

SHORT COMMUNICATION

Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes

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Abstract

Sequence analysis of the mitochondrial DNA control region from 112 southeastern US coyotes (*Canis latrans*) revealed 12 individuals with a haplotype closely related to those in domestic dogs. Phylogenetic analyses grouped this new haplotype in the dog/grey wolf (*Canis familiaris*/*Canis lupus*) clade with 98% bootstrap support. These results demonstrate that a male coyote hybridized with a female dog, and female hybrid offspring successfully integrated into the coyote population. The widespread distribution of this haplotype from Florida to West Virginia suggests that the hybridization event occurred long ago before the southeastern USA was colonized by coyotes. However, it could have occurred in the southeastern USA before the main front of coyotes arrived in the area between male coyotes released for sport and a local domestic dog. The introgression of domestic dog genes into the southeastern coyote population does not appear to have substantially affected the coyote's genetic, morphological, or behavioural integrity. However, our results suggest that, contrary to previous reports, hybridization can occur between domestic and wild canids, even when the latter is relatively abundant. Therefore, hybridization may be a greater threat to the persistence of wild canid populations than previously thought.

Keywords: Allee effect, *Canis familiaris*, *Canis latrans*, hybridization, introgression, mtDNA

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Introduction

Two decades of molecular surveys of plant and animal populations have demonstrated that hybridization between species is more common than once believed (Allendorf *et al.* 2001). Hybridization may have little effect on the genetic integrity of wild populations when it occurs in a narrow zone between two numerous, geographically widespread species (Barton & Hewitt 1985). However, in cases where one population is rare or endangered, hybridization can result in the genetic swamping of one population by another (Rhymer & Simberloff 1996). Examples of endangered species threatened by hybridization and introgression include the Przewalski horse (Van Dierendonck & Wallis de Vries 1996), the Hawaiian duck (Browne *et al.* 1993), the mountain mahogany

(Rieseberg & Gerber 1995), southwestern trout species (Dowling & Childs 1992), and the red wolf (Wayne & Jenks 1991; Roy *et al.* 1996).

Hybridization has been documented in wild canids (Lehman *et al.* 1991; Wayne & Jenks 1991; Gottelli *et al.* 1994; Roy *et al.* 1994, 1996; Vilà & Wayne 1999) and introgression of genes has compromised the genetic integrity of a population of the Ethiopian wolf (Gottelli *et al.* 1994), the red wolf (Wayne & Jenks 1991; Roy *et al.* 1996), and grey wolves from Minnesota and eastern Canada (Roy *et al.* 1994). However, pre-zygotic behavioural barriers are sufficient to prevent hybridization where sympatric and potentially hybridizing species have populations that are healthy and stable (Mengel 1971; Fuller & Keith 1981; Carbyn 1982). The few examples of hybridization between wild canids have occurred when one species is vastly more abundant than the other. Allee effects occur when individuals of one species are present in such low densities that it is difficult to locate an appropriate mate (Allee 1931; Vilà & Wayne 1999).

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Three species of wild *Canis* occur in North America: the widespread and abundant coyote (*Canis latrans*); the patchily distributed and often rare grey wolf (*Canis lupus*); and the highly endangered red wolf (*Canis rufus*). Recent work has suggested that the red wolf is synonymous with the eastern Canadian wolf and that the two taxa should be designated *Canis lycaon* (Wilson *et al.* 2000). The coyote, a North American endemic which has been expanding its range for the last century or so (Parker 1995), will hybridize with its less abundant wild relatives (Lehman *et al.* 1991; Roy *et al.* 1994; Roy *et al.* 1996) in conditions where coyotes are abundant and grey, red, or eastern Canadian wolves are rare. No evidence has been found for maternally inherited grey wolf mitochondrial DNA sequences in coyotes, suggesting that offspring of female grey wolf/male coyote crosses are not integrated into the coyote population, or that they do not occur. It has also been suggested that hybridizing populations of wolves only represent the eastern Canadian wolf and that coyotes may only cross with this wolf and red wolf because of their genetic similarity and recent evolutionary divergence (Wilson *et al.* 2000).

Domestic dogs (*Canis familiaris*) are the oldest domesticated species (Clutton-Brock 1995) and were domesticated in Eurasia from wolves at least 15 000 years ago (Dayan 1994). Despite the long coexistence of wolves and dogs in Europe, there is no evidence for significant introgression of dog DNA into natural wolf populations (Vilà & Wayne 1999; Randi *et al.* 2000). However, in Africa, the critically endangered Ethiopian wolf has been shown to hybridize with local domestic dogs, and as much as 17% of individuals in one population may have hybrid ancestry (Gottelli *et al.* 1994). During the 9000 years that domestic dogs have been present in North America (Schwartz 1997), they have shared the continent with the grey wolf, red wolf and coyote. Despite this prolonged coexistence, introgression of dog genetic material into any of these wild species has not been found in a combined survey of over 700 individuals (Lehman *et al.* 1991; Roy *et al.* 1994; Roy *et al.* 1996). Here we report genetic evidence for a hybridization event between two widely abundant species that led to introgression of domestic dog mitochondrial DNA into the wild coyote population of the southeastern USA.

Materials and methods

DNA extraction, amplification and sequencing

Coyote tissue samples were collected from West Virginia ($n = 24$), Virginia ($n = 61$), North Carolina ($n = 24$) and Florida ($n = 3$). All samples were captured opportunistically either by fur trappers or as a result of predator control projects. Samples from West Virginia and Florida were processed at the University of California, Los Angeles, and samples from Virginia and North Carolina were processed

at the University of Idaho. Different protocols and reagents were used at the two Universities and the samples were obtained and processed by different people. DNA from the West Virginia and Florida samples was extracted using slight variations on phenol–chloroform extraction methods (Sambrook *et al.* 1989). DNA from the Virginia and North Carolina samples was extracted using a QIAmp™ tissue kit (Qiagen). For the West Virginia and Florida samples an approximately 425-base pair (bp) fragment of the control region I of the mitochondrial DNA was amplified by polymerase chain reaction (PCR) in Primus 96plus (MWG-BIOTECH) machines in 40 cycles (94 °C for 30 s, 50 °C for 40 s, 72 °C for 50 s) after an initial denaturation step of 95 °C for 30 s using primers ThrL 15926 (5'-CAATCCCCGGTC TTGTAAACC) and DL-H 16340 (5'-CCTGAAGTAGGAA CCAGATG) as in Vilà *et al.* (1999). The PCR mix consisted of 25 pmol of each primer, 0.5 mM dNTPs, 1× *Taq* DNA polymerase buffer supplied by the manufacturer (Sigma), 2.5 mM MgCl₂ and 0.75 U *Taq* DNA polymerase (Sigma) in 50 µL with approximately 100 ng of DNA extract. For the Virginia and North Carolina samples a 350-bp fragment of the control region I of the mitochondrial DNA was amplified by PCR in PTC-100 (MJ Research Inc.) machines in 40 cycles (94 °C for 30 s, 50 °C for 30 s, 72 °C for 40 s, with final extension of 72 °C for 2 min) after an initial denaturation step of 95 °C for 2 min using primers L16345 (5'-CACCATTAGCACCCAAAGCT) and H16751 (5'-CCTGAAGTAGGAACCAGA) from Ward *et al.* (1991). The PCR mix consisted of 20 pmol of each primer, 0.2 mM dNTPs, 1× *Taq* DNA polymerase buffer supplied by the manufacturer (Applied Biosystems), 2.5 mM MgCl₂ and 0.5 U *Amplitaq* DNA polymerase (Applied Biosystems) in 15 µL with approximately 150 ng of DNA. Negative controls were included in all extractions and PCRs to monitor for contamination. Most PCRs also contained one positive control to verify correct amplification. All samples were sequenced using either the Ceq^{PN} BTCS-Quick Start Kit (Beckman-Coulter) and run on the Ceq 2000XL DNA Analysis System (Beckman-Coulter) or the Big Dye kit version 2.0 (Perkin Elmer) and run on an ABI automated sequencer following the manufacturers' protocols.

Phylogenetic analysis

Sequences were compared to all available canid sequences by a BLAST search on the NCBI website (<http://www.ncbi.nlm.nih.gov>). One haplotype displayed close similarity to dog sequences but did not directly match any of the 88 grey wolf, five coyote and 110 dog control region sequences found on the NCBI website. This haplotype also did not match the previously generated red wolf haplotype. The independent identification of the same haplotype using different procedures with samples of different origins eliminates the possibility that the novel

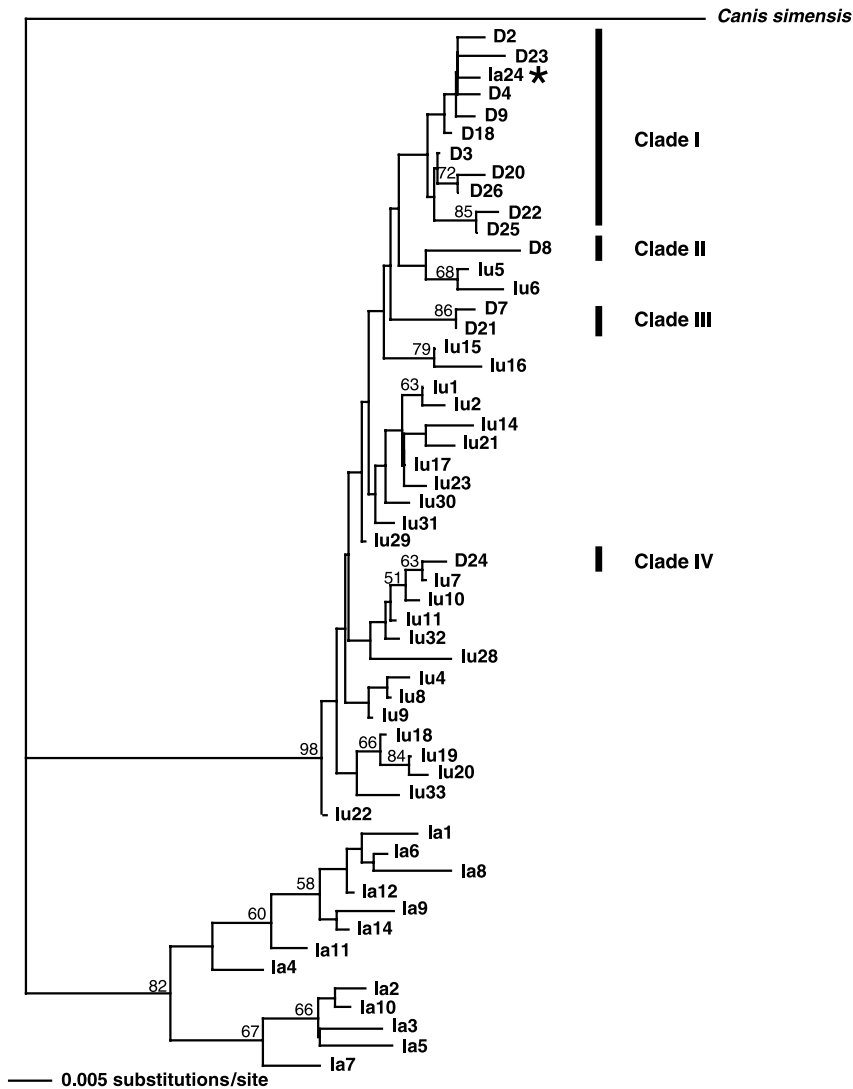


Fig. 1 Neighbour-joining tree of domestic dogs (D), grey wolves (lu) and coyotes (la) based on 394–400 bp of mitochondrial DNA control region sequence (variation due to indels). Dog clades as in Vilà *et al.* (1997). Bootstrap support is indicated at nodes if found in more than 50% of 1000 bootstrap trees. The new haplotype described in this paper is labelled 'la24' and is marked with an asterisk.

haplotype could be the result of contamination. To evaluate the phylogenetic placement of this sequence, a neighbour-joining tree of the longer version of this new haplotype and previously published wolf, dog and coyote sequences (Vilà *et al.* 1997; Vilà *et al.* 1999) was constructed using PAUP 4.0b8a (Swofford 2002) with the HKY85 distance statistic and a gamma parameter of 0.5. The sequences used to construct the tree were 394–400 bp long and were aligned manually. A previously published Ethiopian wolf (*Canis simensis*) sequence was used as an outgroup (Vilà *et al.* 1999). The support for the tree topology was measured by bootstrap analysis (1000 replicates) in PAUP 4.0b8a.

Results

Sequence analysis of 112 southeastern US coyotes revealed 24 unique haplotypes. One haplotype was highly diver-

gent from all other coyote haplotypes with 24–30 bp differences in 394–400 bp, and an average divergence of 8.7%. The sequence did not match any canid sequence in GenBank, and we refer to it as 'la24'. This haplotype is more closely related to haplotypes of grey wolves, differing by 6–11 bp and an average divergence of 2.2%. We compared the divergent sequence found in coyotes to those found in a monophyletic group of dogs, designated clade I (Fig. 1, Vilà *et al.* 1999). This group probably represents the earliest radiation of domestic dog (Vilà *et al.* 1999). The domestic dogs in this clade differ from la24 by 2–5 bp and have an average divergence of 0.8%.

Phylogenetic analyses place haplotype la24 within the main monophyletic clade of dog sequences (clade I in Vilà *et al.* 1997; Fig. 1). This haplotype contains the diagnostic change (A to G at bp 75) that defines clade I dogs (Vilà *et al.* 1997). The assignment of haplotype la24 to the wolf/dog clade as opposed to the coyote clade is supported by a

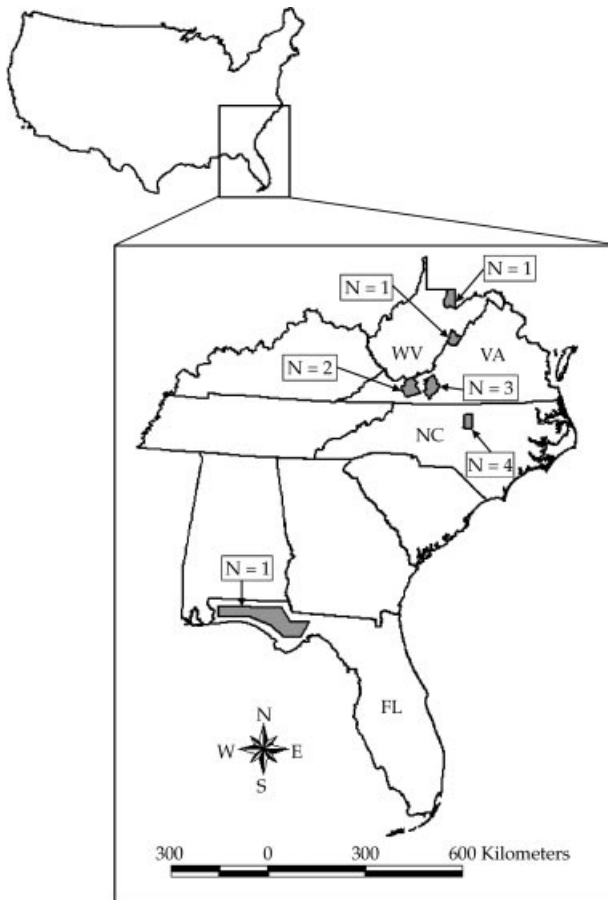


Fig. 2 Map of the United States with inset map of southeastern USA showing localities where the dog haplotype 'la24' was found in coyotes. WV = West Virginia, NC = North Carolina, VA = Virginia, and FL = Florida. Highlighted locations indicate the counties in which the haplotype was found except Florida where the general location is identified. Sample sizes are indicated for each location.

bootstrap value of 98% (from 1000 replicates), as well as by three fixed indels (two insertions in the wolf/dog lineage and one deletion in the coyote lineage).

The haplotype la24 was found in 12 individual coyotes from the southeastern USA (Fig. 2). The haplotype was observed at fairly high frequency across sampling areas: 9.8% in Virginia (6/61), 4.2% in West Virginia (1/24), 16.7% in North Carolina (4/24) and 33.3% in Florida (1/3) with an overall frequency of 10.7%.

Haplotype la24 was submitted to GenBank, accession number AF541876.

Discussion

In previously recorded incidences of hybridization between carnivores in the wild, the species involved were closely related and differed in abundance, one being a rare native and the other an invading form (Hubbard *et al.* 1992;

Gottelli *et al.* 1994; Davison *et al.* 1999). In contrast, our data suggest that the invading coyote has hybridized with abundant local domestic dogs.

Eastern Canadian wolves and coyotes are able to interbreed and produce viable offspring (Iljin 1941; Gray 1954; Lehman *et al.* 1991) and hybrid offspring have been incorporated into the wild paternal population (Lehman *et al.* 1991; Wayne & Jenks 1991; Roy *et al.* 1994; Roy *et al.* 1996). Dogs and coyotes are able to hybridize in captivity (Dice 1942; Kennelly & Roberts 1969; Mengel 1971) and coyote-dog hybrids ('coydogs') have been reported in the wild (Cook 1952; Mengel 1971). However, previous genetic analyses have found no evidence of dog introgression in the coyote population despite extensive continent-wide evaluations using mitochondrial DNA markers (Lehman & Wayne 1991; Lehman *et al.* 1991; Roy *et al.* 1996; Vilà *et al.* 1999) and nuclear microsatellite markers (Roy *et al.* 1994; Roy *et al.* 1996). This lack of evidence for dog introgression into the coyote population has been attributed to physiological and behavioural differences between the two species (Mengel 1971).

F_1 and F_2 coyote-dog hybrid females have a shifted oestrous cycle, so they are fertile in December rather than February (Silver & Silver 1969; Mengel 1971). Allowing for a 2-month gestation period (Evans 1993) hybrid litters would be born during late winter, a time of inclement weather. Moreover, male dogs as well as F_1 and F_2 hybrid males raised in captivity show no parental instinct (Mengel 1971). These observations lead to the hypothesis that hybrid litters would have little chance of surviving long enough to be incorporated into the wild population (Mengel 1971). Additionally, hybrid individuals may experience lowered levels of fertility (Mengel 1971; Fox 1978). However, the backcross of a female hybrid to a male coyote would improve the survivorship of offspring through parental care by the father. This backcross would introduce the maternally inherited dog mitochondrial DNA haplotype into the wild coyote population. This initial hybridization event may have been facilitated by mild winters, which sometimes occur in the southeastern USA.

The wide distribution of the dog-like haplotype in the southeastern USA suggests that the hybridization event between a male coyote and a female dog may have happened a long time ago. The distribution of the coyote has expanded greatly over the last 150 years from the plains of North America to its current distribution including most of North America, from Alaska to Panama (Parker 1995). We observe the dog-like haplotype (la24) in relatively new populations of coyotes in southeastern USA, which were established between 1960 and 1980 (Parker 1995). Therefore, the hybridization event may have occurred in the population of coyotes that is ancestral to southeastern coyotes. However, previous studies of mitochondrial DNA in coyotes elsewhere have not found any wolf-like or dog-like

haplotypes (Lehman & Wayne 1991; Vilà *et al.* 1999). This supports an alternative hypothesis that the introgression event occurred as the ancestral coyote population began to colonize the southeastern USA. Coyotes dispersing along the edge of their range would encounter areas with few potential mates and hybridization with dogs may have been favoured because of density effects. Furthermore, coyotes occur frequently in urban and rural areas where dogs are abundant and may range freely.

Finally the dog-coyote cross could have taken place in the southeast through human activities before the natural range of coyotes expanded to encompass the southeastern USA. The range of the dog haplotype corresponds to the area of the USA where coyotes are purchased from dealers to be released for sport hunting. These animals are generally trapped in an area, such as Texas, where coyotes are abundant, and then trucked to the southeastern USA where they are sold (personal communication, Randy Farrar, Furbearer Biologist, Virginia Department of Game and Inland Fisheries). Additionally, dispersing juvenile males are much more abundant in this trade because they are easier to capture (personal communication, Randy Farrar). Some coyotes were released into areas which previously had no coyotes, and they escaped (personal communication, Randy Farrar). Some releases may have occurred in northwestern Florida (the 'panhandle') and southern Alabama by the mid-1960s (personal communication, Tim Breault, Florida Wildlife and Fisheries Department). These predominately male, released individuals may have been the first coyotes in many areas, thus lacking female counterparts. In this situation one male coyote may have mated with a single female dog. The female hybrid offspring may have been accepted by male coyotes because there were no female coyotes available. The descendants of this cross may have expanded their range in the southeastern USA, with or without the assistance of dealers, before coyotes naturally expanded into these areas. Once coyotes naturally expanded into these areas, the hybrid phenotypes were diluted through backcrossing, although the mitochondrial DNA lineage remained. Releases of coyotes from Texas into Florida were documented as recently as the late 1990s, marked by an outbreak of a strain of Texan coyote rabies in the Gainesville, Florida vicinity (personal communication, Tim Breault).

Our data show that hybridization occurred between a female dog and a male coyote, and that at least one of the female offspring of that cross successfully integrated into the coyote population. Considering the current diversity of dog and coyote haplotypes (Vilà *et al.* 1997, 1999; this report), and that only a single dog haplotype was found, the hybridization event probably involved one or a few females and is not evidence for ongoing hybridization. The biologists and trappers that obtained samples from the 12 coyotes with dog mitochondrial DNA detected no differ-

ences in morphology or behaviour. Thus, we conclude that there has been no appreciable effect on the coyote's genetic, morphological, or behavioural integrity. However, these data warn us of the potential conservation problems posed by domestic species to their wild brethren, even when those wild species are abundant.

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