

Clarifying late Holocene Coyote (*Canis latrans*)–Gray Wolf (*Canis lupus*) sympatry in the western Great Lake states

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Thiel, R.P. 2020. Clarifying late Holocene Coyote (*Canis latrans*)–Gray Wolf (*Canis lupus*) sympatry in the western Great Lake states. *Canadian Field-Naturalist* 134(1): 36–41. <https://doi.org/10.22621/cfn.v134i1.2163>

Abstract

North American *Canis* genetics research varies in interpreting the Pre-Columbian distribution of Coyotes (*Canis latrans*). Many studies have relied on generalized species-distribution maps and a few actually cite earlier genetics works as secondary sources. I use archaeological, paleontological, and settlement era documents to demonstrate that Coyotes were present in portions of Minnesota, Wisconsin, and Illinois thousands of years prior to European arrival. This review provides important clarification of historical Coyote distribution in the region and may have implications on the various interpretations of introgressed Coyote haplotypes present in Gray Wolves (*Canis lupus*) throughout the Great Lakes region.

Key words: Coyote (*Canis latrans*); Gray Wolf (*Canis lupus*); Great Lakes region; Coyote-wolf hybridization; Coyote-wolf sympatry; Coyote-wolf haplotypes

Introduction

Lehman *et al.* (1991) published the first study analyzing DNA of *Canis* spp. in North America, reporting Coyote (*Canis latrans*) mtDNA haplotypes in Gray Wolf (*Canis lupus*) samples from the Great Lakes region and eastern Canada. They described Pre-Columbian Coyote distribution as “confined primarily to plains and deserts” (Lehman *et al.* 1999: 105), asserting Coyotes expanded into the Great Lakes region following anthropogenic changes in Gray Wolf distribution, clearing of forests, and introduction of agriculture. They concluded that hybridization between the two species “is taking place in regions where Coyotes have only recently become abundant” (Lehman *et al.* 1999: 104).

Since Lehman *et al.* (1991) many papers have analyzed the genetics of *Canis* populations inhabiting the Great Lakes region. Most focus on introgression of Coyote genes into large wolf-like canids (hereafter referred to as wolves). At least seven subsequent genetics papers refer to Pre-Columbian Coyote distribution in vague terms (Roy *et al.* 1994; Wilson *et al.* 2000; Leonard and Wayne 2008; Koblmüller *et al.* 2009; Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016). VonHoldt *et al.* (2011) supplied a simplified distribution map (their Figure 1) showing Coyotes as far east as Illinois and northwest Indiana. This contrasts with a vonHoldt *et al.* (2016) map (their Figure 1) showing Coyote distribution reaching east to extreme

southwest Minnesota at least 560 km west of Lake Michigan. The use of generalized species-distribution maps generates inconsistencies, especially in defining boundaries, as noted by Shelton and Weckerly (2007).

A trans-Mississippi-west Pre-Columbian distribution of Coyotes has been promoted by many genetics researchers (Lehman *et al.* 1991; Roy *et al.* 1994; Wilson *et al.* 2000; Leonard and Wayne 2008; Koblmüller *et al.* 2009; Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016). Some cite earlier genetics papers (secondary sources) in describing Coyote distributional limits (Wayne *et al.* 1992; Wilson *et al.* 2000; Leonard and Wayne 2008; Bozarth *et al.* 2011; vonHoldt *et al.* 2011).

At least 13 studies claim Coyotes expanded into the Great Lakes region, seven providing arrival dates ranging from 90 to 200 years ago (approximately 1790 to 1920; Lehman *et al.* 1991; Roy *et al.* 1994; Vilà *et al.* 1999; Wilson *et al.* 2000; Grewal *et al.* 2004; Kyle *et al.* 2006; Leonard and Wayne 2008; Koblmüller *et al.* 2009; Kays *et al.* 2010a,b; Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016). Koblmüller *et al.* (2009: 2313) sums this view succinctly: “Over the last century, coyotes have invaded this region and hybridized with wolves”.

Being certain of the temporal and spatial relationships of the two species is central to the interpretation of when, where, how, and if Coyote-wolf hybridization occurred in the Great Lakes region. Having

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

performed extensive historical work on the demise of Gray Wolves in Wisconsin (Thiel 1993), I recognized the Lehman *et al.* (1991: 105) description of Coyote range limited to “plains and deserts”, and many subsequent papers (Roy *et al.* 1994; Vilà *et al.* 1999; Wilson *et al.* 2000; Grewal *et al.* 2004; Kyle *et al.* 2006; Leonard and Wayne 2008; Koblmüller *et al.* 2009, Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016) as erroneous. In order to rectify this problem, I provide documentation of Coyote presence in Wisconsin, Minnesota, and Illinois between the late Holocene and 1850.

Methods

Paleontological, archeological, and settlement era documents were searched for records of Coyotes in Illinois, Minnesota, and Wisconsin (the tri-state region) before 1920. I did not search fur trade era records, an additional source of potential information. I queried the Neotoma Paleocology Database, (NPD, neotomadb.org—earlier version known as FAUNMAP; Graham and Lundelius 1994), a free-access paleontological database, canvassing for specimens morphologically identified as *Canis latrans* in Minnesota, Wisconsin, Illinois, Indiana, and northeastern Iowa with a timeline of 5000 to 400 years before present (YBP). Archeological periodicals from the tri-state region were also searched for documentation of Coyote and wolf remains at Native American sites. Similarly, pioneer accounts from early county histories within the tri-state region were canvassed for accounts of Coyotes and wolves. Unfortunately, many used the ambiguous term, “prairie wolf” that may refer to either *C. latrans* or *C. lupus*. Species identification was aided in narratives that described canid size (height at shoulder <55 cm, Coyote; >55 cm, wolf), weight (10–18 kg, Coyote; >25 kg, wolf; Way and Hirten 2019; R.P.T. pers. obs.), group size, existence of two varieties of wolf, and/or diet (primarily rodents and lagomorphs, Coyote; primarily ungulates, wolf). I organized spatial data to the county level in the tri-state region and noted whether the area was located in grassland or forested biomes using maps generated by Curtis (1959), Anderson (1970), and McMillan (2006). In specific areas I noted temporal aspects of sympatry. I assumed Coyote occurrences prior to the mid-1800s in Minnesota, Wisconsin, and Illinois represented breeding populations because these areas were well beyond normal dispersal distances for Coyotes (>160 km; Pyrah 1984; Geese *et al.* 1989; Harrison 1992), based on an array of genetics literature that placed the eastern continental edge of Coyote range near the Minnesota-Dakota border (Lehman *et al.* 1991; Roy *et al.* 1994; Wilson *et al.* 2000; Leonard

and Wayne 2008; Koblmüller *et al.* 2009; Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016).

Results

The Neotoma Paleocology Database lists five archaeological sites containing Coyote remains in Illinois, two in Indiana, and one each in Minnesota, Wisconsin, and northeast Iowa, dating from 5000 to 3000 YBP to approximately the year 1650. Table 1 lists Coyotes and wolves recorded in paleontological, archeological, and settlement era documents in the tri-state region. Four archaeological documents report on sites also reported in NPD: (1) the Durst Rockshelter in Wisconsin (Theler 2000; Parmalee 1960a), and from Illinois, (2) the Havana River Group (Parmalee 1960b), (3) the Fisher site (Parmalee 1962), and (4) Riverton (Parmalee and Stephens 1972). Two additional Illinois archaeological sites contained Coyote remains 800–300 YBP (Parmalee 1960b). Three archaeological sites in Minnesota did not go beyond the genus, *Canis*, level (Anfinson 1982; Mather 2004, 2006).

Dated Coyote material extends from 5000 to 3000 YBP (Durst Rockshelter, Wisconsin) to 1910. Settler accounts document the presence of Coyotes in all three states, from 1807–1808 (Minnesota) to about 1910 (Illinois). Scientist-naturalist Increase Lapham lists a wolf from Milwaukee County and a Coyote in adjacent Racine County, Wisconsin (Lapham 1853). Even in eastern sites Coyote material dates to well before European contact (Table 1).

Overall, Coyotes and wolves were reported together in eight of 23 occurrences (35%; Table 1). Two archaeological sites reported remains of both species prior to 2000 YBP; three sites between 1000 and 400 YBP; and three sites in the 1800s. Late Holocene overlap between the two species within this region points toward a shared range through much of the region south of the northern forests (Table 1, Figure 1). Sympatric occurrences were limited to areas that favoured Coyote distribution, i.e., prairie and prairie savannah habitats (Curtis 1959; Anderson 1970; McMillan 2000), whereas wolves seemed to roam more widely throughout the region (Table 1; Thiel 1993). Significantly, three Illinois archaeological sites contained remains of both Coyote and wolf. These dated to roughly 2000 to 400 YBP. Additionally, Coyote and wolf occurrences in adjacent counties leave little doubt that Coyotes and wolves were broadly sympatric within tri-state region grasslands.

Discussion

Coyotes were present within prairie and savannah habitats from the South Dakota-Minnesota border to the Illinois-Indiana border for at least several thou-

TABLE 1. Records of Coyotes (*Canis latrans*) and wolves in Illinois, Minnesota, and Wisconsin based on paleontological, archaeological, and European settlement documents.

State	County	Approximate year	Species*	Reference
Minnesota	Blue Earth	1807–1808	C	Anonymous (1881)
	Becker	1878	C W	West and Wilcox (1907)
	Rock & Pipestone	~1885	C	Rose (1911)
Wisconsin	Sauk	5000–3000 YBP	C W	Parmalee (1960a), Theler (2000), NPD 4614
	LaFayette	1831	C	Kinzie (1975)
	La Crosse	3000–400 YBP	W	Theler (2000)
	Crawford	1000–2000 YBP	W	Theler (2000)
	Vernon	1000–400 YBP	W	Theler (2000)
	Iowa	1832	C	Draper (1903)
	Grant	1838	C W	Butterfield (1884)
	Waukesha	1839	C W	Anonymous (1880)
	Milwaukee	<1852	W	Lapham (1853)
	Racine	<1852	C	Lapham (1853)
Illinois	Crawford	2000–800 YBP	C W	Parmalee and Stephens (1972), NPD 7491
	Will	300–800	C W	Parmalee (1962)
	St. Claire	<1650	C	Parmalee (1960b)
	Pike		C W	
	Calhoun		W	
	Cook		C W	Parmalee (1962), NPD 6137
	Fulton		W	Parmalee (1962), NPD 7626
	Williamson		W	Parmalee (1962)
	Bureau	1911	C	Cory (1912)
	Edgar	1830s	C	Anonymous (1879)

*C = Coyote, W = wolf.

sand years prior to the arrival of Europeans (Table 1). Temporal sympatry in archaeological remains is difficult to ascertain, but occurrences of both species at the same sites extend from earlier than 2000 YBP to the point of European contact (approximately 1650). Temporal sympatry during the settlement period, region-wide, is unambiguous. This was captured in maps of two genetics papers (Kays *et al.* 2010b; vonHoldt *et al.* 2011), but papers by Roy *et al.* (1994), Wilson *et al.* (2000), Leonard and Wayne (2008), Koblmüller *et al.* (2009), Bozarth *et al.* (2011), and vonHoldt *et al.* (2016) stand in contrast.

Habitat destruction ($n = 10$) and deforestation ($n = 5$), along with predator control and changes in *Canis* species distributions ($n = 9$), were the most often cited bases for supposed Coyote invasion into the western Great Lakes region (Lehman *et al.* 1991; Wayne *et al.* 1992; Roy *et al.* 1994; Vilà *et al.* 1999; Wilson *et al.* 2000; Grewal *et al.* 2004; Kyle *et al.* 2006; Leonard and Wayne 2008; Koblmüller *et al.* 2009; Chambers 2010; Kays 2010a,b; Bozarth *et al.* 2011; Rutledge *et al.* 2011; vonHoldt *et al.* 2011, 2016). Although First Nations occupied the Great Lakes region greater than

12 000 YBP, and First Nations people impacted ecosystems (see Delcourt and Delcourt 2004 and Riley 2013), large scale, region-wide anthropogenic ecological disturbances did not likely begin until the period between when each state became a United States Territory and each gained statehood: Illinois, 1809 and 1818; Wisconsin, 1836 and 1848; and Minnesota, 1849 and 1858, respectively (Buley 1950; Smith 1985).

Such ecological upheavals may have occasioned Gray Wolf hybridization event(s) as their numbers declined and Coyotes increased, as suggested by many researchers (Lehman *et al.* 1991; Wayne *et al.* 1992; Roy *et al.* 1994; Vilà *et al.* 1999; Wilson *et al.* 2000; Grewal *et al.* 2004; Kyle *et al.* 2006; Leonard and Wayne 2008; Koblmüller *et al.* 2009; Chambers 2010; Kays 2010a,b; Bozarth *et al.* 2011; Rutledge *et al.* 2011; vonHoldt *et al.* 2011, 2016). However, the timing and circumstances of *Canis* population declines and changes in relative abundance of sympatric Coyote and wolf populations in the western Great Lakes states remain unclear.

Direct impacts in region-wide *Canis* populations in response to persecution and ecological upheavals

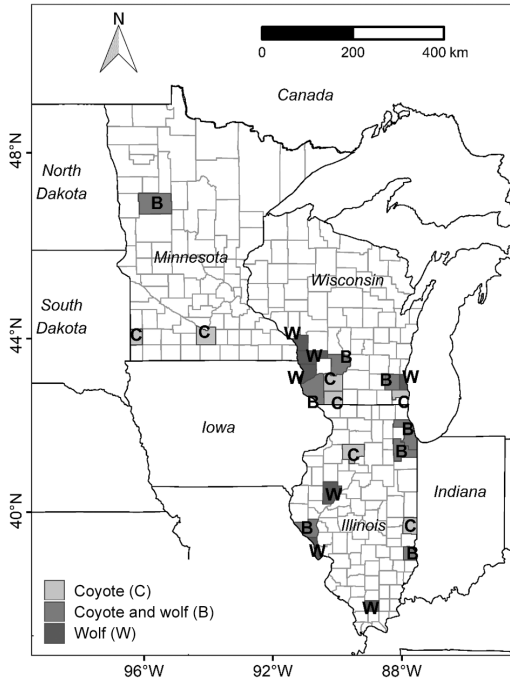


FIGURE 1. The spatial distribution of paleontological, archeological, and settlement era canid records. Occurrences of Coyotes (*Canis latrans*, C), wolves (W), and both Coyotes and wolves (B) are summarized by county in Minnesota, Wisconsin, and Illinois, USA.

caused by settlement likely took decades, generally moving southeast to northwest within the tri-state region. Such impacts likely did not occur during early phases of settlement (e.g., Illinois became a United States Territory in 1809; Minnesota in 1849). Wisconsin territorial bounties on both *Canis* species commenced in 1839, continuing into statehood (1848), but Gray Wolves were not extirpated from southern Wisconsin until the 1880s and northern region until the 1950s. While Coyotes likely expanded their range northwards, they were similarly persecuted throughout Wisconsin during this entire period (Thiel 1993).

Coyotes probably did not occur regularly in the mixed forests surrounding Lake Superior prior to European settlement. However, even there, periodic fire and wind-throw created large temporary openings in which dispersing Coyotes may have occasionally colonized (Schorger 1944, 1953; Loucks 1983). Coyotes expanded north into the Lake Superior basin as anthropogenic destruction of forests resulted in conversion of much of the landscape into impermanent prairie-like conditions (Schorger 1944; Allen 1979; Breitenstein and Thiel *in press*). Kays *et al.* (2010b: 249) map occurrences of museum specimens,

“before 1940” but do not elaborate on the earliest dates these were collected. They demonstrate that by 1940 Coyotes were present throughout the region surrounding Lake Superior.

While not within the scope of this study, the presence of both Coyotes and wolves in three archaeological sites—one along the Illinois-Indiana border (Parmalee and Stephens 1972, NPD site 7491), one in extreme southwestern Indiana (Bergman and Peres 2014, NPD site 6600), and one in central Indiana (NPD site 6602)—extends Coyote presence and possibly the area of sympatry much further east (but see map in Kays *et al.* 2010b). These sites date to 3400 to 350 YBP. An 1830s era settler account affirms an area of sympatry along the Illinois-Indiana border confounding hypotheses for the mechanisms, places and timing of hybridization of sympatric *Canis* populations (Anonymous 1879). These sites position Coyotes much closer to eastern North America than acknowledged by current studies regarding the ancestries of Eastern Coyote, Red Wolf (*Canis rufus*), and Eastern Timber Wolf (*Canis lycaon*; Wilson *et al.* 2000; Kyle *et al.* 2006; Chambers 2010; Kays *et al.* 2010a,b; Rutledge *et al.* 2010a, 2012; Wheeldon *et al.* 2010; Bozarth *et al.* 2011; vonHoldt *et al.* 2011, 2016; Way 2013).

In-depth studies on Holocene–Anthropocene Coyote distribution, using fur-trade records and genetically testing the ancestries of paleontological and archaeological site specimens are necessary to fully understand areas of *Canis* sympatry between the Ohio River and Lakes Erie and Ontario. Archeological specimens subjected to genetic testing, such as that conducted by Rutledge *et al.* (2010b), would aid in determining areas of sympatry, temporal affinities, confirm identities of *Canis* species, and further our understanding of *Canis* haplotypes over distant time.

Acknowledgements

I extend thanks to P. DeWitt who constructed the map.

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Received 7 December 2018

Accepted 6 April 2020