

Climate Events Drive the Dynamics of a Resident Vertebrate Community in the High Arctic

B. B. Hansen,^{1†‡} V. Grøtan,^{1†} R. Aanes,^{1,2*} B.-E. Sæther,¹ A. Stien,³ E. Fuglei,² R. A. Ims,⁴ N. G. Yoccoz,⁴ Å. Ø. Pedersen²

¹Centre for Conservation Biology, Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway. ²Norwegian Polar Institute, Fram Centre, NO-9296 Tromsø, Norway. ³Norwegian Institute for Nature Research, Fram Centre, NO-9296 Tromsø, Norway. ⁴Department of Arctic and Marine Biology, University of Tromsø, NO-9037 Tromsø, Norway.

*Present address: Norwegian Directorate for Nature Management, Tungasletta 2, NO-7047 Trondheim, Norway.

†These authors contributed equally to this work.

‡To whom correspondence should be addressed. E-mail: brage.b.hansen@ntnu.no

Recently accumulated evidence has documented a climate impact on the demography and dynamics of single species, yet the impact at the community level is poorly understood. Here, we show that in Svalbard in the high Arctic, extreme weather events synchronize population fluctuations across an entire community of resident vertebrate herbivores and cause lagged correlations with the secondary consumer, the arctic fox. This synchronization is mainly driven by heavy rain on snow that encapsulates the vegetation in ice and blocks winter forage availability for herbivores. Thus, indirect and bottom-up climate forcing drives the population dynamics across all overwintering vertebrates. Icing is predicted to become more frequent in the circumpolar Arctic and may therefore strongly affect terrestrial ecosystem characteristics.

In the Arctic, climate is now changing rapidly (1), affecting the population dynamics of many species, as well as trophic interactions among them (2). It is well recognized (3) that spatial correlations in climate can enforce synchronous fluctuations among populations within the same species [the “Moran effect” (4)]—increasing the likelihood of species extinctions (5, 6). More far-reaching consequences may be expected if such climate-enforced synchronization acts on the level of ecological communities (7, 8). However, linking cross-species synchrony to common environmental drivers has proven difficult as variation among species in the form of density regulation and response to other environmental drivers often has a desynchronizing effect (9). Thus, observed synchrony usually results from trophic interactions, such as the co-fluctuations among predators because of shared prey (3). Nonetheless, one rare example of vertebrates that fluctuate synchronously but are not linked by trophic interactions comes from the Arctic, where populations of caribou (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) on opposite coasts of Greenland seem synchronized by large-scale weather oscillations (7), but see (10).

Here, we ask how weather events influence population dynamics across the entire overwintering vertebrate community on the high-arctic island of Spitsbergen, Svalbard

(Fig. 1 and fig. S1). In winter, this trophic system at 78°N includes only three herbivores, the wild Svalbard reindeer (*R. t. platyrhynchus*), Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and sibling vole (*Microtus levis*), as well as their shared consumer, the arctic fox (*Vulpes lagopus*). The species are sympatric and widely distributed across the archipelago, except for the vole, which is only found in a small bird cliff area (11). In the short summer season, migratory birds including seabirds, geese, and waders also breed in Svalbard, and polar bears (*Ursus maritimus*) occasionally go on shore throughout the year. However, the few resident terrestrial vertebrates and the lack of widespread endemic arctic rodents with multiannual population cycles, such as arctic lemmings (*Lemmus* spp. and *Dicrostonyx* spp.), makes the Svalbard terrestrial food web and its trophic dynamics simpler than many other high-arctic ecosystems (12).

We found correlated population fluctuations across all four overwintering members of the community (Fig. 1), specifically the presence of positive interspecific correlations in the annual changes in population sizes or population indexes (13) when the arctic fox data were advanced by 1 year (Figs. 2B and 3). One plausible hypothesis explaining this synchrony is that climate influences the herbivores in a broadly similar way because of common effects on plant availability, operating through variation in snowpack properties or vegetation growth. This generates bottom-up effects on their shared consumer. To test this, we fitted linear regressions (13) that modeled population growth rate as a function of log population size (or index) and weather covariates obtained from a local weather station that were expected to influence the herbivore food supply.

Model selection (table S1) suggested that, after accounting for density dependence, the number of rainy days in winter (hereafter, “winter rain”) (Fig. 2A) was the best predictor of annual population growth rates across species. Winter rain had a significantly negative effect on all species (tables S2 to S5). Model selection also revealed an additional positive effect of summer temperature on the species’ growth rates. We evaluated the synchronizing effect of climate by testing whether estimates of the among-species correlation in model residuals were reduced when compared with estimates from a model including only effects of density dependence (14). The correlation in model residuals was lower for all species pairs (Fig. 3) and, on average, was significantly reduced (mean $r = 0.10$ versus $r = 0.43$; Fig. 4) when we included winter rain and summer temperature as predictor variables (Fig. 2, C and D). As hypothesized, this suggests that climate enforces the synchrony among the herbivores and induces lagged fox-herbivore correlations through changes in abundance of prey and reindeer carrion.

Fluctuations in summer and winter climate can influence the herbivores’ food supply directly and indirectly, respectively. First, at these latitudes, even a slight increase in summer temperature increases the green biomass available for herbivores (15). Second, there is emerging evidence that warmer and rainier winters can generate a similar negative response in many northern populations of small (16–18) and large herbivores (19–21) owing to changes in snowpack characteristics. Warm spells and rain generate crust-ice layers through thaw-freezing cycles, and heavy rain may percolate through the entire snowpack and cause ground icing (19, 22). A thick ice layer can build up on the deeply frozen ground and encapsulate most of the short-growing vegetation on the high-arctic

tundra (19). Previous studies of other populations of Svalbard reindeer have shown that extreme winter rain (many rainy days) and associated icing dramatically suppress food accessibility (19) and contribute significantly to the population dynamics (19, 21) by simultaneously reducing survival (causing mass mortality in calves and old animals) (21) and fecundity (21, 23). Rain-on-snow and icing events also have a negative effect on the sibling voles (11), and their fluctuations in abundance therefore follow changes in local reindeer fecundity (23). Our analyses demonstrate that particularly rainy (≥ 4 rainy days) (Fig. 2A) and, hence, icy winters generate simultaneous population crashes in all overwintering herbivores. This drives them into 2 years or more of synchronous fluctuations, as the decline is followed by an increase because of reduced food competition and, in the case of vole and ptarmigan, possibly reduced predation pressure. The dynamics of the herbivores may subsequently diverge because of contrasting density regulation and other environmental drivers (9) and then be forced back into synchronous decline with the next icing event. None of the herbivores seem able to recover during the summer following icing. This is due to low fecundity in reindeer (23) and, most likely, few breeding voles (11) and ptarmigans (for which springtime body condition also affects fecundity) (24). The vole and ptarmigan may also be subject to a top-down effect of fox predation. Accordingly, climate drives the herbivore synchrony, but the mechanisms can differ among species.

A lagged correlation is not uncommon for fox-prey population abundance dynamics (12). In the lemming-free Svalbard ecosystem, foxes are not functional predators of reindeer, and the fox population abundance is most likely related to the availability of reindeer carrion (25, 26)—the most important terrestrial food at the onset of fox breeding. More important, a rainy and icy winter with excess of carrion is likely to be followed by a winter with distinct scarcity of carrion (table S6). This occurs because high mortality of calves and old individuals in the icy winter and low subsequent calf production result in a low-density population with reduced food competition and predominantly high-quality individuals entering the next winter (21, 23). The combination of these highs and subsequent lows in carrion availability influences the fox growth rate (table S7 and fig. S2) and is most likely the mechanism that forces the observed dynamics of reindeer and foxes into lagged correlations. The icy conditions that cause these correlated population fluctuations have been frequent in Svalbard since the mid 1990s, i.e., during most of our study period, because of high temperatures and frequent rain on snow (19). If, however, icing occurs even more frequently, a different pattern of co-fluctuations may emerge because consecutive severe winters would cause less distinct ups and downs in carrion.

This study has demonstrated cross-species synchronization of population dynamics by climate that operates among unrelated species (3) with different patterns of density regulation (9) and a large variation in life-history strategies, ranging from the slow (reindeer) to the very fast (vole) (11) end of the life-history continuum (27). The Svalbard tundra is characterized by few species, a lack of specialist predators, and multiannual predator-prey cycles. This eliminates the potential for trophic interactions to cause synchrony (3, 28, 29) and obscure synchronizing effects of climate. Although not shown previously, in such a simple ecosystem it may not be surprising that climate-induced vegetation “blocking” generates a trophic effect on all primary consumers that wells up to the secondary consumer. It thus appears that rapid responses to environmental change are

particularly pronounced in arctic herbivores. Svalbard is characterized by large weather fluctuations and has been considered an “early warning” system (30) for the projected increase in extreme events and rainfall during winter across the Arctic (1). As demonstrated here, such extreme events may have broad ecological implications (2). Warmer and rainier winters may already have contributed to dampened fluctuations in many rodent populations (16, 18) and the decline in many caribou and reindeer populations in the northern hemisphere (31). Such changes are, in turn, expected to influence other ecosystem components (17, 32), as shown here. The present study therefore represents a bellwether of how future changes in climate and extreme events during winter may contribute to shape ecosystem functioning and stability in the terrestrial Arctic.

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Supplementary Materials

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Materials and Methods

Figs. S1 and S2

Tables S1 to S8

References (33, 34)

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Fig. 1. The study system in high-arctic Svalbard. Annual population abundances (or indexes) are shown for the overwintering vertebrates: (A) wild reindeer, (B) rock ptarmigan, (C) sibling vole, and (D) arctic fox (advanced by 1 year).

Fig. 2. Annual fluctuations in weather and population parameters for the vertebrates overwintering in Svalbard. (A) Weather variables acting as synchronizing agents across

species, i.e., total number of rainy days during the core winter season [December year (t) through March year ($t + 1$), bars] and mean temperature in summer [July–August year (t), solid line]. **(B)** Standardized population growth rates ($\log[N_{t+1}] - \log[N_t]$) of sibling vole (purple), wild reindeer (red), rock ptarmigan (orange), and arctic fox (blue; advanced by 1 year). **(C and D)** Residuals from linear models of population growth rates when including **(C)** only density versus **(D)** density and weather variables as covariates.

Fig. 3. Pairwise correlations in population parameters between the vertebrates overwintering in Svalbard. Correlation coefficients are given for population growth rates (r_1) and residuals from linear models of population growth rates when including density (r_2) versus including density and climate (r_3), i.e., winter rain and summer temperature, as covariates. Note that the fox data were advanced by 1 year.

Fig. 4. Effect of climate (winter rain and summer temperature) on population synchrony. **(A)** Simulated mean between-species correlations in residuals from linear models of population growth rates including only density (light gray bars) versus including density and weather (dark gray bars). **(B)** Difference in between-species correlations in model residuals when excluding versus including weather (median difference = -0.334 , 5th percentile = -0.614 , 95th percentile = -0.025). Note that the fox data were advanced by 1 year.