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Comment

Colonization history and ancestry of northeastern coyotes

Recently Kays *et al.* (2010) reported on mitochondrial DNA (mtDNA) sequence data and skull measurements to demonstrate a hybrid origin for northeastern coyotes. They suggested that, as western coyotes (*Canis latrans*) expanded their range in the last century, they colonized Ontario from Minnesota and hybridized with wolves, and subsequently colonized the northeastern United States via movement across the Saint-Lawrence River. We support the conclusion that northeastern coyotes are derived from wolf–coyote hybridization, and we agree that introduced adaptive variation resulting in larger body size and more wolf-like cranial features probably allowed them to better hunt deer and facilitated their colonization of the northeast. However, data do not support the proposed route of western coyote colonization into Ontario from Minnesota and we criticize their use of the term 'Great Lakes wolf' (GLW) in describing *Canis* species taxonomy. We provide mtDNA data from southern Ontario (SON) coyotes and refer to the literature to demonstrate that the most probable route of western coyote colonization was from the lower Michigan peninsula near Detroit into SON, where hybridization with eastern wolves (*Canis lycaon*) occurred (figure 1).

We observed 10 mtDNA haplotypes in our SON sample ($n = 310$); two were of eastern wolf origin and the other eight were of coyote origin (see the electronic supplementary material, figure S1). The predominant haplotypes were C1, C9 and C19, with other haplotypes observed in low frequency, similar to the haplotype composition reported by Kays *et al.* in the northeast (figure 1; see the electronic

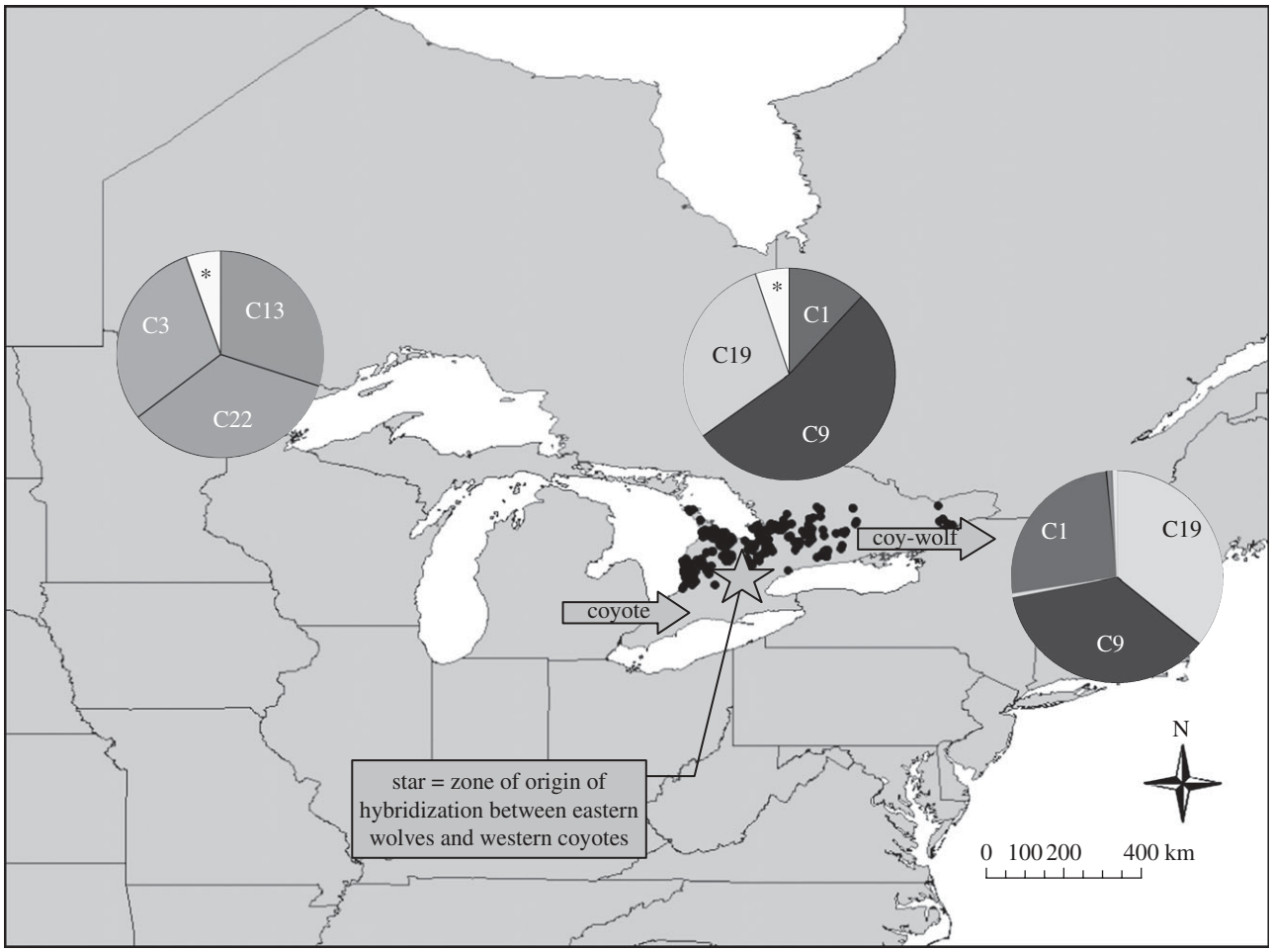

Figure 1. Sampling distribution of southern Ontario coyotes, and mtDNA haplotype frequencies of southern Ontario coyotes ($n = 310$), northeastern coyotes ($n = 453$; modified from Kays *et al.* 2010, fig. 2), and Minnesota/northwestern Ontario wolves ($n = 130$; data from Wheeldon 2009). Asterisk in pie charts indicates combined low frequency haplotypes. Arrows indicate colonization paths.

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supplementary material, table S1). The haplotype composition of Minnesota and northwestern Ontario wolves is different from that of eastern coyotes (figure 1), and there is no morphological or biological evidence to support wolf–coyote hybridization occurring in the western Great Lakes region (Nowak 2009). Eastern wolf–western coyote hybridization has been extensive in SON, supported by genetic (Wilson *et al.* 2009) and morphological data (Sears *et al.* 2003), suggesting it is the probable origin of the wolf–coyote hybrids that colonized the northeast.

Way *et al.* (in press) also presented mtDNA sequences and microsatellite genotype data to demonstrate the hybrid nature of northeastern coyotes (*C. latrans* × *C. lycaon*). They used genetic distance measures to demonstrate the colonization path of 'coywolves' from southeastern Ontario into New York, followed by expansion into the northeast. This independent study confirms the hybrid nature of the animals reported by Kays *et al.* but supports western coyote colonization from the lower Michigan peninsula and hybridization in SON.

The use of the term GLW as a species designation by Kays *et al.* ignores literature on the eastern wolf, and perpetuates confusion over *Canis* taxonomy. Although Leonard & Wayne (2008) presented mtDNA data to demonstrate the GLW was a distinct species, Wheeldon & White (2009) demonstrated that the GLW sequences were similar or identical to those of the eastern wolf. Thus, it is disturbing that Kays *et al.* cite Wheeldon & White (2009) in the sentence preceding their use of the term GLW. In reporting on the same samples as Leonard & Wayne (2008), Koblmuller *et al.* (2009) did not recognize the GLW as a distinct species in their mtDNA phylogeny. This further demonstrates that the term GLW used to describe a phylogenetically distinct mtDNA lineage lacks support and consistency. Additionally, the failure on the part of Koblmuller *et al.* (2009) to distinguish between coyote and eastern wolf lineages obscures the view that western Great Lakes region wolves contain grey and eastern wolf genetic material, and thus are grey–eastern wolf hybrids (*C. lupus* × *lycaon*) and not wolf–coyote hybrids (Wheeldon 2009; Wheeldon & White 2009; Wilson *et al.* 2009). In addition to a more careful analysis of the probable colonization routes of western coyotes into northeastern North America, Kays *et al.* should have considered this alternative hypothesis, which has considerable support in the literature (see Kyle *et al.* 2006).

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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.* (in press) on our study on the evolution of northeastern coyote and the new data they present in their comment and new paper (Way *et al.* in press). 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.* (in press) 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 (Koblmuller *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.* (in press) 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.* (in press) 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.* in press; 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 cla28 and 2 cla29; UP: 3 cla28; LP: 11 cla28 and 1 cal29), 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.* (in press) 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

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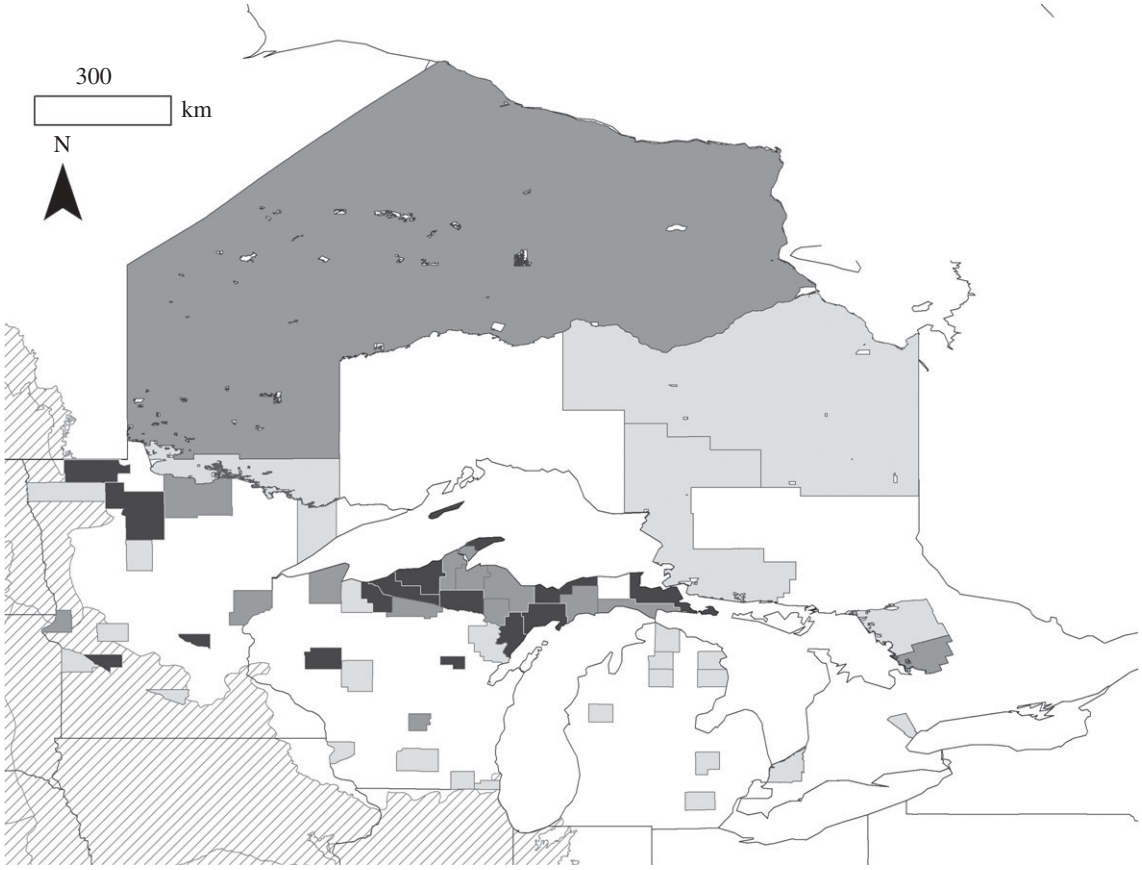

Figure 1. Coyote specimens recorded in the Great Lakes Region before 1940 suggests their eastward colonization moved along a route through Western Ontario and/or the Upper Peninsula of Michigan. The 311 specimen records come from 11 museums and are mapped per county. Hatching shows the original range 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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