Hybridization between Wolves and Dogs

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Abstract: *Concern has been expressed that European populations of gray wolves (*Canis lupus*) have extensively hybridized with domestic dogs (*C. familiaris*). We reviewed and analyzed surveys of mitochondrial and biparentally inherited genetic markers in dogs and wild populations of wolf-like canids. Although dog-wolf hybrids have been observed in the wild, significant introgression of dog markers into wild wolf populations has not yet occurred. Our investigation suggests that hybridization may not be an important conservation concern even in small, endangered wolf populations near human settlements. The behavioral and physiological differences between domestic dogs and gray wolves may be sufficiently great such that mating is unlikely and hybrid offspring rarely survive to reproduce in the wild.*

Hibridación entre Perros y Lobos

Resumen: *En algunas ocasiones se ha sugerido que las poblaciones europeas de lobos (*Canis lupus*) pueden estar profundamente hibridadas con perros domésticos (*C. familiaris*). Revisamos y analizamos estudios que utilizan marcadores genéticos mitocondriales y de herencia biparental en perros y poblaciones silvestres de cánidos del grupo del lobo. Aunque existen observaciones de híbridos entre perros y lobos en condiciones naturales, nunca se ha observado una significativa introducción de marcadores genéticos de perros en las poblaciones de lobos. Nuestra revisión sugiere que la hibridación puede no ser un problema importante ni tan sólo para la conservación de poblaciones de lobos pequeñas y amenazadas, cerca de asentamientos humanos. Las diferencias fisiológicas y de comportamiento entre perros y lobos pueden ser suficientemente grandes como para que su apareamiento sea improbable y los híbridos tengan escasas posibilidades de sobrevivir y reproducirse en libertad.*

Introduction

All species in the genus *Canis* are closely related (Wayne et al. 1997) and can interbreed and produce fertile offspring (Gray 1954). Interbreeding may present conservation problems if it threatens the genetic integrity of endangered wild canids. There are numerous reports of wild or domestic canids hybridizing with rare or endangered species. For example, the Ethiopian wolf (*C. simensis*), a unique wolf-like species and the world's most endangered canid, is threatened by hybridization with domestic dogs (*C. familiaris*) (Gottelli et al. 1994). Red wolves (*C. rufus*) may hybridize with coyotes in the wild (Nowak 1979; Wayne & Jenks 1991), and gray wolves (*C. lupus*) and coyotes (*C. latrans*) interbreed in the Great Lakes region of North America (Lehman et al. 1991).

Gray wolves and dogs are the most closely related large canids. During the last 100,000 years domestic dogs may have originated from and interbred with wolves several times (Vilà et al. 1997). Dog breeders and many North American cultures occasionally crossed their dogs with wolves to improve vigor (Schwartz 1997). More than 10,000 wolf-dog hybrids may exist in the United States (García-Moreno et al. 1996). Dog-wolf interbreeding may have an ancient history: archaeological remains from Agate Basin Site in Wyoming suggest that wolf-dog hybridization may have occurred in North America 10,000 years ago (Schwartz 1997).

Hybridization between gray wolves and dogs is thought to be most frequent near human settlements where

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wolves are found in low densities and where feral and domestic dogs are common (Boitani 1983; Bibikov 1988; Blanco et al. 1992). Boitani (1984) hypothesized that after a severe bottleneck before 1980, Italian wolves were numerically augmented through hybridization with dogs. Recently, Butler (1994) suggested that European wolf populations were in fact mainly hybrids between dogs and wolves. Although such inferences are based on anecdotal evidence, the genetic integrity of wild wolf populations is a real concern among conservationists (Blanco et al. 1992; Boitani 1993). Few genetic tests, however, have been done to determine the magnitude of hybridization in the wild.

Recent studies provide evidence that natural hybridization between gray wolves and domestic dogs is a much rarer event than is implied by the level of concern. The most extensive genetic studies have utilized maternally inherited mitochondrial DNA (mtDNA) markers that can identify individuals with an ancestry involving interbreeding between a female dog and a male wolf. Studies of nuclear markers are fewer and less conclusive but detect introgression regardless of sex. To assess claims of hybridization, we evaluate recent studies of maternally and biparentally inherited genetic markers in dogs and gray wolves. We conclude that the genetic data do not support widespread hybridization. To better understand why dogs and gray wolves may not successfully hybridize in the wild, we discuss hybridization in the Ethiopian wolf, a species whose genetic integrity is threatened by hybridization with dogs.

Maternally Inherited Markers

Vilà et al. (1997) sequenced a segment of 261 base pairs (bp) of the mitochondrial control region of 162 gray wolves from 27 localities worldwide and 140 dogs from 67 breeds. They found 27 different sequences in wolves and 26 in dogs. Remarkably, only one of the sequences found in dogs (D6) was identical to a sequence found in wolves (W6; Fig. 1). Moreover, with additional sequencing these two sequences were found to be different (Vilà et al. 1997). Okumura et al. (1996) also sequenced 900 bp of the control region of 73 Japanese dogs from 8 indigenous breeds and 21 non-Japanese dogs. We compared the homologous 240-bp region in both studies and found a total of 35 different haplotypes in dogs (n = 213), and only one of them was identical to a wolf sequence, again W6, from the study by Vilà et al. Moreover, as with the Vilà et al. study, the dog sequences that showed identity to wolves in the 240-bp segment could be differentiated from them when the full 900-bp region was analyzed.

Wolf populations in some Mediterranean countries such as Spain, Portugal, Italy, Greece, and Israel have been suggested to be at high risk of hybridization because of their small population size and extensive contact with dogs (Boitani 1993). Nevertheless, none of 100 wolves from these countries analyzed by Vilà et al. (1997) or the 30 wolves from Italy characterized by Randi (1993) have mtDNA genotypes found in any dog.

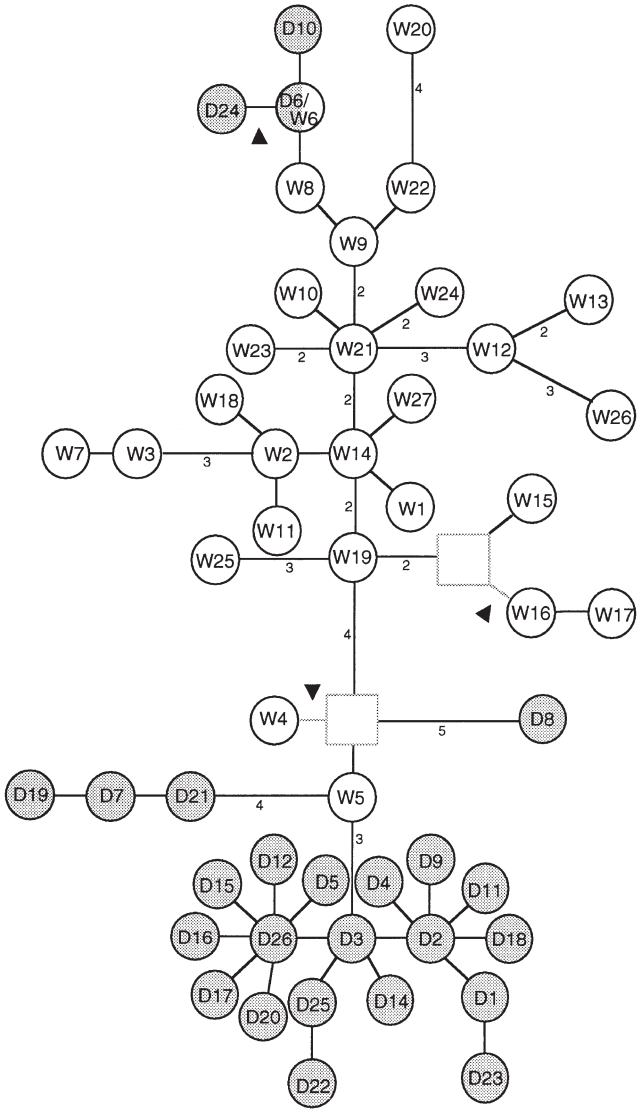

Figure 1. Relationship between wolf (W, unshaded circles) and dog (D, shaded circles) control region haplotypes. A minimum spanning network was constructed with the wolf sequences, and the dog sequences were added to the network at the point requiring the fewest changes (Vilà et al. 1997). The number of substitutions, when different from one, is indicated by the numbers on lines connecting haplotypes. Arrows show insertions of one or two nucleotides. Boxes indicate hypothetical ancestral genotypes prior to the insertion event. Alternative links are not represented but involve minor changes in the association of genotypes.

In Spain, wolves are found in agricultural areas where dogs are abundant and human density is 50 humans/km^2 or more (Blanco et al. 1992). The total wolf population is

estimated between 1500 and 2000 individuals. Over the last few decades wolves have established territories in severely disrupted areas where less than 5% of the area is forested and domestic dogs are common. These marginal populations are small, and human-induced mortality is high (Barrientos 1989). Consequently, many areas of Spain seem well suited for dogs and wolves to hybridize.

To better assess the frequency of dog-wolf hybrids in Spain, we genetically typed a 355-bp segment of the control region in 107 Spanish wolves from throughout Spain. Three different haplotypes were found: two matched the W1, W3 haplotypes identified previously (Vilà et al. 1997), and one new genotype was a single substitution different from W1. These three haplotypes are distinct from all sequences found in dogs. Therefore, interbreeding between female dogs and male wolves followed by backcrossing to wild wolves is a rare event. If it was common, we would have found dog sequences in wild wolf populations.

Biparentally Inherited Markers

Conceivably, male dogs and female gray wolves may interbreed and the offspring backcross to wild gray wolves. Such hybrids would not have been detected in genetic surveys using maternally inherited mtDNA markers. Female wolves have been observed to cross with male dogs in Italy and Israel (Randi et al. 1993). In Spain, feral dogs have been found to have mtDNA sequences otherwise present only in Iberian gray wolves (C.V., personal observation). Although these observations show that male dogs and female wolves can cross in the wild, analysis of morphologic and nuclear markers in European wolves has not detected introgression into wild wolf populations. Two independent studies on allozyme variation in Italian wolves and domestic dogs failed to show evidence of introgression of dog genes into the Italian wolf population (Randi et al. 1993; Lorenzini & Fico 1995). Similarly, morphologic analysis of 600 wolf carcasses in Spain showed no evidence of hybridization (Blanco et al. 1992), suggesting that, if hybrids are produced, they rarely breed successfully with wolves. Genetic studies using these biparentally inherited markers are less definitive, however, and the surveys are less extensive than those involving mtDNA.

Lessons about Hybridization from the Ethiopian Wolf (*C. simensis*)

Hybridization with domestic dogs has substantially altered the genetic composition of Ethiopian wolves, a distinct wolf-like species. Morphologic and nuclear evidence suggested that 8–17% of one population had a hybrid ancestry (Gottelli et al. 1994). Sexual asymmetry in mating has been observed in Ethiopian wolves, where only female wolves mate with male dogs (Gottelli et al. 1994). Consequently, only biparentally inherited markers could identify Ethiopian wolves of hybrid ancestry.

The difference in the degree of introgression of dog genes into gray wolf and Ethiopian wolf populations may reflect differences in the mating system of the two species. The breeding season of the Ethiopian wolf is very short, and females leave their natal pack to copulate with males from neighboring territories (Sillero-Zubiri et al. 1996). In areas where hybrid Ethiopian wolves have been observed, free-roving domestic dogs greatly outnumber Ethiopian wolves (Gottelli et al. 1994). Thus, females searching for mates may encounter dogs at a high frequency and mate with them. After mating, female Ethiopian wolves return to their natal pack to give birth and get assistance in the raising of young from other pack members. Consequently, hybrid pups are socialized as Ethiopian wolves and can easily integrate into the population. In fact, dog-Ethiopian wolf hybrids have been observed as the dominant member of their packs (C. Sillero-Zubiri, personal communication).

In contrast, dispersing female gray wolves do not return to their natal pack because the reproducing alpha pair holds dominance over reproduction. Rather, dispersing female wolves attempt to form a new pack with their mate (Smith et al. 1997). Because male dogs often do not assist in the rearing or care of offspring (Boitani et al. 1995) or form long-term bonds with females, offspring of wolf-dog matings may not survive in the wild; if they do survive, hybrids may not be well socialized and may have difficulty integrating into a wolf pack. The lack of assistance in the rearing of young by male dogs can be one of the reasons for the high pup mortality observed in Italian feral dog packs (L. Boitani, personal communication).

Physiological differences also distinguish dogs from wild wolf-like canids. Gray wolves and Ethiopian wolves follow the general breeding pattern of wolf-like canids: females have a single estrus per year, and males show seasonal increases in testosterone, testis size, and sperm production (Asa 1997). Gray wolf females generally come into estrus from late January through April (Mech 1970). Most dog breeds are an exception to this pattern: females can produce two litters per year, and males continuously maintain elevated testosterone levels (Asa 1997). Estrus usually occurs twice a year, in spring and fall, although it may occur in any month (Evans 1993). Consequently, the breeding cycle of male gray wolves may not be well timed for interbreeding with female dogs. In contrast, male dogs can potentially mate with dispersing female wolves during peak receptivity.

In conclusion, hybridization between gray wolves and domestic dogs does not appear to have materially affected the genetic composition of gray wolf populations. Offspring of male dogs and female wolves may rarely survive because male dogs provide limited parental care, whereas the reverse cross may not often occur because

sperm production and estrus cycle are not coincident in dogs and gray wolves.

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