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Response

Northeastern coyote cannot be a distinct species without isolation: a response to Way and Lynn

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Article

We strongly oppose the proposal by Way and Lynn (2016) to recognise the coyote (*Canis latrans*) in northeastern North America as a unique species, *Canis oriens*. There is no reproductive isolation from surrounding coyote populations. Genetic data show continued gene flow throughout the eastern half of the continent, and morphological data show a pattern of clinal variation expected for a broad-ranging species.

Although evolutionary biologists argue about exactly what level of differentiation is needed to separate species, there is general agreement that speciation cannot occur without some form of reproductive isolation between populations (Arnold 2015). There are no obvious barriers to dispersal separating coyotes in northeastern North America from surrounding populations, and numerous studies have documented extensive gene flow across broad geographic regions. For example, Monzón et al. (2014) showed the continuity of genetic composition of coyotes from Ohio to Maine. The coyote populations of Virginia and North Carolina descended from multiple sources of colonisation, indicating that admixed hybrids dispersing from the north readily interbreed with another wave of colonising coyotes dispersing from the west (Bohling and Waits 2011, Bozarth et al. 2011). More recently, vonHoldt et al. (2016) suggested that the introgression of wolf genes into coyotes has given them such an evolutionary advantage that the genes rapidly spread from their origin in the Great Lakes as far south as Mississippi. Even the graphs provided as evidence of the genetic distinctiveness of northeastern coyotes (Figures 1c and 1d in Way and Lynn 2016) show contemporary admixture among canid populations in the northeast USA, Ohio, North Carolina, Texas and Ontario. We are not the first to point this out, the interpretation of the northeastern coyote as a new species has already been refuted by Chambers (2010).

The lack of isolation is also evident in measures that show northeastern coyotes are not much genetically differentiated from midwestern/southern coyotes ($F_{ST} = 0.02$) or from western coyotes ($F_{ST} = 0.05$) (vonHoldt et al. 2011). These values are lower than expected for different subspecies, and they are even less genetically different than various populations of grey wolves (*Canis lupus*) such as Yellowstone National Park vs. Isle Royale National Park wolves ($F_{ST} = 0.10$), or between Italian and Spanish wolves ($F_{ST} = 0.16$) (vonHoldt et al. 2011). Coyotes are known to be long-distance dispersers (Gompper 2002), and the body of genetic evidence suggests a diverse but well-mixed gene pool with continual variation across eastern North America.

Although Way and Lynn (2016) emphasised the morphological differences between eastern and western coyotes, their graphs (Figures 1a and 1b) actually show continuous variation from east to west, as seen in many broad-ranging species. It is not surprising that specimens from opposite ends of a cline would be statistically different from each other in size, and this should not be mistaken for evidence of speciation.

Wolves and coyotes around the world have been shown to form 'ecotypes' that are distinct populations adapted to their local environment or particular type of habitat (Futuyma 1998). Neighbouring ecotypes typically have unique genetic signatures and phenotypes, but maintain enough gene flow between them to be considered the same species. For example, one genetic study identified six coyote ecotypes associated with different habitat types in California (Sacks et al. 2008). We suggest that the coyotes living in eastern deciduous forests should be recognised as a new ecotype. The eastern ecotype is a hybrid swarm - a population of individuals with mosaic genomes containing coyote, wolf and dog genes - with continual morphological and genetic variation across their range. The spread of coyote hybrids into the forests of eastern North America over the last century has provided an amazing evolutionary experiment, with natural selection favouring an animal that is somewhat larger than the western coyote, presumably allowing it to more effectively hunt the abundant white-tailed deer (*Odocoileus virginianus*) in the region (Kays et al. 2010).

Coyotes are likely to continue to specialise within this region. For example, preliminary evidence suggests that eastern coyotes might be locally adapting based on the availability of white-tailed deer (Monzón 2012, Monzón et al. 2014), and one can imagine local specialisations on different habitats within the region, be they natural or urbanised, mountainous or low-lying. Is it possible that one of these ecotypes could become sufficiently isolated from the rest of the coyote populations that it could be recognised as a unique species? Yes. Indeed, biologists have long considered the importance of hybridisation in generating evolutionary innovations that accelerate the speciation process (Anderson and Stebbins 1954). However, this speciation scenario would require extremely strong, and spatially heterogeneous, natural selection for the specialised form to counter the continual gene flow of dispersing animals. Given that the coyote is one of the most generalist and highly mobile species in the world, this is an unlikely scenario. If it did occur, evidence for a unique species would be seen as discontinuous breaks in the morphological and genetic variation corresponding to boundaries in the geographic range of the new species. Levels of ge-

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netic differentiation (F_{ST}) between populations would be high, reflecting their isolation and differentiation. None of this is observed in today's eastern coyote populations.

Life on earth is made up of hierarchies of variation. We use the word 'species' to recognise groups of animals that are substantially different and rarely or never exchange genetic material. Within a species, natural selection hones populations to fit their local environments, even as limited gene flow between them continues, creating local variations we recognise as subspecies, races, or ecotypes. There is no doubt the northeastern coyote is a new type of coyote, but with continued genetic connections to the broader coyote population throughout North America, and relatively minor physical differences. It should not be recognised as a distinct species, instead, we propose that the eastern coyote be recognised as a coyote ecotype specialised on eastern forests.

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Biographical sketch

Roland Kays is Head of the Biodiversity Research Laboratory at the North Carolina Museum of Natural Sciences, and a Research Associate Professor at NC State University. He has a broad interest in ecology and conservation, especially of mammals. Roland studies research questions which are scientifically interesting but also have real-world relevance through educational or conservation value.

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