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Review

Warring brothers: The complex interactions between wolves (*Canis lupus*) and dogs (*Canis familiaris*) in a conservation context

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ABSTRACT

Although both wolves and dogs have been the subjects of numerous studies in many disciplines, the complex relationships between them have not yet been synthesized within a common review, and neither has it been placed in a holistic conservation context. Information and data are spread across numerous publications from different disciplines that rarely interact. Dogs have become the most common carnivore and their population is still increasing. In a context of wolf recovery in multi-use landscapes, there is a growing concern among conservationists for the potential negative impact of dogs on wolf conservation. With this paper we aim to review the numerous and complex interactions existing between wolves and dogs, using literature from disciplines as diverse as history, archeology, anthropology, genetics, ecology, and epidemiology in order to better understand the wolf–dog relationship and its potential impact on wolf conservation. Starting with their phylogenetic relationship and following a summary of the current knowledge on the dog's ancestry we explore how dogs can represent a direct threat for wolves through hybridization, disease transfer and competition. The review highlights a number of ways in which dogs can impact wolf conservation, although a general lack of data and conclusive studies is a common theme that emerges for many topics. Then we analyse how dogs can mitigate human–wolf conflicts through their role as livestock guardians or wolf hunters. Finally we describe the complex phenomenon of wolf predation on dogs before discussing the wolf–dog relationships in general, with a special focus on including a more anthropological perspective. The review highlights the diversity of interactions between wolves and dogs, that can be both negative and positive for wolf conservation. However, more important than these direct impacts, the review highlights how the wolf–dog relationship challenges human attempts to construct simple dichotomies between wild and domestic, or between nature and culture. The borders between these concepts are in fact much more fluid and elusive than is often appreciated, and wolf conservation must adapt to this more complex reality.

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1. Introduction

Wolves and dogs are two powerful icons of the complex relationships that humans form with animals (Jenkins, 1957; Lopez, 1978; Serpell, 1995; Ariel de Vidas, 2002; Foltz, 2006). Although the exact mechanism, location and timing of domestication is subject to constant debate it is apparent that animals resembling domestic dogs had begun to appear between 15,000 and 10,000 years BP (Larson et al., 2012). Since then the history of humans and wolves has been complex, but by the early 20th century humans had exterminated wolves from much of Europe and North America (Boitani, 1995; Mech, 1995; Pluskowski, 2006). However, recent decades have seen a dramatic recovery in many areas (Kaczensky, 1996; Mech, 2010a; Kaczensky et al., 2012).

On the other hand, the history of the dog appears as a linear success story. In a few thousand years, they spread across all continents following humans. They became the object of a wide variety of uses; a source of food and fur, useful working tool as hunter, carrier, hauler, guard, fighter, helper for disabled people, and loving companion. Dogs have become one of the most ubiquitous domestic species and the most common carnivore. Their worldwide population is estimated to be close to 900 million and certainly growing (Gompper, 2014a).

Although they have gone through different historical processes, wolves and dogs are still interacting across a large part of the northern hemisphere. Wolf–dog interactions constitute a unique example of a widespread relationship between a domestic animal and its wild ancestor, since most ancestors of the other actual domestic species are extinct (e.g. aurochs *Bos primigenius*, wild horse *Equus ferus*) or have a greatly reduced distribution (e.g. wild goat *Capra aegagrus*, wild sheep *Ovis orientalis*, wild camel *Camelus ferus*). In addition, the variety of ways that dogs are used results in a variety of wolf–dog interactions. As well as providing a fascinating and rich case study in the field of human–nature interactions, these interactions are actually central elements in the ongoing process of wolf conservation.

Dogs in general are the object of an abundant scientific literature and the various impacts of dogs on wildlife is an emerging research topic, notably in Africa and India, and has been the object of several reviews (Butler et al., 2004; Vanak and Gompper, 2009; Hughes and Macdonald, 2013; Gompper, 2014b; Vanak et al., 2014). However, the relationships between dogs and wolves are not the most studied and have not been the object of a holistic review including the full variety of complex interactions linking these two animals, especially in a conservation context. Through this review we hope to address this gap and provide an overview on wolf–dog relationships and their implication for conservation.

We review the various relationships between wolves and dogs, starting with the phylogenetic one which is fundamental for understanding the other types of relationships. Following the clarification of current thinking on the ancestry of dogs we question how dogs can represent a threat for wolf conservation through hybridization, disease transfer and competition. Then we analyse how dogs can help modulate human–wolf conflicts through their role as livestock guardians or wolf hunters. Finally we describe the complex phenomenon of wolf predation on dogs before discussing future research direction which could be taken to better understand human–wolf–dog relationships and the way they could be managed to minimize conflicts in a context of wolf conservation. Understanding these consequences requires taking into account the existence of culturally constructed conceptual boundaries that humans have established between wolves and dogs that parallel those between wild and domestic, or nature and culture.

2. Methods

Because of the diversity of disciplines and topics covered by this review the information was gathered using a variety of methods. Firstly, a range of literature databases (ISI, SCOPUS, Google Scholar, JSTOR) were searched for relevant key words. Secondly, we manually searched through literature cited sections of relevant papers using "snowball" sampling. Thirdly, we discussed many aspects with colleagues from different disciplines who pointed us towards key publications from their specific fields. Finally, we drew on our own archives of publications, books and technical reports that have been collected during more than 20 years of research. The fact that the resulting review is very heavily built on resources published in sources that are not routinely covered in the databases of peer-reviewed papers underlines the importance of this type of ad hoc data collection which is especially important when touching on disciplines outside the natural sciences. Linguistically, we were biased towards English, French, Spanish and Scandinavian language publications, but we managed to include several sources from other languages such as Russian throughout our network of contacts.

3. Wolves and dogs: ancestors and descendents

Dog ancestry has been and is still the object of numerous studies, reviews and debates. Our aim here is not to contribute to this debate but to present the current state of knowledge as most of the interactions between wolves and dogs, as well as our perceptions of these interactions, must be seen within the context of a domestic animal interacting with its wild ancestor. This therefore requires a clarification of current thinking in this relationship.

According to archaeological data, hominids and wolves have had a relatively close relationship for at least 300,000 years (Olsen, 1985). At that time, they were sharing the same habitat, the same caves and a similar way of life, living in family groups and hunting large ungulates. Indeed, wolf bones have been found in association with hominid bones in very ancient sites dated from 150,000 up to 400,000 Before Present (BP) (de Lumley, 1969; Olsen, 1985; Clutton-Brock, 1995). It is likely that this close relationship led to the progressive emergence of commensal wolves partly living on human refuse, thus entering into a domestication process eventually leading to the emergence of domestic dogs (Morey, 1994; Clutton-Brock, 1995). Notably, an unconscious or conscious selection for tameability could quickly drive to changes in behaviour, morphology and physiology (Trut et al., 2009). Even though it is still contested by a few authors (see e.g. Koler-Matznick, 2002), most genetic, archaeological and behavioural studies tend to

confirm that the extant grey wolf (*Canis lupus*) is the main ancestor of the dog (Clutton-Brock, 1995; Vilà et al., 1997, 1999; Savolainen et al., 2002; Lindblad-Toh et al., 2005).

However, the debate remains open about when, where, and how the process of domestication happened. Both archaeologists and geneticists have recently made important advances in their study of the topic. Some fossils morphologically identified as dog remains have been dated from ca. 30,000 years BP (Germonpré et al., 2009, 2012, 2013; Ovodov et al., 2011). Whether they are domestic dogs or other types of wild canids is still debated since the morphological distinction between wild canids and domestic dogs is difficult for the early phase of the domestication process (Pionnier-Capitan et al., 2011; Larson et al., 2012). According to Larson et al., (2012) who recently reviewed the archaeological literature, the first undisputed domestic dog remains date back to ca. 15,000 years BP in Europe and ca. 12,000 years BP in several places including Syria, Cyprus, Iraq, northern China, and the Russian far east.

Genetic studies using mitochondrial DNA (mtDNA) and based on a molecular clock first suggested that wolf–dog separation could have occurred as long ago as 135,000 years BP and with multiple events (Vilà et al., 1997), but the use of molecular clocks has been critiqued for recent divergences (Ho et al., 2005). Another important study based on mtDNA suggested a more recent domestication event around 15,000 years BP with a single origin in eastern Asia (Savolainen et al., 2002). A more recent analysis supports these findings suggesting a single origin in southern China less than 16,300 years BP (Pang et al., 2009). This origin was already suspected earlier because of the existence of osteological details present in dogs and Chinese wolves (Olsen and Olsen, 1977; Pang et al., 2009).

However, a study showing the same mtDNA haplotype diversity in African village dogs as in east Asian village dogs clearly challenges east Asia as the single origin for dog domestication (Boyko et al., 2009). In addition, another recent study using a genome-wide survey instead of only mtDNA indicates that wolves from the Middle East have been a dominant source for the genetic diversity of dogs (Gray et al., 2010; vonHoldt et al., 2010), even if Chinese wolves probably contributed as well (vonHoldt et al., 2010). Another study based on the genetics of the Major Histocompatibility System (MHC) revealed a higher diversity in Asian dogs (Niskanen et al., 2013), while another analysis based on dogs, wolves, and prehistoric canid mtDNA suggests a dog origin in Europe (Thalmann et al., 2013). It also appears that interbreeding (backcrossing) between dogs and local wolf populations often occurred in the early stages of the domestication process (Vilà et al., 1997; vonHoldt et al., 2011; Wayne and vonHoldt, 2012).

The combination of archaeological and genetic data has begun to provide a better understanding of the dog domestication process. Thus, the complexity of the process and frequent interbreeding between dogs and wolves would reinforce the suggestion that dog domestication, at least in its first stages, was probably more a stochastic evolutionary process rather than one guided by human design, implying no intention of domestication but more a specialization of some wolves to a new niche offered by humans (Morey, 1994; Coppinger and Coppinger, 2001; Galibert et al., 2011; Larson et al., 2012). It is all the more probable since the dog was the first domesticated animal implying that humans had no prior experience with domestication. According to the most recent studies combining archaeology and genetic data, livestock domestication events for other species (cattle, sheep, goats, pigs) all occurred in the Near East around the same period between 8500 and 11,000 years BP (Zeder et al., 2006; Zeder, 2008, 2011; Vigne et al., 2011). At the time and place these domestication events occurred, dogs were already domesticated in Eurasia and certainly present in the Near East (Dayan, 1994; vonHoldt et al., 2010; Larson et al., 2012). It could well be that the definitive separation between dogs and wolves is relatively recent and would have followed Neolithic animal domestication which implied a physical separation between dogs and wolves as a consequence of the incompatibility of wolf presence around human settlements where livestock were kept (Clutton-Brock, 1995; Sablin and Khlopachev, 2002; Verginelli et al., 2005).

The difficulty in defining the exact nature of the relationship between domestic dogs and wolves is epitomised in the uncertain taxonomic status of the dingo in Australia, which is variously viewed as either a wolf subspecies, *C. lupus dingo*, or a feral dog, *Canis familiaris dingo* (Newsome et al., 1980; Newsome and Corbett, 1982, 1985; Corbett, 1995). The situation is made even more complex because of documented hybridization between domestic dogs (of European origin) and dingoes (Daniels and Corbett, 2003). Similar taxonomic uncertainty also exists for many other wild canids, such as the status of the eastern wolf in North America (*C. lupus* vs. *Canis lycaon*), the role of hybridization between coyotes and wolves in the origins of the red wolf (*Canis rufus*) (Nowak, 1992; Nowak et al., 1998; Wayne et al., 1998; Wilson et al., 2000; Grewal et al., 2004; Mech, 2010b; Benson et al., 2013) and the identity of the Great Lakes wolves (Leonard and Wayne, 2008, 2009; Cronin and Mech, 2009; Mech, 2009). Most recently it has been claimed that North African jackals could potentially be considered as African wolves *C. lupus lupaster* (Rueness et al., 2011; Gaubert et al., 2012). This pattern of cryptic relationship is beginning to emerge as a recurrent theme among the larger canid species and may reflect more fluid species borders than many biologists, and almost all legislation, are used to dealing with.

The fact that wolves and dogs are so closely related is at the heart of many controversial and problematic situations within wolf conservation. For example, this taxonomic proximity allows hybridization between these two species as well as the sharing of numerous diseases.

4. Dogs as a threat to wolf conservation

4.1. Hybridization between wolves and dogs

As a consequence of wolves and dogs being closely related, they share identical karyotypes, and can interbreed and produce fertile offspring. Thus, for centuries humans have been deliberately crossbreeding wolves and dogs in order to obtain wolf–dog hybrids. The first written record of this practice comes from Aristotle (ca. 2400 BP), and Pliny (ca. 1900 BP) who reported that people from Gaul tied their bitches to trees so they could mate with wolves and produce hybrids (Iljin, 1941). Deliberate wolf–dog crossbreeding in order to improve dog breeds was apparently widespread in the 17th and 18th century, even if only occasionally practiced, and has been reported for Indian dogs, Eskimo dogs, Hungarian dogs, etc. (Iljin, 1941). Nowadays, several wolf–dog breeds exist (e.g. the Saarloos wolf dog, the Czechoslovakian wolf dog, the Lupo Italiano, the Kunming wolf dog). These dogs are often subject to specific legislation and even forbidden in some countries, more for public safety reasons than for concerns for backcrossing with wild populations of wolf.

While humans have been, and still are, crossbreeding wolves and dogs, hybridization can also occur in uncontrolled situations. As we saw in the previous section, hybridization was certainly a reoccurring part of the early dog domestication process and there was probably a frequent flow of genes between wolf populations and early dog populations. This was possible because humans and wolves were living in close contact and also because early dogs and wolves were not morphologically so different.

Nowadays, uncontrolled hybridization between dogs and wolves still occurs. In order to have an impact on wolf populations,

hybridization has to go through two steps. Firstly a crossbreeding between wolves and dogs must generate hybrids (generation F1). These hybrids can reproduce among themselves but can also backcross with wolves. Ultimately an introgression of dog genes can occur into wolf populations (Randi, 2011). Anecdotal evidence for modern day hybridization in the wild has been detected in numerous places including; Bulgaria, Canada, Italy, Latvia, Spain, and Scandinavia (Vilà and Wayne, 1999; Randi et al., 2000; Andersone et al., 2002; Randi and Lucchini, 2002; Verardi et al., 2006; Klütsch et al., 2010; Muñoz-Fuentes et al., 2010; Godinho et al., 2011; Caniglia et al., 2013a).

Analyses based on mtDNA rarely detect much introgression of dog mtDNA into wolf populations (Muñoz-Fuentes et al., 2010). Therefore, either wolf–dog hybridization is a very rare event, or female F1 hybrids cannot easily reproduce with wolves, or hybridization is mainly occurring between male dogs and female wolves (Vilà and Wayne, 1999; Muñoz-Fuentes et al., 2010; Randi, 2011). It has been hypothesized that crossing between male dogs and female wolves is unlikely to be successful since male dogs do not assist females in pup rearing and care (Vilà and Wayne, 1999). However, recent genetic studies that include Y-chromosome analysis tend to show that crosses between male dogs and female wolves occur and are primarily responsible for the hybridization process (Vilà et al., 2003; Iacolina et al., 2010; Godinho et al., 2011). Crosses between female dogs and male wolves can occur but remain rare (Hindrikson et al., 2012).

Hybridization can also occur between both wolves and dogs and other canids like coyotes (Leonard and Wayne, 2008; Kays et al., 2010; Rutledge et al., 2012). It is often assumed that the risks of hybridization are higher in areas where wolves are either rare, highly perturbed, or in contact with a large population of free-ranging dogs (Vilà and Wayne, 1999; Randi et al., 2000; Andersone et al., 2002; Randi and Lucchini, 2002; Hailer and Leonard, 2008) or coyotes (Rutledge et al., 2012). However, it appears that hybridization between wild canids and domestic dogs can also occur even when the wild canid population is relatively abundant (Adams et al., 2003).

Conservation biologists and wildlife managers are concerned with hybridization as a potential threat to small wolf populations in close contact with free-ranging and feral dogs (Randi, 2008; Iacolina et al., 2010). Indeed, hybridization could drive species or populations to lose specific adaptations and even cause their extinction as a distinct taxon (Gottelli et al., 1994; Simberloff, 1996; Randi, 2008; Muñoz-Fuentes et al., 2010; Allendorf et al., 2013). On the other hand, it has been shown that introgression can also be adaptive (Castric et al., 2008; Hedrick, 2013) and it could be that hybridization with dogs could sometimes provide advantages for their descendants. For example, the black coat colour in wolves is probably the result of the introgression of a mutation resulting from hybridization with dogs (Anderson et al., 2009; Caniglia et al., 2013a). Under certain circumstances, black wolves may have a better life expectancy, especially in the face of environmental changes (Anderson et al., 2009; Hedrick, 2009; Coulson et al., 2011) even if its rarity in wolf populations and its early appearance in dogs would suggest this mutation was strongly counter selected in strictly wild contexts (Ollivier et al., 2013).

Whatever the consequences, hybridization between dogs and wolves appears as a great challenge for wildlife managers and conservation biologists for a number of reasons. Firstly, identification of wolf–dog hybrids remains complex even with the latest advances in genetic techniques (cf. notably Lorenzini et al., in press). Secondly, the legal status of these hybrids is very difficult to assess. If the wolf is protected, what is the status of a wolf–dog hybrid? The only international legislation that specifically addresses the issue is the Convention on International Trade in Endangered Species which offers hybrids the same protection as the wild species (CITES, Conf. 10.17, Rev. Cop14). These issues lead to a range of difficult questions that nature conservationists need to address about the management of hybrids.

The question has been raised as to whether all black wolves or wolves with dewclaws (cf. Ciucci et al., 2003) should be removed from the wild in Italy because there has been an introgression of dog genes in their karyotype at some point in their history. This leads to further technical questions about what is an acceptable level of introgression, as well as more philosophical questions concerning the borders between wild and domestic. Finally, a wide range of ethical questions about the acceptability of various management interventions are apparent. Practices in different countries vary, from the use of lethal control of hybrids (e.g. Norway in 2004) to live capture and placement in a captive setting (e.g. Latvia in 2000, Germany in 2003 and Italy in 2013). Virtually all discussions around hybrid management take place in very emotional debates, and there are no widely accepted best practice management protocols for their management.

An interesting parallel exists with domestic horses which are often used in nature conservation projects to take on the ecological role of their extinct wild ancestors (through conservation grazing). The desirability of wolf–dog hybrids being ecological surrogates for wolves has never been raised in the mainstream conservation literature, although there has been some local public debate about it. One of the main problems is that there is virtually no data about the behaviour and ecology of wolf–dog hybrids under free-ranging conditions.

4.2. Disease transmission between wolves and dogs

Due to their close genetic similarity, dogs and wolves share many of the same parasites and diseases. More than 350 pathogens have been identified which can infect dog populations (Cleaveland et al., 2001). Dog populations, and especially feral dogs, can be a maintenance population for diseases, meaning their critical community size is sufficient to allow the infection to persist (Knobel et al., 2014). Thus, diseases maintained in a dog population (reservoir) can potentially affect wildlife (target) through a spill-over mechanism (Daszak et al., 2000) and be considered as a threat to conservation (Haydon et al., 2002). On the other hand, wolves can also transmit parasites and diseases to dogs, either through a spill-back mechanism or if wolves are themselves a disease reservoir, causing veterinary problem as well as health concerns if dogs in turn transmit parasites to humans. In addition, both wolves and dogs can play a role in disease transmission without being a maintenance population if they are part of a maintenance community or just vectors for transmitting infection from maintenance population or community to a target population (Knobel et al., 2014). Among the numerous pathogens affecting dogs, only a few are believed to be of concern for wild canid conservation, and only three of them have been well studied: rabies virus (RABV), canine distemper virus (CDV) and canine parvovirus (CPV) (Knobel et al., 2014).

The rabies virus is of primary concern, notably because it also impacts human health. Indeed, the World Health Organisation (WHO) estimates number of deaths from rabies between 37,000 and 86,000 for 2010 (95% confidence intervals) with most cases (35,000–82,000) occurring in Asia and Africa (World Health Organization, 2013). It has been suggested that the different clades of RABV come from an ancestor occurring in domestic dogs from the Indian subcontinent, and dogs are probably the main vector for interspecies transmission of rabies (Bourhy et al., 2008). Dogs are also thought to be at the origin of the most widespread lineage of rabies present in South America, North and Central Africa (cf. Smith et al., 1992), originating in Europe and spreading with dog movements during colonisation (Baer, 2007; Knobel et al., 2014).

However, apart from intercontinental and large scale translocations, human movements do not appear to be responsible for rabid animal movements and therefore RABV transmission (Bourhy et al., 2008). Dogs are still considered as the main reservoir for rabies in Asia and Africa (Knobel et al., 2005).

Rabies has been frequently documented among wild wolf populations and can locally be important for wolf demographics (Chapman, 1978; Theberge et al., 1994; Ballard and Krausman, 1997; Holmala and Kauhala, 2006). In addition, wolves can be responsible for directly transmitting rabies to humans (Tabel et al., 1974; Cherkasskiy 1988; King et al., 2004; Türkmen et al., 2012). Wolves tend to develop the furious form of rabies and their ability to travel long distances makes them effective transmitters of the disease (Holmala and Kauhala, 2006). Rabid wolves are very dangerous and there are numerous well documented episodes from throughout history during which one wolf can bite several people (cf. King et al., 2004; Baer, 2007; Moriceau, 2007). In addition, to the transmission of rabies, attacks by rabid wolves frequently result in the immediate death of victims from their injuries. However, considering the few attested cases of rabid wolves compared with other host animals, wolves do not appear to be a primary host or reservoir for rabies, even if the situation could have been different when they were more abundant in Europe in the past (Linnell et al., 2002). From a human safety point of view, most of the countries highly concerned with human rabies are outside wolf range, with the notable exception of India (6000–14,000 deaths in 2010) (World Health Organization, 2013). The epidemiology of rabies among wild canid species is complex. Both dogs and wolves can transmit rabies to each other. However, there is no evidence that wolf rabies occurs as a result of spill-over from dogs. Even if wolf rabies can be connected with stray dogs, it also appears to be linked with foxes and jackals (Johnson, 1995; Linnell et al., 2002; Holmala and Kauhala, 2006). On the other hand, it appears unlikely that wolves could be a long term reservoir host since they have not acquired a unique virus variant (Hanlon et al., 2007). However, with their long dispersal distances wolves represent challenges in areas where wildlife rabies is being eradicated through vaccination campaigns.

While some evidence points to dogs serving as a potential reservoir for RABV, their role in the transmission of other pathogens like CDV and CPV to grey wolves is less clear. Dogs appears to be responsible for transmission of these diseases to other wild canids like Ethiopian wolves (*Canis simensis*) and African wild dogs (*Lycaon pictus*) (Cleaveland et al., 2001; Haydon et al., 2006; Woodroffe et al., 2012). Both CPV and CDV affect wolves (Mech et al., 1986; Bailey et al., 1995; Sobrino et al., 2008) and it has been shown they can affect wolf pup survival (Johnson et al., 1994; Mech et al., 2008). Increased contacts with dogs are suspected to be responsible for the transmission of CPV and CDV to wolves in some cases (Bailey et al., 1995; Müller et al., 2011) although there is no confirmation that domestic dog is a host reservoir for these pathogens (cf. Knobel et al., 2014). One of the most notable episodes of disease transfer from dogs to wolves with a conservation context was on the well-studied Isle Royale population. An outbreak of parvovirus (of domestic dog origin) led to a dramatic crash in the wolf population and a dramatic change in the dynamics of the entire ecosystem (Wilmers et al., 2006).

Although RABV, CDV, and CPV are the most studied diseases in canids, other diseases are beginning to be studied in a conservation context, e.g. canine adenovirus, canine parainfluenza virus, and *Toxoplasma gondii* among others (Philippa et al., 2004; Almberg et al., 2009). In addition, apart from viruses and microparasites, dogs also share macroparasites with wild carnivores and notably with wolves. Among internal parasites, cestodes *Echinococcus multilocularis* and *Echinococcus granulosus* are of great concern since they are responsible for echinococcosis in humans (Davidson et al., 2012; Grosso et al., 2012; Otero-Abad and Torgerson, 2013). Both dogs and wolves are definitive hosts for these parasites (Martínek et al., 2001; Foreyt et al., 2009). *E. granulosus* has two cycles, a domestic one with dogs and sheep and a sylvatic one with wolves and wild ruminants, but these cycles are linked when dogs eat wild ruminant carcasses and wolves eat domestic animals (Gortázar et al., 2007). Dogs are the main vectors of transmission towards humans (Grosso et al., 2012). The increase in dog numbers as well as dog movements by people are considered to be responsible for the increasing range of *E. multilocularis* (Jenkins et al., 2011; Davidson et al., 2012). Also in this context the long dispersal distances of wolves has raised public health concerns because of the risk of wolves bringing the parasites to areas from which it is absent (Martínek et al., 2001; Hirvelä-Koski et al., 2003; Romig et al., 2006; Romig, 2009). Although it has not been documented that this has actually happened, the potential has become a part of anti-wolf discourse in both Europe and North America (Geist, 2010).

External parasites are also shared and wolves in Alaska have been infected by dog lice (*Trichodectes canis*) which were introduced via dogs, causing pediculosis with various consequences (Gardner et al., 2013). Dog lice can cause individual morbidity and could affect fitness but does not appear as a threat to wolf populations (Mech et al., 1985; Jimenez et al., 2010a). Sarcoptic mange *Sarcoptes scabiei* can affect both dogs and wolves and cross transmission of some strains is possible between species (Jimenez et al., 2010b) and between wild and domestic hosts (Pence and Ueckermann, 2002), even though early experimental attempts with transmission from wolf to dog were unsuccessful (Samuel, 1981). Sarcoptic mange epidemiology remains unclear and up to now there is no indication of transmission between dogs and wolves (Knobel et al., 2014).

Because of wildlife recovery, globalization and international trade, there is a general trend for increasing disease transmission between people, domestic animals and wildlife, with the emergence of new diseases and the re-emergence of others that had almost disappeared (Daszak et al., 2000; Cook and Karesh, 2008). Due to their widespread presence inside human communities, dogs clearly appear as a potential reservoir of emerging and re-emerging infectious diseases for humans (Macpherson, 2005; Salb et al., 2008; Quinnell and Courtenay, 2009). As a rather positive consequence, dogs can also play a useful role as sentinel hosts for disease (Cleaveland et al., 2006).

In a conservation perspective, it appears that dogs can transmit numerous diseases to wildlife populations and could serve as a reservoir host, notably because of their population size. However, our knowledge of the epidemiology and ecology of the various pathogens is insufficient to assess whether dogs are the main responsible host or if their management would lead to a reduction of pathogen frequency in wildlife populations (Knobel et al., 2014). If disease transmission through dogs appears as a threat to wild canids like in the case of Ethiopian wolves and African wild dogs, its impact on grey wolf demography remains to be assessed. There is notably a lack of monitoring for diseases and parasites (e.g. tuberculosis, erlichiosis, and leishmaniasis) considered as less important which may cause mortality or reduced fitness, even if only sporadically or chronically. Moreover, considering the numerous diseases and parasites shared by dogs and wolves, it is important to take into account the possibility of co-infections potentially driving die-off episodes.

In a context of wolf–dog hybridization, the question of potential better resistance of hybrids to diseases could raise some concern. Indeed, introgression can sometimes provide more variation in the Major Histocompatibility Complex (MHC) and then better resistance to disease as exemplified by coyotes (*Canis latrans*) and red wolves (*C. rufus*) (Hedrick et al., 2002; Hedrick, 2013).

4.3. Wolf–dog competition

When they have the possibility to do so, dogs generally act as carnivores, becoming a part of the carnivore community and compete with other carnivores. Being in fact the most abundant carnivore in the world, feral and free-ranging dogs have the greatest potential to compete with wolves for wildlife (Young et al., 2011). Vanak and Gompper (2009) identify three types of intraguild competition:

- Exploitative competition: competition for limited resources.
- Interference competition: spatial exclusion, harassment or intraguild predation.
- Apparent competition: differential sensitivity to a shared predator or parasite.

Although there has been a growing interest in research on dog-wildlife interactions in recent years (Hughes and Macdonald, 2013), our knowledge of dog interactions with sympatric carnivores still remains severely limited (Vanak and Gompper, 2009). A review of the different studies analysing or reporting competitive effects of dogs on sympatric carnivores does not mention any research on competition between wolves and dogs (Vanak et al., 2014). This is surprising considering the extent of sympatry between the two and the fact that being both canids they should show more intense interference competition (Donadio and Buskirk, 2006). Some early studies could only suggest the high probability of competition existing between wolves and dogs considering the low number of wolves and the high number of dogs, as well as the fact they were sharing the same resources, i.e. garbage and livestock (Rjabov, 1980; Boitani, 1983; Gipson, 1983; Ovsyanikov and Poyarkov, 1996). Indeed, if dogs do not appear as good exploitative competitors to wolves in more natural environments, they can be at an advantage when using human-derived materials (HDM) or as scavengers close to human settlements (Vanak and Gompper, 2009). Interference competition can also occur between wolves and dogs but in general it favours the wolf which is known to kill dogs in a context of intraguild predation. However, wolves tend to live in pairs or in small packs in areas where they are highly persecuted, giving them a disadvantage facing large dog groups (Boitani, 1983).

As we saw in the previous part, dogs can be a potential reservoir for diseases affecting wolves and as such it could be there is apparent competition in that case, wolves being more sensitive to the parasite because of their smaller population (as compared to the massive dog population).

Another potential factor of apparent competition between wolves and dogs could be differences in the immune system. Indeed, small and isolated wolf populations can show a low variability in MHC alleles (Seddon and Ellegren, 2004), even if variability is often maintained in wolf populations (Seddon and Ellegren, 2002; Galaverni et al., 2013). Although it remains unclear if loss of MHC variation poses a threat to population viability (Radwan et al., 2010), it is probable that high numbers of MHC alleles are crucial to deal with the variety of pathogens in a context of competition with large populations of dogs.

Some authors suggest that wolves are often blamed for dog predation on livestock, notably in places where feral and free-ranging dogs are numerous (Boitani, 1983; Cozza et al., 1996). This phenomenon could arise where wolf attacks are compensated and not dog attacks (Cozza et al., 1996), and is also the result of difficulties in distinguishing between wolf and dog attacks based on field autopsies (Caniglia et al., 2013b). In the case that this phenomenon leads to legal management actions like regulation or elimination of wolves, or to an increased poaching activity targeting wolves, it could be seen as a form of apparent competition, as wolves and dogs would share humans as a common predator.

It has been shown that dogs can kill livestock, notably sheep (Bergman et al., 2009), and can even have an important economic impact in some wolf-free areas (Taylor et al., 2005). A study in Spain even found dog faeces contained far more domestic animal remains than wolf faeces from the same area but could not make the distinction between predation and scavenging (Echegaray and Vilà, 2009). Thus, even if there appears to be some indications that dogs could be responsible for damages attributed to wolves, there are no relevant published data confirming this phenomenon. Moreover, some longitudinal studies have shown that when wolves return in a region the damage on livestock substantially increases as compared with when they were absent (Garde et al., 2004; Garde, 2005).

In fact, despite the potential impact of dogs on livestock, and because of the difficulties to assertain the origin of predation, there is a lack of information on this phenomenon. The use of a forensic approach availing of DNA analysis from saliva in bite marks could probably help to better understand this phenomenon in the future (Caniglia et al., 2013b).

5. Dogs as a tool to help conserve wolves

5.1. Livestock guarding dogs

If dogs can become a threat to wolf populations through hybridization, competition, and the spread of diseases, they have also been, and are still, employed to protect livestock from wolf predation. Therefore they can contribute to mitigating human–wolf conflicts and are often proposed as a non-lethal management tool in the wolf conservation toolbox (Shivik, 2006).

It is quite common that shepherds are accompanied by a few dogs that will alert humans of the presence of any intruder, but not all of them can deter the attack of wild carnivores. While many dogs can be used to guard livestock against predators, as shown by the effective use of small mongrels by Navajos (Coppinger et al., 1982; Black and Green, 1985), some types of dogs appear to be the result of a specific selection for this activity. These specific dogs originate from Eurasia and are generically called Livestock Guarding Dogs (LGDs) or Livestock Protection Dogs (LPDs). LGDs present specific morphological and behavioural characteristics. These characteristics are probably the result of an adaptation to the harsh conditions of transhumance, mountain life, and confrontation with wild carnivores as well as a post-zygotic selection of behavioural traits favoured by shepherds (Coppinger and Coppinger, 2001). Thus, LGDs generally weight at least 30–40 kg and reach 50–60 cm in height (Coppinger and Schneider, 1995). Considering they show a specific morphology, Breber proposes that they be categorized as mastinoid types (Breber, 2008).

The behavioural characteristics of LGDs result from the combination of specific innate traits with the reinforcement of some behaviours and the prevention of others at specific developmental periods (Coppinger and Schneider, 1995). Thus, being raised among livestock, LGDs should develop attentiveness, i.e. build social bonds with livestock. The prevention of any attempt to play with livestock or show predatory motor patterns is an important part of their trustworthy behaviour. The combination of attentiveness and trustworthiness should drive the dog to develop a protective behaviour towards the flock (Coppinger and Schneider, 1995; Coppinger and Coppinger, 2005). Although an appropriate environment is essential for the development of attentiveness, trustworthiness, and protectiveness to the flock, LGDs show some behavioural predispositions that facilitate the emergence of these qualities. Indeed, they tend to have a longer period of social bonding than other breeds, to maintain juvenile behaviours during

adulthood, and their predatory motor patterns rarely emerge or remain rather weak (Coppinger and Schneider, 1995).

According to Coppinger and Schneider (1995), LGDs are not fierce and brave animals defending the flock. They rather protect livestock by disrupting wolf predatory behaviour and displaying ambiguous and context-maladapted behaviours (barking, social greeting, play, and sometimes aggression). However, in some contexts, notably facing large predators like wolves, a higher level of aggressiveness could be more efficient to deter attacks (Green and Woodruff, 1990; Sedefchev, 2005). Widespread historical use of LGDs against wolves in Eurasia (Coppinger and Coppinger, 1995) as well as numerous popular accounts (Smith et al., 2000) shows that LGDs have been, and can potentially be, efficient against wolf predation in many contexts. A study in France has shown that the ability of LGDs to reduce wolf depredation on sheep depends of several factors, notably the size of the herd and the wider husbandry practices within which they are integrated (Espuno et al., 2004). LGDs are sometimes killed by wolves (Bangs et al., 2005; Mertens and Schneider, 2005) and their efficiency could notably be limited in silvo-pastoral systems where sheep are split in several small flocks (Garde, 1996) or else do not flock at all (see notably Hansen and Smith, 1999). It appears that additional research is needed to assess the effectiveness of LGDs in protecting flocks from wolf depredation (Smith et al., 2000; Gehring et al., 2010), notably considering the variety of pastoral systems in Eurasia and America, as well as the changes in social and economic context (see e.g. Lescureux and Linnell, 2013) which are affecting pastoralism worldwide.

LGDs are now used to protect livestock from wild carnivores in general, but also from wild ungulates that can transmit diseases (VerCauteren et al., 2012). They now occur on almost all continents to protect against carnivores as diverse as cheetah (*Acinonyx jubatus*) in Africa (Marker et al., 2005), coyotes, pumas (*Puma concolor*) and black bears (*Ursus americanus*) in America (Andelt and Hopper, 2000), and dingoes in Australia (Jenkins, 2003). However, historically they originate from Eurasia and their existence appears to be linked with extensive sheep grazing, the availability of whey (as a waste product from cheese production) to feed such large dogs, and wolf depredation. Indeed, in several cases like in the British Isles, LGDs disappeared quickly after wolf extermination (Pluskowski, 2006; Breber, 2008).

According to Coppinger and Coppinger (2001), livestock guarding dogs are among the oldest working dogs. Dog breed supporters have constructed a diversity of unsubstantiated myths around LGDs' origins, suggesting they could originate as far back as 6000 years BP (Rigg, 2001). While some authors trace their origins to the Tibetan Mastiff, others suggest LGDs come from Molossers given to Alexander the Great by an Indian king (Guardamagna, 1995) or even that some breeds like the Slovensky Cuvac are derived from Arctic wolves (American Kennel Club, 2013). There is no archeological data supporting any of these hypotheses (see notably Brewer et al., 2001). The most ancient association between dogs and sheep in archaeological records dates back to 3585 BC (Olsen, 1985) and the oldest written mention of dogs dedicated to guarding livestock appears in Aristotle's *History of Animals*, dated from 343 BC (cf. Cummins and Lore, 2006). Livestock guarding dogs are described in detail in Varro's (116–27 BC) *Rerum rusticarum libri III*. *De re rustica* is a compilation of Cato the Elder, Varro, Columella and Palladius texts about agriculture and remained the main reference on agronomy in Europe until the 17th century (Nisard, 1851) and includes sections on LGDs.

Concerning the origin of different breeds, it has been shown that the term breed is problematic when it comes to dog history and that it would be more relevant to consider that some broad classes of dogs existed like sight hound, scent hunters, shepherd dogs, etc. Modern breeds as we know them, based on morphologic appearance and closed bloodlines, only appeared in the 19th century (Larson et al., 2012). It is probably all the more the case for LGDs since these dogs were mainly used by transhumant shepherds, and gene flow between dogs from different regions was probably important (Coppinger and Schneider, 1995; Coppinger and Coppinger, 2001, 2005). Thus Breber points out that overall similarity between LGDs is so obvious that splitting them into different breeds appears arbitrary (Breber, 2008) probably explained by hobbyist rationales within recent national or regional boundaries (Coppinger and Coppinger, 2001) that are separated from their original working contexts.

From a wolf conservation perspective, LGDs appear as a potentially useful tool to mitigate human–wolf conflicts, although their role in mitigation will vary strongly according to the socio-cultural and ecological context. In places where they have always been used, they are usually well integrated into the pastoral system and the ecological and social environment, even though conflicts can still exist with other land users, notably hunters (Sedefchev, 2005, Lescureux unpublished data). They are not only perceived as a carnivore conflict mitigation tool but more as a pastoral tool used in combination with other types of measures, including night-time enclosures, shepherding and lethal control. Nonetheless, the fact they reduce predation on livestock probably allows a more peaceful coexistence with wolves. In places where they are introduced or reintroduced after the return of wolves, the situation is far more complex. Livestock breeders generally see LGDs as a new constraint. LGDs generate additional costs and work (Gehring et al., 2010), pastoral systems are not always adapted to their presence, and there can be a lack of information, resources and proper dog lineages (Garde, 1996). The legal status of LGDs should also be taken into account notably when reintroduced into a country, as livestock breeders have been prosecuted and fined for LDG attacks on hikers in France (Linder and Durand, 2001). In transhumant systems, the management of LGDs during the winter period can also be challenging if they have to be confined close to human settlements, which has sometimes led local authorities to forbid LGDs within their communities (Gehring et al., 2010).

From a more anthropological point of view, LGDs constitute a striking example of the complex relationships established between humans and their environment, with the use of a wolf descendant to protect livestock from wolves. This example shows how pastoral systems have evolved in close interaction with predators and brings a focus on the role of both the herding and the guarding dogs in the evolution of pastoral systems.

5.2. Dogs used for hunting wolves

While some dogs can be used to protect flocks from wolf attacks, others have also been widely used in the past to hunt wolves (Association des Lieutenants de Louveterie, 1925; Lopez, 1978; Martin, 2005; Hickey, 2011), and are still used in some countries like Kyrgyzstan (Lescureux, 2007). Various hunting breeds, notably hounds, have been used to hunt wolves, but some breeds have been specifically selected for wolf hunting, like the Borzoi wolfhound, the Irish wolfhound, or the Kyrgyz Tajgan. If wolfing with dogs has been described as an aristocratic amusement (Lopez, 1978), it has to be mentioned that wolf hunting also provides products with a direct utilitarian use like pelts and organs used in traditional medicine (Lescureux, 2007). More importantly from a conservation point of view, large carnivore hunting can also be considered as a management tool (Parker et al., 2009; Treves, 2009; Bischof et al., 2012) and in some cases can help mitigate conflicts between humans and carnivores (Lescureux, 2006; Lescureux and Linnell, 2010; Mech, 2010a; Knott et al., 2013; Treves et al., 2013). In historic periods, it appears that wolfhounds were important tools for wolf management. For example, the export of Irish

wolfhounds was forbidden by a council order of Cromwell in 1652 in order to help deal with growing wolf problems in the country (Hickey, 2011). However, to our knowledge hunting wolves with dogs is not in use anymore in Europe. Although wolf hunting with dogs was authorized in Wisconsin in 2012 (cf. Treves et al., 2013), dogs were not used in the 2012 season due to a non-resolved lawsuit (Wisconsin Department of Natural Resources, 2013), showing the potential controversy existing over this hunting form, both from wolf protectionists concerned with wolf hunting and animal right and animal welfare activists concerned with the possibility of dogs being injured or killed by wolves.

6. Wolf predation on dogs

In contrast to the cases where dogs are used to reduce conflicts with wolves, dogs can also be central in the escalation of conflicts between people and wolves. This refers to cases when wolves kill dogs. The role of dogs as prey or predators in various ecosystems is well documented (Butler et al., 2004, 2014) but while wolf predation on dogs is widely known from the grey and popular literature, it is not well documented in the scientific literature (Butler et al., 2014). Information on the killing of dogs comes from two sources. The first is from wildlife management agencies who keep records of domestic animals killed by large carnivores, usually in situations where compensation is paid for conflicts. This data will only cover the killing of dogs that have a clear owner and where dogs are kept close to the owner such that the attack can be documented. It will not cover issues where wolves kill feral dogs, for example. The second source is from wolf diet studies that quantifies the extent of dog hair in wolf scats or stomachs, and will not be biased towards certain types of dogs.

We were able to obtain wildlife management agency records from seven European countries and six states within the US (Table S1). With the exception of Croatia, the picture that emerges is of dog killing being a chronic but low intensity conflict with relatively few dogs being killed per year. However, the data also show a lot of spatio-temporal variation within the study areas. In addition to these systematic records a brief survey among our colleagues working with wolves in other countries indicated that such attacks also occur in areas as diverse as Albania, Macedonia, Bulgaria, Slovakia, Germany, Spain, Italy, Mongolia and Kyrgyzstan. The situation where most dogs are killed is where loose dogs are used for recreational hunting (30–80% of the cases, see Butler et al., 2014). In Fennoscandia this mainly concerns moose (*Alces alces*) or hare (*Lepus timidus*) hunting dogs, whereas in the Great Lakes region of the US it is mainly black bear hunting hounds. Killing these dogs is associated with considerable emotional trauma due to the loss of a companion animal. Additionally there is an economic aspect considering the value of these dogs for sale as trained dogs or as breeding material. The role of the cooperation between hunter and dog as a motivation to hunt is well documented in the hunting literature and can therefore serve to erode an already fragile tolerance among hunters for the presence of wolves. The second common situation concerns where pet or guard dogs are taken close to houses or in recreational areas. Such attacks particularly induce a sense of fear to rural people with predatory attacks occurring close to their homes. A final situation concerns the killing of livestock guarding dogs that are trying to defend livestock.

The data on dog occurrence in wolf diet also indicates that dog killing is widespread, but rarely intense, with dog presence typically constituting just a few percentage points in occurrence (Table S2). The exception is for some parts of Russia and Spain in places and periods where wild prey were only present at low densities, and some data from Romania for specific wolf packs that lived close to large towns. It is only in these cases that dogs can be viewed as a major dietary component of wolves (Bibikov, 1988; Cuesta et al., 1991; Pozio et al., 2001).

Although the numbers of dogs killed per year are relatively low, this killing can be the driver of very intense conservation conflicts (Redpath et al., 2013) that can have negative impacts on human willingness to share space with wolves due to the special relationship that exists between people and their pet dogs and the induced fear linked with wolves entering villages and farmyards to take dogs close to houses. Indeed, in many cultures there are strong social and emotional bonds between humans and dogs and the latter can be seen as family members and/or working/sporting team members (Sanders, 1993; Hart, 1995; Haraway, 2003; Guillo, 2009). In these situations the loss of dogs can lead to strong emotional responses. At least in Fennoscandia and Wisconsin, the issue of dog attacks has become a central driver of rural opposition to wolves and demands for more liberal wolf hunting and lower population recovery goals (Skogen and Krange, 2003; Skogen et al., 2006; Bisi et al., 2007; Sjolander-Lindqvist, 2009). In addition, good hunting or working dogs are valuable animals which cannot be quickly replaced (see e.g. Lescureux and Linnell, 2010).

As a consequence, wolf predation on dogs clearly weakens community and political support for wolf conservation (Skogen and Krange, 2003; Skogen et al., 2006; Bisi et al., 2007; Sjolander-Lindqvist, 2009), and if some of the dog killing can be mitigated by avoiding having dogs lose or tied in yards at night, the hunting dog issue is nearly impossible to mitigate as it is part of a strong tradition, at least in Europe and parts of North America. An additional aspect that can be detrimental for wolf conservation is the fact that the killing and consumption of dogs opens for the transmission of diseases and parasites from dogs to wolves (Pozio et al., 2001).

There has been relatively little research investment in this topic (Fritts and Paul, 1989; Kojola and Kuittinen, 2002; Kojola et al., 2004; Edge et al., 2011) and there have been even fewer analyses that try to explain variation in dog killing in space and time (Butler et al., 2014). Wolf population size, low wild prey density, the way in which dogs are kept or used, and the existence of specialized problem packs are four factors that are often cited as being important for determining the numbers of dogs killed (Cuesta et al., 1991; Pozio et al., 2001; Kojola and Kuittinen, 2002; Sidorovich et al., 2003; Kojola et al., 2004). However, there has never been a formal analysis of these patterns. A further uncertainty lies in the motivation for wolves to kill dogs, which seems to be both motivated by predation for food and territorial defence (Karlsson and Jaxgård, 2004), but again these patterns have never been formally analysed.

7. Discussion

Through this review which has crossed multiple disciplinary boundaries we have explored several complex interactions between dogs and wolves. Despite the relatively large number of publications and even reviews that touch on either dogs or wolves, the relationship between them has been rarely investigated specifically and it appears there is a strong need for more research on this topic.

Thanks to progress in genetic studies, numerous recent publications have shed light on dog ancestry, wolf–dog hybridization, and the overall relationships between large canid species. It is almost uncontested now that dogs descend from wolves and were found in several places from Europe to the Middle-East and Far Eastern Russia between 15,000 and 12,000 years BP. Wolf–dog hybridizations were probably numerous then, and it appears they also occurred in the recent past, and they still occur nowadays in numerous places (Randi, 2011). In fact, hybridization also occurs

between other large wild canids, and species borders in the genus *Canis* appear to be rather blurry with many cryptic relationships existing, generating controversies over species names and conservation status.

7.1. The impacts of dogs on wolves

From a conservation point of view, the direct impact of dogs on wolves has yet to be assessed with any certainty. While several publications suggest there could be multiple pathways to competition between wolves and dogs, there is a lack of studies confirming the strength of the interactions. In the same way, knowledge of the epidemiology and ecology of the pathogens common to wolves and dogs appears to be insufficient to confirm that dogs actually constitute a threat to wolf conservation through disease transmission. Finally, the greatest direct threat that dogs could cause to wolves appears to be through hybridization since its occurrence has been confirmed. The extent of this phenomenon will probably vary a lot according to context and it urgently needs to be investigated in many places, notably southern and eastern Europe and India where free-ranging dogs are numerous and sympatric with wolves. However, its impact on wolf conservation status has not yet been confirmed, and both the identification (Lorenzini et al., in press) and management of hybrids are quite challenging, from both technical and legal points of view.

Finally, it is important to consider the potential additive impact of the different potential impacts that dogs could have on wolves, as it is likely that the areas which are predisposed to one impact will also be predisposed to other impacts. The impact of dogs is likely to vary between areas depending on the way in which dogs are kept, and modulated by proximity to human settlements and potential access to anthropogenic food. In general there is a desperate need for more studies of the ecology of dogs of all forms, including free-ranging, stray and feral, even if some studies have already been published (Vanak and Gompper, 2009; Young et al., 2011; Paschoal Ana Maria et al., 2012).

Considering that the main threat to wolf populations is usually direct killing (legally and illegally) due to conflicts with humans (Fritts et al., 2003), the role dogs play in human–wolf conflicts is probably as important as their direct impact, if not more so. This impact can be either positive or negative, depending on the type of interaction and the context. Once again, this impact is difficult to measure and more research is needed to assess the role of the dogs according to the context and notably the dog status.

While free-ranging and feral dogs clearly represent potential direct threats to wolf populations, their impact on human–wolf conflicts is not obvious, except in the case where wolves are blamed for dog attacks on livestock. In that case the few existing results cannot be generalized, considering many factors can influence the relative impact of dogs and wolves on livestock according to the status and populations of dogs as well as the different pastoral systems.

Although wolf hunting dogs had a negative impact on wolf conservation status in the past this practice is currently quite rare and its proposed reintroduction is likely to increase conflicts, notably with animal rights and animal welfare activists (with concerns for both wolf and dog welfare). Hunting dog in general are associated with increasing human–wolf conflicts since dog killing by wolves appears to be one of the major drivers of negative attitudes towards wolf conservation in many areas. Butler et al. (2014) proposed a Dog Development Index (DDI) measuring the human–dog relationships which could permit the evaluation of the potential conflicts emerging from wild carnivore predation on dogs, depending also on the human–wild carnivore relationship. Once again, more research is needed to assess the social and ecological factors associated with wolf predation on dogs as well as its effect on human–wolf conflicts.

Livestock Guarding Dogs (LGDs) have the most positive impact on wolf conservation by reducing damages on livestock caused by both wolves and dogs and thus mitigating conflicts with humans. However, their effectiveness varies according to the ecological and social context, and their introduction or reintroduction to pastoral systems that are not used to them can generate new conflicts, notably if they do not have a clear legal status. A comparison between different pastoral systems using LGDs in various ecological and social contexts appears necessary for a better understanding of LGDs' impacts on wolf damages as well as for improving their incorporation and use in new areas. Nonetheless, if suitably combined with other protection measures, LGDs appear as one of the best mitigation tools in many areas.

7.2. Conceptual boundaries between wolves and dogs

Beyond the biological and technical problems, the management of wolf–dog relationships in a conservation context raises the question of the boundaries between these animals. Indeed, dogs almost certainly descend from wolves and the two can interbreed to produce hybrids. While *natural* hybridization (between wild living forms) is seen as having a role in speciation, *anthropogenic* hybridization (between wild and domestic forms) and the introgression of dog genes into wild wolf populations is seen as a *pollution* potentially compromising the genetic *integrity* of existing taxa (cf. Lorenzini et al., in press). This concern which is expressed in several papers about the introgression of dog genes into wolf populations directly raises the questions of *boundaries*, *purity* and *pollution* which are well developed concepts in disciplines such as the anthropology of nature and the sociology of sciences (see e.g. Douglas, 1966; Latour, 1993; Knight, 2000; Forsyth, 2003). Milton (2000) suggested that conservationists invoke three culturally defined boundaries: (1) the interspecies boundary, (2) the boundary between natives and aliens, and (3) the boundary between human and non-human processes, which reflects the dichotomy between nature and culture on which modern western science is largely based (Latour, 1993; Descola, 2005). In such contexts purity is associated with the respect for boundaries whereas pollution occurs when boundaries are crossed, i.e. when the social understanding of the contextualised environmental order is disturbed (Knight, 2000).

Wolf–dog hybridization and dog genetic introgression into wolf populations are perceived as pollutions because they not only cross the boundary between two species but also the boundary between wild and domestic, which is well established in western societies (Descola, 2004). In this dichotomic view, dogs – as domestic animals – are already "polluted" by human processes and do not belong to nature anymore. This could probably explain the previous lack of interest among biologists in studying dog ecology (Vanak and Gompper, 2009) as dogs are not regarded as "pure" objects of interest for wildlife ecologists. A similar purification process has been shown in India with the choice of protected areas as study sites (Ghosal et al., 2013).

Therefore, when dogs become feral, they fall between the two categories as they are not domestic anymore but they do not belong to wildlife. They already "pollute" nature and they are perceived as a conservation problem, and an anthropogenic threat to nature. When they interbreed with wolf populations, they cross the interspecies boundary as well as the domestic/wild one generating disorder in conservationists' social understanding of the environment. However, the boundaries generating this sense of pollution are not rigidly established once and for all. On the one hand it appears that boundaries between species (with canids being an especially potent example) are more fluid than many

biologists, and almost all legislation, are used to dealing with, and on the other hand the socially constructed concept of nature as separated from humans is being increasingly questioned in some disciplines and generating numerous conceptual "hybrids" (Latour, 1993). This generates what Robbins and Moore (2012) call ecological anxiety disorder. Thus, the current debates on land-sharing vs. land-sparing (Phalan et al., 2011) within conservation biology are probably as much motivated by the different values associated with the relative place of humans with respect to nature as with the efficiency of the strategies to conserve biodiversity.

Blurry boundaries and the impact of human society on wolf–dog relationships is notably reflected in the varying legal status of wolf–dog hybrids and the legal status of free-ranging dogs. The latter is in general much more diverse than the legislation governing wolves and shows great variation between countries, from the shoot on sight policy for loose dogs in the Baltics to the full protection provided for them in Italy. Ironically the LGDs which can potentially mitigate conflicts with wolves also have a highly variable legal status and they appear to be at the border between domestic and wild, being owned but generally free-ranging, more attached to livestock than to humans, working outside enclosures and often without supervision.

This anthropological view on wolf–dog relationships does not de-legitimise conservationists' concerns for feral dog impacts on wolf and hybridization but shows that in addition to legal and technical aspects their concern is based on values linked with culturally defined (socially constructed) boundaries. Therefore the management of feral dogs and of wolf–dog hybridization goes beyond being a biological problem and requires consideration of the perceptions of society.

The main conclusion from this review is that there is a dramatic need for more research on the issue of how dogs modulate the relationship between humans and wolves, which should include good field studies of all the ecological issues that we address above, as well as studies of the perceptions that the public and experts have of the relationship. As well as being a necessary topic with respect to wolf conservation, it also represents a fascinating case study for exploring the wider human relationship with nature. Given the thousands of years with which humans have lived with both dogs and wolves, and the fact that these interactions have been played out across the entire Holarctic, it should not come as a surprise that there is a huge diversity of social, cultural and ecological contexts that will need to be taken into account.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.01.032.

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