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Dispelling myths about the origins of wolf–coyote hybrids and related *Canis* species in Ontario

Tyler Wheeldon^{1,*} and Brent Patterson¹

¹Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Trent University, DNA Building, 2140 East Bank Drive, Peterborough, Ontario K9L 1Z8 Canada

*Corresponding author: tyler.wheeldon@ontario.ca

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Abstract

Long-standing myths exist about the origins of wolf-coyote hybrids and related *Canis* species in Ontario. Specifically, there is a perceived controversy whether they are the product of natural hybridization that occurred between wolves and coyotes in the wild during the last century or the descendants of animals that escaped or were released from captive colonies or controlled breeding experiments. We review the relevant evidence and conclude that captive colonies and controlled breeding experiments were unlikely to have played any role in the origins of wolf-coyote hybrids and related *Canis* species in Ontario.

Key words: Algonquin Wolf; Eastern Coyote; Eastern Wolf; wolf-coyote hybrids; captive colonies; controlled breeding experiments

Introduction

Long-standing myths exist about the origins of wolf-coyote hybrids and related Canis species in Ontario, the latter of which include Algonquin Wolf (Canis sp.) and Eastern Coyote (Canis latrans var.). Specifically, there is a perceived controversy whether they are the product of natural hybridization that occurred between wolves and coyotes in the wild during the last century or the descendants of animals that escaped or were released from captive colonies or controlled breeding experiments. The myths that caused this perceived controversy held by a vocal minority of public stakeholders relate to the Ontario Ministry of Natural Resources and Forestry (OMNRF; formerly the Ontario Department of Lands and Forests and the Ontario Ministry of Natural Resources) and their alleged direct or indirect role in breeding wolves, coyotes, and/or their hybrids for release into the wild; encouraging hybridization or augmentation of canids in Ontario; and releasing hybrid or non-native canids into the wild. Although these myths, propagated decades ago by members of the public, have been debunked by employees of the OMNRF (Kolenosky et al. 1964), they persist.

A detailed review of the taxonomy of *Canis* species in Ontario and interbreeding among them is beyond the scope of this article, but interested readers are encouraged to consult available literature reviews for relevant information (Chambers et al. 2012; Way and Lynn 2016; vonHoldt and Aardema 2020). Way and Hirten (2019) also provide a pictorial representation of North American Canis species that may be helpful. Briefly, Algonquin Wolf (sensu COSSARO 2016) derive from Eastern Wolf (Canis lycaon) that hybridized with western Coyote (Canis latrans) and Gray Wolf (Canis lupus; Rutledge et al. 2010, 2012); Eastern Coyote (sensu Hilton 1978; Parker 1995) derive from western Coyote that hybridized with Eastern Wolf and Domestic Dog (Canis familiaris; Wheeldon et al. 2010, 2013). Notably, Algonquin Wolf has effectively replaced Eastern Wolf, whereas Eastern Coyote has merely extended the range of western Coyote (albeit in modified form). Hybridization occurs between Algonquin Wolf and Eastern Coyote in central Ontario, including near Algonquin Park, such that wolves, coyotes, and their hybrids occur across the landscape (Benson et al. 2012), complicating management of wolves and coyotes (Beacon Environmental Limited and Wildlife 2000 Consulting 2018).

There were contrasting views of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the Committee on the Status of Species at Risk in Ontario (COSSARO) regarding the taxon known as both Eastern Wolf and Algonquin Wolf. In 2015, COSEWIC recognized Eastern Wolf as a unique species (defined under the federal *Species at Risk Act* [SARA]), *Canis* sp. cf. *lycaon*, and assessed it as Threatened in Canada, noting that its range included central Ontario and southern Quebec. It was listed as Special Concern under SARA in 2003, a status it retains (SARA Registry 2021). COSEWIC (2015: iv) stated that

Eastern Wolf is best defined by a combination of genetic distinctiveness, morphological characters, and an ecological role associated with a feeding preference for smaller prey than fed on by Gray Wolf.

COSEWIC (2015: iv) recognized that "the taxonomy of Eastern Wolf is under debate" and that "the Eastern Wolf population has a degree of hybridization with Coyote".

In 2016, COSSARO recognized Algonquin Wolf as a unique species (defined under Ontario's *Endangered Species Act* [ESA]), *Canis* sp., and assessed it as Threatened in Ontario, noting that its occurrence was concentrated in various protected areas of central Ontario. It was listed as Threatened under Ontario's ESA in 2016. COSSARO (2016: 8) stated that "Algonquin Wolf is most appropriately described as a hybrid group that collectively represents a genetically discrete cluster with distinct morphological characteristics". COSSARO (2016: 9) explained that it

named this taxon Algonquin Wolf to a) differentiate it from other populations that have been [inappropriately] labelled 'Eastern Wolf' (e.g., hybrids in the Great Lakes region, which are genetically distinct from the Algonquin Wolf), and b) acknowledge the hybrid ancestry of this evolutionarily significant unit.

However, although COSEWIC and COSSARO used different names for this taxon (Eastern Wolf versus Algonquin Wolf), COSSARO (2016: 9) clarified that "these two taxa are considered to have the same genetic characteristics". Accordingly, Eastern Wolf and Algonquin Wolf were synonymous in a contemporary context, but the former supplanted the latter in a historical context (i.e., before the wolf-coyote hybridization that occurred during the last century), because only the former was appropriate when referring to this taxon in its original form. Notably, in late 2021, COSSARO adopted a name change for Algonquin Wolf to "better reflect the outcome of discussions regarding genetics", whereby it will be referred to as Eastern Wolf, consistent with COSEWIC (COS-SARO 2021). We have used the names Algonquin Wolf and Eastern Wolf for this taxon, where appropriate, based on prior context and for the purpose of differentiating between its contemporary and historical forms, respectively.

The 2016 listing of Algonquin Wolf as Threatened under Ontario's ESA led to additional protection for wolves and coyotes in parts of central Ontario, which elicited criticism from some public stakeholders, some of whom cited the perceived controversy regarding the origin of Algonquin Wolf. Indeed, the aforementioned myths were propagated in response to the 2016 listing of Algonquin Wolf as Threatened and the subsequent posting of the draft recovery strategy (Beacon Environmental Limited and Wildlife 2000 Consulting 2018) on the Environmental Registry. Hence, it is important to resolve the issue.

Here, we review the relevant evidence to resolve the origins of wolf-coyote hybrids and related *Canis* species in Ontario. First, we address the history of captive colonies and controlled breeding experiments. Second, we address the results of morphological and genetic investigations.

Captive Colonies

Between 1956 and 1968, the OMNRF maintained captive colonies of wolves, coyotes, and coyote–dog hybrids for research purposes at the Wildlife Research Station in Algonquin Park. The history of the captive colonies is documented by several sources (e.g., Standfield 1954; Pimlott 1961; Kolenosky *et al.* 1964; Rutter and Pimlott 1968; Pimlott *et al.* 1969).

Standfield (1954) documented that a litter of seven coyote-dog hybrids and a litter of five "brush wolves" (i.e., coyotes) were removed from dens in the Niagara Peninsula and raised to sexual maturity in captivity. He noted that the captive animals were maintained at the Southern Research Station at Maple (they were later transferred to the Wildlife Research Station in Algonquin Park). He also detailed planned breeding experiments, including hybrid brother × sister matings, brush wolf and Domestic Dog matings, and a brush wolf brother × sister mating, which were intended to be completed in 1956. Standfield (1954) indicated that the purpose of the planned breeding experiments among captive animals was to study the inheritance of certain morphological characters noted in hybrids collected in Ontario. He noted that the female parent of the hybrid litter was being used in the breeding program. Standfield (1954: 5) stated that "Two brother \times sister matings of hybrid animals have been successful: three young being produced in one litter and four in the other". He indicated that the breeding program would continue until 1956 and that the breeding population would probably continue at a level of 12 animals.

Pimlott (1961) noted that coyote–dog hybrids in the captive colony at one time numbered over 40 animals. He also mentioned obtaining a series of tape recordings of the howls of the captive animals, which were played to elicit replies from wild wolves, a technique applied to locate wolf packs in Algonquin Park (Joslin 1967).

Kolenosky *et al.* (1964: 1, 10) acknowledged that "the purposes and activities of the [OMNRF's] program have been occasionally misrepresented and often misunderstood" and that "[occasionally] some extravagant rumours have circulated about the research program in Algonquin Park". Commenting on the purpose of the captive colonies, Kolenosky *et al.* (1964: 10) clarified that

These are used for breeding experiments, as a basis for identifying wild-caught hybrids [referring to coyote–dog hybrids] which are presented for bounty, for developing methods to determine ages of wild wolves, for testing the effects of poisons and drugs, for testing new marking devices such as collars and tags and for other experimental purposes as they are required.

They documented that in 1959 and 1960 the program biologist used tame "Eastern Timber Wolves" from the captive colony to travel with him in the bush to locate wild packs, but the animals were returned to captivity at the end of each trip. Kolenosky *et al.* (1964: 10–11) also stated the following:

Wolves are not being bred for releasing in Algonquin Park ... All the timber wolves that have ever been part of this captive colony are either still caged or are now dead. None have been released to augment the wild population. There has never been any research or management program to breed and release wolves in any area of Ontario nor has it ever been contemplated. Wolves are not being imported from Alaska or any other area to be released in Algonquin Park ... The importation and release of wolves has never been suggested for any area of Ontario; least of all for Algonquin Park.

Rutter and Pimlott (1968) documented multiple wolves from the captive colony, including two litters of five wolf pups, which were obtained from Moosonee, Ontario, in spring 1960 and Black Donald, Ontario, in spring 1961, and whose fates were explicitly detailed. They documented that the wolf pups from these litters were temporarily placed on an island in Potter Lake in Algonquin Park in the summers of 1960 and 1961 (with a pair of yearling wolves in the latter). They also documented multiple instances of certain wolves from the captive colony temporarily roaming freely (i.e., lost and found).

Pimlott *et al.* (1969) confirmed that captive colonies of wolves, coyotes, and coyote–dog hybrids were maintained at the Wildlife Research Station in Algonquin Park from 1956 to 1968. They also mentioned captive wolves in the context of two studies on wolf howling and captive wolves and coyotes in the context of testing drugs for use in capturing and handling wolves.

Notably, none of these sources mention that any wolves from the captive colonies escaped or were released into the wild permanently, i.e., those that escaped or were released into the wild were later returned to captivity. Similarly, none of these sources mention that any coyotes or coyote–dog hybrids from the captive colonies escaped or were released into the wild permanently or even temporarily. Collectively, these sources indicate that the captive colonies were used for research purposes, not manipulation of wild canid populations.

Controlled Breeding Experiments

Between 1969 and 1983, the OMNRF carried out a series of controlled breeding experiments with Ontario canids for research purposes (Kolenosky 1971; Schmitz and Kolenosky 1985a).

Kolenosky (1971) reported that a female wolf mated with a male coyote and produced two hybrid litters in captivity. The wolf was taken from Lawrence Township, Algonquin Park (captured in the wild on 24 August 1964) and the coyote was taken from East Gwillimbury Township, York County (removed from a den on 23 April 1966). On 14 May 1969, the wolf produced the first hybrid litter of five pups; two pups were killed and consumed by the wolf on 7 July 1969. On 20 May 1970, the wolf produced the second hybrid litter of five pups; one pup was killed and consumed by one of the parents (probably the wolf) ~17 days after birth. Kolenosky (1971: 449) stated that "Further crosses involving the original parents and the two litters of offspring [were] planned". Interestingly, Standfield (1970: 35) stated that "a reciprocal cross was not successful", indicating that an attempt was made to cross a male wolf and a female coyote, which was not reported by Kolenosky (1971).

Schmitz and Kolenosky (1985a) reported further crosses, including sibling crosses of F1 hybrids, which produced F2 hybrids. They also reported the crossing of one F1 hybrid female with the male coyote parent, which produced back-crosses. The numbers of F1 hybrids, F2 hybrids, and back-crosses produced during the controlled breeding experiments were not explicitly detailed. However, carcasses from 28 adults were used for comparison of body morphometrics among the parents, F1 hybrids, F2 hybrids, and backcrosses. Thus, it seems that all the animals involved in the controlled breeding experiments were euthanized for the collection of data or died in captivity.

Neither Kolenosky (1971) nor Schmitz and

Kolenosky (1985a) reported any instances of escape or release of captive wolf–coyote hybrids into the wild. Schmitz and Kolenosky (1985a) indicated that the controlled breeding experiments were carried out to test the wolf–coyote hybrid hypothesis, which was formulated to explain the origins of the "wild canids of questionable identity" (Kolenosky 1971: 446) in eastern North America, specimens of which Silver and Silver (1969) observed in captivity with the objective of establishing their identity. The controlled breeding experiments clarified that wolf–coyote hybridization was possible and that the "wild canids of questionable identity" in eastern North America plausibly originated from wolf–coyote hybridization that had occurred naturally in the wild.

Wolf–Coyote Hybridization in the Wild

Several studies provide evidence that wolf–coyote hybridization had occurred naturally in the wild in Ontario before the controlled breeding experiments.

Schmitz and Kolenosky (1985b) analyzed and compared body morphometrics and skull characters among various Canis specimens, including several groups of wolves and coyotes for which data were obtained from carcass samples collected in Ontario by the OMNRF between 1959 and 1969 (i.e., before the controlled breeding experiments), and wolf-coyote hybrids for which data were obtained from specimens raised in captivity (i.e., originating from the controlled breeding experiments). They tentatively concluded that the most parsimonious explanation was that coyotes in southeastern and central Ontario, which resembled wolf-coyote hybrids, descended from coyotes that hybridized with wolves. Their tentative conclusion implicitly suggests that wolf-coyote hybridization had occurred naturally in the wild in Ontario before the controlled breeding experiments.

Rutledge et al. (2012) analyzed genetic data of historical (1964-1965) and contemporary (1987-1999; 2002-2007) wolf samples from Algonquin Park. These wolf samples showed evidence of mixed ancestry, including varying levels of autosomal admixture and haplotype introgression from coyotes and other wolves. Rutledge et al. (2012) demonstrated that wolves in Algonquin Park (i.e., Algonquin Wolf) descended from Eastern Wolf that hybridized with western Coyote and Gray Wolf, thereby clarifying the evolutionary history of Algonquin Wolf. Their findings indicate that wolf-coyote hybridization had occurred naturally in the wild in Ontario before the controlled breeding experiments. Moreover, genetic data revealed that wolf-coyote admixture and the proportion of coyote-like animals occurring in Algonquin Park increased between 1964-1965 and 1987-1999, a finding seemingly corroborated by morphological

data of Algonquin Park wolves that revealed a reduction (although not statistically significant) in the body weight and skull size of females and males, respectively, between those periods (Theberge and Theberge 2004). Rutledge et al. (2012) concluded that the wolf culls conducted in Algonquin Park in 1964-1965 as part of the wolf research program transformed the genetic composition of the Algonquin Park wolf population by facilitating coyote introgression. They suggested that extensive wolf culling prompted some of the remaining wolves in Algonquin Park to mate with individuals from the expanding coyote population. However, the culled wolves already showed evidence of coyote introgression, indicating that wolf-coyote hybridization had occurred before the wolf culls, and, thus, implying that the wolf culls merely exacerbated wolf-coyote hybridization in Algonquin Park.

Wheeldon et al. (2013) analyzed genetic data of historical (1974-1984) and contemporary (2005-2010) coyote samples from southeastern Ontario. These coyote samples showed evidence of mixed ancestry, including varying levels of autosomal admixture and haplotype introgression from wolves and dogs. Wheeldon et al. (2013) demonstrated that coyotes in southeastern Ontario (i.e., Eastern Coyote) descended from western Coyote that hybridized with Eastern Wolf and Domestic Dog, thereby clarifying the evolutionary history of Eastern Coyote. Their findings indicate that wolf-coyote (and coyote-dog) hybridization had occurred naturally in the wild in Ontario not only at the time of the controlled breeding experiments, but also earlier, because the contrasting levels of autosomal admixture and haplotype introgression from wolves (and dogs) observed in the coyote samples imply that backcrossing of wolf-coyote (and coyote-dog) hybrids with coyotes had occurred naturally in the wild in Ontario then, which implies that initial hybridization must have occurred earlier. The coyote-dog hybrids from the captive colony predated the coyote samples, but this seems irrelevant, because suspected covote-dog hybrids occurred in the wild in Ontario before development of the captive colony (Standfield 1954).

Conclusions

The findings of these studies collectively support the origins of wolf-coyote hybrids and related *Canis* species in Ontario via natural hybridization that occurred in the wild. Indeed, the haplotype diversity of Algonquin Wolves (Rutledge *et al.* 2010, 2012) and Eastern Coyotes (Wheeldon *et al.* 2010, 2013) does not support either originating from the descendants of a relatively small number of animals from captive colonies or controlled breeding experiments. Land clearing associated with logging and agriculture, as well as the decline of larger predators, such as wolves, likely facilitated the eastward expansion of coyotes (Young and Jackson 1951; Moore and Parker 1992; Hody and Kays 2018), which brought them into contact with declining wolves in Ontario and resulted in wolfcoyote hybridization (Schmitz and Kolenosky 1985b; Rutledge et al. 2012; Wheeldon et al. 2013). Coincident with the beginning of the controlled breeding experiments, Standfield (1970) described the species and types of canids that occurred in Ontario, including wolves (two types), coyotes, wolf-coyote hybrids, wolf-dog hybrids (infrequent), and coyote-dog hybrids. Standfield (1970: 36) stated that "To the best of our knowledge the present occurrence and distribution of these species and types has been in response to habitat changes and natural movements", which reflects our current understanding of their past and present occurrence and distribution. Standfield (1970: 36) also stated that "There has been no intentional manipulation of populations by man", which, to the best of our knowledge, was true then and remains true at the time of this writing.

In summary, there is no evidence that animals from the captive colonies or controlled breeding experiments escaped or were released into the wild permanently or even temporarily (except certain wolves from the captive colony) in Ontario. The captive colonies were used for research purposes, and the controlled breeding experiments were carried out to test the wolf–coyote hybrid hypothesis. The results of morphological and genetic investigations indicate that wolf–coyote hybridization had occurred naturally in the wild in Ontario before the controlled breeding experiments. We conclude that captive colonies and controlled breeding experiments were unlikely to have played any role in the origins of wolf–coyote hybrids and related *Canis* species in Ontario.

Author Contributions

Writing – Original Draft: T.W. and B.P.; Writing – Review & Editing: T.W. and B.P.

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Please also see the comment by John Theberge in News and Comment, whose work on Ontario canids began during the late 1950s and was present in the early days.