Colonization of the arctic archipelago Svalbard

We have more knowledge on colonization to the Arctic Archipelago of Svalbard than to any other arctic region. Previous analyses include the only native terrestrial mammals, reindeer (Flagstad and Røed 2003) and arctic fox (Dalen et al. 2005), the only fresh water fish, arctic charr (Brunner et al. 2001), several Daphnia species (Weider et al. 1999), the moth Plutella xylostella (Coulson et al. 2002), and many vascular plant species (Brochmann et al. 2003, Alsos et al. 2007). Recently, also the colonization routes for the only resident terrestrial bird, the Svalbard rock ptarmigan (Lagopus muta ssp. Hyperborea, Figure 1) have been analysed (Sahlman et al. 2009).

Svalbard represents an ideal model system for studying colonization for several reasons. It was almost entirely glaciated during the last glacial maximum 20,000 years before the present (Landvik et al. 1998, Landvik et al. 2003) and thus glacial survival can mainly be ruled out as explanation for the presence of species. Fossil evidence indicates sparse arctic vegetation from 10,000 years B.P. (Birks et al. 1994), which thus gives the maximum time frame for colonization events. It is geographically isolated, and the distances to nearest lands are 470 km to northeast Greenland, 650 km to N Norway, 870 km to Novaya Zemlya, and 240 km to the high arctic archipelago Frans Josef Land.

The Svalbard rock ptarmigan, L. muta ssp. hyperborea, is restricted to Svalbard and Frans Josef Land. It belongs to the large rock ptarmigan species complex (Lagopus muta) which originated in Beringia (Lucchini et al. 2001), and now consists of up to 30 different subspecies which are found throughout the circumpolar region as well as in many temperate alpine regions (Storch 2007). The Svalbard rock ptarmigan is commonly seen from March to October, but it is a puzzle where they spend the winter, as the dark polar night makes visual observations difficult. Rock ptarmigan in other regions have seasonal migrations of up to 500 km (arctic Russia) or 1,000 km (coastal Greenland). It is assumed that Svalbard rock ptarmigans stay in Svalbard during winter, possibly

Figure 1. The Svalbard rock ptarmigan (Lagopus mutus ssp. hyperboreus) colonized Svalbard from Russia or Greenland according to a recent study (Sahlman et al. 2009). Photo: Bjørn Erik Sandbakk.
feeding below the bird cliffs (Kovacs and Lydersen 2006). However, it has also been claimed that they migrate and, recently, satellite transmitters have been fitted to eight individuals in order to elucidate this question (http://svalbardtype.npolar.no/en/index.html).

In their paper titled ‘Island in the ice: colonization routes for rock ptarmigan to the Svalbard archipelago’, Sahlman, Segelbacher and Höglund (2009) present molecular data on rock ptarmigan, having genotyped populations from Svalbard, W Greenland, Iceland, Scandinavia and Taymyr for 12 microsatellite loci. In addition, they sequenced the mitochondrial control region (mtCR). The sequences represent a nice expansion of previous studies mainly from the Nearctic and the Bering region e.g. (Holder et al. 1999, Holder et al. 2004), and the sequences were aligned with all previously identified sequences available in Genebank. They thereby fill in a gap in the circumpolar phylogeography of rock ptarmigans.

On a circumpolar scale, populations from Svalbard, Taymyr and W Greenland were closely related to other arctic populations, whereas populations in Scandinavia and the Pyrenees are most differentiated from all other populations. The Scandinavian populations were also differentiated from the arctic populations based on the microsatellite data. Thus, Scandinavia could be ruled out as a source region for Svalbard rock ptarmigan (Sahlman et al. 2009). It is striking how few of the species analysed so far show a colonization route from Scandinavia to Svalbard (Brochmann et al. 2003, Alsos et al. 2007), suggesting that the open ocean between these regions constitutes a larger dispersal barrier than the sea-ice covered oceans between Svalbard, NW Greenland and Russia, although the distance to Russia is longer. This emphasizes that we should be cautious with assuming a northward migration due to current climate warming. One has to look for both likely dispersal barriers and dispersal bridges, as this might strongly modify the migratory route of the species.

It remains uncertain whether rock ptarmigan colonized Svalbard from east or west, but as Svalbard and Taymyr populations had one haplotype in common, an eastern colonization route is slightly more likely (Sahlman et al. 2009). These colonization routes are not mutually exclusive as, for example, has been shown for several plant species that most likely colonized Svalbard from several source areas (Alsos et al. 2007). To answer this question for Svalbard rock ptarmigan, samples from East Greenland should be included, as different subspecies have been found in different parts of Greenland (Holder et al. 2004). Also, more and better quality samples are needed from northwestern Russia. For all studies addressing the phylogeography of arctic species, it is a challenge to obtain good samples from Russia. The feather obtained from Taymyr by Sahlman et al. (2009) gave poor genotyping success. This is a pity, as this turned out to be the most likely source area. More predictable condition for field work in Russia as well as easier transfer of samples would not only greatly improve our knowledge on the Russian part of the arctic, but also shed more light on the biogeography, ecology and systematics of the arctic region in general.

The most common haplotype found in Svalbard rock ptarmigan was also the most widespread one, and it was placed in the center of the haplotype network. This is a striking similarity to what has been observed in the circumpolar bird-dispersed species *Vaccinium uliginosum* (Alsos et al. 2005, Eidesen et al. 2007). In the purple saxifrage, *Saxifraga oppositifolia*, too, only the most widespread haplotypes were found in Svalbard (Abbott et al. 2000). A possible explanation for this is that Svalbard was colonized from long distance, and just by chance the most frequent haplotypes are most likely to survive and establish a local population.

Both the sequence data and the microsatellite data showed lower levels of genetic diversity in Svalbard than in other regions. This suggests that a strong genetic bottleneck has occurred in the past (Sahlman et al. 2009). In arctic vascular plants, a similar bottleneck is seen in rather therophilous species but not in species well adapted to the local climate conditions (Alsos et al. 2007). Whether the bottleneck occurred during colonization, or was due to some other processes later on, is unknown. Even though hunting pressure has been extreme for other Svalbard animals, and has almost lead to their extinction, the Svalbard rock ptarmigan most probably has not been hunted that much (Løvenskiold 1964).

Based on the accumulating phylogeographical studies of arctic species, there is a good potential to study immigration routes also to other arctic and subarctic archipelagoes. Especially good datasets exist for the North Atlantic regions,
where meta-analyses of existing data could indicate migration routes to Iceland and Greenland. For rock ptarmigan, additional samples from east Greenland would be needed to answer this question. The data also allows exploring for differences in colonization routes for different functional groups. For example, while birds might disperse plants, the presence of plants might determine if any occasional dispersed birds will survive and be able to establish a population. Thus, having data on many different organisms, as we are now compiling for Svalbard, will open up new research perspectives.

References

Inger Greve Alsos
The University Centre in Svalbard, Norway
e-mail: ingera@unis.no
http://www.unis.no/

Edited by Spyros Sfenthourakis