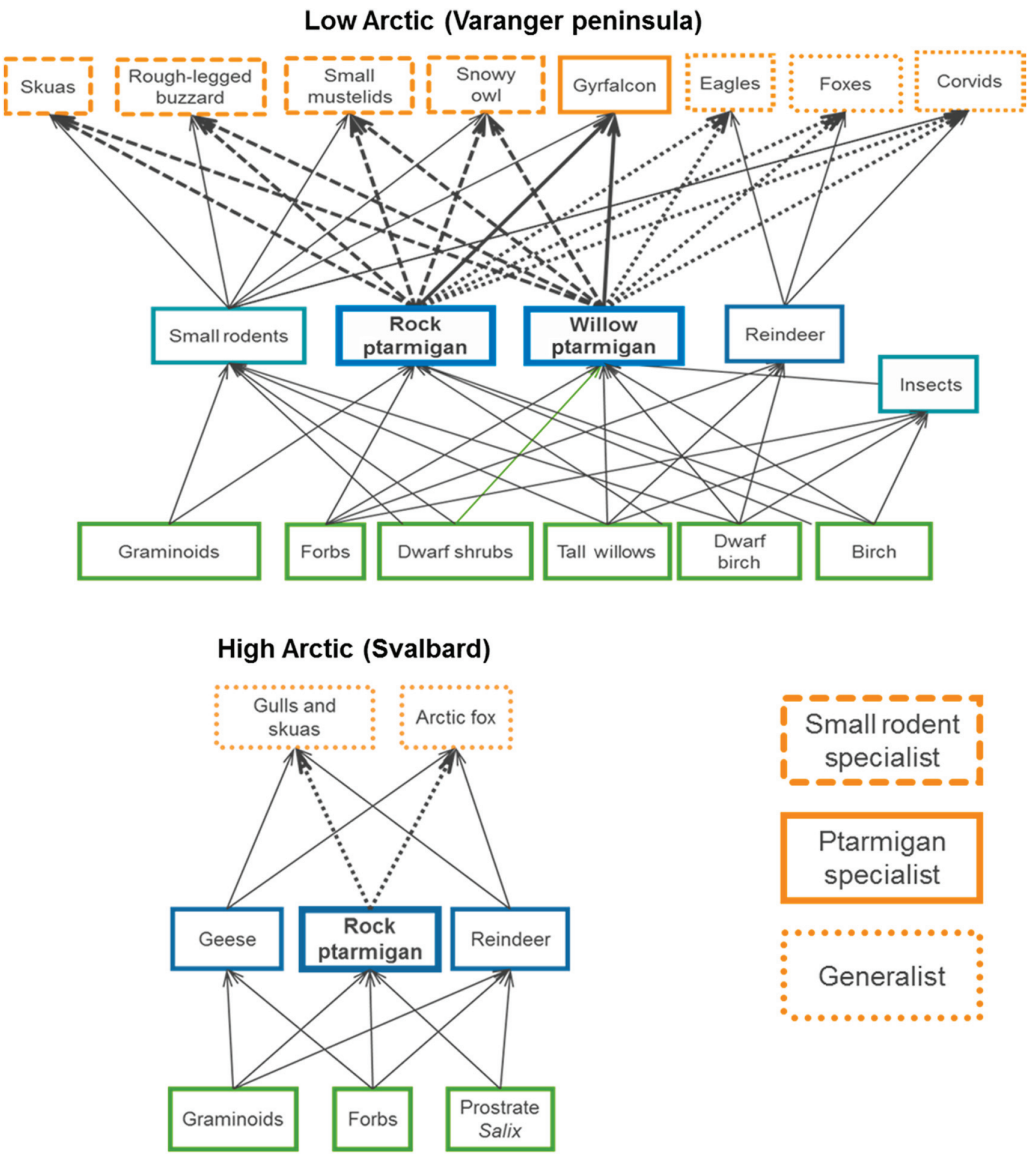

Figure 1. Ptarmigan in low-arctic and high-arctic food webs in Norway with contrasting complexities. Three functional groups of predators are distinguished. Only species or functional groups (directly or indirectly) linked to ptarmigan through trophic interactions (arrows) are included in the diagrams (modified from Ims et al. 2013c).

other ecosystems (Moss and Watson 2001). However, the importance and outcome of the interaction between predators and ptarmigan is likely to be dependent on the complexity of the food web, and in particular, the structure and functioning of the predator guild. For instance, in the fairly simple terrestrial food web of Iceland, the 10-year population cycle of the rock ptarmigan is mainly driven by an interaction with its key specialist predator – the gyrfalcon *Falco rusticolus* (Nielsen 1999). The gyrfalcon acts on the ptarmigan population as a typical specialist predator both in terms of the numerical and functional response (Clum and Cade 1994, Booms and Fuller 2003). In contrast, ptarmigan populations in the low-arctic continents in both Eurasia and North America often find themselves in a more complex ecological setting with predator species belonging to three guilds (Fig. 1b) that may have significant impacts on different ptarmigan life stages. The gyrfalcon is present as a "ptarmigan specialist" (Tømmerås 1993), partly along with the golden eagle *Aquila chrysaetos*, which to some extent relies on adult ptarmigan as prey during the breeding season (Krebs et al. 2001, Nyström et al. 2006). The golden eagle also partly belongs to a guild of "generalist predators" that to a large degree subsist on ungulate carrion in winter (Killengreen et al. 2012, Henden et al. 2014). Other prominent members in the guild of generalists are raven *Corvus corax*, hooded crow *Corvus cornix* and red fox *Vulpes vulpes*, which are important ptarmigan predators, particularly on eggs and chicks (Erikstad et al. 1982, Parker 1984, Munkebye et al. 2003, Fletcher et al. 2010). The last predator guild of interest are "facultative rodent specialists" where small mustelids probably are the most important ptarmigan predators (Parker 1984). Specialist rodent predators, and to some extent those of the generalist predators that responds functionally and numerically to the cyclic rodent dynamics

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(Ims et al. 2013b), have been proposed to cause 3–5-year cycles in Fennoscandian willow ptarmigan through the "alternative prey mechanism" (Hagen 1952, Myrberget 1982, Moss and Watson 2001, Ims and Fuglei 2005).

Climate warming and changed enemy–victim interactions

Synchronized cycles of small rodents and willow ptarmigan were clear from time series data from Fennoscandia until the 1980s (Myrberget 1982, 1985, Steen et al. 1988) when the synchrony and cyclicity has become weaker and even vanished in many areas (Kausrud et al. 2008, Henden et al. 2011). The classical small rodent population cycle with high amplitude peak densities, has recently changed into non-cyclic low amplitude dynamics or a dynamic with longer periodicity in large parts of Fennoscandia (Holmstad et al. 2005, Ims et al. 2008, Kausrud et al. 2008) and elsewhere (Schmidt et al. 2012, Cornulier et al. 2013). Changes in small rodent population cycles have been attributed to increasing frequencies of freeze-melt events during winter (Korslund and Steen 2006). Accordingly, Kausrud et al. (2008) showed that willow ptarmigan populations rapidly declined and cyclicity was lost simultaneously with the sudden collapse of the small rodent cycle in an alpine region in southern Norway. Based on the alternative prey hypothesis, they attributed the decline of the willow ptarmigan to increased predation impact from specialist rodent predators (Fig. 1b) after the rodent population cycle collapse. However, Henden et al. (2011) could not find any effect of the different phases of the rodent cycle on temporal dynamics of willow ptarmigan in low-arctic northern Norway, where the rodent cycle has prevailed. That is, the decline rate of the ptarmigan population appeared to be unaffected by the increase, peak and crash phases of the rodent population (but see Kvasnes et al. 2014). Due to the strong trophic link between typical small rodent predators and their primary prey (Hanski et al. 1991) one would not expect such predators to exert a sustained negative impact on alternative prey (e.g. ptarmigan). Hence, as their main prey source of small rodents collapse, these predators would also decline to very low densities or even be extirpated as they have done in high-arctic Greenland (Schmidt et al. 2012). Hence, other factor(s) than those predators that usually act to cause synchronous dynamics of rodents and ptarmigan, are likely responsible for the long-term depression of ptarmigan population growth in this region.

There are reasons to suspect that increasing abundance of generalist predators may be acting on several ptarmigan populations in a negative way. Generalist predators such as foxes and corvids have increased in abundance worldwide in recent decades, expanding their distribution into arctic and alpine areas (Tapper 1992, Gregory and Marchant 1996, Tannerfeldt et al. 2002). Ground-nesting species are particularly susceptible to predation by avian and mammalian predators, and negative impacts of predation have been documented for game birds and waterfowl (Marcström et al. 1988, Newton 1993, Fletcher et al. 2010, McKinnon et al. 2010). Recently, Fletcher et al. (2010) found that a large-scale reduction in abundance of carrion crow *Corvus corone* (–78%) and red fox (–43%) led to an average threefold increase in breeding success of red grouse, highlighting the potential high impact of such generalist predators. Moreover, there are indications that corvids may play a similar role in the decrease of sage grouse *Centrocercus* spp. in North America (Bui et al. 2010, Coates and Delehanty 2010). With a warmer climate, such predators may increase in tundra or alpine areas simply due to lower physiological demands at higher temperatures or even as a direct consequence of increased human activity or settlements in alpine and arctic regions (Hersteinsson and Macdonald 1992). More important in the case of northern Fennoscandia and North America, is increased availability of human-mediated subsidies or carcasses from large herbivores (Côté et al. 2004, Henden et al. 2014). In northern Fennoscandia, the availability of reindeer carcasses have increased due to changed management policies combined with more variable winters with ice-crust formation (Hausner et al. 2011, Killengreen et al. 2012), while in high-arctic Svalbard mortality rates of reindeer increase in winters with high frequency of "rain-on-snow" events (Stien et al. 2012, Hansen et al. 2013). Crows and red fox were recently able to establish and breed at the Yamal peninsula in the Russian arctic after a winter with catastrophic reindeer mortality due to an extreme rain-on-snow event (Sokolov et al. 2016). Generalist predators stabilise at high densities in response to high reindeer abundance, due to increased access to carcasses during the long and limiting winter period (Henden et al. 2014). This, in turn, is likely to promote strong and continuous predation pressure on ground nesting species in the summer (Fletcher et al. 2010, Ims et al. 2013b). Moreover, as many generalist predators are known to respond numerically and functionally to small rodents and other keystone herbivores (Ims et al. 2013b), changes in the dynamics of these keystone herbivores will likely be transferred to alternative prey species, such as ptarmigan. Recent changes in small rodent dynamics in Fennoscandia and elsewhere may therefore have resulted in additional and more continuous predation pressure on ptarmigan, as ptarmigan are increasingly deprived of predation-free years associated with small rodent peak years (Gilg and Yoccoz 2010). Thus, the fact that low-arctic ptarmigan populations are subjected to the simultaneous impacts of up to three guilds of predators (generalists, rodent specialists and ptarmigan specialists), with different numerical and functional responses as well as different responses to climate change, provides a scope for complex cumulative impacts on ptarmigan populations that cannot be ignored.

Compared to the complex impacts that may be implied by the functionally diverse predator community in low- and sub-arctic areas, predator impacts on high-arctic and high-alpine rock ptarmigan is likely to be simpler. For instance, in high-arctic Svalbard predation is mainly due to one terrestrial predator species – the arctic fox *Vulpes lagopus* (Fig. 1a). While the impact of arctic fox predation on the Svalbard rock ptarmigan is mostly unknown (but see Steen and Unander 1985), it has been proposed that, owing to the lack of lemming cycles, arctic fox predation rates on ground breeding birds is likely to be continuously high (Gilg and Yoccoz 2010). Still, temporal and spatial variability in predation rates on Svalbard rock ptarmigan may be caused by climate induced fluctuations in the

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abundance of alterative food sources for the arctic fox, such as reindeer carrion and breeding geese (Fuglei et al. 2003, Eide et al. 2012).

Camouflage is likely essential for ptarmigan as they live year-round in open areas where they are particularly vulnerable to predation. There is now evidence for an increasingly later onset of snow cover in autumn and an advanced spring with earlier snow melt in both arctic and alpine areas (cf. Ims et al. 2013a). Hence, a white plumage against bare ground represents a conspicuous contrast that could increase predation risk (Montgomerie et al. 2001, Mills et al. 2013). Considering that predation constitute the main form of adult mortality in most ptarmigan populations (Smith and Willebrand 1999, Martin 2001, Munkebye et al. 2003), the impact of a mismatch between moult and onset of winter snowfalls and spring snowmelt can be high. For instance, as autumn is the season when willow ptarmigan mortality is the highest due to natural predation (Smith and Willebrand 1999) and tend to coincide with the timing of snow fall (Sandercock et al. 2011), such mismatch in plumage coloration due to late snowfall could lead to a higher vulnerability in this part of the year. Ptarmigan can likely cope with potential mismatch, at least to a certain degree, with behavioral mechanisms such as plumage maintenance (Montgomerie et al. 2001), and by selective use of different microhabitats (Steen et al. 1992). However, as winter moult is mainly triggered by changes in the photoperiod (Höst 1942), it will be increasingly difficult for ptarmigan to forecast such changing and variable weather events precisely and consequently respond by behavioural mechanisms. The impact of mismatched plumage coloration on the dynamics of ptarmigan populations is likely to depend on food web structure and in particular on the relative abundance of different predator guilds (Fig. 1). It could be expected to be strongest in food webs with abundant predators that use mainly vision for detecting and pursuing prey; i.e. raptors like the golden eagle and the gyrfalcon. We are not aware of empirical studies that have targeted the issue of plumage coloration mismatch in boreal, alpine and arctic vertebrates beyond those on the snowshoe hare (Mills et al. 2013).

Climate change will likely also induce changed geographic distributions and changed dynamics of parasites and infectious diseases (Lioseau et al. 2012, Harvell et al. 2002, Kutz et al. 2005). Climate warming is expected to lead to expansion of the geographical northern range of parasites, it may modify the timing of parasite life cycles (Kutz et al. 2005) and thereby possibly enhancing transmission and outbreaks (Laaksonen et al. 2010, Loiseau et al. 2012). In particular, new pathogens and parasites arriving from the south may constitute a threat to Arctic and Alpine birds given that they constitute naïve hosts. Transmission, spread and infection by novel pathogens will, however, likely depend on the density of the host populations. Thus colonial species such as seabirds, may be more prone to outbreaks of parasites and diseases than low-density Arctic and Alpine ptarmigan.

Changed food web interactions involving plants

Increased interspecific competition due to facilitated growth of certain species is one of the main hypothesised consequences of climate change (Root and Schneider 2006, Hitch and Leberg 2007). Ptarmigan are herbivorous birds that share food plants with other herbivores, both in the high- and low-Arctic (Fig. 1), thus a potential for intra-guild competition is present. Three cases of increased abundances of competing herbivores may be of concern in the arctic: reindeer, arctic geese and forest insects.

Rock and white-tailed ptarmigan prefer rocky ridges, diversely structured slopes and boulders offering good viewpoints and shelter (Watson 1972, Marti and Bossert 1985, De Juana 1994) where they forage on sparse vegetation composed of dwarf shrubs and herbaceous plants (Savory 1989). In Fennoscandia, the transition zone between the heath and rocky ridges is heavily used by reindeer (Ims et al. 2007), especially when temperatures and insect harassment peak during summer. Consequently, increased competition between reindeer and rock ptarmigan for limited food resources as summer warming increases could potentially be a catalyst for negative impacts on ptarmigan numbers. In winter, competition could intensify when ice-crusts from 'rain-on-snow' events limit the available foraging habitats for both reindeer and rock ptarmigan. Ims et al. (2007) found a negative spatial association between the abundance of reindeer and rock ptarmigan in northern Norway, but were not able to pinpoint the underlying mechanism.

In the high-Arctic, intraguild competition from climate induced increases of pink-footed goose *Anser brachyrhynchus* is more important and a possible threat to the rock ptarmigan. For instance, in Svalbard the populations of pink-footed geese has increased substantially over the last decades, with climate change suggested as one of the major drivers, especially in recent years (Madsen and Williams 2012). Hence, the impact of this rapidly increasing population of pink-footed geese on vegetation, which already is substantial, is a key concern (Madsen and Williams 2012). The necessary condition for competition to take place is that geese and ptarmigan overlap in habitat use, share food plants, and food availability is limited (Van Der Wal et al. 2000). The pink-footed goose share key food plants with the Svalbard rock ptarmigan (Unander et al. 1985, Fox and Bergersen 2005), and it is well known that intensive goose grazing and grubbing may reduce plant biomass, and cause habitat degradation (Speed et al. 2009). Currently these effects are most profound in wetland habitats that are relatively unimportant to the rock ptarmigan, but it is not known to what extent the two species will overlap in habitat use if the geese population continues to grow and/or have depleted their food plants in optimal goose habitats (Jensen et al. 2008). In the Canadian arctic, population declines in ptarmigan (Sandercock et al. 2005) have been attributed to expanding populations and severe habitat destruction impacts from snow geese *Anser caerulescens*, which substantiate the possibility that a similar situation may develop in Svalbard and elsewhere with increasing populations of geese.

Model-based projections of vegetation responses to climate change in boreal, arctic and alpine ecosystems yields positive plant growth effects (Xu et al. 2013), in particular of shrubs in tundra, which is now confirmed by many empirical observations (Myers-Smith et al. 2015). In turn, this may be expected to increase the habitats for shrub-dependent species like the willow ptarmigan. However, the most recent remote

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sensing based studies have shown surprising recent declines in the biomass in arctic tundra – so-called "tundra browning" (Epstein et al. 2015). In northernmost Fennoscandia, large tracts of sub-arctic birch forest, including the sensitive tundra–forest ecotone, have been transformed by outbreaks of temperature sensitive forest pest insects (Jepsen et al. 2012). These insect outbreaks have caused a vegetation state shift from dwarf shrubs to a community dominated by graminoids (Karlsen et al. 2013) and with a concurrent shift in the herbivore guild from a dominance of browsers to grazers (Jepsen et al. 2013). Outbreaks of shrub-defoliating insects have also been documented in arctic Greenland (Post and Pedersen 2008). Intensified outbreaks of forest insects, as climate warming intensifies, may constitute a rapid and large negative impact on low- and sub-arctic ptarmigan species, through removal of key food plants. It is important to note that such outbreaks often result from non-linear responses that are hard to predict (Hagen et al. 2008). On the other hand, model-based predictions from many alpine areas have shown that habitat availability is predicted to decline and become increasingly fragmented, especially in summer (Revermann et al. 2012, Jackson et al. 2015). Some studies have already shown elevational shifts in the distribution of Alpine ptarmigan populations leading to a considerable shrinkage in the distributional area (Revermann et al. 2012, Pernollet et al. 2015). Many Alpine populations are thus in danger of being pushed off the mountaintops as available habitat will be confined to increasingly fragmented mountain tops. Hence, Alpine ptarmigan may be especially vulnerable as the spatial climate gradient is much steeper and their distribution is more patchy leading to more fragmentation and edge effects.

Summer food availability has been suggested as a critical factor influencing grouse chick mortality (Ludwig et al. 2010). Ptarmigan might be affected through climate-induced temporal asymmetry between the availability of important food resources and ptarmigan reproduction, a phenomenon called trophic mismatch (cf. Post and Forchhammer 2008) and for which many bird studies have offered illustrative cases (Møller et al. 2010). Young rock and willow ptarmigan chicks typically consume large quantities of invertebrates (Ford et al. 1938, Spidsø 1980, Jørgensen and Schytte Blix 1985, Savory 1989) and newly emerged and highly nutritious reproductive plant parts (Dixon 1927, Choate 1963, Weeden 1969, Savory 1977, Spidsø 1980, Williams et al. 1980, Pullianen and Eskonen 1982) to meet growth and energetic demands. This highlights the potential of chicks to be particularly vulnerable to changes in the phenology of important food resources. A trophic mismatch would depend on the climate sensitivity of bird life-history events and/or food items that are particularly important. In general, graminoids and forbs show greater variability in reproductive phenology than shrubs (Molau et al. 2005). For instance, reproduction in the forb *Bistorta vivipara* (syn. *Polygonum bistortum*), known to be an important food item for ptarmigan (Unander et al. 1985), has been found to fail in the warmer parts of its distributional range (Doak and Morris 2010). On the other hand, Williams et al. (1980) found in a study from Alaska that willow ptarmigan chicks can alter food preferences in consecutive years. Thus, as willow and rock ptarmigan seem capable of switching between different food sources depending on their availability (Spidsø 1980, Williams et al. 1980), phenological mismatch may not constitute the most imminent threat to ptarmigan, at least in low-arctic habitats.

In contrast, in the high-Arctic, with its less diverse plant communities and limited access to above-ground macroinvertebrates, alternative food resources may be less available to ptarmigan chicks. Consequently, the Svalbard rock ptarmigan has a highly specialised diet during the early chick stage (Unander et al. 1985), where newly hatched chicks almost entirely feed on protein-rich bulbils of *B. vivipara* (Unander et al. 1985). Hence, this arctic endemic rock ptarmigan may be more prone to trophic mismatch than ptarmigan in the low-Arctic. Reported egglaying dates in Svalbard span a limited range, coinciding with ambient temperatures above freezing (Steen and Unander 1985). The phenotypic plasticity in time of egglying is likely to be limited by a genetically determined photoperiodic effect on gonadal development (Stokkan et al. 1986), which suggests that the high-arctic Svalbard rock ptarmigan may be vulnerable to rapid changes in climate that affect the phenology of its key food plants. With climate warming, soil temperature and soil nutrient availability likely increase in most habitats (Sjögersten et al. 2008). Hence, one might expect increased bulbil production. However, the amount of energy allocated to flower production rather than bulbil production has also been shown to increase with temperature along both altitudinal and latitudinal gradients (Bauert 1993, Fan and Yang 2009). Thus, climate warming may result in less bulbil production and higher seed production, with seeds available later in the growing season than bulbils, and thereby reducing food availability for chicks. The highly specialised diet of the Svalbard rock ptarmigan and the simplicity of the food web (Ims et al. 2013a, 2014) makes this ptarmigan species an interesting case for studying the possibility that arctic ptarmigan populations may be impacted by climate change though a trophic mismatch.

Direct climate effects: adverse effect of weather

Young chicks of ptarmigan are highly sensitive to adverse conditions, and survival of chicks through the first few weeks is a critical component of the demography in grouse and ptarmigan populations (Hannon and Martin 2006, Ludwig et al. 2006). Adverse weather conditions shortly after hatching has been shown to be detrimental for chick survival (Erikstad and Spidsø 1982, Erikstad and Andersen 1983, Steen and Unander 1985, Ludwig et al. 2006, Novoa et al. 2008, Kobayashi and Nakamura 2013). If climate change involves an increased frequency of extreme weather events such as heavy rain or drought during this critical life stage, it may represent a strong direct impact on arctic ptarmigan populations.

As ptarmigan are adapted to the harsh and cold environments of the arctic and high-alpine areas (Martin 2001, Martin and Wiebe 2004), increasing temperatures in spring and summer could be unfavourable. While several studies have found a positive effect of advanced snowmelt on ptarmigan reproductive success (Novoa et al. 2008, Imperio et al. 2013, García-González et al. 2016), some studies have indicated potential negative effects of

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increased temperatures during the summer season (Imperio et al. 2013). Revermann et al. (2012) found, in a study of rock ptarmigan in the Swiss Alps, that areas with lower temperatures and higher amounts of precipitation in July represented more suitable habitats. Hence, because of their adaptation to cold environments, ptarmigan might have temperature constraints with regard to their ability to dissipate body heat. According to the "heat dissipation hypothesis" (cf. Speakman and Król 2010), endothermic animals might be limited by their ability to dissipate body heat rather than by the competition for a limited energy supply. Hence, ptarmigan species may therefore be favoured by an early snowmelt, likely mediated by early plant growth and thereby foraging conditions before egglaying (Watson et al. 1998, Høye et al. 2007), but simultaneously negatively affected by high summer temperatures, mediated through hyperthermia, despite the potential increased resource availability in warmer years.

Perspectives for ptarmigan research in the age of rapid climate change

Human impacts on the planet, including anthropogenic climate change, affect arctic and alpine tundra ecosystem structure and functioning in unprecedented ways (Ims et al. 2013a). If we are to meet the challenge of conserving biodiversity and ecosystem integrity in a rapidly changing world, we must understand how species and communities and their food web interactions respond to novel conditions (Post et al. 2009a). In the Arctic and in alpine environments this is especially pressing, as the rate of warming in regions at high altitudes and latitudes has been much higher than the global average (Brunetti et al. 2009, Ims et al. 2013a), and consequently some of the largest ecological impacts of climate warming are documented in the Arctic (Post et al. 2009b). In this paper, we have shown that arctic and alpine ptarmigan potentially face a multitude of challenges that involves both direct and complex indirect bottom–up and top–down trophic interactions, mediated through changes in predation pressure, vegetation and competition from other herbivores. We have argued that the nature of these impacts will depend on the food web setting of the different ptarmigan populations because arctic and alpine food webs differ much, depending on biogeography and bio-climate. Hence, we suggest that ptarmigan research in light of climate change requires a food web approach, which currently lacks almost entirely in the mainstream studies of ptarmigan, but also generally in birds as noted by Møller et al. (2010). A food web approach has several advantages. Academically, it provides a structured framework for simultaneously assessing alternative hypothesis and the partial strength of multiple impacts. This approach is also management relevant. For instance, some detrimental food web interactions resulting from climate change (i.e. invasive predators–native prey interaction) can be subjected to management interventions. Moreover, knowing that low-density and/or declining ptarmigan populations are subjected to enhanced top–down control due to dampened populations cycles of key-stone

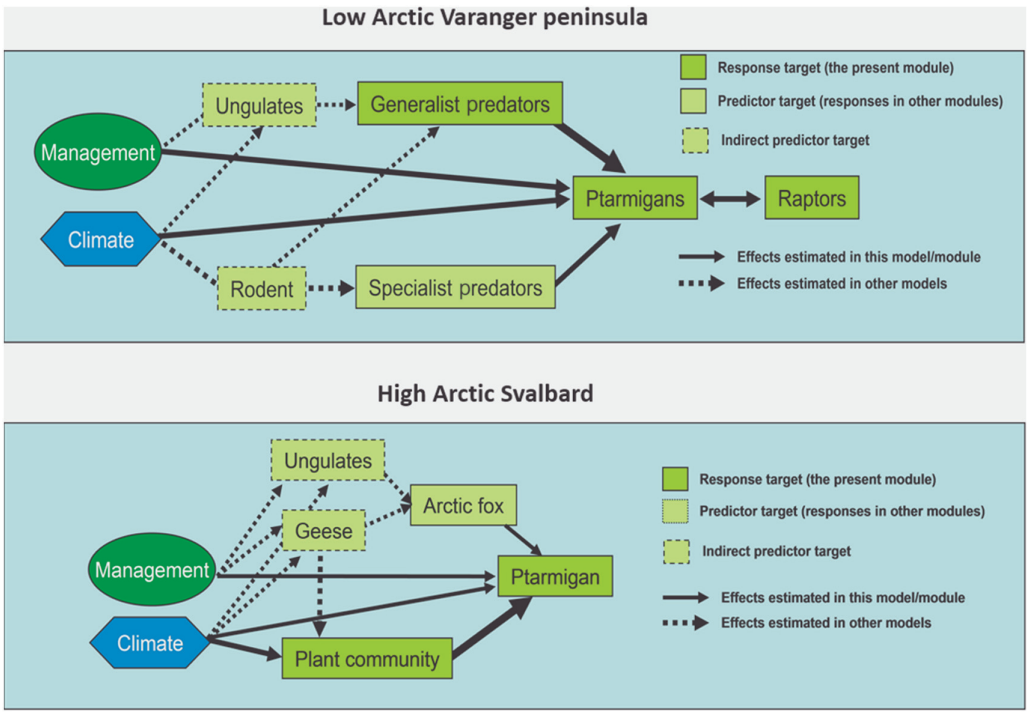

Figure 2. Conceptual 'path' models for the expected effects of climate and climate change on ptarmigan populations in the Low Arctic Varanger peninsula and High Arctic Svalbard. The two 'climate-effect-chain' models are taken from the ptarmigan module in the COAT monitoring science plan (Ims et al. 2013c, COAT Science Plan), depicting the most likely climate sensitive aspects for ptarmigan in each food web setting (Fig. 1), based on the current knowledge of the systems. Also highlighted is how management actions can be implemented to buffer unwarranted effects. Note that the COAT monitoring program consists of eight monitoring modules. Hence, in the 'path' models for ptarmigan, the Predictor targets and Indirect predictor targets represents Response targets in other modules.

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mammal herbivores, is useful for devising sustainable harvesting strategies. This is because harvest mortality is likely to be additive under such circumstances.

We advocate that ptarmigan researchers should team up with specialists on other taxa in order to adopt a food web approach to their research. A necessary and productive start is to outline the food web for the system under study, centred around the species in focus; e.g. as (cf. Krebs 2012) did for boreal snowshoe hare and arctic lemming in Canada, and as we have here done for ptarmigan at our two study sites in the Norwegian arctic (Fig. 1). A next step could then be to develop a conceptual model that specify the pathways for how climate is most likely to affect the focal ptarmigan populations. Figure 2 outlines such 'climate impact path models' for ptarmigan in the two food webs depicted in Fig. 1. These models were developed in collaboration with 20 colleagues within the Norwegian COAT initiative (Climate-ecological Observatory for Arctic Tundra; Ims et al. 2013c). The conceptual models reflect what our team assessed to be the most rapid and imminent threats to ptarmigan at the two sites. Specifically, for the low-Arctic food web on Varanger Peninsula an enhanced top–down impact from the functionally diverse community of predators, under a dampened small rodent cycle and increased abundance of carrion from reindeer, was assessed to be more important than any climate-induced changes in the plant community. In contrast, bottom–up impact from food plants was assessed to be important for the high-Arctic Svalbard food web through an increased potential for phenological mismatch and intensified competition with increasing populations of geese.

The developments of such conceptual models is beneficial in several respects (cf. Lindenmayer and Likens 2010). 1) It forces researchers to delimit the general scope of their future research based on the current knowledge of the system. 2) It demands that priorities are made on the most likely hypotheses among many possible. 3) It helps to highlight critical components and links in the food web that presently misses data essential for empirical testing or that require theoretical modelling for checking assumptions. 4) Simplified food web diagrams (Fig. 1) and conceptual climate impact models (Fig. 2) provides, in our experience, a very structured way to communicate knowledge and ideas among researchers and between researchers and managers. Concerning the last point, we believe that our approach can facilitate important comparative studies across the arctic and alpine biomes that can allow insights into how climate shapes the current dynamics and future fate of ptarmigan in a rapidly warming world.

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