

Synthesis

Northeastern coyote/coywolf taxonomy and admixture: A meta-analysis

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Keywords: *Canis latrans*, *Canis lycaon*, *Canis lupus*, *Canis oriens*, cladogamy, coyote, coywolf, eastern coyote, eastern wolf, hybridisation, meta-analysis, northeastern coyote, wolf.



Abstract

A flurry of recent papers have attempted to taxonomically characterise eastern canids, mainly grey wolves *Canis lupus*, eastern wolves *Canis lycaon* or *Canis lupus lycaon* and northeastern coyotes or coywolves *Canis latrans*, *Canis latrans* var. or *Canis latrans* x *C. lycaon*, in northeastern North America. In this paper, we performed a meta-analysis on northeastern coyote taxonomy by comparing results across studies to synthesise what is known about genetic admixture and taxonomy of this animal. Hybridisation or cladogamy (the crossing between any given clades) between coyotes, wolves and domestic dogs created the northeastern coyote, but the animal now has little genetic input from its parental species across the majority of its northeastern North American (e.g. the New England states) range except in areas where they overlap, such as southeastern Canada, Ohio and Pennsylvania, and the mid-Atlantic area. The northeastern coyote has roughly 60% genetic influence from coyote, 30% wolf and 10% domestic dog *Canis lupus familiaris* or *Canis familiaris*. There is still disagreement about the amount of eastern wolf versus grey wolf in its genome, and additional SNP genotyping needs to sample known eastern wolves from Algonquin Provincial Park, Ontario to verify this. Given its mixed species origin and morphological and genetic uniqueness, the most appropriate name for this animal is “coywolf”, which accounts for its two main genetic influences (i.e. coyotes and wolves) in portmanteau order; this name still applies even with the relatively small amount of dog introgression in its genome since dogs are essentially domesticated grey wolves and dog DNA is found in many other wild *Canis* species including grey wolf populations. It is important for managers to acknowledge that this animal was produced through cladogamy events ~100 years ago, but there is now minimal recent admixture throughout most of its northeastern range. The fact that the coywolf is clearly morphologically and genetically different to any other described population of *Canis* should qualify the animal for species status. We suggest that they be scientifically classified as *Canis oriens*, meaning “east”, or more specifically “eastern canid”, in Latin. This nomenclature gives them a distinct stand-alone name separating them from their parental *Canis* species/types and the associated relative amounts of *latrans*, *lycaon*, *lupus*, and domestic dog genes contributing to their hybrid background. Efforts should be made to monitor the southern wave of western coyote expansion converging with coywolves to document any genetic introgression that might take place between these closely related *Canis* and whether these two canids will remain distinct.

The following is the established format for referencing this article:

Way, J.G. and Lynn, W.S. 2016. Northeastern coyote/coywolf taxonomy and admixture: A meta-analysis. *Canid Biology & Conservation* 19(1): 1-7. URL: http://www.canids.org/CBC/19/northeastern_coyote_taxonomy.pdf.

Introduction

Hybridisation is progressively being more recognised in nature, having been discovered in many taxa (Way 2013). Vargas Pêgas (2013) noted that hybridisation may be a phenomenon misconceived and underestimated by many modern evolutionary biologists and may need revisions in order to respect the new perspectives on hybridisation's role in evolution, including with humans. Vargas Pêgas (2013) suggested the use of the term "cladogamy" to substitute with "hybridisation" to refer to the crossing between any given clades, due to difficulties from scientists and arbitrary means of separating species from lower taxa. Cladogamy is a term that can apply to crossings between two species given any species concept and any two clades (subspecies or varieties) distinguished by taxonomy, ecology, genetics, geography or phylogeny. Stronen and Paquet (2013) believed that certain hybrids, like northeastern coyotes/coywolves (*Canis latrans* or *Canis latrans* x *C. lycaon*; hereafter northeastern coyotes for consistency purposes), resulting from human actions should be preserved if the animal has replaced the ecological role of extirpated or extinct parent taxa. They argue for conservation policies focusing on protecting the ecological role of taxa affected by hybridisation.

Numerous recent papers have attempted to taxonomically characterise eastern canids, mainly grey wolves *Canis lupus*, eastern wolves *Canis lycaon* or *Canis lupus lycaon*, and northeastern coyotes in eastern North America (Chambers et al. 2012, Fain et al. 2010, Monzón et al. 2013, Way 2013, Wilson et al. 2009). Until the publications of Kays et al. (2010) and Way et al. (2010), there had been more of an emphasis on wolf than coyote genetics. But since then, there has been a flurry of additional research on the topic culminating with Way (2013), Monzón et al. (2013) and Wheeldon et al. (2013). At the same time genetic research on coyotes south of the Northeast U.S. has discovered that these animals are more coyote-like compared to northeastern coyotes. Coyotes in the mid-Atlantic region have small amounts of wolf and dog introgression (Bozarth et al. 2011), and southeastern coyotes are more typical western coyotes that have little wolf but some domestic dog *Canis lupus familiaris* or *Canis familiaris* (see Dinets 2015 for discussion of domestic dogs being a separate species from grey wolves) admixture (Parker 1995, von Holdt et al. 2011). In this paper, we synthesise contemporary morphological and genetic studies on northeastern coyotes to come to a better understanding of which research findings are largely agreed upon and which have differing conclusions or interpretations of the data. We conclude by making recommendations for northeastern coyote taxonomy.

Methods

We conducted a meta-analysis of northeastern coyote taxonomy by reviewing all of the literature on northeastern coyote genetics and morphology. Sources were obtained by acquired scientific papers as well as from the references of recent scientific papers; we believe that all papers relating to northeastern coyote taxonomy were obtained from 1995–2014. Each paper was analysed, coded to specific observations/conclusions, categorised and grouped in order to gain a better understanding of similarities and differences between studies (Table 1). There was no method for assessing risk of bias of individual studies as we simply categorised observations gleaned from each study. We analysed all studies therefore we do not believe there is a risk of bias that may affect the cumulative evidence (e.g. publication bias, selective reporting within studies). However, to ensure that the studies conducted by the first author were not over-represented in the results, those studies and their times used in Table 1 were compared to the overall average of all studies considered in the analysis using an unpaired t-test.

Parker (1995) is used here to represent all previous references that are summarised in that book, most of which are also discussed in Way (2007a), Way et al. (2010) and Way (2013). Parker (1995) was published at the very beginning of genetic work being conducted on eastern canids (and wildlife in general) and most of the studies cited in Parker (1995) do not necessarily add unique data to this study, even though they were important in framing recent studies on the morphology (e.g. Way 2007a and 2013) and genetics (Kays et al. 2010,

Way et al. 2010) of northeastern coyotes. The results are presented here in two sections: 1) agreed upon conclusions, and 2) differing results or interpretations (Table 1).

Recent research indicates that the medium-sized eastern wolf (Rutledge et al. 2010b, Chambers et al. 2012, Rutledge et al. 2010b, 2012a, b) was probably the original wolf native to northeastern North America, with potential influence from grey wolves (or more likely their hybrids) from the north (Kyle et al. 2008, Wilson et al. 2009, Fain et al. 2010, Chambers et al. 2012, Wheeldon and Patterson 2012). Most of the reviews on eastern North American *Canis* have concluded that the eastern wolf is a distinct species (e.g. Fain et al. 2010, Mech 2011, Chambers et al. 2012, Rutledge et al. 2012a) including Rutledge et al. (2015) who, at the time that this paper was going to press, published a paper definitively clarifying that the eastern wolf is indeed a unique species. However, given that there is ongoing debate about the taxonomic identity of the eastern wolf (e.g. Koblmüller et al. 2009, von Holdt et al. 2011, Table 1b), when we refer to the eastern wolf herein it could be in reference to either a distinct species, *Canis lycaon*, or a unique, small type/race of grey wolf, *Canis lupus lycaon* (also see Nowak 2002).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "<http://zoobank.org/>". The LSID for this publication is: urn:lsid:zoobank.org:pub: C273DE33-CA6F-4B9D-A602-D878FCEA8BFD; and the specific Nomenclature Act can be found at: urn:lsid:zoobank.org:act:4DE0DDA0-0089-4A0B-8997-E85A799722D1. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Results and discussion

We analysed 25 studies which occurred from 1995–2013 and were related to northeastern coyote taxonomy and admixture. We generated 13 coded categories with agreed upon findings (Table 1a) and six of differing results or interpretations of data (Table 1b). All of the 25 studies reviewed were included in Table 1 and were categorised between 4–15 times (mean \pm SD = 7.7 ± 3.0) and were referenced a total of 184 times per 19 combined categories (9.7 sources/category). For Table 1a, studies were referenced 2–11 times (4.2 ± 2.3) for a total of 101 times in the 13 categories (7.8 sources/category), while Table 1b sources were referenced 2–6 times (3.5 ± 1.2) for a total of 83 times in the six categories (13.8 sources/category). There was no difference ($P = 0.7429$, $t = 0.3315$, $df = 26$) in the average number of times the first author's studies were categorised (8.3 ± 4.7 ; range 5–15) compared to all 24 of the studies (7.7 ± 3.0); therefore, we believe that all of the studies were analysed and coded in an unbiased fashion.

Agreed upon findings

As noted by Monzón et al. (2013), molecular evidence has unequivocally confirmed coyote-wolf admixture in the creation of the northeastern coyote in northeastern North America (hereafter Northeast, see map in Way 2013) around the year 1919 in southeastern Canada (Table 1a; Nature 2014). Initial genetic studies using mitochondrial DNA (mtDNA) and nuclear microsatellite loci documented only eastern wolf and western coyote influence (Figure 1a–d, Way et al. 2010, Wilson et al. 2009) but more recent studies, using Y-chromosomes and single-nucleotide polymorphisms (SNPs), have conclusively discovered low levels of grey wolf and domestic dog admixture (Table 1a, Monzón et al. 2013, Wheeldon et al. 2013, Wilson et al. 2012). Wilson et al. (2012) noted that despite an absence of grey wolf mtDNA, there

was a surprisingly high frequency of grey wolf-like Y-chromosomes in northeastern coyotes that were different from the haplotypes found in northern grey wolves, which may reflect an origin of introgression related to the declining Great Plains wolves *C. lupus nubilus* or alternatively, these Y-chromosomes may have originated from dogs, as the majority of the Zfy-2 haplotypes in northeastern coyotes are common in dog breeds. Additionally, Wilson et al. noted the presence in north-

eastern coyotes of Y-chromosome haplotypes observed in grey wolves but not dogs and, overall, noted that similar to the Y-chromosome patterns, there is a stark contrast in the mtDNA composition of western coyote populations compared with that of eastern *Canis* populations (i.e. eastern wolves and northeastern coyotes/coywolves).

Table 1. Results of recent northeastern coyote/coywolf studies showing agreements and disagreements over data interpretation. Sources used, in roughly chronological order: 1. Parker 1995¹; 2. Way and Proietto 2005; 3. Way 2007a; 4. Koblmuller et al. 2009; 5. Wilson et al. 2009; 6. Way et al. 2010; 7. Kays et al. 2010a; 8. Wheeldon et al. 2010a; 9. Kays et al. 2010b; 10. Wheeldon et al. 2010b; 11. Chambers 2010; 12. Rutledge et al. 2010a; 13. Rutledge et al. 2010b; 14. Bozarth et al. 2011; 15. vonHoldt et al. 2011; 16. Benson et al. 2012; 17. Rutledge et al. 2012a; 18. Rutledge et al. 2012b; 19. Wheeldon and Patterson 2012; 20. Way 2013; 21. Wheeldon et al. 2013; 22. Monzón et al. 2013; 23. Benson and Patterson 2013; 24. Brockerville et al. 2013; 25. Wilson et al. 2012.

Results from recent eastern coyote/coywolf studies	Source(s)
(a) Agreed upon results	
Larger than other coyote populations	1-3, 7, 13, 16, 19, 20
Smaller than other wolf populations	13, 16, 19, 20, 23
Product of hybridisation with coyotes and wolves ²	4-25
Product of hybridisation with coyotes, wolves, and dogs ²	13, 15, 19, 21, 22, 24, 25
Minimal recent admixture with other <i>Canis</i> after original hybridisation episode(s) ~100 years ago	4, 20-22
Genetically distinct from western coyotes	4, 15, 20, 22, 25
Adapted well to northeastern North America	1-25
Acquisition of adaptive alleles confers a selective advantage	5, 6, 7, 20, 22
Morphologically distinct	1-3, 7, 13, 16, 19, 20,
Protecting all <i>Canis</i> will better conserve ecological processes	4, 5, 12, 13, 18, 20, 22
Protecting them may facilitate wolf recovery as has been shown elsewhere	4, 5, 12, 13, 18, 20
Reliance on larger prey (i.e. deer) than most other coyote populations	7, 22, 23
Unique appearance, especially in relation to other populations of coyotes	20, 24
(b) Differing results or conflicting interpretations of results	
Common name referenced to or suggested term for animal: eastern coyote	1-5, 12, 13, 16-19, 21-23, 25
northeastern coyote	7-11, 14, 15, 22, 24
coywolf	6, 20
Referenced to scientifically as: <i>Canis latrans</i> x <i>C. lycaon</i>	5, 6, 8, 13, 17, 20
<i>Canis latrans</i> var.	1, 12
<i>Canis latrans</i>	2-4, 14-16, 18, 19, 21-23, 24
Hybrid background with just eastern wolves	5, 6, 11, 17, 18, 20
Hybrid background with eastern wolves and grey wolves	4, 15, 16, 19, 21, 22, 25
Refer to the wolf in the east as: eastern wolf	5, 6, 11-13, 16-21, 23, 25
Great Lakes wolf	4, 7, 14, 15, 22
Where colonisation and hybridisation took place: SE Ontario (south of Algonquin Provincial Park)	5, 6, 8, 10, 18, 20, 21, 23
Western Great Lakes states	7, 9, 22

¹Parker (1995) is used here to represent all previous references that are summarized in that book, most of which are also discussed in Way (2007a), Way et al. (2010) and Way (2013).

²Earlier sources (e.g. 4 and 5) did not detect dog DNA in those studies because of techniques used (i.e. mitochondrial DNA and/or nuclear microsatellites) versus newer methods (e.g. Y-chromosomes and SNPs) that have detected dog DNA.

Overall, and accounting for variability between studies, the northeastern coyote is roughly 60% coyote, 30% wolf, and 10% domestic dog. It was also agreed upon that there has been minimal recent admixture with other *Canis* after original hybridisation episode(s) ~100 years ago (Table 1a), meaning that the animal is now breeding with other northeastern coyotes throughout the vast majority of its northeastern range and much less frequently with any of its parental species, except at the edge of its range in southeastern Canada with eastern wolves and in Ohio, Pennsylvania, and the mid-Atlantic area with western coyotes (Monzón et al. 2013, Way 2013).

The genetic background of the northeastern coyote has contributed to its intermediate body size whereby it is larger than all other populations of coyotes (Figure 1a) but smaller than wolves (Table 1a, Figure 1b). This is documented in its robust cranial features compared to coyotes (Kays et al. 2010) and large body size where individuals are regularly ≥20kg (Way and Proietto 2005, Way 2007a, Way 2013). Genetic evidence from STRUCTURE analysis (Figure 1c) and factorial correspondence analysis (Figure 1d) of microsatellite genotypes also indicates that northeastern coyotes cluster separately from western coyotes, eastern wolves and grey wolves.

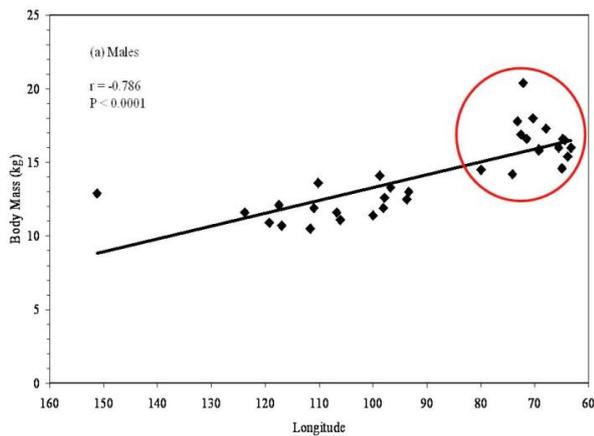


Figure 1a.

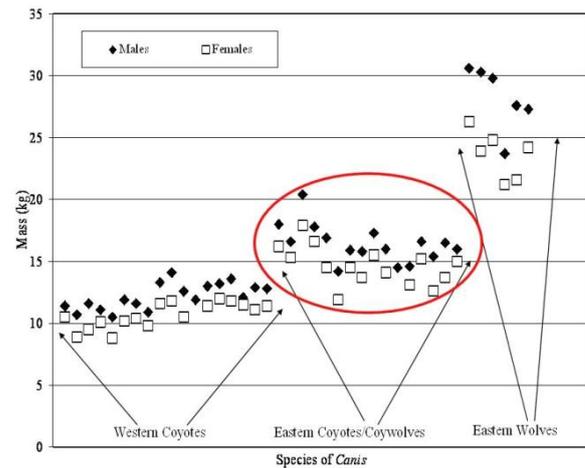


Figure 1b.

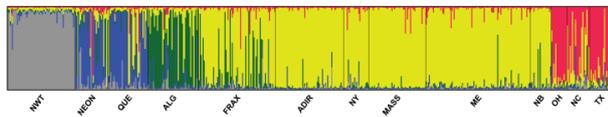


Figure 1c.

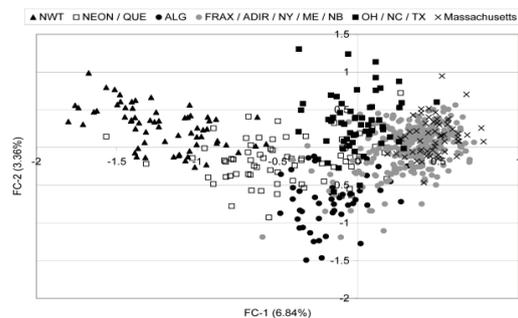


Figure 1d.

Figure 1 (a-d). Graphs illustrating the morphological and genetic distinctiveness of northeastern coyotes/coywolves. They are larger than any other coyote population outside of the Northeast (Figure 1a; from Way 2007), are morphologically distinct between western coyotes and eastern wolves (Figure 1b; from Way 2013), and STRUCTURE analysis (Figure 1c; from Way et al. 2010 where grey = grey wolves, blue = grey/eastern wolf hybrids, green = eastern wolf, yellow = northeastern coyote/coywolf, and red = western coyote) and factorial correspondence analysis (Figure 1d; from Way et al. 2010 where northeastern coyotes = FRAX/ADIR/NY/ME/NB and MA) of microsatellite genotypes indicate that northeastern coyotes cluster separately from western coyotes, eastern wolves and grey wolves.

Larger prey, such as white-tailed deer *Odocoileus virginianus*, is commonly described as a major food item for northeastern coyotes (Table 1a, Harrison and Harrison 1992). However, it is important to point out that the majority of those studies occur in northern, forested areas, with relatively low amounts of alternative prey. There is evidence that northeastern coyotes have a more diverse diet of small to medium sized prey in other areas, such as agricultural or mixed forested areas, which separates them from most wolf populations that typically do not inhabit human-dominated areas or feed on smaller prey (Harrison and Harrison 1992, Sears et al. 2003). Way and White (2013) noted that coyotes commonly predate on rodents and that they may be important to help regulate Lyme disease in the Northeast, especially when living at natural (i.e. not human exploited) densities. Thus, northeastern coyotes are wolf-like in that they are known to regularly kill larger prey such as deer, but they are also coyote-like in that they are capable of having a diverse diet, especially in altered landscapes (i.e. agricultural, suburban areas). Monzón et al. (2013) even noted that northeastern coyotes are more wolf-like genetically in areas of high deer density, supporting the idea that introgressive hybridisation with wolves facilitated the colonisation of eastern forests and introduced adaptive genetic variation that allowed northeastern coyotes to exploit a prey base rich with ungulates. Those authors pleaded the importance of restoring and encouraging natural predator-prey dynamics given the abundance of deer in the eastern U.S.

All studies noted, either explicitly (i.e. by documenting its success; Parker 1995) or implicitly (reporting on the animal given that it is common in the region), that the northeastern coyote is adapted very well to the Northeast given its colonisation of all available habitats in the region (Table 1a). Through the acquisition of adaptive alleles, whereby the hybrid background of this animal has made it more successful than its parental species, the northeastern coyote has a combination of genes (not necessarily all in heterozygous forms in most individuals) that confers a selective advantage since both western coyotes and wolves do not inhabit this region where northeastern coyotes are ubiquitous. Monzón et al. (2013) stated that the introgression of adaptive genetic variation via hybridisation with wolves presumably permitted admixed “coyotes” to rapidly colonise the Northeast, something that did not happen until they hybridised with wolves. However, it should be noted that this statement, i.e. that northeastern coyotes are a product of historical hybridisation that has succeeded specifically because of selection on the particular hybrid genome, is merely a hypothesis. An equally valid hypothesis is simply that coyotes, regardless of whether they had interbred with eastern wolves or not, would have succeeded in colonising the northeast because human persecution of wolves tipped the competitive balance in favour of the more reproductively responsive coyotes (in any form). That is, the larger size of the northeastern coyote (i.e. resulting from hybridisation with wolves) could be irrelevant to the coyotes’ success rather than the driving force behind it. Coyotes colonising the east from the south have been equally successful in response to the decline

of red wolves, *C. rufus* (essentially the southern remnant of eastern wolves), as they were driven to extirpation by various anthropogenic causes and eventually hybridised with coyotes (Bozarth et al. 2011, Mech and Nowak 2010).

Even though the term “hybrid” has negative connotations, animals with a cladogamy background may have particular adaptations that permit them to succeed in their environment and that unless the parent taxa is still present (e.g. eastern wolves), the focus should be on preserving the ecological role currently held by hybrids (e.g. northeastern coyotes; Stronen and Paquet 2013). Numerous studies agreed that better protection of northeastern coyotes will conserve evolutionary and ecological processes as they continue to evolve and adapt to the modern landscape, and increased protection may also facilitate wolf recovery as has been shown elsewhere (Table 1a, Rutledge et al. 2010a, Way 2014). Rutledge et al. (2010a) noted that the role of social groups in long-term population persistence is routinely overlooked by wildlife managers, but minimising the anthropogenic impact (i.e. human-caused killings) on social structure in populations that form highly related groups (also see Way et al. 2010 for northeastern coyotes) is likely to improve overall fitness by allowing evolutionary processes to occur in response to natural selection, not human-mediated mortality. It has been suggested that reducing levels of exploitation by expanding no-harvest zones is a relatively simple and inexpensive long-term solution to promote persistence of top predators that are integral to healthy ecosystems (Rutledge et al. 2010a, Way 2013).

Differing results or interpretations between studies

A major difference between studies was the vernacular name and scientific classification of the northeastern coyote, with most calling them a type of coyote, specifically “eastern coyote” (Table 1b). Monzón et al. (2013) did not believe that “coywolf” was a suitable term for “northeastern coyotes” since they are the product of cladogamy of four different *Canis* species or *Canis* types/races (western coyote, eastern wolf, grey wolf and domestic dog;) yet offered no suggestions for accurately describing this animal. However, these authors, as previously noted, stated that the introgression of wolf DNA has allowed “coyotes” to colonise and thrive in the northeast, which hints that coyotes alone were not capable of accomplishing that feat (although see the alternative hypothesis presented in the previous section). Chambers (2010) stated that “northeastern coyote” was the most appropriate term for these animals since they are mostly coyote, but did acknowledge that they have ~33% wolf introgression in their genome (Table 1b, Parker 1995). Most recently, Way (2013) declared that the best name for this hybrid animal is “coywolf”, *Canis latrans* x *C. lycaon*, rather than a type of coyote, since they are morphologically and genetically distinct, being larger than any other population of coyote but smaller than the eastern wolf. Furthermore, Way (2013:9-10) provided five lines of morphological and genetic evidence on why the vernacular terms “coyote”, “eastern coyote”, and “northeastern coyote” undervalue the importance of the wolf in the ancestry of this canid. Way (2013) stated that the recent discovery of domestic dog DNA in eastern coyotes (von Holdt et al. 2011, Wheeldon and Patterson 2012, Wheeldon et al. 2013) need not change this terminology, since this discovery does not appear to affect the phenotype and ecology of this animal. Also, Way (2013) and Monzón et al. (2013) summarised the literature and documented many other wild *Canis* that also hybridise with dogs (especially populations of grey wolves), yet those animals retain their wild species name.

Northeastern coyotes have been referred to scientifically as *Canis latrans*, *Canis latrans* var. (a variation of coyote), and *Canis latrans* x *C. lycaon* (Table 1b). However, the recent discovery of low amounts of domestic dog and grey wolf admixture in the genome of the northeastern coyote (Wheeldon et al. 2013) fail to account for this introgression in their scientific classification. Since dogs are generally regarded as a subspecies of grey wolf (but see Dinets [2015] who argued for full species status for dogs) it may be most accurate that this animal be designated as *Canis latrans* x *C. lycaon* x *C. lupus* to account for its mixed species hybrid background, with the relative importance of each species listed in order.

A continued conflicting interpretation between research papers was using the term “eastern wolf” as synonymous with the Great Lakes wolf (Table 1b; see methods and most recently, Rutledge et al. 2015). While it is generally agreed upon that Great Lakes wolves are grey x eastern wolf hybrids (Wilson et al. 2009, Fain et al. 2010, Chambers et al. 2012), a number of authors incorrectly refer to wolves in the western Great Lakes region of Minnesota, Michigan and Wisconsin as *C. lycaon* (eastern wolves) (e.g. vonHoldt et al. 2011, Monzón et al. 2013). Eastern wolves are known to be most representative in and around Algonquin Provincial Park, Ontario (APP; Rutledge et al. 2012a, b; 2015), not in the Great Lakes region. Due to von Holdt et al. (2011) not properly sampling eastern wolves and claiming some eastern wolf DNA was coyote, they initially gave lower percentages of wolf (<10%) in the genetic makeup of northeastern coyotes than is now commonly believed (~25-30%). Future studies, using SNPs, may tweak the percentage of eastern and grey wolf (most likely derived from hybrid Great Lakes wolves) in the genome of northeastern coyotes (see Monzón et al. 2013) once known eastern wolves are sampled from APP (Rutledge et al. 2012a). In other words, it is likely that the northeastern coyote has a higher percentage of eastern wolf than grey wolf in its genome and some of the grey wolf classified by Monzón et al. (2013) may in fact be from eastern wolves (Wilson et al. 2009; Rutledge et al. 2012a, 2015; Way 2013). Rutledge et al. 2015 specifically stated that the presence of a unique species, the eastern wolf, would explain the hybridised background of the “eastern coyote” (i.e. northeastern coyote/coywolf) whereby it was mainly the product of hybridisation between western coyotes and eastern wolves. However, independent research does verify low levels of grey wolf (and dog) admixture in northeastern coyote populations in the Northeast (Wheeldon et al. 2013, Wilson et al. 2012).

A final discrepancy between investigations was where the initial hybridisation event(s) took place to create the northeastern coyote ~100 years ago (Table 1b). While it is largely agreed upon that the majority of admixture took, and continues to take place in southeastern Ontario around APP (Benson et al. 2012, Benson and Patterson 2013), there is an additional possibility of hybridisation occurring in the western Great Lakes states. But this is probably in much lower frequency than in southeastern Ontario where the eastern wolf mediates gene flow between coyotes and grey wolves (Wilson et al. 2009, Rutledge et al. 2010b, 2012b). In the Great Lakes region there is little documented hybridisation between wolves and coyotes (Wheeldon et al. 2010c), even if some coyotes colonised the northeast via north of the Great Lakes in Ontario (Kays et al. 2010b) rather than south of the Great Lakes by way of the Lower Peninsula, Michigan (Wheeldon et al. 2010a, b).

Conclusions and recommendations

Cladogamy of *Canis* in eastern North America is clearly an ongoing and well documented process (Table 1; Mech and Nowak 2010, Way 2013). The northeastern coyote has been very successful in colonising and is well adapted to the Northeast given its range and abundant population in the region; this implies that they acquired adaptive alleles through genetic introgression between coyotes and wolves which conferred a selective advantage. However, the hypothesis that these animals are more successful than their parental forms is merely a hypothesis as it is still unproven whether western coyotes could/would have colonised this region via a southern route south of the Great Lakes states, even if slower than northeastern coyotes did via a northern route (Kays et al. 2010, Table 1).

It is unquestionable that northeastern coyotes derived from the product of hybridisation/cladogamy between western coyotes and wolves with additional genetic input from domestic dogs (Table 1a). It is larger than other coyote populations (Figure 1a-b) and generally eats larger prey than western coyotes, yet feeds on smaller prey than wolves. This suggests that this animal has a unique ecological niche in the region (Way 2013, Way and White 2013). Many sources noted that better protecting northeastern coyotes will help conserve ecological processes and evolutionary adaptations (e.g. social pack living) and allow it to continue to adapt to the area through natural selection

while also allowing for the potential recovery of wolves into portions of the Northeast (Table 1a; see also Stronen and Paquet 2013).

There was still confusion among papers over separating the eastern wolf and Great Lakes wolf (a grey x eastern wolf hybrid), which may affect the final agreed-upon genomic percentages that each species or canid type/race contributed toward creating the northeastern coyote (Monzón et al. 2013, Rutledge et al. 2015). Given that there has been minimal contemporary hybridisation throughout most of the Northeast compared to historical introgression (~100 years ago; Wheeldon et al. 2013), accurately deciphering the amount of eastern versus grey wolf in its genome is likely the most significant finding remaining to be gleaned about the genetic background of the northeastern coyote.

The various investigations that we reviewed differed on the appropriate common name and scientific classification of this animal (Table 1b). Many sources found that the animal is distinctive, both morphologically (Figure 1a-b) and genetically (Figure 1c-d) from other *Canis* (Table 1a, Way 2013), therefore we suggest that the most appropriate name for this animal is not a form of coyote (specifically, northeastern coyote) but rather “coywolf” which accounts for its two main genetic influences (i.e. coyotes and wolves) in a simple one-word portmanteau order (i.e. combining two words into one with the dominant descriptor first). Quite simply the animal is statistically neither a coyote nor a wolf, but rather a hybrid of the two. The name “coywolf” still applies even with the relatively small amount of dog introgression in its genome since dogs are generally believed to be domesticated grey wolves (but see Dinets 2015) and dog DNA is found in many wild *Canis* species including grey wolves (see references in Monzón et al. 2013 and Way 2013). It is important for managers to acknowledge that this animal was produced through cladogamy events ~100 years ago, mostly in southeastern Ontario (Table 1b), but there is now minimal recent admixture throughout the Northeast after those original hybridisation events occurred, except at the edge of its range (Way 2013, Wheeldon et al. 2013). However, coywolves, with their mixed species heritage, are no doubt still evolving and adapting to the landscapes of the Northeast (e.g. see Brockerville et al. 2013 for white “coyotes” in Newfoundland).

It may be difficult to change the vocabulary of the general public and state wildlife departments from using the common moniker “eastern coyote” (e.g. Parker 1995, Way 2007b), which is not even that accurate of a term given that colonising “coyotes” in the Northeast, mid-Atlantic region and Southeast are considerably different from each other, but education may help in making the transition to coywolf in order to most accurately describe the canid found throughout the Northeast. For example, a recent national television documentary introduced the term “coywolf” (Nature 2014) which was likely the result of acquired learning through scientific research (Table 1, Kays et al. 2010, Way 2013) and education efforts (for example, see www.EasternCoyoteResearch.com).

Because the coywolf is clearly morphologically and genetically different than any other described population of *Canis* (Table 1a, Figure 1a-d), it should qualify for species status throughout the majority of its range in the Northeast (Way 2013). We suggest that they be scientifically classified as *Canis oriens*, meaning “east”, or more specifically “eastern canid”, in Latin. This positions the coywolf on species level and stands them apart from the parent contributions of *latrans*, *lycaon*, *lupus* and domestic dogs that created them. Cladogamy is a natural process through which a lineage can evolve or perish as a consequence of the complexity of sexual reproduction (Vargas Pêgas 2013), and a separate species name will recognise the uniqueness of this animal formed both naturally (i.e. canids mating with each other in the wild) and through human-induced habitat changes that likely facilitated coyote and wolf (and dog) populations coming together.

One unique challenge of preserving the genome of coywolves is the possibility of them becoming genetically swamped by “western” coyote genes from the south and west. This other flank of colonising “eastern coyotes” (from the mid-Atlantic and Southeast USA – Bozarth et al. 2011, Parker 1995), which is more western coyote-like (i.e. has less wolf genes), is only just now contacting the range of the coywolf in the Northeast. Thus, it remains to be seen whether this entity will

remain distinct as opportunities increase for introgression with southeastern coyotes which may potentially influence future systematic perspectives. Efforts should be undertaken to monitor eastern *Canis* genomics now and in the future.

Acknowledgements

We conducted this review paper with no specific funding and completed the paper on our own time. We were not paid during the completion of any part of this study. L.D. Mech, B. Sacks and an anonymous reviewer provided helpful comments.

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