Invited reply

Reply to Wheeldon *et al.* 'Colonization history and ancestry of northeastern coyotes'

The history of hybridization and range change of *Canis* in eastern North America has created an interesting evolutionary story that researchers are still untangling. We welcome the comment by Wheeldon *et al.* (2010) on our study on the evolution of northeastern coyote and the new data they present in their comment and new paper (Way *et al.* 2010). Their comment raises two issues, one taxonomic and one biogeographic. Here we briefly defend our taxonomic treatment of northeastern wolves, and present new data supporting our original biogeographic interpretations.

Wheeldon *et al.* (2010) criticized our decision to refrain from using any formal (binomial) species designation for eastern wolves, choosing instead the geographical descriptor 'Great Lakes Wolf' (GLW). We recognize the ongoing controversy over wolf taxonomy and wished to avoid taking sides on a debate which our data did not directly address. Our data show that northeastern coyotes are the descendants of coyotes that hybridized with wolves, but do not contribute anything new to the understanding of the taxonomy of that wolf. Wheeldon *et al.* erroneously assert that Leonard *et al.* (2008) concluded that the GLW is a distinct species when that study actually made no taxonomic recommendations, and a more detailed follow-up (Koblmüller *et al.* 2009) considered the GLW an ecotype of *Canis lupus*, one of several ecotypes in North America (Munoz-Fuentes *et al.* 2009). Additionally, this diagnosis was based primarily on an analysis of 26 nuclear microsatellite loci, not mtDNA, as suggested by Wheeldon *et al.* The matter is hardly settled regarding the species status of the eastern wolves, but all data suggest that species limits in the genus are fluid in this region and poorly captured by traditional binomial taxonomy.

Wheeldon *et al.* (2010) also state that 'data do not support the proposed route of western coyote colonization into Ontario from Minnesota', and they presented new data which they suggest indicate a southern Ontario origin of hybridization following a colonization through the lower peninsula (LP) of Michigan near Detroit. Their data show that southern Ontario coyotes have hybridized with wolves. However, the presence of hybrids in southern Ontario

today does not bear on the geographic origin of this hybridization event, nor does it favour an immigration route through Detroit compared with a more northern route.

Our initial interpretation that coyotes immigrated into Ontario from Minnesota (MN) was based on a general history of coyotes across the entire region (Parker 1995). To examine the colonization in greater detail we surveyed museum collections for coyote specimens early in their range expansion (before 1940) in the Great Lakes region (figure 1). These records do not support an LP colonization route, but do show that western Ontario and Michigan's upper peninsula (UP) had recorded multiple coyotes by 1940. This suggests early migration through western Ontario and the UP, both of which support our earlier conclusion (Kays *et al.* 2010) that a northern front of hybrid coyotes colonized much more rapidly than non-hybrid animals moving through Ohio.

Wheeldon *et al.* (2010) suggest that coyote colonization could not have started in MN or Western Ontario (WON) on the basis of new data, suggesting that the two coyote-like haplotypes we found in the northeast were not present in MN or WON (Wheeldon *et al.* 2010; figure 1). However, these data were from wolves, not coyotes. Since our paper appeared, we have sequenced the same mtDNA region for 19 coyotes from MN and 18 from Michigan (five UP, 13 LP). The two coyote-like haplotypes characteristic of northeast coyotes (GenBank accession nos.: GQ863718.1 and GQ863719.1) are present in all these populations (MN: 4 cl28 and 2 cl29; UP: 3 cl28; LP: 11 cl28 and 1 cl29), as also noted by Wheeldon (2009). Furthermore, the wolf-like haplotype present in eastern coyotes was found in a wolf collected in Wisconsin near the time of coyote expansion (1908; Wheeldon & White 2009). Thus, all the genetic haplotypes common in eastern coyotes could have originated from this region.

Finally, Wheeldon *et al.* argue against an MN or WON origin for the coyote–wolf hybridization on the basis of recent genetic (Wheeldon 2009) and morphological data (Nowak 2009); once again the papers they cite focus on wolves. In fact, a morphological study that included coyotes from the region did find evidence for hybridization, although not as extreme as we found in northeast coyotes. MN coyotes showed a shift toward a more wolf-like morphology, were intermediate between western coyotes and northeast coyotes in a linear discriminant function, and exhibited greater morphological variation than western coyotes, a characteristic of hybrid populations (Lawrence & Bossert 1969).

Taken together, these studies suggest that hybridization had different impacts on populations of coyotes and wolves. The lack of genetic and morphological signatures in wolf populations noted by Wheeldon *et al.* (2010) suggests that backcrosses of F1 coyote–wolf hybrids with wolves are not as successful as with coyotes. Conversely, the widespread hybrid signatures in the morphology and genetics of coyote populations throughout the northeast and southern Ontario suggests that hybrids backcrossing into the coyote population had offspring that were well adapted to

Figure 1. Coyote specimens recorded in the Great Lakes Region before 1940 suggests their eastward colonization moved along a route through Western Ontario and/or the Upper Peninsula of Michigan. The 311 specimen records come from 11 museums and are mapped per county. Hatching shows the original range of coyotes in western grasslands. Coyote specimens: light grey shading, 1–2; dark grey shading, 3–10; black shading, more than 11.

the human-dominated landscapes common in the region.

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