

## Is the glacial refugium concept relevant for northern species? A comment on Pruett and Winker 2005

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Pruett and Winker (2005) recently published a phylogeographic study of the rock sandpiper (*Calidris ptilocnemis*) in Beringia. They found that the species was variable with partitioned genetic diversity which did not, however, reflect the different subspecies that have been described. They concluded that this diversity had evolved in multiple refugia in Beringia and that these refugia were in operation during the last glaciation or between 117,000 and 10,000 years BP. Other authors have also published interpretations of phylogeographies of taxa today restricted to high-latitude areas concluding that glacial refugia are likely to have existed (Tremblay and Schoen 1999; Holder et al. 1999; Fedorov and Stenseth 2002; Loehr et al. 2006; Anderson et al. 2006). However, these studies would benefit from an alternative interpretative perspective.

The traditional view of refugia in non-tropical areas focuses on temperate taxa during glacial stages where populations are believed to have been pushed away from the cold into southern refugia (Hewitt 1996, 1999, 2000; Taberlet et al. 1998). This has recently been questioned as incomplete with a suggestion that cryptic northern refugia had supplemented the southern ones (Stewart and Lister 2001; Stewart 2003). This cryptic northern refugium hypothesis is finding support in the phylogeographic studies of a whole host of temperate organisms including small mammals (Wójcik et al. 2002; Jaarola and Searle 2003; Deffontaine et al. 2005), ferns (Trewick et al. 2002), sedges (Tyler 2002), snails (Pfenninger et al. 2003; Haase and Bisenberger 2003) and reptiles (Ursenbacher 2006).

However, while it is clear that temperate (mid-latitude) taxa were restricted to refugia of various kinds during glacial phases, taxa found in more northern latitudes today are known to have had greater distributions in the glacial stages (Musil 1985; Faunmap Working Group 1996; Markova et al. 2002; Stewart 2003). This implies that colder adapted species are in more restricted refugia during interglacials, including that of today (the Holocene), and not during glacials (Stewart and Lister 2001; Dalén et al. 2005). This does not

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completely preclude the significance of isolated refugial populations during glacials, and particularly during the maxima of such phases. During the glacial maxima population distributions were probably restricted and discontinuous in more northern latitudes as stated by Pruett and Winker (2005) although it seems clear that for more northern/cold adapted taxa it is the interglacials that cause populations to be most restricted in refugia.

During most of the glacials, as exemplified by the last such period, the Weischelian or Wisconsin glaciation, the climate in the mid to northern latitudes was colder than today but not usually glaciated or devoid of life forms. As already mentioned it was during such times that northern European tundra species like the Norway lemming *Lemmus lemmus*, the reindeer *Rangifer tarandus*, the arctic fox *Alopex lagopus*, the ptarmigans *Lagopus* sp., the dwarf birch *Betula nana* and mountain avens *Dryas octopetala* had larger geographical ranges than in interglacials, including today. The reindeer, for instance, reached as far south as the Cantabrian Mountains in northern Spain during the Late Pleistocene (Musil 1985). A related problem is that the European ice sheets have been recently re-evaluated and most of the time during glacial phases it appears that they were less extensive than previously thought (Arnold et al. 2002). Therefore, it is only during the glacial maxima that the stereotypical “Ice Age” conditions existed and even during such times there was considerable variation through time and space. It is clear that too little attention has been paid in phylogeographic studies to sub-Milankovitch scale climatic variation such as the interstadials or Heinrich events of the last glaciation. Although shorter in duration they were not necessarily less significant in amplitude and are likely to have affected animal distributions quite considerably (Lister 1997). The relatively shorter time spent in isolation during sub-Milankovitch cold events would presumably confer less genetic differentiation.

In the case of the rock sandpiper, a small migratory wader living today in Beringia, there appears to be little of no fossil record for the taxon at lower latitudes during the last glaciation. Despite this lack of evidence for a greater distribution during the last glaciation it would seem very likely that this was the case as seen from the distribution of other northern organisms including a number of birds (Tyrberg 1991). The ptarmigan for instance had a far greater distribution over the mid-latitudes of the last glaciation (Bochenski 1974; Mourer-Chauviré 1979; Tyrberg 1995 and Stewart 1999, 2002 and 2007). In our view, it is therefore not surprising that Pruett and Winker (2005) could not find any support for their hypothesis of a postglacial population expansion.

However, what remains to be demonstrated, or tested, is whether the more southern populations of these taxa, in the glacials have contributed to the genetic make up of modern populations at high latitudes. Stewart et al. (2003) questioned whether it was likely that the arctic fox or Norway lemming populations, present at significantly lower latitudes than today during the late Pleistocene glaciation (the Weischelian), contributed to the genetics of the populations living in Scandinavia today. This is because there were arctic fox and Norway lemming living at Skjonghelleren Cave and Hansundhelleren Cave, both on the Norwegian coast at about 61.8° latitude at around 30,000 years old (Larsen et al. 1987 and Valen et al. 1996). The consensus for the population distribution change involving contraction seems to be that it takes place by the extinction of metapopulations rather than actual movement of individual organisms (Lister 1997). The latter has now been confirmed for arctic fox (Dalén et al. 2007). The geographical expansive phases of populations, on the other hand, take place by leading edge or leptokurtic dispersion (Hewitt 1996).

The consequence of this to the interpretation of Pruett and Winker (2005) is therefore dependent on how the actual process of population contraction towards the present distribution took place. If, as hypothesized by Stewart et al. (2003), cold taxa like the rock sandpiper had more extensive and more southwards extending populations during the last,

and previous, glacials they may have been found in more extensive parts of the North American and Asian continents. The populations seen today are the refugial populations likely to have resulted from a major contraction along the coasts of both continents. From an evolutionary perspective, geographical regions that have been continuously inhabited during both glacials and interglacials are of special importance. These are the “true refugia” where genetic diversity evolves, and between which there is sufficient time for strong population divergence to evolve. In the case of the rock sandpipers, two such regions seem to exist: (1) Kamchatka including the Commander Islands, and (2) St. Matthew Island and the Pribilof Islands. Other regions that rock sandpipers inhabit, or have inhabited, were either not coastal habitats during the last glacial or are today inundated by the sea. It is therefore interesting to note that the two most strongly supported clades in the rock sandpiper phylogeny originate from these two regions.

The aforementioned description of the likely times during which high-latitude organisms are in refugia as opposed to the more commonly discussed or conceived refugia for more temperate taxa is important and has wide ranging implications to the interpretation of phylogeographic studies. There appears to be some confusion among molecular biologists about the ecology of Pleistocene glacials and interglacials and a lack of realisation that glacials are complex episodes with dramatic variations of climate and ice extent. It is also not apparent that there is a clear understanding that species today restricted to high latitudes are in refugia today and not necessarily in the Late Pleistocene. All of this is important because these different types of refugia are operational for different lengths of time, during which populations are in isolation and hence, during which they can accrue genetic differences. This is because glacials last an order of magnitude longer than interglacials.

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