

Coyote Continent



Pack of hybrid coyotes caught on camera trap

EMAMMAL/ROLAND KAYS

Historically native to open country in the west, this canid now lives in all habitats across the continent.

By Roland Kays

Photographs by Robert Michelson

From the Atlantic to the Pacific seaboards and from Alaska to Panama, coyotes, *Canis latrans*, have conquered the entire North American continent, despite widespread management that treats them as a “varmint,” or pest species. In the last century, when most predator populations have declined, the highly adaptive coyote has dramatically increased in numbers. The expansion of its range prompts ecological questions related to what roles it plays in these new ecosystems and evolutionary questions related to its hybridization with dogs, and wolves.

There are three factors that set the stage for coyote expansion. First, the local extermination of larger predators helped this mesopredator expand by reducing predation risk as well as competition for larger prey. Specifically, the extirpation of wolves and cougar, *Puma concolor*, across most of eastern North America, and the decline of cougar and jaguar, *Panthera onca*, in Central America, created a kind of ecological vacuum that coyotes filled. Second, conversion of once-forest landscapes to agriculture likely facilitated coyote expansion by creating prime hunting habitat in areas that were previously unsuitable due to thick

forest cover. The northwestern expansion of coyotes into western Canada and Alaska has been attributed to the creation of new human settlements during gold rushes in the late 1880s, although this explanation has not been critically tested. Finally, the hybridization of coyotes with wolves and domestic dogs in eastern North America introduced new genetic variation that may have promoted colonization and survival in forested habitats. Although there has been no report of coyote hybridization in their populations expanding northward, coyotes moving into Central America are suspected, based on morphological characteristics, to be hybridizing with dogs.

This ongoing range expansion poses a new challenge for conservationists, as the ecological implications of spreading coyotes are still largely unknown. If coyotes are the new top predator in eastern North America and other parts of the continent, what are the cascading effects on predator

communities? Will this have impacts on down the ecosystem—for example, on over-browsing by deer, or in the lifecycle of ticks and Lyme disease? Likewise, the recent arrival of coyotes in Panama may poise them to colonize South America, with unknown implications for tropical ecosystems. Rigorously testing the causes and consequences of coyote range expansion requires an accurate historical context for where the species previously occurred. Current accounts of coyote distribution, however, have two major problems.

First, the historical distribution of coyotes prior to the westward expansion of European settlers in the 1800s remains poorly defined. Although taxonomically modern coyotes have occurred in North America since the Pleistocene (2.6 million to 11,700 years ago), the historical limits of their range are unclear as widely cited accounts of their historical distribution conflict with available data. The most popular narrative suggests that coyotes were re-

stricted to true prairie ecosystems prior to European settlement, bounded between the Mississippi River and the Rocky Mountains from southern Canada to central Mexico. In this scenario, coyotes presumably only expanded to coastal states since the late 1800s. However, historical accounts and coyote specimens in California suggest a wider western distribution. In the 1937 book, *Fur-Bearing Mammals of California* (University of California Press, Berkeley), Joseph Grinnell (1877-1939) stated that coyotes occurred in California well before European settlement. Moreover, the genetic structure of Californian coyote populations suggest that they occurred in the area well before European colonization, contradicting the hypothesis of a recent westward expansion.

The original northern and southern range limits of coyotes are also uncertain. In Alaska and northern Canada, researchers have debated whether coyotes historically occurred in low densities, arrived during the 1880s, or arrived during the 1900s. The original southern extent of coyote range has been similarly controversial. Fossil evidence confirms that coyotes were present in the Yucatán Peninsula



2 Hybrid coyotes. Their head and body size are larger, and more closely resemble that of a German Shepherd.

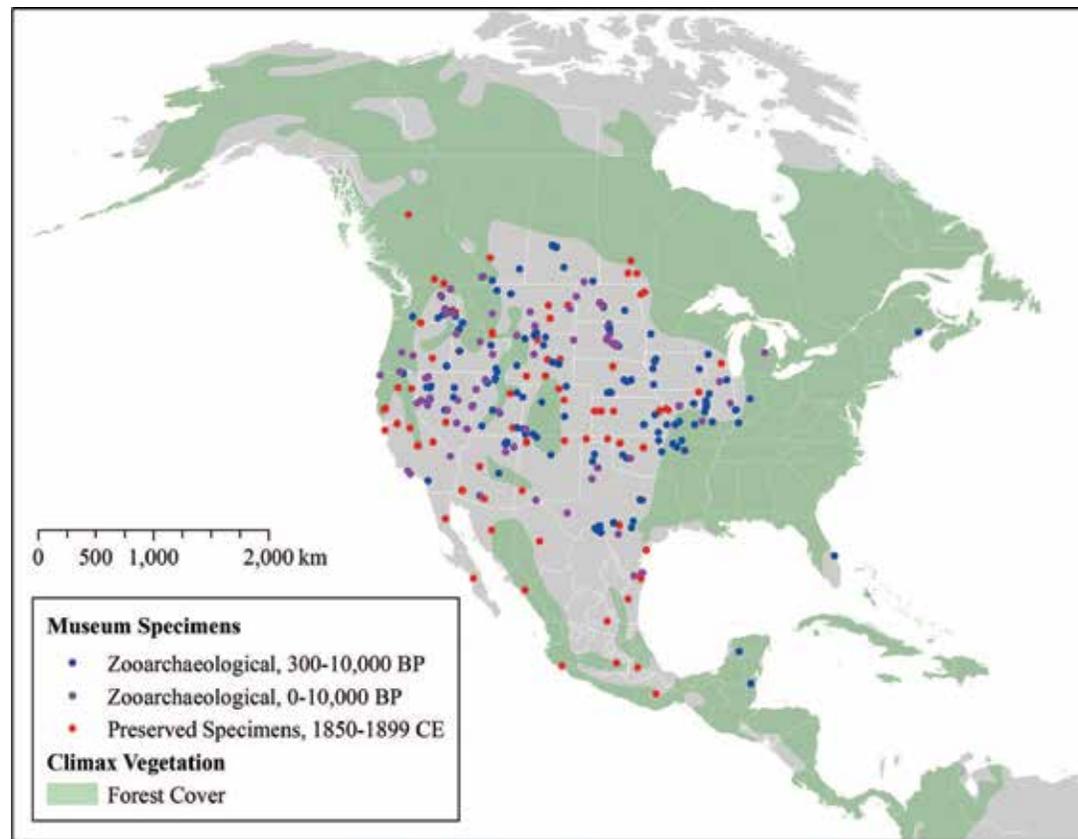
and northwestern Costa Rica during the Pleistocene, but their southern distribution after climatic changes of the late-Pleistocene is less clear. In their 1951 seminal work on coyote ecology, *The Clever Coyote* (University of Nebraska Press), Stanley P. Young and Hartley H. T. Jackson suggested that coyotes only recently colonized Central America, although the written accounts of coyote-like canids in the 1500s and late 1800s provide anecdotal evidence other-

wise. Also, pre-Columbian coyote remains have been found at two known sites, and possibly more, in the Yucatán Peninsula, lending credibility to this hypothesis. Overall, the historical distribution of coyotes during the Holocene remains poorly characterized, warranting reexamination.

A second problem with existing large-scale accounts of coyote range is that their recent expansion has been coarsely described, without clear detail about where or when. Maps are typically hand-drawn, without citing reference material, and with few, widely scattered time points. Consolidating and improving continent-wide descriptions of coyote range expansion would facilitate testing hypotheses about their effects on newly colonized ecosystems.

Fortunately, coyotes are well represented in museum collections, having been hunted extensively due to their abundance and widespread reputation as a nuisance species. Furthermore, coyotes are well represented in fossil and zooarchaeological records, allowing inferences about their distribution several thousand years ago. North Carolina State University graduate student James Hody, now at Clemson University, and I compiled museum records from recent biological surveys, fossil and zooarchaeological collections, peer-reviewed literature, and game department reports to characterize the historical distribution of coyotes prior to European settlement and to catalogue their expansion decade-by-decade from 1900 to 2016.

Our findings indicate that coyotes historically occupied a larger area of North America than generally suggested in the literature. They more closely match the historical range presented by Young and Jackson in 1951 and by Ronald M. Nowak, at the University of Kansas Museum of

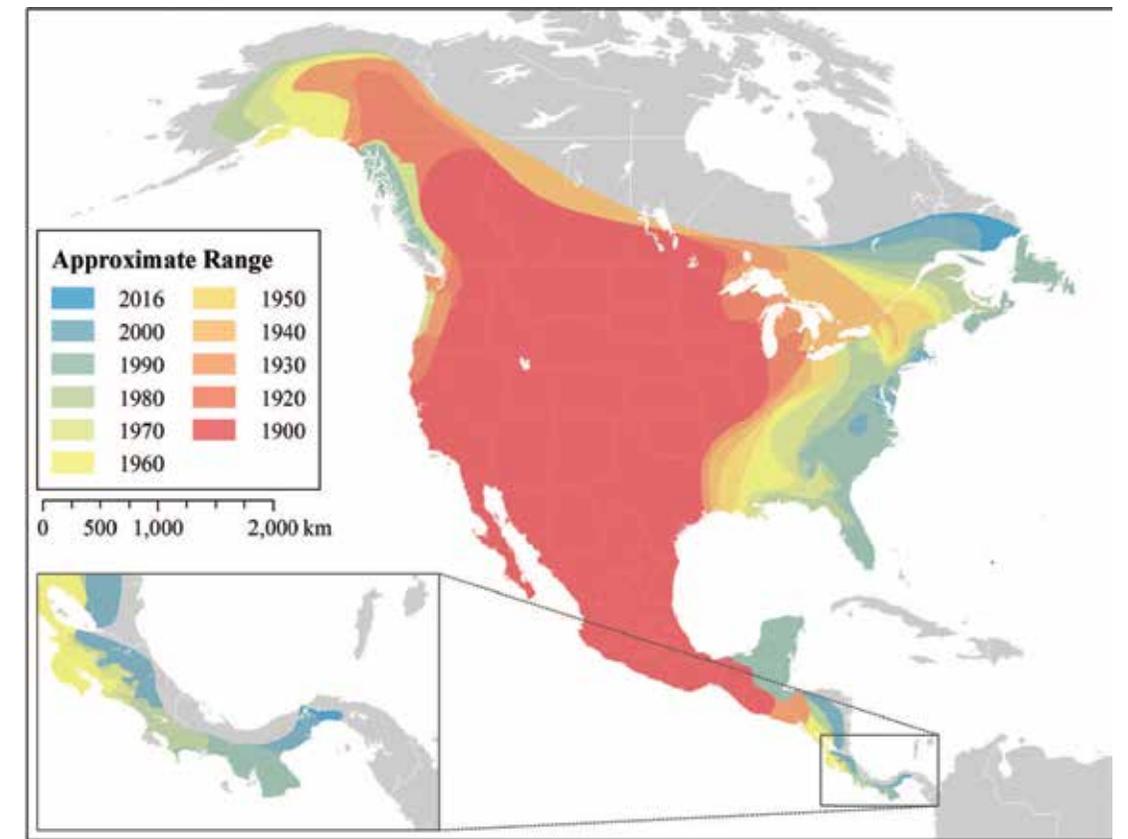


Color shading shows the timing of coyote expansion and was drawn from museum specimens and state game commission reports.

Natural History, in a 1979 monogram, “North American Quaternary Canis.”

The distribution of excavated coyote remains—300 years or older—matches the distribution of preserved coyote specimens collected between 1850 and 1899, almost identically, suggesting that the geographic range of coyotes in the late-1800s had already been established prior to the 1700s. This same spatial pattern emerges when our mapped data is subdivided in other ways, suggesting that this is not an artifact of how we defined our time intervals. Excavated coyote remains—4,000 years or older—confirm the presence of coyotes as far east as Arkansas and central Texas and as far south as the Yucatán Peninsula. These records predate the rise of civilizations with large permanent settlements in North and Central

Coyotes inter-bred with Grey wolves as they migrated North and East into Ontario, on their way to the Eastern half of United States beginning in 1900. Grey wolf pictured left



Color shading shows the timing of coyote expansion and was drawn from museum specimens and state game commission reports.

America, suggesting that coyotes were widely distributed throughout the Holocene independent of large-scale land use change by Pre-Columbian civilizations.

Nineteenth-century museum records show excavated coyote remains occurred throughout most non-forested habitats in North America. Thus, before humans arrived in the Americas, the great conifer forests of the North, deciduous forests of the East, and rainforests of the tropics were apparently unsuitable habitat, and barriers to coyote dispersal. These specimen records show that coyotes occurred in the Rocky Mountains and arid West throughout the Holocene, disproving the proposed western expansion of coyotes during the late 1800s, although there was a smaller expansion into forests of the Pacific Northwest in the early 1900s.

The distribution of excavated remains includes four notable outliers: one in southern Florida, one in the Province of New Brunswick, and two on the Yucatán Peninsula. Although we consider the New Brunswick sample questionable (likely a domestic dog), the Florida and Yucatán specimens might reflect historical range dynamics of coyotes. The Florida record is dated to the early Holocene, but its estimated range age overlaps with the late Pleistocene. Coyote fossils from this geological epoch have been documented throughout Florida, which was previously dominated by grassland ecosystems.

The two Yucatán specimens suggest a historical presence of coyotes in parts of Central America, and possible range expansion associated with Mayan land use and de-

forestation. The westerly record is dated to the early Holocene, suggesting a longstanding presence of coyotes in the area. This record occurs near relatively open habitat along the western coast of the Yucatán Peninsula, possibly facilitating their historical presence there. The eastern record is much younger, associated with Postclassic Mayan ruins in Belize, and may indicate that coyotes existed in areas deforested by the Maya civilization. Written accounts spatially coincide with areas that were most heavily cultivated and deforested prior to European contact. One possibility is that the southern distribution of coyotes was eruptive during the Holocene, with populations extending eastward across the Yucatán Peninsula and southward along the Pacific coast of Central America in periods when barriers of forested habitat were broken. Additional research is needed to clarify their historical distribution of coyotes south of Mexico, but all available evidence suggests that this species was restricted to habitats north of the Nicoya Peninsula in northwestern Costa Rica until the mid-1900s.

Our map of coyote records from 1900–2016 shows how and when coyotes expanded their range into forested biomes. Agriculture was widespread in these previously forested regions by 1900, so this more open, fragmented landscape presumably helped them expand, although eastern coyotes now occur in large forested wilderness





Hybrid coyote looking more like a German Shepherd than a coyote.

ing in the largest mammalian hybrid zone known, populated with a larger variety of coyote that is presumably more fit for surviving in eastern North America than either parental species. Research suggests that natural selection enhances the fitness of hybrid individuals of intermediate body size. In this case, eastern coyotes may be more appropriate predators of white-tailed deer than smaller western coyotes while still small enough in size to live in densely populated landscapes.

Coyotes have now covered nearly all prime habitat in eastern North America and are now also pushing into cities. Coyotes are good swimmers, and also known to run along bridges, and are even now expanding to isolated islands on the east coast, with recent sightings in the Florida Keys and Long Island, New York.

Although coyote range expansion into eastern Canada has been well studied, historical reasons for the northward expansion of coyotes into western Canada and Alaska are sparse. Early northwestern expansion is generally attributed to land clearing and refuse left by settlers during the gold rushes of the late 1800s. This explanation appears chronologically appropriate, but it is doubtful that these disturbances alone would provide coyotes with enough momentum to establish resident populations in western Canada and further colonize southeastern Alaska in the 1900s.

However, coyotes have now established at least one breeding population in the Taiga Shield Ecozone, near Yellowknife, Northwest Territories. It is unclear whether this population extends into undeveloped areas, or if it is restricted to disturbed habitats.

Likewise, coyote expansion southward across Central America is also not well studied. Coyotes have rapidly expanded into deforested habitats in eastern Panama. The dense forests of the

and are not dependent on open habitats. Eastward expansion occurred along two isolated expansion fronts. The first major wave began in the early twentieth century and consisted of two routes: across the northern Great Lakes region and southern Canada into New England, and along the southern Great Lakes eastward to Pennsylvania. These two fronts likely converged in New York and Pennsylvania during the late 1940s, and now operate as a single front of expansion. The second major coyote expansion began in the mid-twentieth century and followed a southeastern route from Texas to the Carolinas by the 1980s.

The relatively rapid colonization of the Northeast in comparison with the Southeast may be due to higher levels of wolf introgression, allowing a more rapid evolution of larger body size. The two species hybridized in the Great Lakes region prior to coyote expansion further east, result-

ing in the largest mammalian hybrid zone known, populated with a larger variety of coyote that is presumably more fit for surviving in eastern North America than either parental species. Research suggests that natural selection enhances the fitness of hybrid individuals of intermediate body size. In this case, eastern coyotes may be more appropriate predators of white-tailed deer than smaller western coyotes while still small enough in size to live in densely populated landscapes.



Coyote pup just outside of her den opening.



Close-up of "Molly" at the Buttonwood Zoo, New Bedford, Massachusetts. She was orphaned in Texas. Molly is much smaller than the hybrid animals shown on the previous pages, and has the typical coloration, and body/head size of a Western coyote.

Darién now appears to be the last major barrier between coyote populations and South American savannah ecosystems. However, this barrier may be more permeable than previously thought, especially along the coastlines, raising concerns that coyotes might reach South America in the near future.

The grassland and agricultural habitats in Colombia and Venezuela would likely be prime habitat for coyotes, unless competition with native carnivores prevents them

from colonizing. It's improbable that coyotes would expand into the continuous parts of the Amazon rainforest, but the open habitats of the Andes might offer suitable coyote habitat and facilitate further expansion. Regardless of its extent, coyote colonization of South America would be an event of profound ecological significance; expansion of a North American predator into South American ecosystems has

not been observed since the Great American Biotic Interchange, about three million years ago, and its potential effects on native mammal species is entirely unknown.

Coyotes are one of the most adaptable species on the planet and have shown they are capable of living in almost any habitat they have encountered so far. Despite being targeted for removal by varmint hunters, the overall balance sheet shows that coyotes benefit enormously from the impacts of humans on the environment. Our fragmentation of forests and removal of larger predators, combined with occasional supplementation of genetic variation from dogs and wolves, has helped coyotes evolve from a predator of grasslands and deserts, to an omnivore who is as at home in forested wilderness as they are in suburbia. Museum specimens and camera trap pictures allowed us to map this transition in great detail and will no doubt help document the next chapter of the remarkable expanding coyote.

Roland Kays is a zoologist in the Department of Forestry and Environmental Resources at North Carolina State University, and a scientist at the North Carolina Museum of Natural Sciences, both in Raleigh. **Robert S. Michelson** is an underwater marine and wildlife photographer/videographer based in Braintree, MA.