

# Impact of hybridization with domestic dogs on the conservation of wild canids

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## 7.1 Introduction

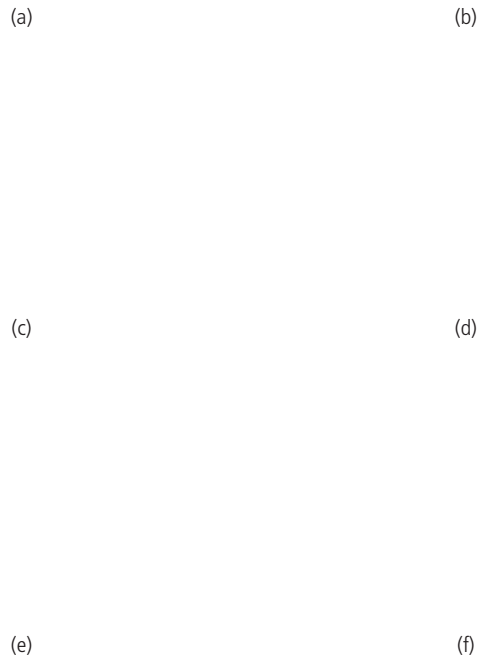
Dogs (*Canis familiaris*) were domesticated from gray wolves (*C. lupus*) in the late Pleistocene (Vilà et al., 1997; Wayne et al., 2006). Dogs retain the ability to hybridize with gray wolves and produce fertile offspring. However, gray wolves are not the only wild species that can hybridize with dogs. All wolf-like canids (*Canis* spp. and *Lycyaon*; Figure 7.1) have the same number of chromosomes ( $n = 78$ ) and may have the capacity to interbreed and produce viable offspring (MacDonald and Sillero-Zubiri, 2004; Vilà and Wayne, 1999).

Dogs are distributed across the entire range of all wild canids, and are much more abundant than any other canid species. The wild canid with the greatest natural distribution is the gray wolf, which, despite having been extirpated from large parts of its native range, has approximately 115,000 to 139,000 individuals distributed across Europe, Asia, and North America (Mech and Boitani, 2003). On the other end of the scale, only a few small populations remain of the Ethiopian wolf (*C. simensis*), totaling about 500 individuals in the wild (Ethiopian Wildlife Conservation Authority, 2012; MacDonald and Sillero-Zubiri, 2004). For comparison, there are approximately 700 million to 1 billion dogs worldwide (Baker et al., 2010; Hughes and MacDonald, 2013; WHO-WSPA, 1990; Gompper, Chapter 1), and a large fraction of this dog population could be considered free-ranging

(reaching up to 75%, according to World Society for the Protection of Animals, 2010 as cited in Massei et al., 2010). Dogs not under control of an owner are considered 'free-ranging,' although some of these animals likely have owners that provide regular care, but allow them to roam for periods of time (Gompper, Chapter 1; Ritchie et al., Chapter 2). The abundance of free-ranging dogs in areas with small and endangered populations of other wolf-like canids could represent a serious conservation threat via risk of hybridization. A special case is that of the dingo, a divergent dog population that hybridizes with dogs of recent arrival to Australia (see Box 7.1).

## 7.2 Effects of hybridization

Hybridization can affect wildlife in a number of ways, most of them negative but some potentially positive as well (i.e., Grant and Grant, 1992; Larsen et al., 2010; McDonald et al., 2008; Schwenk et al., 2008). The negative impacts are better known and they include loss of reproductive potential, lowered fitness of individuals that hybridize, introduction of maladaptive alleles into wild populations, loss of genetic integrity, potential for disease transfer, and legal consequences that may affect the individual or population's conservation status (i.e., Barilani et al., 2007; Casas et al., 2012; Pierpaoli et al., 2003; Puigcerver et al., 2007; Randi, 2008; Schwartz et al., 2004).



**Figure 7.1** Some canids that potentially could be affected by hybridization with free-ranging dogs (a) Iberian wolf (*Canis lupus*) in Spain (photo: Jorge Echegaray); (b) coyote (*Canis latrans*) in Montana, USA (photo: Jorge Echegaray); (c) Ethiopian wolf (*Canis simensis*) in the afroalpine highlands of Ethiopia (photo: Martiño Nercellas); (d) African wild dog (*Lycaon pictus*) in South Africa (photo: Martiño Nercellas); (e) golden jackal (*Canis aureus*) in Hungary (photo: Miha Krofel); (f) black-backed jackal (*Canis mesomelas*) in South Africa (photo: Martiño Nercellas).

### Box 7.1 Dingoes: mixing of ancient and recent dog populations

Dingoes are free-roaming dogs in Australia that descend from dogs brought to the region by ancient hunter-gatherer societies 3,500–5,000 years BP (Corbett, 1995; Elledge et al., 2006). This population of dogs has been largely isolated from other dogs for thousands of years (Oskarsson et al., 2012) until the arrival of the British with their dogs in 1788. These new arrivals bred with the local dog population, yielding the current mixed population (Corbett, 1995; Dickman et al., 2009). There are still some animals that are considered ‘pure’ dingo, although, according to skull morphomet-

rics, they have been declining in numbers for the last century (Corbett, 1995). Dingoes have been and are still an important component of native Australian culture.

While the dingo is a protected species in parts of Australia (for example, it is protected in the Northern Territory and is regarded as having important conservation value) in other areas it is considered a pest and there is a legal mandate to decimate or eradicate its populations. Efforts to control the dingo population have grown out of the conflict between

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**Box 7.1** *Continued*

dingoes and ranchers due to predation on livestock, especially sheep. The best example of this campaign has been the construction of the world's longest fence: the dingo fence, a man-made defense that stretches 5,614 kilometers.

There is a recent and growing body of research that suggests that dingoes may be playing an important role as apex predators (Johnson et al., 2007; Letnic et al., 2009; Wallach et al., 2009; Ritchie et al., Chapter 2). It has been suggested that these free-ranging dogs could be helping to restore the biodiversity in several environments (see e.g., Dickman et al., 2009) by direct predation on introduced competitors of marsupial native communities (i.e., feral goats and pigs), and indirectly benefiting native species through suppression of introduced mesopredators (i.e., fox and cats).

In areas where dingoes are protected, the main threat to their conservation is crossing with dogs of recent arrival to Australia (Elledge et al., 2006). However, quantitatively assessing the extent of this mixture, as well as the extent of genetic transfer between populations, is a difficult task since no diagnostic tools exist that can readily separate the two lineages, and dingoes are heavily admixed over the entire Australia with the possible exception of some remote and protected areas. This implies that it is difficult to find pure dingoes that can be used as reference for the identification of mixes (see Box 7.2). It is not clear how many pure dingoes may exist today and conservation efforts sometimes aim at identifying and removing animals below a specific threshold of dingo ancestry (e.g., quarter or half dingoes, Elledge et al., 2006).

In small populations, hybridization may result in a loss of intraspecific mating opportunities and a subsequent reduction in the effective number of breeders. This implies a loss in the population's reproductive potential and may reduce the population growth rate to a level that is below what is needed for its long-term survival. In this way, hybridization may present a demographic threat to a species or population even if hybrids die and do not lead to genetic admixture through introgression (introduction of genes of one species into the gene pool of another, see Box 7.2).

Introgression following hybridization can introduce maladapted genes into wild populations. The gene pool of each population and species is the result of thousands to millions of years of selection and adaptation to specific environmental conditions. A rapid influx of genes from another species or population, that evolved under different conditions and with a different set of co-evolved genes, usually precipitates a decline in fitness. Despite strong negative selection, these genes have a real chance of achieving high frequencies or even becoming fixed in small populations through random genetic drift. These genes could reduce the population's chances of long-term survival. In cases of high frequency of hybridization and introgression, a major conservation threat is the potential for the loss of the genetic integrity of a species.

Several of these negative effects of hybridization in the wild are observed in the Ethiopian wolf. The distribution of Ethiopian wolves has been reduced and fragmented to a handful of very small populations, some of which are in populated areas with high numbers of free-ranging dogs. In at least one of these populations, Web Valley, these endangered canids hybridized with dogs, and the hybrids have integrated into the population and backcrossed (Gottelli et al., 1994). The level of hybridization and backcrossing is high enough to threaten the integrity of this population, and dog alleles were also identified in another population. Currently, small size, strong population structuring with low gene flow, demographic stochasticity, and hybridization with dogs are considered the main threats for the survival of this species (Gottelli et al., 2013). The contact during successful or attempted intercrossing with dogs has also further threatened Ethiopian wolves by spreading rabies (Laurenson et al., 1998).

Hybridization with dogs can threaten wild populations of canids even when the hybrids do not backcross into the population, by changing people's perception of the population and, in some cases, changing their legal conservation status. Popular perception of wildlife, expectations of wildlife management, and feelings about hybridization involving wildlife are drastically different across the range of all species in the genus *Canis*, even

between North America and Europe. For example, a female gray wolf from the highly endangered Scandinavian population hybridized with a male dog in Norway (Vilà et al., 2003). Concern about the presence of hybrids led the authorities to allow killing any wolf-like canid in the area by government officials and hunters despite it being outside the hunting season. In other countries such as Finland, some hybridization events were reported in areas geographically distant from the known established wolf packs. The suspected wolf-dog individuals inspired fear in local people with their apparent lack of shyness, aggressive behavior, and some livestock damage possibly caused by them (Ministry of Agriculture and Forestry, 2005). In Spain, the existence of some suspected hybrids has recently fanned persecution of both wolves and dogs in areas where hybridization may have taken place. Wolf conservation and management programs across Europe emphasize the eradication of hybrids as a priority (for example, in Estonia, Lohmus, 2001; Italy, Genovesi, 2002; Finland, Ministry of Agriculture and Forestry, 2005), and this is also emphasized in the *Action plan for the conservation of wolves (Canis lupus) in Europe* (Boitani, 2001). Although this priority has been widespread, the scientific basis is not clear.

Hybridization and introgression are generally assumed to be negative. However, they can act as a source of genetic variation that could be beneficial in

some cases, promoting rapid diversification or even speciation, and introduction of alleles with adaptive value (i.e., Cadieu et al., 2009; Grant and Grant, 2008; Larsen et al., 2010; Pardo-Díaz et al., 2012). When populations are large, hybridization and subsequent introgression could provide additional genetic material for selection to act upon. An example of this seems to have happened when a gene coding for melanistic coloration was transferred to wild populations of both gray wolves and coyotes (*C. latrans*) in North America from dogs through ancient hybridization (Anderson et al., 2009). Analysis of the gene and surrounding sequence (haplotype) in wolves, coyotes, and dogs showed that the causative mutation arose in dogs and then entered the wolf and coyote gene pools. The mutation likely arose many thousands of years ago in dogs and was more recently transferred, likely in pre-Columbian times, to gray wolves from Native American dogs. The very low diversity in the wolf haplotypes and the high frequency of this allele in certain populations suggests that this locus had been positively selected for in some populations of wild wolves. In this case, the populations of wolves and coyotes were large enough that the positive selection for the introgressed gene was able to separate it from other linked genes, and it increased in frequency in some populations. This would have been less likely if the populations were small.

### Box 7.2 Identifying hybrids and assessing introgression

The terms ‘hybridization’ and ‘introgression’ are related, but not the same. Hybridization, interbreeding between two different species, even when it results in viable, fertile offspring does not always lead to introgression. Introgression is the transfer of genetic material from one species to another. Introgression starts with hybridization, but then those hybrid offspring must backcross with the parent species for the DNA from one species to be incorporated into the gene pool of the second species (Allendorf and Luikart, 2007).

Although morphological irregularities can indicate a hybrid origin of an individual (Ciucci et al., 2003), there are no unambiguous traits that definitively distinguish dog–wild canid hybrids. The difficulty in identifying hybrids is especially

great in this case because of the huge phenotypic diversity present in the domestic species (Boyko and Boyko, Chapter 8). For this reason, the unambiguous identification of hybrids and of individuals with signs of introgression demands the application of genetic tests.

There are thousands of genetic markers that are useful for the study of gray wolves and dogs. The markers inform about variants (alleles) in very small portions of the genome of these species. When investigating hybridization, researchers look for genetic markers (such as short repetitive sequences called microsatellites, or single nucleotides that differ from one sequence to another, called SNPs) that are present in the

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**Box 7.2** *Continued*

two species with different frequencies. The genetic identification of hybrids involves typing a panel of genetic markers (often between 10 and 20 microsatellite loci) in the suspect individuals and comparing the alleles observed with the frequencies previously found in dogs and in the wild canid. Since the two species are relatively well separated, the allele frequencies tend to be different. Genetic markers showing fixed or almost fixed differences between the two species are the most useful ones because they are expected to generate heterozygote genotypes in the first hybrid generation, following Mendel's laws. Alleles that are present with high frequency in dogs, but are rare in the wild canid, can thus be considered 'dog alleles.' First generation (F1) hybrids will tend to have a 'dog allele' and a 'wild canid allele' for each one of the genetic markers studied. Even if species-specific alleles cannot be identified, the genotype found for a hybrid should have a very low probability of being found in each one of the parental species and should fit with the expectation of an admixed genotype.

Even though the genetic identification of hybrids is relatively easy (except for dingoes; see Box 7.1), the identification of cases of introgression is much more difficult. If a hybrid mates with the wild parental species, only half of the genetic markers would be expected to show a mix of dog and wild canid alleles. This proportion will continue to decrease in subsequent generations. This implies that the robust identification of individuals with admixed ancestry requires a much larger number of genetic markers in order to increase the chances of unambiguously finding regions of the genome originating in the other species. The number of markers required will exponentially increase as one tries to identify older introgressions. This is further complicated by the difficulty of characterizing true parental populations and because hybridization may be episodic or fluctuating, particularly in anthropogenic cases of hybridization. Only more sophisticated genomic approaches, currently being developed, promise to provide this robust identification of old introgression events (Anderson et al., 2009; vonHoldt et al., 2011).

**7.3 Hybridization is often directional**

Hybridization between wild canids and dogs typically seems to be directional. Vilà and Wayne (1999) surveyed all of the maternally inherited mitochondrial DNA data available for gray wolves at that time and found no instance of introgressed dog mitochondrial DNA in any gray wolf population. Since then, thousands more mitochondrial DNA sequences have been published (i.e. Koblmüller et al., 2009, 2012; Leonard et al., 2005; Muñoz-Fuentes et al., 2009; Musiani et al., 2007; Pilot et al., 2010; Randi et al., 2000; Vilà et al., 1999) and very few instances of introgression of a dog mitochondrial haplotype into a wild canid population have been reported, each of which is most likely explained by a single hybridization event (Adams et al., 2003; Muñoz-Fuentes et al., 2010). This implies that hybrid matings involving a female dog and a male wolf are extremely rare, or that those hybrids fail to integrate themselves in the wolf populations.

On the other hand, almost all confirmed hybridization events between these two species involved the mating of female wolves and male dogs. Thus the hybrids carry wolf mitochondrial DNA

(Andersone et al., 2002; Godinho et al., 2011; Khosravi et al., 2013; Randi, 2011; Randi and Lucchini, 2002; Verardi et al., 2006; Vilà et al., 2003; but see Hindrikson et al., 2012). These cases could not be identified through mitochondrial DNA analyses because this marker is maternally inherited, so paternally or bi-parentally inherited nuclear markers must be employed (Iacolina et al., 2010; Vilà et al., 2003). A similar pattern was also observed in Ethiopian wolves (Gottelli et al., 1994).

In the case of gray wolves, the asymmetric pattern of hybridization has been explained by the lack of synchrony in breeding time with that of dogs (Vilà and Wayne, 1999). In most wild canids, females have a single estrus per year, and males are only sexually active at that time of year. This differs fundamentally from dogs, where females have two non-synchronized estrus cycles per year and males are ready to breed throughout the year. This means that whenever a female, wild or domestic, is ready to breed, male dogs are also ready. However, many female dogs will not be in estrus during the short window that wild male canids are able to breed (Vilà and Wayne, 1999).

In some of the few cases where it has been documented that a male wild canid hybridized with a female dog, those males were the first or among the first individuals of their species to (re)colonize an area, and there were either few, or possibly no, conspecific females in the area (Adams et al., 2003; Muñoz-Fuentes et al., 2010). This specific social/ecological condition is an extreme example of an Allee effect (Allee, 1931) where it is not only difficult, but potentially impossible, for an individual to find an appropriate mate. These conditions are probably rare in less disturbed systems. However, in both of these cases this condition was anthropogenically facilitated. In one case young coyote males were trapped, transported outside the range of the species, and released, so there was no possibility of them finding female coyotes with which to mate (Adams et al., 2003). In the second case the local wolf population in Vancouver Island was eradicated, and the first natural recolonizers to reach it found a large population of dogs, but no conspecific potential mates (Muñoz-Fuentes et al., 2010).

#### 7.4 Hybridization, but limited introgression

Theoretically, the arrival of just a few effective migrants—individuals contributing to the reproduction and to the population's gene pool—per generation is enough to erase the differentiation between two populations (Fisher, 1941; Mills and Allendorf, 1996; Wright, 1978). The frequency of hybridization between dogs and wolves in small, frag-

mented European populations where hybrids have been reported (Figure 7.2) appears to be close to 3–5% (Andersone et al., 2002; Godinho et al., 2011; Randi, 2011; Randi and Lucchini, 2002; Verardi et al., 2006; Vilà et al., 2003). Gottelli et al. (1994) reported that 8–17% of the Bale Mountains Ethiopian wolf population had hybrid ancestry. Therefore, reported levels of hybridization should quickly lead to the complete admixture and loss of differentiation of the two species if the hybrids are incorporated into the wild canid populations and do not have a lower fitness. These cannot be taken as species-wide estimates of hybridization rates. Genetic studies of hybridization are costly and are not likely to be undertaken unless there is reasonable chance (lots of dogs and few wild canids) or indirect evidence of hybridization. However, these rate estimates show that hybridization can be locally frequent.

Nevertheless, all these studies show that the hybridizing species remain genetically distinct, suggesting that the genetic admixture may be lower than that estimated by the estimates rates of hybridization. In part this may be due to the fundamentally different behavior of dogs as compared to wild canids (Miklósi, 2007). Many of these behaviors and behavioral complexes have been shown to be genetically inherited, and not a product of the environment. For this reason it is expected that hybrid offspring will share some of their behaviors with each parental species (Box 7.3). Some dog behaviors, such as a tendency to promiscuous matings without forming stable pairs and a low level of contribution by males to raising pups, may seriously impede or

(a)

(b)

**Figure 7.2** Gray wolf–domestic dog hybrids (a) born and living in the wild in Asturias, Spain (photo: Xurde Gayol); (b) born and living in the wild in Italy (photo: Lorenzo Rigacci).

### Box 7.3 Behavior of hybrids

Many behavioral characteristics are genetically determined, and have been differentially selected for in wild and domestic canids. Because hybrids are a combination of two genetic lineages, their behavioral characteristics are likely to be a mix of both. Nevertheless, our knowledge about inheritance of behavior is limited.

The modern advances in molecular genetics have found links between genes, brain function, and a wide range of social behaviors on diverse organisms (Moon-Fanelli, 2011; Robinson et al., 2008). For example, in silver foxes, a naturally occurring melanistic variant of the red fox (*Vulpes vulpes*), an extensive study including genetics, pedigree, biochemical and morphological data, found that some behavioral phenotypes have a genetic basis (i.e., Kukekova et al., 2012). In this sense, each hybrid could show very different personality traits, depending on the degree of admixture and also on chance inheritance of specific alleles. In the course of domestication, dogs have been selected for traits that enable them to understand some human signals and to produce a wider range of communication signals (Hare et al., 2002; Miklósi,

2007). The development of these skills likely has a genetic basis (i.e., Kukekova et al., 2012), as it has also been shown through training experiments with socialized wolves and dogs (Miklósi, 2007; Miklósi et al., 2004). This ability does not seem shared with either wolves or wolf–dog hybrids.

In general, wolf–dog hybrids are less predictable and manageable than dogs. They generally exhibit unpredictable behavior, often including absence of tameness, lack of fear, anti-social behavior, and aggressiveness towards both animals and humans, even if they have been raised with them. Wildlife and livestock may be much more vulnerable to predation by hybrids than dogs because of their higher prey drive instinct (Fritts et al., 2003). There are even reports of fatal attacks by wolf–dog hybrids on unattended children (Hope, 1994).

Dogs are the result of thousands of generations of selection for tame animals. Hybridization represents the disruption of this co-selected set of genes, altering the behavioral repertoire in an unpredictable way. This makes hybrids poor pets in almost all circumstances.

even prevent hybrids from integrating into the wild canid society and achieving breeder status (Vilà and Wayne, 1999). This factor may be especially important in the more social canids, such as the gray wolf and the Ethiopian wolf.

In some cases, physiological differences between the species can contribute to reduce the fitness of the hybrids and their chances of integrating into the wild populations. The timing of estrus in females is genetically based. In dog X coyote crosses, female F1 and F2 hybrids have an estrus cycle that is shifted by two months, from February to December (Mengel, 1971; Silver and Silver, 1969). If these females are able to find mates and breed, their offspring will be born in winter instead of spring, which is likely to increase mortality in colder portions of their range (Adams et al., 2003). A similar effect on the physiology of hybrids with other wild species is probable.

## 7.5 Cases of introgression

Despite the lower fitness of hybrids, there are a few clear cases of introgression of dog alleles into wild

canid populations, including both the Vancouver Island gray wolf population and the south-east United States population of coyotes examples mentioned above (Adams et al., 2003; Muñoz-Fuentes et al., 2010). These examples involve the rare introgression of mitochondrial DNA, often considered to be selectively neutral. Selectively neutral autosomal microsatellite alleles have also been reported to have introgressed from domestic dogs to wild canids, for example in the case of the Ethiopian wolf (Gottelli et al., 1994). Neutral loci should not have any major impact on the phenotype or fitness of the carriers of these introgressed alleles.

Alleles at functional genes associated with coat color appear also to have introgressed from domestic dogs to wild canids. The best-documented case is that of the introgression of a *k* locus allele, which causes a melanistic coat color in dogs, into wild populations of both wolves (Figure 7.3) and coyotes in North America (Anderson et al., 2009), as described above (Section 7.2). Once this mutation was in the wolf population, it provided some selective advantage and spread, although the specific advantage incurred is not known. The black color

**Figure 7.3** Pack of wolves comprising gray and black individuals in Yellowstone National Park, USA (photo: Dan Stahler/NPS photo).

in North American wolves has been correlated with ecological factors, and its high frequency in some areas is suggested to be an adaptation to specific ecological conditions (Coulson et al., 2011; Musiani et al., 2007). Thus, modern black wolves carry in their DNA evidence of an ancient introgression of dog genes, but this does not imply that they are hybrids or that they have a recent hybrid ancestor.

Similarly, results from Italian wolves suggest that introgression of portions of the dog genome in the gene pool of wild wolves can be selected for, affecting only some parts of the genome, while other genomic regions remain virtually untouched (Randi, 2011). In both of these cases the functional or putatively functional gene or region seems to be very discrete and not to have ‘carried along’ much else. This suggests strong selection against most dog DNA in wild canids.

Due to the strong effect of selection in wolves, the rate of gene introgression cannot be directly related to the frequency of hybridization. If hybrids fail to reproduce or to integrate themselves into the wild canid population, these crosses do not result in the transfer of dog genes, reducing the threat posed by hybridization. As mentioned above, the observation that the species remain differentiated indicates that hybrids often do not transfer their genome into the wild populations. This, together with the observation that most of the genome of

the wild canids remains virtually untouched (see vonHoldt et al., 2011 for genome-wide analyses involving multiple populations of dogs and wolves), suggest that introgression in nature might be strongly counteracted by selection (Randi and Lucchini, 2002; Vilà and Wayne, 1999). In very small populations, however, random genetic drift can overwhelm selection and even deleterious alleles can rise in frequency or even become fixed. For example, recessive deleterious alleles likely cause the observed inbreeding depression in the Scandinavian wolf population (Liberg et al., 2005), which was highly inbred because of its extremely small founder population of just three individuals (Vilà et al., 2003), and removing those maladaptive alleles from the gene pool has proven difficult because the effects of selection are likely offset by genetic drift (Hagenblad et al., 2009). This may have impacted the population recovery.

## 7.6 When does hybridization occur?

The factors driving hybridization between wild and domestic canids are multiple and likely complex (Randi, 2008; Vilà and Wayne, 1999). Hybridization has been primarily documented in cases where the wild species exists as a small population, on the edge of its distribution, or when dispersing individuals fail to find suitable mates. Allowing wild can-



ids to exist in populations that are large enough to be demographically and genetically self-sustaining would greatly alleviate this threat (i.e., Wayne and Brown, 2001; Gottelli et al., 2013).

Additionally, hybridization between wild canid species has been shown to increase under conditions of anthropogenic disturbance, such as changes in land-use and high human-caused mortality, likely due to social structure disruption (Hailer and Leonard, 2008; Koblmüller et al., 2009; Rutledge et al., 2010; Stronen et al., 2012; vonHoldt et al., 2011). The same conditions that facilitate hybridization between wild canids may also facilitate hybridization between wild and domestic canids. In this case, the hunting or removal for management of wolves or other wild canids, especially in small, isolated, or 'edge' populations, may be an important factor resulting in hybridization (Andersone et al., 2002).

## 7.7 Conservation implications

Despite the huge capacity of large canids, such as gray wolves, Ethiopian wolves, and coyotes, to disperse, these species have been shown to have a strong population structure likely associated with local adaptation (Carmichael et al., 2001; Geffen et al., 2004; Muñoz-Fuentes et al., 2009; Musiani et al., 2007; Pilot et al., 2006; Sacks et al., 2004, 2005; Gottelli et al., 2013). This pattern is probably common to all wild canids distributed across multiple habitats. Hybridization has the potential to break down both species-level and population-level adaptations.

Most of the documented hybridization between wild and domestic canids has been between gray wolves and dogs (i.e., Randi, 2008). This is primarily a reflection of the amount of effort that has gone into studying the population genetics of gray wolves versus other wild canids. However, hybridization has also been documented between dogs and coyotes (Freeman and Shaw, 1979; Gipson et al., 1974) and Ethiopian wolves (Gottelli et al., 1994). It seems likely that, as more studies are undertaken with other large canids, more examples of hybridization will be identified. The golden jackal (*C. aureus*) is a widespread species that inhabits many human-dominated areas, and has expanded its distribution in some European countries (Arnold

et al., 2012). Recently, two jackals with anomalous phenotypes were collected in Dalmatia (Croatia). Preliminary genetic analyses suggested that they are probably first generation hybrids with dogs (E. Randi, pers. obs.). Hybridization between dogs and common, widespread species such as coyotes and gray wolves (and probably golden jackals) does not usually threaten the wild species due to loss of breeding opportunities. However, hybridization between dogs and rarer wild species, such as the Ethiopian wolf, can reduce its effective number of breeders (MacDonald and Sillero-Zubiri, 2004) and so contribute to the erosion of its genetic diversity (Randall et al., 2010).

At the same time, dog-transmitted diseases have caused dramatic die-offs and local extinctions (Knobel et al., Chapter 6), such as rabies in Ethiopian wolves (Laurenson et al., 1998; MacDonald and Sillero-Zubiri, 2004) and canine parvovirus in gray wolves in Isle Royale (Peterson, 2007). This may constitute an anthropogenic 'edge effect' originating from the large and uncontrolled presence of dogs in many environments (Woodroffe and Ginsberg, 1998), which could also favor hybridization between dogs and some wild canids (e.g., Vilà and Wayne, 1999).

A less biological, but still important, threat to wild canids resulting from hybridization with dogs can be a change in social or legal status. Many populations of canids are protected by regional, national, and/or international laws and treaties. A few individuals hybridizing in these populations may remove the legal protection from either those individuals, their social group, or the whole population. Ironically, the populations under the highest conservation threat, and thus most in need of legal protection, are also those most likely to be involved in hybridization, as discussed above. Perhaps the observation of hybridization in wild populations of canids should be an indicator of poor population health, and a reason for more, not less, protection.

A common response to the presence of wolf-dog hybrids in an area is trying to remove the individuals to minimize the impact of those hybrids on the native population. However, most studies suggest that hybrids often fail to introduce themselves in the wild population and reproduce (see Section 7.4). Consequently, those management measures may

not be necessary. Increased hunting pressure and disturbance of social groups created during the hybrid removal efforts could translate into increased chances of hybridization, and thus amplify rather than contain the problem. Allowing populations to grow and to reach stability could be a more efficient (and cheaper) management measure to reduce the impact of hybrids.

The risk of hybridization between wild and domestic canids could be further diminished by reducing contact between them (Randi, 2008). This would require the control of free-ranging dog populations and, most importantly, allowing an increase in the numbers of wild canids where they exist as small populations so they can form functional populations. This is simple in principle, but complex in practice (Randi, 2011; Young et al., 2011). Fertility control through immunocontraception and surgical sterilization has been shown as an efficient alternative for the long-term reduction of dog numbers (Woodroffe et al., 2004; Young et al., 2011). Direct lethal measures focused on dogs and presumed hybrids are very costly, complex, difficult in practice, and ineffective to implement in the long term. A more effective way to control dog populations would be intense public education and reduced access to anthropogenic food resources such as carrion and garbage dumps (Butler et al., 2004; Woodroffe and Donnelly, 2011; Woodroffe et al., 2004).

## 7.8 Conclusion

Introgression of dog genes into wild canid populations does not seem to be a large problem for widespread wild species, as selection against the hybrids seems generally to be strong enough to remove them from wild populations. The ability of selection to favor adaptation and remove unfit alleles is dependent on large population sizes. In cases where populations are small, selection will not be able to counteract drift and deleterious genes may increase in frequency or even become fixed. For this reason, it is important to allow small, isolated populations of canids to increase in numbers. This includes both rare species, such as the Ethiopian wolf, and isolated populations of more common species, such as the Mexican wolf and the Scandinavian wolf popu-

lations (Hagenblad et al., 2009; Hailer and Leonard, 2008).

## 7.9 Future research

The frequency, distribution, and impact of hybridization between domestic and wild species are just now being realized, largely with the use of increasingly sensitive genetic and genomic tools (Randi, 2008; vonHoldt et al., 2010, 2011). Many of these same patterns of hybridization are also being identified in other taxonomic groups that include both wild and domestic species (Alemayehu et al., 2011; Allendorf et al., 2001; Halbert et al., 2005; Scandura et al., 2011; Silbermayr et al., 2010).

In addition to documenting and characterizing hybridization, we need to better understand the conditions that promote it. This will require an integration of field ecology and genetic approaches. Europe is a good place to study these interactions because of high human and dog density, overlapping with fragmented and relatively small wolf populations. In many regions, conservation guidelines and laws aim at establishing a functional system of connected landscapes and wilderness areas to allow natural dispersal of wildlife. This could support the conservation of marginal or small wild canid populations (Boitani and Ciucci, 2009; MacDonald and Sillero-Zubiri, 2004; Gottelli et al., 2013).

Most of the documented hybridization and introgression has been between dogs and their wild ancestor, the gray wolf. However, this may primarily be a reflection of effort. Very little work has been done on interactions between other *Canis* species and dogs. In particular, golden jackals could be prone to hybridization. Golden jackals may live in humanized areas, are opportunistic, and are likely increasing their distribution in Europe (Arnold et al., 2012). Other species of jackals and wild dogs also co-occur with free-ranging dogs and could potentially hybridize.

Hybridization in *Canis* species is likely not a novel phenomenon. Understanding the history of hybridization over the course of the dog domestication process and over the course of the past several thousand years of change in human societies would be informative. Such information (which could be

achieved through the ancient DNA analysis of Pleistocene and Holocene populations of co-distributed dogs and wild canids) would provide insight into the conditions under which hybridization is most common, and the longer-term effect(s) of that hybridization on natural populations.

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