Reproductive phenology in terrestrial ecosystems

The timing of reproduction in plants and animals, also termed ‘reproductive phenology’, is probably the most frequently reported indicator of a species response to climate change and possibly one of the most sensitive. Along with the growing awareness of climate change, shifts in species phenology have been reported from the Arctic [1] and most other biomes globally [2]. Most Arctic species breed during the short summer, and they face the double challenge of avoiding severe weather during spring while ensuring sufficient time for offspring growth and development. Different reproductive strategies explain why, for instance, musk oxen, *Ovibos moschatus*, give birth long before the spring thaw, while the hatching of eggs of migratory birds like the ruddy turnstone, *Arenaria interpres*, takes place during the peak of summer. Musk oxen are able to provide their young with milk during late winter even with limited access to forage, while migratory shorebirds need to build up body reserves for egg formation after their arrival on Arctic breeding grounds. Yet, the short Arctic summer poses a constraint on successful breeding in most species, and changes to the duration of the breeding season can be expected to have profound consequences for the production of offspring and survival.
Despite the current focus on global climate change, the number of studies on trends in Arctic reproductive phenology is very limited. This was evident in a recent analysis where very few relevant studies were identified north of 60°N [3]. There are some examples of phenological recordings that have been made over extended time periods but there are no explicit attempts to quantify the rates of change [4, 5]. Logistical challenges and funding constraints associated with maintaining long-term monitoring in the Arctic have no doubt contributed to the scarcity of data sets.

It is clear from lower latitudes that phenological trends are linked to temperature changes [6] and experimental warming also results in earlier plant phenology [7]. Yet, in Arctic and alpine ecosystems, the melting of the winter snow pack rather than temperature per se determines the onset of biological activity like the timing of flowering in plants and emergence in invertebrates [8–10]. As such, the phenology of these groups of organisms, or taxa, could be advancing considerably in response to earlier snowmelt. In fact, in a study covering a range of taxa carried out at Zackenberg Research Station in Northeast Greenland, the phenology of these groups of organisms, or taxa, could be advancing considerably in response to earlier snowmelt. In fact, in a study covering a range of taxa carried out at Zackenberg Research Station in Northeast Greenland (adapted from [11]). The species in the photos are: (C) Arctic fritillary, *Boloria chariclea*, (D) eggs of ruddy turnstone, *Arenaria interpres*, and (E) purple saxifrage, *Saxifraga oppositifolia*.
Greenland, it was found that not only is reproductive phenology showing stronger trends in the Arctic than elsewhere, trends were also stronger the later, on average, that an event (e.g., flowering in plants, emergence in arthropods, and egg-laying in birds) took place during the season [11] (Figure 12.1). There are clearly limits to such phenological flexibility. In a situation with extreme changes to the physical environment, the timing of reproductive phenology may be more influenced by other cues like day length.

The timing of reproductive phenology in birds and mammals may respond to changes in food availability as well as to changes in the abiotic environment [12, 13]. Calf production in muskox populations in West and East Greenland benefit from earlier plant phenology when accounting for variation in winter harshness [14]. In migratory species like the ruddy turnstone, however, the timing of producing offspring at breeding areas is dependent upon the timing of migration away from wintering areas, which is likely triggered by day length and so may not be a good predictor of conditions at breeding areas [15, 16]. This can have consequences for reproductive success and predation rates in situations where predators are also migrating [17].

It appears that Arctic species of plants and invertebrates exhibit considerable flexibility in their reproductive phenology. Individual plants can change their date of flowering by several weeks between years. This is particularly evident in species inhabiting areas with extensive snow cover. In mountain avens, *Dryas octopetala*, for instance, late-flowering individuals (i.e., those in late snow-free microhabitats) show more year-to-year variation in timing of flowering than early-flowering individuals (i.e., those in early snow-free microhabitats) of the same species [9]. Although the evidence is sparse, there are indications that Arctic birds and mammals are less responsive in their reproductive phenology, and their migration and breeding strategies may explain why this is the case [11].

**Concerns for the future**

As stated above, variation in the timing of snowmelt in time and space has a strong influence on variation in phenological events of plants and insects in the Arctic. At Zackenberg, warmer temperatures have resulted in markedly earlier snowmelt despite no trend across years in the thickness of the end-of-winter snowpack. Across the entire Northern Hemisphere, the extent of snow cover during spring and summer is rapidly declining suggesting that a strong shift in the reproductive phenology of these taxa is a circum-Arctic phenomenon [1]. The reproductive phenology of birds and mammals appears to be less responsive to changes in the physical environment but a conclusive comparison among taxa is hampered by the scarcity of data. Importantly, responsiveness can be either advantageous or disadvantageous and lack of responsiveness should not be confused with lack of flexibility.

The effect of climate change on the population dynamics of plants and animals can be both beneficial and detrimental. Longer growing seasons may allow more southern species to invade Arctic ecosystems, but could also be advantageous in terms of growth and reproduction for Arctic species. One of the serious risks, however, is the disruption of food webs due to differing phenological responses among trophic levels resulting in a so-called trophic mismatch. The timing of calving in caribou in West Greenland, for example, varies little among years despite pronounced advancements of the plant growing season there. In years where calving is mistimed to the emergence of plant forage, calf production and survival are lower [15]. Indications of a similar trophic mismatch has been reported for greater snow geese, *Chen caerulescens atlantica*, in the Canadian Arctic, suggesting that this could be a geographically and taxonomically widespread phenomenon [18]. Our ability to understand whether trophic mismatch or other effects of changes to reproductive phenology will put species and populations at risk, hinges upon a continued effort to gather long-term data from the rapidly changing Arctic.