The Canadian Field-Naturalist

Volume 127, Number 1 January–March 2013

Taxonomic Implications of Morphological and Genetic Differences in Northeastern Coyotes (Coywolves) (*Canis latrans* × *C. lycaon*), Western Coyotes (*C. latrans*), and Eastern Wolves (*C. lycaon* or *C. lupus lycaon*)

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Way, Jonathan G. 2013. Taxonomic implications of morphological and genetic differences in Northeastern Coyotes (Coywolves) (*Canis latrans* × *C. lycaon*), Western Coyotes (*C. latrans*), and Eastern Wolves (*C. lycaon* or *C. lupus lycaon*). Canadian Field-Naturalist 127(1): 1–16.

The eastern Coyote or Coywolf (*Canis latrans* × *C. lycaon*) inhabiting northeastern North America resulted from hybridization between the expanding population of the western Coyote (*Canis latrans*) and the remnant population of Eastern Wolf (*C. lycaon*) and possibly domestic dogs (*C. lupus familiaris*) in the early 20th century. This study compares the body mass of eastern (i.e., northeastern) Coyotes, western Coyotes, and Eastern Wolves and synthesizes the recent literature to gain better insight into the taxonomic relations and differences of closely-related *Canis* species. Northeastern Coyotes (males = 16.5 kg; females = 14.7 kg) were statistically ($P < 0.0001$) intermediate in mass between western Coyotes (males = 12.2 kg; females = 10.7 kg) and Eastern Wolves (males = 28.2 kg, females = 23.7 kg), consistent with their hybrid origin, but were numerically closer to western Coyotes. Large Cohen's *d* (3.00–8.56),^{2} (0.915–0.929), and Cohen's *f* (3.28–3.62) values indicated large effect sizes from the body mass comparisons. Eastern Wolves were 61–71% heavier than the same sex in the northeastern Coyotes, which in turn were ca. 35–37% heavier than the same sex in the western Coyotes. Alternatively, western Coyotes were 73–74% of the size of the same sex in the northeastern Coyotes, which in turn were 59–62% of the size of the same sex in the Eastern Wolves. I also attempted to relate mitochondrial DNA (mtDNA) haplotypes to body mass. Six of 17 (35.3%) adult female northeastern Coyotes captured in Massachusetts weighed ≥18 kg, heavier than any other described Coyote from outside northeastern North America. Mitochondrial DNA haplotypes associated with these heavy female northeastern canids were C9 = 4, C19 = 1, and C48 = 1. Body mass (kg) and mtDNA haplotype data of 53 northeastern Coyotes (males = 28, females = 25) showed no difference between haplotype and body mass for males ($P < 0.852$) or females ($P < 0.128$), suggesting that there is not a particular haplotype (e.g., C1) that is associated with the heavier animals. I propose that the most appropriate name for this hybrid animal is Coywolf (*Canis latrans* × *C. lycaon)*, rather than a type of Coyote. Coywolves are distinct, being larger than any other population of Coyotes but smaller than Eastern Wolves. I propose that the 5 distinct types of *Canis* be recognized as: western Coyote, Coywolf (northeastern Coyote), Eastern Wolf (including Red Wolf *C. rufus*), Gray × Eastern Wolf hybrids ('Great Lakes' Wolves; *C. lupus* × *C. lycaon* or *C. lycaon* × *C. lupus*), and Gray Wolf (*C. lupus*). The implications for wolf recovery in the northeastern United States is discussed.

Key Words: *Canis latrans* × *C. lycaon*, northeastern Coyote, Coywolf, *Canis latrans*, Coyote, Domestic Dog, Eastern Wolf, *Canis lycaon, Canis lupus lycaon,* Gray Wolf, *Canis lupus,* hybridization.

Hybridization is increasingly being recognized as common in nature, having been documented in amphibians, insects, fish, birds, and especially within closely related plant species (Berger 1973; Arnold 1992; Fritz et al. 1994; Haddad et al. 1994; Parris et al. 1999; Arnold et al. 1999; Albert et al. 2006; Schierenbeck and Ellstrand 2009; Meyerson et al. 2010). Allendorf et al. (2001) noted that hybridization is more common in fish than in other vertebrates, and hybridization in fish has been facilitated by the extensive introduction of non-native fish species worldwide. Within mammals, hybridization has rarely been documented, but canids represent a notable case of widespread interspecies mating (Wheeldon and White 2009; Wilson et al. 2009; Way et al. 2010; vonHoldt et al. 2011).

The canid currently inhabiting northeastern North America was originally described in the 1960s as being a large Coyote-like animal that is the result of hybridization with wolves and dogs (Lawrence and Bossert 1969; Silver and Silver 1969; Lawrence and Bossert 1975). This animal has been variously called coydog, eastern Coyote, Tweed Wolf, brush Wolf, northeastern Coyote, Coyote, new Wolf, and Coywolf, and it has scientifically been described as *Canis latrans* var. (Lawrence and Bossert 1969; Silver and Silver 1969; Lawrence and Bossert 1975; Parker 1995) and as *Canis latrans* × *C. lycaon* (Way et al. 2010; Wheeldon et al. 2010a).

It is now generally accepted that northeastern Coyotes formed in the early 1900s (Hilton 1978; Parker 1995;

Wheeldon et al. 2010a) in southern Ontario through hybridization between colonizing Coyotes (*Canis latrans*) from the west and remnant populations of Eastern Wolves (*C. lycaon*) (Wilson et al. 2000, 2003, 2009; Rutledge et al. 2012a, 2012b) or *C. lupus lycaon* (a subspecies of Gray Wolf) (Nowak 2002; vonHoldt et al. 2011). The hybrid was originally called the Tweed Wolf (Kolenosky and Standfield 1975; Wilson et al. 2009).

Recent research indicates that the medium-sized Eastern Wolf (Rutledge et al. 2010b; Chambers et al. 2012; Rutledge et al. 2012a, 2012b) was probably the original species native to northeastern North America, with potential influence from Gray Wolves (*Canis lupus*) (or their hybrids) from the north (Kyle et al. 2008; Wilson et al. 2009; Fain et al. 2010; Mech 2010; Chambers et al. 2012; Wheeldon and Patterson 2012), but see the discussion in vonHoldt et al. (2011) for an alternate interpretation. In addition, a new theory (vonHoldt et al. 2011) (also see Wheeldon and Patterson 2012) holds that domestic dogs (*C. lupus familiaris*) contributed ~9% to the genetic composition of the northeastern Coyote (previous genetic studies detected no dog influence (Way et al. 2010) or insignificant amounts (Kays et al. 2010)).

Way (2007a) noted that body mass is a useful index to gauge size differences among regions or species because this metric is more commonly reported in the literature than other measurements, such as body length or cranial measures. Furthermore, MacNulty et al. (2009) found that body mass in Gray Wolves ($n = 304$) was strongly correlated with chest girth, body length, and height, indicating that mass is a valid index of overall size. Thus, a large sample of body masses from different regions should give a good approximation of morphological differences in closely related canid species (or hybrids).

In the past 75 years, northeastern Coyotes have colonized northeastern North America (Figure 1) east

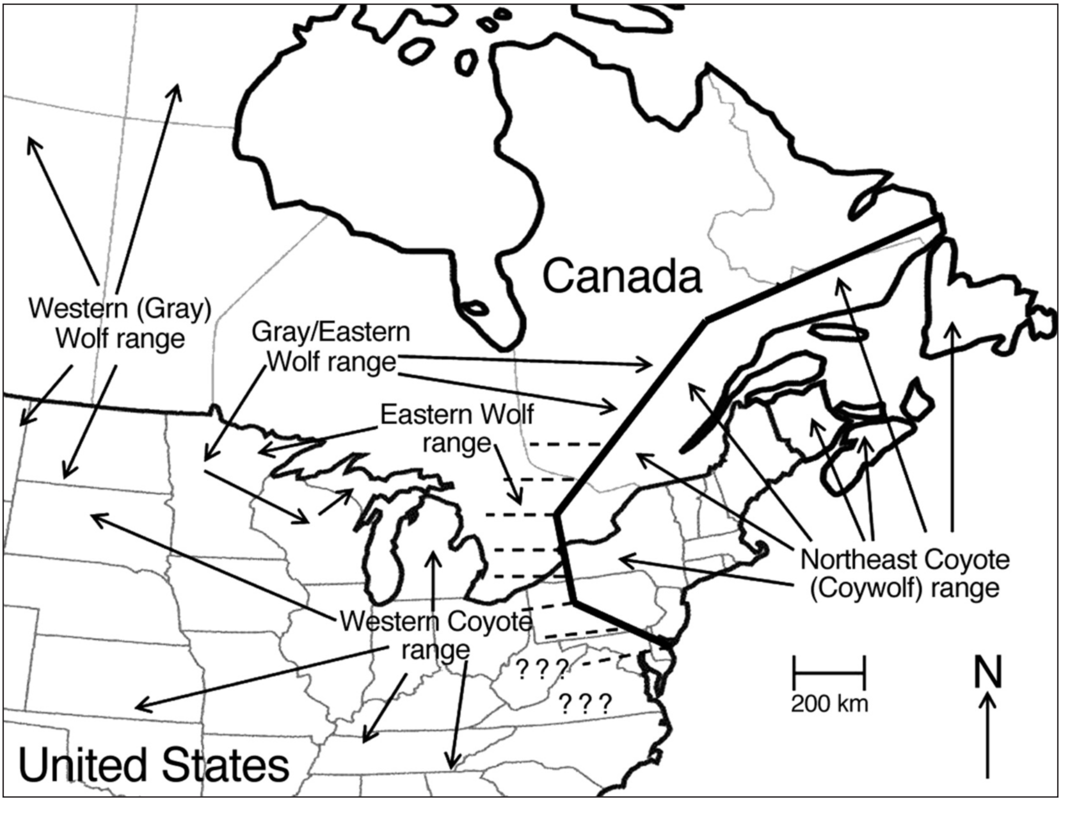

FIGURE 1. Approximate regions where various contemporary *Canis* in North America can be found, focusing on northeastern Coyote/Coywolf range. Dashed lines (e.g., southern Ontario, western Pennsylvania) denote the probable zone of hybridization between the northeastern Coyote (*Canis latrans* × *C. lycaon*) and the Eastern Wolf (*C. lycaon* or *C. lupus lycaon*) and between the western Coyote (*C. latrans*) and the northeastern Coyote. Question marks and dashed line at the southern edge of the range of the northeastern Coyote reflect uncertainty in the mid-Atlantic United States about where the range of the northeastern Coyote ends and the southern wave of expansion by the western Coyote continues (Kays et al. 2010; Bozarth et al. 2011). Boundaries should not be considered static, as there is hybridization between canids at the edges of their respective ranges (see text). Thus, rather than sharp lines separating taxa, boundaries should generally be thought of as intergrade zones of variable width (Chambers et al. 2012).

of 80° west longitude from western Pennsylvania and New Jersey in the United States to southern Ontario and the Maritime provinces in Canada. Much controversy continues to surround the taxonomic nature of this animal (e.g., see Chambers 2010 vs. Way et al. 2010). Mech (2010, page 134) noted that no one has attempted to correlate wolf (or canid) genetics with morphology, and Mech and Paul (2008) proposed that, because both the taxonomic descriptions and the mitochondrial DNA (mtDNA) haplotype assessments recognized two types of wolves (i.e., Eastern Wolves and Gray Wolves) in Minnesota, a correlation might be found between morphology and genetics. Subsequently, Kays et al. (2010) compared northeastern Coyote skull and mtDNA characteristics to those of other *Canis* populations. Wheeldon and Patterson (2012) differentiated hybridized wolves and coyotes in northeastern Ontario through genetic and morphological analysis but did not directly correlate the two variables. Similarly, Benson et al. (2012) characterized spatial genetic and morphologic structure of wolves and coyotes around Algonquin Park in Ontario and compared mass to *Canis* type but did not explicitly correlate mass to DNA haplotypes within a given *Canis* type.

Following the analysis by Thurber and Peterson (1991) of Coyote body size, Way (2007a) provided a comprehensive review of the size differences of Coyotes throughout North America. However, Way (2007a) did not compare the weights of the Coyote and the Eastern Wolf or compare their genetics (Eastern Wolf weights and genetics are rarely reported in the literature) (Mech and Paul 2008). Therefore, the objectives of this paper were to add to the knowledge of northeastern Coyote systematics by (1) conducting a comparison of northeastern Coyote body mass to those of both western Coyotes and Eastern Wolves, the putative parental species; (2) comparing northeastern canids mtDNA haplotypes with mass; and (3) reviewing the literature and describing northeastern Coyotes (Coywolves) as the 5th major *Canis* grouping in North America.

Most of the recent reviews on eastern North American *Canis* have focused on Eastern Wolves and have concluded that the Eastern Wolf is a distinct species (e.g., Fain et al. 2010; Mech 2010, 2011; Chambers et al. 2012; Rutledge et al. 2012a). However, there has also been an abundance of recent papers on Coyote genetics in eastern North America (e.g., Chambers 2010; Kays et al. 2010; Way et al. 2010; Wheeldon et al. 2010a; Bozarth et al. 2011), and I therefore attempt to synthesize these papers. Lastly, I discuss the implications of Coyote taxonomy and management in northeastern North America with regards to the recovery of the Eastern Wolf in the northeastern United States, similar to the discussion in Wheeldon and Patterson (2012, page 1229).

Methods

Body mass comparisons

I reviewed the literature to compare the body mass of northeastern Coyotes, Coyotes from areas outside northeastern North America, and Eastern Wolves using previously published data from Way (2007a) for Coyotes, from Theberge and Theberge (2004, pages 19–24) for Eastern Wolves (including three Red Wolf (*Canis rufus*) populations from both the historical ($n = 2$) and current ($n = 1$) North Carolina range), and from any additional papers discovered reporting Coyote and Eastern Wolf mass (Appendix 1).

Although Chambers et al. (2012) recommended that Eastern Wolves and Red Wolves be treated as distinct but closely related species, I include Red Wolf values in the Eastern Wolf category (Appendix 1) because of the genetic and morphological similarity of the two putatively North American evolved species (Theberge and Theberge 2004; Rutledge et al. 2010b, 2012a, b; Wilson et al. 2000, 2009). Mech (2010) summarized genetic studies and deduced that most of Minnesota is home to hybrid Gray × Eastern wolves. For this study, I retained samples from extreme northeastern Minnesota (Van Ballenberghe 1977) (cf. Mech and Paul 2008), as those were taken where Mech believed the highest content of Eastern Wolf resided and fell within the range of the values reported by Theberge and Theberge (2004) (Appendix 1).

All studies included in Appendix 1 report ≥10 individuals (of both sexes) from a given locale and include only adults (≥2 years old), similar to the analysis by Way (2007a).

Comparing northeastern canids mtDNA haplotypes with mass

Previous studies have classified the three main mitochondrial DNA haplotypes found in northeastern Coyotes as C1 (Eastern Wolf derived), C9 (eastern-specific haplotype that groups with Coyote haplotypes but is mainly found in Eastern Wolves and northeastern Coyotes; it has also been found in low frequency in Great Lakes states and mid-Atlantic region coyotes) (Wheeldon et al. 2010b, Bozarth et al. 2011), and C19 (western Coyote derived) (Kays et al. 2010; Rutledge et al. 2010b; Way et al. 2010; Wheeldon et al. 2010a; Rutledge et al. 2012b). Using this information, I report the body mass of large adult (≥2 years old) female northeastern Coyotes ≥18 kg captured in conjunction with a radio-monitoring study in Massachusetts (Way 2007b) and compare mitochondrial haplotypes in these females using the samples reported by Way et al. (2010).

I also correlated the mean body mass of adult and yearling northeastern Coyotes of each associated mtDNA haplotype reported from Massachusetts using data from Way (2007a) and Way et al. (2010). Unlike in the comparisons of body mass among regions, yearlings (which are technically full-grown animals) were retained here to increase sample size for statistical testing.

Statistical analyses

Analysis of variation (ANOVA) (SPSS Inc., Chicago, Illinois) was used to compare the mass of the three groups/species of canids. The individual study or population of canids was considered to be the sampling unit. ANOVA tests were conducted separately for male and female canids. Tukey's Honestly Significant Different (HSD) post-hoc tests were conducted when significant ($P < 0.05$) differences were detected in ANOVA.

I also used ANOVA to test for differences among the various haplotypes for both males and females, and Tukey's HSD tests were used when significant ($P < 0.05$) differences were detected in ANOVA.

Effect size is a term used to describe a family of indices that measures the magnitude of a treatment effect (Kotrlik and Williams 2003). Effect size is different from significance tests, because effect size focuses on the meaningfulness of the results and allows for comparison between studies (Cohen 1988; Kotrlik and Williams 2003). I calculated the effect size of body mass comparisons using the following measures:

(1) Cohen's *d* and effect size *r* using the online program (http://www.uccs.edu/~faculty/lbecker), where mean body mass and standard deviation for a given canid were compared to the mass and standard deviation of a second canid (Table 1). A small effect size for Cohen's $d = 0.2$, a medium effect $= 0.5$, and a large effect $= \geq 0.8$ (Kotrlik and Williams 2003).

(2) Cohen's *f*, after first calculating η^2. This required calculating:
(A) $\eta^2 = SS_{between} / SS_{total}$ (SS = sum of squares calculated from ANOVA table); and
(B) Cohen's f = square root of $\eta^2 / (1 - \eta^2)$. A small effect size for Cohen's $f = 0.10$, a medium effect $= 0.25$, and a large effect $= \geq 0.40$ (Kotrlik and Williams 2003).

Results

Body mass comparisons

Body mass (mean and standard deviation) of western Coyotes ($n = 18$ populations) were as follows: males = 12.2 kg (SD 1.1), females = 10.7 kg (SD 1.0); northeastern Coyotes ($n = 17$): males = 16.5 kg (SD 1.5), females = 14.7 kg (SD 1.5); and Eastern Wolves ($n = 6$): males = 28.2 kg (SD 2.6), females = 23.7 kg (SD 1.9) (Figure 2) (Appendix 1). ANOVA of the three groups of canids revealed significant differences for both males ($F_{2,37} = 242.2$, $P < 0.0001$) and females ($F_{2,35} = 187.9$, $P < 0.0001$). All pair-wise comparisons (e.g., northeastern to western Coyotes, Eastern Wolves to both Coyote groups) were significant ($P < 0.0001$).

These data can be interpreted as showing that northeastern Coyotes are statistically intermediate in size between western Coyotes and Eastern Wolves, although numerically closer to western Coyotes (Figure 2). Although the largest population of northeastern Coyotes almost approached the smallest Eastern Wolves, there were individual northeastern Coyotes not shown in Figure 2 that overlapped (i.e., 22–25 kg range) the smaller Eastern Wolves (Appendix 1). Because northeastern Coyotes were numerically closer to western Coyotes than to Eastern Wolves (Figure 2) (Appendix 1), the largest western Coyotes approached the smallest northeastern Coyotes. For instance, female northeastern Coyotes were 20.5% larger than male western Coyotes while female Eastern Wolves were 43.6% larger than male northeastern Coyotes.

Effect size was robust for all calculations and comparisons (Table 1). In practical biological terms, adult male Eastern Wolves were on average 1.71 times (71%) heavier than male northeastern Coyotes, which in turn were ca. 1.35 times (35%) heavier than adult male western Coyotes. Or put another way, adult male western Coyotes were 74% of the size of male northeastern Coyotes, which in turn were 59% of the size of male Eastern Wolves. Similarly, adult female Eastern Wolves were on average 1.61 times (61%) heavier than female northeastern Coyotes, which in turn were ca. 1.37 times (37%) heavier than adult female western Coyotes. Adult female western Coyotes were 73% of the size of female northeastern Coyotes, which in turn were 62% of the size of female Eastern Wolves.

TABLE 1. Effect size variables comparing the body mass of three *Canis* in North America. The square of the *r* value is the percentage of variance in the dependent variable that is accounted for by membership in the independent variable groups. Effect size *r* values are typically presented rather than r^2.

Comparison	Cohen's *d*	Effect size *r*	r^2	η^2	Cohen's *f*
Males					
Western Coyote and northeastern Coyote	3.27*	0.853	0.727		
Western Coyote and Eastern Wolf	8.02*	0.970	0.941		
Northeastern Coyote and Eastern Wolf	5.51*	0.940	0.884		
Overall (from ANOVA)				0.929	3.62*
Females					
Western Coyote and northeastern Coyote	3.14*	0.843	0.711		
Western Coyote and Eastern Wolf	8.56*	0.973	0.947		
Northeastern Coyote and Eastern Wolf	5.26*	0.935	0.874		
Overall				0.915	3.28*

* Large effect size based on Kotrlik and Williams (2003).

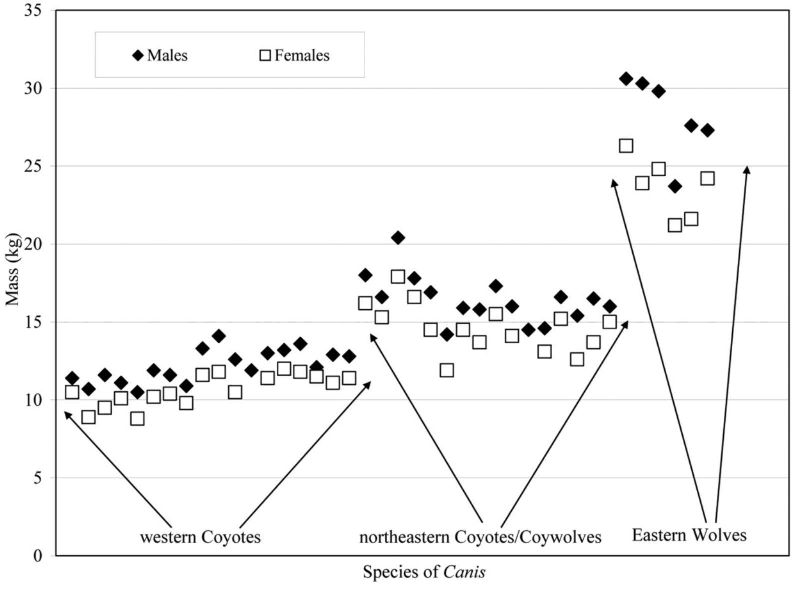

FIGURE 2. Ranges of average body mass (kg) of western Coyote (*Canis latrans*), northeastern Coyote/Coywolf (*C. latrans* × *C. lycaon*), and Eastern Wolf (*C. lycaon* or *C. lupus lycaon*) populations.

Comparing northeastern canids mtDNA haplotypes with mass

I also obtained body mass (kg) and mtDNA haplotype data for 53 northeastern Coyotes (males = 28, females = 25) from Massachusetts. Six of 17 (35.3%) radio-collared female northeastern Coyotes captured weighed ≥18 kg. Haplotypes associated with these heavy females were as follows: C9 = 4, C19 = 1, C48 (western Coyote derived) = 1. However, there was no difference between haplotype and body mass (mean (kg) and standard deviation) for males (C1: 16.9, SD 2.1, $n = 5$; C9: 16.7, SD 1.3, $n = 13$; C19: 17.2, SD 3.1, $n = 10$; ANOVA: $F_{2,25} = 0.161$, $P < 0.852$) or females (C1: 15.2, SD 2.2, $n = 8$; C9: 17.3, SD 2.4, $n = 11$; C19: 15.5, SD 2.1, $n = 6$; ANOVA: $F_{2,22} = 2.263$, $P < 0.128$).

Appearance

Qualitatively, northeastern Coyotes appeared more wolf-like than Coyote-like. The appearance of 50 individual northeastern Coyotes captured in Massachusetts was as follows: white-faced animals ($n = 10$); dark brown and grizzled gray animals ($n = 13$) often described as being like a German Shepherd; light brown and blondish ($n = 5$), red ($n = 2$); or dull gray animals ($n = 5$) (Figures 3A, 3B, 3C, and 3D).

FIGURE 3A. Wild northeastern Coyote/Coywolf (*Canis latrans* × *C. lycaon*) from Cape Cod, Massachusetts, showing grizzled-gray coloration and whitish face. Photo: J. Way, January 9, 2008, Barnstable, Massachusetts.

FIGURE 3B. Wild northeastern Coyote/Coywolf (*Canis latrans* × *C. lycaon*) from Cape Cod, Massachusetts, showing reddish-yellow coloration and white face. Photo: J. Way, January 20, 2004, Barnstable, Massachusetts.

FIGURE 3C. Wild northeastern Coyote/Coywolf (*Canis latrans* × *C. lycaon*) from Cape Cod, Massachusetts, showing dark gray coloration and whitish face. Photo: Anne Middleton, 2004, Dennis, Massachusetts.

FIGURE 3D. Wild northeastern Coyote/Coywolf (*Canis latrans* × *C. lycaon*) from Cape Cod, Massachusetts, showing a robust German Shepard-like appearance. Photo: Anne Middleton, 2004, Dennis, Massachusetts.

Discussion

Morphology

Northeastern Coyotes typically weighed 13.6−18.2 kg but reached 25 kg (Figure 2) (Appendix 1) (Parker 1995; Way and Proeitto 2005; Way 2007a). These weights are similar to the estimated mass of Ice Age Coyotes during the Pleistocene era, believed to be "super-sized" compared to modern Coyotes (Meachen and Samuels 2012). Chambers (2010) asserted that previous researchers (e.g., Lawrence and Bossert 1969, 1975) measuring canid morphometics grouped northeastern Coyotes with other populations of Coyotes and hence they should continue to be called Coyotes. However, those earlier researchers acknowledged that northeastern Coyotes were larger, were a variation of the species, and proposed calling them *Canis latrans* var. until further research was conducted (Lawrence and Bossert 1969; Silver and Silver 1969).

The Eastern Wolf has only recently been described (Wilson et al. 2000, 2003) (supported by Kyle et al. 2006, 2008; Fain et al. 2010; Mech 2010; Rutledge et al. 2010b; Mech 2011; Chambers et al. 2012; Rutledge et al. 2012a). The work of earlier researchers (including Lawrence and Bossert 1969; Silver and Silver 1969; Kolenosky and Standfield 1975; Hilton 1978; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987) did not acknowledge, or know of, the presence of this smaller species of wolf, instead recognizing it as a subspecies of Gray Wolf (*C. lupus lycaon*). However, these authors (Kolenosky and Standfield 1975; Schmitz and Kolenosky 1985) recognized several forms of wolves and noted that coyotes mated with the smaller Algonquin type wolf (i.e., the Eastern Wolf).

The reanalysis of data in this paper incorporating western Coyotes, northeastern Coyotes, and Red/Eastern Wolves shows that canids in northeastern North America are statistically intermediate between western Coyotes and Eastern Wolves (Figure 2). These results are further supported by large effect sizes (Table 1); also see Rutledge et al. (2010b) and Benson et al. (2012) for Eastern Wolf-Coyote body size comparisons. Furthermore, western Coyotes close to the range of the northeastern Coyote (i.e., in the Midwest or the Great Lakes area) are no bigger than Coyotes found elsewhere (Figure 1) (Appendix 1).

Way (2007a) noted that Coyotes from northeastern North America were so much larger than the typical reported weight for the species that they would be classified in a different size category (based on the body mass) than western Coyotes in many review studies of carnivore-sized guilds. Way (2007a) also summarized a wide range of weights reported for northeastern Coyotes. The mass of northeastern Coyotes from all sites in northeastern North America averaged higher than Coyotes elsewhere—so much so, that longitude accounted for >4 times the amount of variation in body mass than latitude. Six of 17 (35.3%) adult females captured in Massachusetts weighed ≥18 kg, a mass that to my knowledge has not been reported for western Coyotes and approaches the size of female Eastern Wolves (21–26 kg) (Appendix 1). Recent genetic analyses (Kays et al. 2010; Way et al. 2010; Wheeldon et al. 2010a) have confirmed that northeastern Coyotes are hybrids between western Coyotes and Eastern Wolves and this undoubtedly contributes to their larger, statistically intermediate size.

Comparing northeastern canids mtDNA haplotypes with mass

Four of 6 (66.7%) of the heaviest females in this study had the C9 (eastern specific) haplotype (Grewal et al. 2004; Rutledge et al. 2010b; Way et al. 2010) and individuals with the C9 haplotype had the numerically largest average value for females. None of the heavy females carried the Eastern Wolf specific C1 mtDNA haplotype. However, caution should be used when interpreting these results because of a small, non-significant sample size. For example, a possibility exists that these large animals carrying the C9 haplotype came from the same local large-bodied female lineage reported in Way and Proietto (2005). There was only a slight difference in male weights, but males with the C19 mtDNA haplotype were the numerically heaviest males.

Since both males and females with the C1 (i.e., Eastern Wolf derived) mtDNA haplotype were not the heaviest subset of this population, there has probably been sufficient genetic exchange among northeastern Coyotes for them to be one homogenous population, as discussed in Way et al. (2010). In other words, while there are likely to be a range of sizes (since this animal recently (ca. 75–100 years ago) formed from two (Coyotes and Eastern Wolves) or possibly three (domestic dogs) parental species) (Wheeldon et al. 2010a; vonHoldt et al. 2011; Wheeldon and Patterson 2012), it has likely been long enough for this animal to have had sufficient genetic admixture where large animals would potentially carry any of the major mtDNA haplotypes. Further, since morphological differences likely do not correlate with mtDNA haplotypes (mtDNA is inherited maternally and without recombination), the presence of a particular haplotype in an individual or population may represent contemporary hybridization or historical introgression from one or more distant hybridization events. Northeastern coyotes likely experienced historical introgression (i.e., in the early 1900s) because there is little or no opportunity for ongoing (contemporary) hybridization between Coyotes and Eastern Wolves across the majority of the range of the northeastern Coyote (e.g., in most of New England; Figure 1), and the wolf DNA present in northeastern Coyotes represents that which was introgressed in the early 20th century in Ontario (Wheeldon et al. 2010a).

Ecological role of northeastern canids

Kays et al. (2010) found that northeastern Coyotes have larger skulls (up to 15% bigger than western Coyotes), which they speculated would allow them to better exploit White-tailed Deer (*Odocoileus virginianus*), consistent with other studies in northeastern North America that documented high amounts of White-tailed Deer in the diet of Coyotes (Ballard et al. 1999; Patterson and Messier 2000, 2001). Kays et al. (2010) also found significant craniodental differences in these animals that would better facilitate preying on White-tailed Deer. A greater reliance on White-tailed Deer would put the northeastern Coyote intermediate in an ecological context between the western Coyote and the Eastern Wolf (Parker 1995; Theberge and Theberge 2004). The findings of Kays et al. (2010) are similar to previous studies (i.e., Lawrence and Bossert 1969; Silver and Silver 1969) that documented that the skulls of northeastern Coyotes were larger than those of any extant Coyote population.

Future studies should attempt to elucidate the role of the northeastern Coyote as either a mesocarnivore or an apex (top-down) carnivore (Prugh et al. 2009). No studies have documented the ability of the northeastern Coyote to kill Moose (*Alces alces*) (although the role of Eastern Wolves in limiting Moose populations is also debatable—see Theberge and Theberge 2004). It may be that northeastern Coyotes act as apex carnivores in systems dominated by White-tailed Deer (i.e., southern New England and most urbanized areas) but likely as mesocarnivores in systems dominated by Moose (e.g., northern New England).

Appearance

The observed wolf-like characteristics of northeastern Coyotes (Figures 3A, 3B, 3C, and 3D) make them appear similar to Red Wolves and Eastern Wolves (see photos in Smith 1996; Whitaker 1991, Plate 256; Theberge and Theberge 1998; Way 2007b, color plates). In addition, tracks of northeastern Coyotes measure 7.6−9.5 cm (3.0−3.75 inches) in length, which exceeds any described track measurements for western Coyotes (6.4 cm) (2.5 inches) and approaches the size of the tracks of Red Wolves (~10.2−11.4 cm) (4.0−4.5 inches) (J. Way, unpublished data) (Miller 1981; Stokes and Stokes 1986; Whitaker 1991). These 2 characteristics (i.e., appearance and track size) support the intermediate morphology of northeastern Coyotes.

Taxonomy and hybridization in eastern Canis: *Eastern Wolf influence*

Based on the majority of the recently published literature (Wilson et al. 2000; Nowak 2002; Wilson et al. 2003; Kyle et al. 2006, 2008; Wilson et al. 2009; Fain 2010; Mech 2010; Rutledge et al. 2010a, 2010b; Mech 2011; Chambers et al. 2012; Rutledge et al. 2012a, 2012b), I have assumed that the wolf that hybridized to form the northeastern Coyote is a North American-evolved wolf species (*C. lycaon*) that is independent of the Gray Wolf and closely related to the Coyote.

Hybridization between coyotes and wolves is limited to eastern North America, with the Eastern Wolf being a conduit of hybridization between both western Coyotes and western Gray Wolves (Table 2) (Roy et al. 1996; Wilson et al. 2000; Wheeldon and White 2009; Wilson et al. 2009; Fain et al. 2010; Kays et al. 2010; Mech 2010; Rutledge et al. 2010b; Way et al. 2010; Benson et al. 2012), with potential influence from Gray Wolves and dogs in the southeastern U.S. (Adams et al. 2003a, 2003b). The geographic extent of wolf × Coyote hybridization is consistent with the historical range of both the Eastern Wolf and the Red Wolf (Wilson et al. 2000; Nowak 2002; Wilson et al. 2003; Kyle et al. 2006; Wilson et al. 2009; Mech 2010, 2011; Chambers et al. 2012).

TABLE 2. Summary of types of *Canis* currently described in North America. As depicted in this continuum, the Eastern Wolf (*Canis lycaon* or *C. lupus lycaon*) serves as the conduit of hybridization for both the Gray Wolf (*C. lupus*) (in the western Great Lakes and southeastern Canada) and the Coyote (*C. latrans*) (in the southeastern United States and southern Ontario) and has created two hybrid types: the northeastern Coyote/Coywolf (*C. latrans* × *C. lycaon*) (no. 2) and the Gray Wolf × Eastern Wolf hybrids (*C. lupus* × *C. lycaon* and *C. lycaon* × *C. lupus*) (no. 4). See the Discussion for literature citations regarding each type, including a competing theory of canid identity and evolution (vonHoldt et al. 2011).

Body mass (smallest to largest)	Ability to hybridize
1. Western Coyote (*Canis latrans*), 8.2–13.6 kg Range: Most of North America south of the Arctic Circle excluding northeastern North America Remarks: Eastern and western coyotes meet in western Pennsylvania and New York, with relatively pure western Coyotes in Ohio	
2. Northeastern Coyote/Coywolf (*Canis latrans* × *C. lycaon*), 13.6–22.7 kg Range: Northeastern North America from southeastern Canada to the New Jersey–New York region Remark: Status of canids in the southeastern United States is still not fully established, but zones of hybridization between western Coyotes and Red Wolves are believed to occur	
3. Eastern Wolf (*Canis lycaon* or *C. lupus lycaon*), 22.7–31.8 kg Range: Formerly eastern North America from southeastern Canada to the southeastern United States; now relict populations (see text) Remarks: The Red Wolf (*C. rufus*) in the southeastern United States is included in this category	
4. Gray Wolf × Eastern Wolf hybrids (*Canis lupus* × *C. lycaon* and *C. lycaon* × *C. lupus*), 27.3–40.9 kg; "Great Lakes wolf" Range: Great Lakes region between the ranges of the Eastern Wolf and the Gray Wolf, including Minnesota, Michigan, Wisconsin, and southern Ontario around the Great Lakes	
5. Gray Wolf (*Canis lupus*), 36.4–59.1 kg Range: Western North America into eastern North America, where it hybridizes with the Eastern Wolf around the western Great Lakes region Remarks: Largest types are found in Alaska south to the Rocky Mountains	

Although the majority of scientists accept the Eastern Wolf as a distinct taxon, vonHoldt et al. (2011), using high-density single nucleotide polymorphism (SNPs) genotyping arrays, describes only the Coyote and the Gray Wolf as distinct entities in North America and treats all other types of canids (e.g., northeastern Coyote, Red Wolf, Eastern Wolf, "Great Lakes" Wolf) as hybrids with varying degrees of admixture between Coyotes and Gray Wolves. Because all members of the genus *Canis* are karyotypically identical and they interbreed, Coppinger et al. (2010) argued that the different *Canis* could be recognized as subspecies of an overall species.

However, a comprehensive review of the taxonomy of wolves in North America supports the Eastern Wolf as a distinct taxon (Chambers et al. 2012). Furthermore, in a reply to vonHoldt et al. (2011), Rutledge et al. (2012a) stated that SNPs should not be viewed as an indiscriminate replacement for other biological (e.g., body size) and complementary genetic data (e.g., mtDNA, microsatellites, Y-chromosomes) and that there was indeed compelling evidence to support the Eastern Wolf as a distinct species.

Domestic dog influence

vonHoldt et al. (2011, page 7) described the northeastern Coyote as being much more like a Coyote (82%) than a wolf (~9%) (and dog, ~9%). vonHoldt et al. (2011) also describes the Red Wolf as being more like a Coyote (75%) than a wolf (25%). The more accepted theory of the Eastern Wolf being distinct and closely related to Coyotes, however, would suggest that the degree of wolf influence found in northeastern Coyotes (and in Red Wolves) could be underestimated by vonHoldt et al. (2011). Furthermore, there is considerable evidence that Gray × Eastern Wolf hybrids (i.e., Great Lakes Wolves) and Gray Wolves do not hybridize with western Coyotes (Mech 2010; Wheeldon et al. 2010b; Mech 2011). Thus, the alternative theory or interpretation proposed by vonHoldt et al. (2011) requires confirmation that interspecific mating between western Coyotes and Gray Wolves occurs (Mech 2010).

The discovery of domestic dog DNA in northeastern Coyotes (vonHoldt et al. 2011) warrants additional research. Previously, Coyote × domestic dog interbreeding was suspected to occur only in the southeastern U.S. (Adams et al. 2003a). Way et al. (2010), using mtDNA and nuclear microsatellites, detected no domestic dog DNA in northeastern Coyotes and outlined reasons why Coyote × domestic dog interbreeding probably did not occur in northeastern canids. Kays et al. (2010) found one partial sequence of a domestic dog-like haplotype (from Vermont) in 453 samples from throughout the northeast. The authors did not elaborate on this but it is possible that this animal was an F_1 Coyote × domestic dog hybrid which might have never reproduced in the wild.

vonHoldt et al. (2011) claimed that this hybridization took place ~30 years ago (1980s), yet by that time Coyotes had already colonized most of northeastern North America (Parker 1995), making it unlikely that they repeatedly hybridized with domestic dogs once they were already well established in the region (i.e., compared to a more ancient hybridization scenario) (see Adams et al. 2003a).

Conclusions regarding hybridization in eastern Canis

With changing land use patterns, hybridization should not be viewed as a negative influence, as it may enhance the adaptive potential of both western Coyotes and Eastern Wolves, allowing northeastern Coyotes to more effectively exploit available resources in northeastern North America (Kyle et al. 2006), similar to what has been observed in hybrid amphibians (Parris et al. 1999) and eels (*Anguilla* spp.) (Albert et al. 2006).

Because the currently accepted view that the original species of wolf found in northeastern North America was the Eastern Wolf and not the Gray Wolf (Wilson et al. 2009; Fain et al. 2010; Mech 2010, 2011; Chambers et al. 2012; Rutledge et al. 2012a, 2012b) (although see vonHoldt et al. 2011), the northeastern Coyote (harboring Eastern Wolf genes) likely retains some of the original genetic diversity of canids from northeastern North America, even from areas where the Eastern Wolf has been extirpated (Murray and Waits 2007; Kyle et al. 2008).

Hybridization can be important for adaptive evolution when hybrid genotypes have high fitness levels (Arnold et al. 1999). Albert et al. (2006) similarly noted that natural selection may influence the relative fitness of hybrids in terms of differential survival and may therefore modulate the observed proportion of hybrids. Given that Eastern Wolves are functionally extinct in most of northeastern North America (Benson et al. 2012; Wheeldon and Patterson 2012) and northeastern Coyotes colonized the region five times faster than western Coyotes coming from south of the Great Lakes through the Ohio area (Kays et al. 2010), the elevated survival and fitness levels of northeastern Coyotes in anthropogenically altered northeastern North America suggest that this canid is better adapted to this region—at least in areas south of the Moose-dominated "North Woods" of northern New England. Thus, it appears that hybridization in this case positively benefited two closely related species, whereby Eastern Wolf genes now persist in an area where the animal has been extirpated, and western Coyote genes have spread to an area where they previously did not exist (Kays et al. 2010). Finally, Coppinger et al. (2010) argued that hybridization should not be artificially prevented, as it may increase genetic variability and in some instances creates phenotypic novelties (such as the northeastern Coyote).

Nomenclature of hybrid canids in eastern North America

Hybridization of Eastern Wolves and western Coyotes (and potentially domestic dogs) over the past century has produced a highly adaptable animal with the potential for divergence along a spectrum of Coyote and wolf-like characteristics. Recent considerations of introgressive hybridization have suggested that the transfer of genetic material can be a source of genetic variation for adaptive characteristics, distinct from the parental species, thereby promoting reticulate evolution (Jiggins and Mallet 2000; Allendorf et al. 2001). Evidence of this adaptive potential is the convergence of northeastern Coyotes to more wolf-like phenotypes (Figure 3) (Way and Prioetto 2005; Way 2007a).

Renaming the northeastern Coyote to "Coywolf"

Chambers (2010, page 209) suggested that northeastern Coyotes are a part of a larger Coyote population that extends to the west and south (see Figure 1). Conversely, a similar argument could be made that northeastern Coyotes are a southern extension of hybridized Eastern Wolf populations (Wilson et al. 2009, Benson et al. 2012). I suggest that northeastern Coyotes should most appropriately be called "Coywolves," *Canis latrans* × *C. lycaon,* as this terminology most succinctly describes their mixed heritage and current unique genetic (Kays et al. 2010; Way et al. 2010; vonHoldt et al. 2011, page 5 and Figure S5) and morphological characteristics (this study; Way 2007a).

The term Coywolf uses the portmanteau method (i.e., a word formed by combining two other words) of naming, whereby the first word (i.e., Coyote) of the combined two is the more dominant or robust descriptor of that term. It does not suggest that this animal is equally or more wolf than Coyote. Furthermore, I believe that the vernacular terms Coyote, eastern Coyote, and northeastern Coyote (Parker 1995; Chambers 2010; vonHoldt et al. 2011) undervalue the importance of the Eastern Wolf in the ancestry of this canid, effectively ignoring the fact that (1) ~1/3 of the population's mtDNA (C1 haplotype) is derived from the Eastern Wolf (Kays et al. 2010; Rutledge et al. 2010b); (2) another >1/3 (C9 haplotype) is not found in western Coyote populations but is found in Eastern Wolves (Rutledge et al. 2010b; Way et al. 2010; Rutledge et al. 2012b, page 26); note: the C9 haplotype has also been found in low frequency in Great Lakes states (Wheeldon et al. 2010b) and mid-Atlantic region coyotes (Bozarth et al. 2011) but this may also be a product of Coyote × Eastern Wolf hybridization); (Wheeldon et al. 2010b, Bozarth et al. 2011); (3) microsatellite DNA indicate they are unique and separate from western Coyotes and Eastern Wolves (Way et al. 2010), despite the objections recorded in Chambers (2010); (4) they share Y-microsatellite haplotypes with Eastern Wolves (Rutledge et al. 2012b); and (5) they are morphologically unique from both of their parent species (this study). These points run counter to the claim in Chambers (2010) that they are mostly coyotes.

The recent discovery of domestic dog DNA in northeastern Coyotes (vonHoldt et al. 2011; Wheeldon and Patterson 2012) need not change this terminology, since (1) this discovery does not appear to affect the phenotype and ecology of this hybrid animal; (2) the term Coywolf most accurately describes this animal, especially since Red Wolves are described by vonHoldt et al. (2011) as only 7% less (75% vs. 82%) like the Coyote than northeastern Coyote; and (3) Chambers et al. (2012, page 32) acknowledges the introgression of domestic dog DNA into wild populations of some other *Canis*, such as Red Wolves. In addition, Anderson et al. (2009) asserted that domestic dogs are responsible for melanism in Gray Wolves in North America indicating that dogs also hybridized with wolves historically.

Future research should examine the biological species concept (Mayr 1942) in northeastern Coyotes and related *Canis*. For example, Albert et al. (2006) noted that populations that remain reproductively isolated and are almost entirely genetically distinct fulfill the criteria of distinct biological species despite the potential for gene flow with other species. Using this description, it appears that the Coywolf would qualify as a species in most of its range even though they hybridize with Eastern Wolves and western Coyotes where they are sympatric such as southeastern Canada and western New York and Pennsylvania (Figure 1).

Five types of Canis

"Here, I propose the five types of *Canis* found in North America (from smallest to largest) as (1) the western Coyote (*Canis latrans*); (2) the northeastern Coyote or Coywolf (*C. latrans* × *C. lycaon*) (east of 80° west longitude, including New England, New York, New Jersey, Pennsylvania, Ontario, and Quebec); (3) the Eastern Wolf (*C. lycaon*, including *C. rufus*); (4) the Eastern × Gray or Gray × Eastern wolf hybrids (also called the Great Lakes Wolf) (*C. lupus* × *C. lycaon* and *C. lycaon* × *C. lupus*) in the Minnesota–Ontario (western Great Lakes) area (see Koblmuller et al. 2009; Wheeldon and White 2009; Fain et al. 2010; Mech 2010); and (5) the western Gray Wolf (*C. lupus*) (Figure 1) (Table 2).

In addition to the five types of *Canis* described in Table 2, three possible additional genetic and morphological groupings could consist of the Mexican Gray Wolf (*Canis lupus baileyi*) (vonHoldt et al. 2011; Chambers et al. 2012), the mid-Atlantic Coyote (*Canis latrans*) (Bozarth et al. 2011), and the southeastern Coyote (*Canis latrans*) (Adams et al. 2003a, b; vonHoldt et al. 2011). Wolves in Mexico are possibly the remnant of an early expansion of the Gray Wolf into North America, while research in the mid-Atlantic (Virginia) area indicates that Coyotes there are a product of hybridization between northeastern Coyotes from the north and western Coyotes from the west; hence they are an intermediate form between the northeastern Coyote and the western Coyote. vonHoldt et al. (2011) noted that mid-Atlantic and southeastern Coyote also have domestic dog genetic influence, and the southeastern Coyote may also have Red Wolf and/or Gray Wolf influence as well (Adams et al. 2003a, b).

The classification scheme (Table 2) that I propose is also supported by recent research (e.g., vonHoldt et al. 2011, page 1 and Figure 1). Despite their belief that the Eastern Wolf (which they incorrectly grouped with the Great Lakes Wolf) never existed in a pure form, vonHoldt et al. (2011) divides the four morphologically distinct wolf-like canids into the Gray Wolf, Red Wolf (i.e., Eastern Wolf), Great Lakes Wolf (i.e., Gray Wolf × Eastern Wolf hybrids), and Coyote. This study and Way (2007a) confirm that northeastern Coyotes or Coywolves are also morphologically distinct and hence warrant a fifth grouping of *Canis* in North America. Furthermore, vonHoldt et al. (2011, Figure S5) even recognized them as being a unique form of "Coyote". The continuum proposed here is applicable even with conflicting genetic interpretations (e.g., Koblmuller et al. 2009; Wilson et al. 2009; Fain et al. 2010; Mech 2010, 2011; vonHoldt et al. 2011; Chambers et al. 2012; Rutledge et al. 2012a).

Wolf recovery in the northeastern U.S.

With this "*Canis* soup" of different, but closely related, species (there is gene flow from *C. lycaon* to *C. lupus*) (Grewal et al. 2004; Wheeldon and White 2009; Wilson et al. 2009) and from *C. lycaon* to *C. latrans* (Wilson et al. 2009; Way et al. 2010; Rutledge et al. 2012b), distinct species status for any canid complicates conservation efforts, including *C. lupus* in eastern North America (e.g., Kolenosky 1985; Wilson et al. 2009; Fain et al. 2010; vonHoldt et al. 2011).

Wolves are listed under the Endangered Species Act in the northeastern U.S. with the goal of re-establishing viable populations of the "Eastern Timber Wolf" (stated as *Canis lupus lycaon*) (Eastern Timber Wolf Recovery Team 1992) but revised to *Canis lycaon* (Chambers et al. 2012)). From a conservation/recovery perspective, initiatives involving the re-introduction of Eastern/Red Wolves (i.e., Type 3 Wolf) or Gray Wolf × Eastern Wolf hybrids (Type 4) (Table 2) into the region will be affected by their relationship with northeastern Coyotes (Wilson et al. 2009). Any Eastern Wolves colonizing northeastern North America may already be assumed to be large "Coyotes" by state wildlife agencies because of their morphological and genetic similarities to northeastern Coyotes (Benson et al. 2012).

If the reintroduction of the Eastern Wolf into the northeast is intrinsically important because it historically existed in the northeastern U.S. and was extirpated as a result of human activities (Fain et al. 2010; Chambers et al. 2012), the feasibility of maintaining such a population sympatric with the northeastern Coyote must be addressed. The movement of Eastern Wolves into the northeastern U.S. states, such as New York and Maine, might serve only to increase introgression of *C. lycaon* into the current *C. latrans* × *C. lycaon* gene pool without achieving the re-establishment of a more wolf-like canid (i.e., Types 3–5) (Table 2), especially if all *Canis* in the region are not adequately protected (Rutledge et al. 2012b).

Alternatively, a Type 4 or Type 5 canid may be more appropriate to fill the role of an apex canid in the Moose-dominated system of northern New England and, perhaps most importantly, a Type 4 or Type 5 canid does not commonly hybridize with northeastern Coyotes (Wheeldon et al. 2010b; Benson et al. 2012; Wheeldon and Patterson 2012). Nonetheless, a recovery plan for the northeastern U.S. might allow the northeastern Coyote to evolve, given the potentially adaptive hybrid genome inhabiting these regions, as observed through the recent emergence of large wolf-like "Coyotes" in New England, and allow naturally colonizing (or reintroduced) wolves either to hybridize with them or to form their own populations.

This would require levels of protection (e.g., such as listing *Canis* Types 2–4 or 2–5 under the Endangered Species Act due to similarity of appearances between them) (Figure 3) not currently afforded to northeastern Coyotes in the northeastern United States. Therefore, I agree with Rutledge et al. (2010a) that reducing levels of exploitation by expanding no-harvest zones and/or instituting bag limits and strict harvest regulations would be a relatively simple and inexpensive long-term way to promote the persistence of top predators, especially in a region experiencing hybridization, such as in northeastern North America (Rutledge et al. 2012b).

Acknowledgements

B. White and his research team analyzed the DNA samples and have provided many important theories and perspectives over the past decade that greatly influenced this article. L. D. Mech provided useful comments throughout the manuscript. J. T. Bruskotter provided valuable suggestions on a refined version of the manuscript. Four anonymous reviewers provided helpful comments through two revisions.

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Received 8 February 2012
Accepted 30 December 2012

APPENDIX 1. Average body mass of western Coyotes (*Canis latrans*) (areas outside of northeastern North America), northeastern (eastern) Coyotes/Coywolves (*Canis latrans* × *C. lycaon*), and Eastern Wolves (*C. lycaon* or *C. lupus lycaon*).

Location	Mean mass		Source	Comments
	Male	Female		
Western Coyote				
Western United States	11.4	10.5	Bekoff and Jameson (1975)	Extrapolated male and female based on 11 kg average
Idaho	10.7	8.9	Barnum et al. (1979)	*n* = 56 total males and females
New Mexico	11.6	9.5	Windberg et al. (1997)	*n* = 21 males, 13 females
New Mexico	11.1	10.1	Young and Jackson (1951)	*n* = 446 males, 383 females; maximum = 18.6 kg for males, 15 kg females
Northeastern Arizona	10.5	8.8	Witham (1977)	*n* = 10 males,7 females; maximum = 12.7 kg male
Tucson, Arizona	11.9	10.2	Grinder and Krausman (2001)	*n* = 6 males,7 females; maximum = 15.5 kg
North-coastal California	11.6	10.4	Neale et al. (1998)	*n* not given
California	10.9	9.8	Hawthorne (1971)	*n* not given
Kansas	13.3	11.6	Gipson and Kamler (2002)	*n* = 5 males, 8 females
Kansas	14.1	11.8	Gier (1968)	*n* not given
Texas	12.6	10.5	Young and Jackson (1951)	*n* = 46 males, 38 females
Oklahoma	11.9	NA	Young and Jackson (1951)	*n* = 196 males
Iowa	13	11.4	Andrews and Boggess (1978)	*n* not given
Northern Minnesota	13.2	12	Berg and Chesness (1978)	*n* = 204 total males and females
Yellowstone National Park	13.6	11.8	Crabtree and Sheldon (1999)	*n* not given, but many captures (B. Crabtree, personal communication)
Jasper National Park, Alberta	12.1	11.5	Bowen (1982)	*n* = 19 males, 20 females
Alaska	12.9	11.1	Thurber and Peterson (1991)	*n* = 26 males, 28 females
Minnesota	12.8	11.4	Smith et al. (unpublished data) *cited by* Mech and Paul (2008)	*n* = 39 males, 30 females
Mean	12.2	10.7		
Standard deviation	1.1	1.0		
Northeastern Coyote/Coywolf				
Cape Cod/eastern Massachusetts	18.0	16.2	this study, Way (2007a)	*n* = 18 males, 17 females; 12.3–25 kg for males, 25.1 kg for 1 female
Rhode Island	16.6	15.3	C. Brown, Rhode Island Fish and Game (personal communication)	*n* = 21 males, 15 females; maximum male = 20.9 kg, maximum female = 21.4 kg
New Hampshire	20.4	17.9	Silver and Silver (1969)	*n* = 15 males, 13 females
Vermont	17.8	16.6	Person (1988)	*n* = 10 males, 7 females; maximum = 21.4 kg
Western Massachusetts/Vermont	16.9	14.5	Lorenz (1978)	*n* = 24 males, 18 females; 5 males and 1 female ≥19 kg; maximum = 25 kg male
Adirondacks, New York	14.2	11.9	Brundige (1993)	*n* = 19 total males and females
Maine	15.9	14.5	Hilton (1976)	*n* = 37 males, 22 females
Maine	15.8	13.7	Richens and Hugie (1974)	*n* = 28 males, 20 females
Maine	17.3	15.5	Harrison (1986)	*n* = 60 total males and females; maximum = 20.5 kg

APPENDIX 1. (*continued*)

Location	Mean mass: Male	Mean mass: Female	Source	Comments
Southeastern Quebec	16	14.1	Poulle et al. (1995)	*n* = 28 males, 21 females; autumn samples
Ontario	14.5	NA	Kolenosky (1971)	*n* = 19 males
Eastern New Brunswick	14.6	13.1	Dumond and Villard (2000)	*n* = 44 males, 43 females
New Brunswick/Nova Scotia	16.6	15.2	Moore and Millar (1986)	*n* = 50 males, 23 females
Nova Scotia	15.4	12.6	Sabean (1993)	*n* = 85 males, 44 females; maximum = 21.7 kg male
Nova Scotia	16.5	13.7	Parker (1995)	*n* = 89 total males and females; maximum = 25.9 kg male
Prince Edward Island	16	15	Parker (1995)	*n* = 90 total males and females; maximum = 25 kg male
Northeastern Ontario	17.3	14.7	Wheeldon and Patterson (2012)	*n* = 44 males, 38 males; maximum = 22.8 kg male, 18.0 kg female
Mean	16.5	14.7		
Standard deviation	1.5	1.5		
Eastern Wolf				
Extreme northeastern Minnesota	30.6	26.3	Van Ballenberghe (1977); cf. Mech and Paul (2008)	*n* = 36 males, 32 females
Algonquin Provincial Park	30.3	23.9	Theberge and Theberge (2004)	*n* = 48 males, 40 females
Algonquin	30	26	Rutledge et al. (2010b)	Not included in analysis because Algonquin Provincial Park data already reported by Theberge and Theberge (2004); Benson et al. (2012) also provided similar values from the Algonquin region.
Red Wolves reintroduced into North Carolina	29.8	24.8	G. Henry (personal communication); *cited in* Theberge and Theberge (2004)	*n* = 21 males, 29 females
Red Wolves captured in Texas 1968–1972	23.7	21.2	Riley and McBride (1975)	*Cited in* Theberge and Theberge (2004)
Arkansas Red Wolves	27.6	21.6	Paradiso and Nowak (1972)	*n* = 23 males, 34 females
Algonquin 1964–1965	27.3	24.2	Pimlott et al. (1969)	*n* = 40 males, 33 females
Mean	28.2	23.7		
Standard deviation	2.6	1.9		