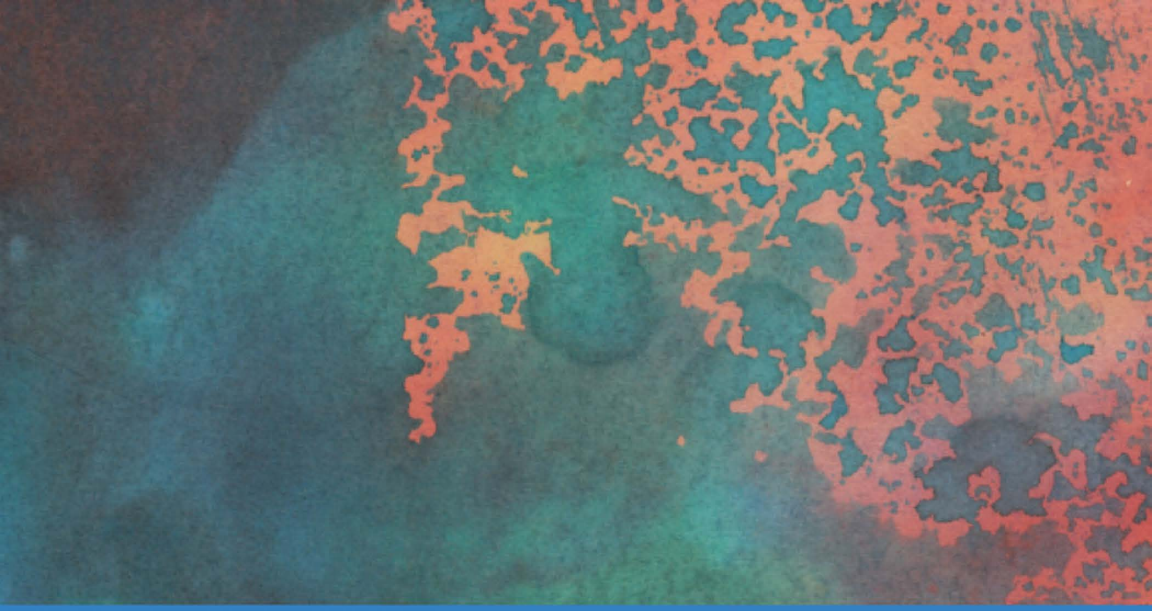
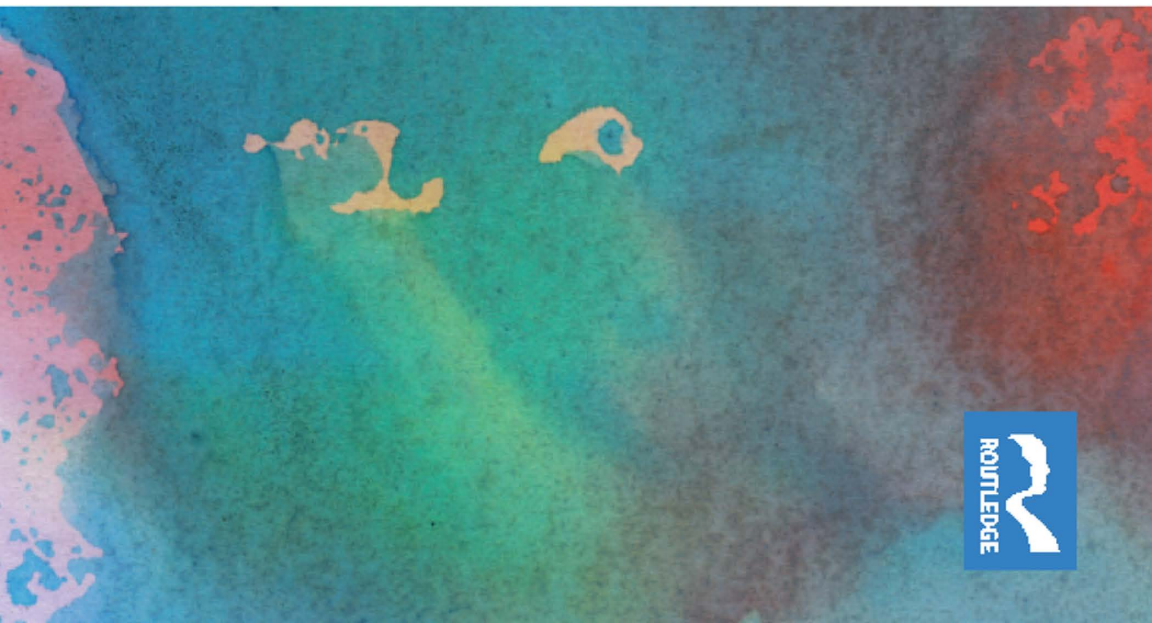


Routledge Studies in Anthropology

HYBRID COMMUNITIES

BIOSOCIAL APPROACHES TO DOMESTICATION AND OTHER TRANS-SPECIES RELATIONSHIPS

Edited by
Charles Stépanoff and Jean-Denis Vigne



Beyond wild and domestic

Human complex relationships with dogs, wolves, and wolf-dog hybrids

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Abstract:

Dog domestication is probably the result of the forging of particularly close relationships between two social species, humans and wolves, around 15,000 years ago. However, a few thousand years later, wolves were progressively excluded from human settlements because of livestock domestication. Then, dogs and wolves took radically different historical pathways, dogs becoming more and more integrated into human societies whereas wolves were rejected and persecuted in large parts of their range until recently. Indeed, under the combined effects of rural abandonment and nature protection laws, wolves are now coming back to their former territories and their populations co-occur not only with humans but also with large populations of dogs, either owned or free-ranging. This co-occurrence produces numerous hybrids, causing difficulties for conservation scientists and wildlife managers. The development of the wolf-dog hybrid problem highlights underlying categorizations behind scientific discourses and questions the relevance of established categories and borders – both interspecific and domestic/wild ones – to describe the diversity of our relationships with animals.

This is an edited author's version of the chapter:

Lescureux, N. 2018. Beyond wild and domestic. *Human complex relationships with dogs, wolves, and wolf-dog hybrids*, in Hybrid Communities. Biosocial Approaches to Domestication and Other Trans-species Relationships, C. Stepanoff and J.-D. Vigne, Editors. Routledge: London. p. 83-98.

Introduction

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. The last two categories clearly reflect the dichotomy between nature and culture on which modern western science is largely based (Latour 1993; Descola 2013). The same is true of the boundary between wild and domestic, which is a consequence of the distinction between human and non-human processes, and appears to not be universal (Descola 2004). Interestingly, the complex relationship between humans, dogs, and wolves – and notably the hybridization between the latter – questions both the interspecies boundary and the boundary between wild and domestic. Indeed, dogs descend from wolves and although they have gone through different historical processes, wolves and dogs still interact across a large part of the Northern Hemisphere. Questioning these boundaries also implies reflecting on conservation discourses and actions about wolf-dog hybrids and hybrids in general, both conceptually and practically.

After clarifying current thinking on the ancestry relationships between wolves and dogs, we will quickly draw the almost antithetical historical trajectories of human-dog and human-wolf relationships from the time dogs first became domesticated. Then we will discuss the question of wolf-dog hybridization, its definition, its level, and how it can be perceived as a double pollution from the nature conservation perspective. This will lead us to question the relevance of interspecies and wild-domestic boundaries used in science in general and in the conservation sciences in particular in the case of wolf-dog hybrids. Beyond its biological aspects, hybridization thus appears as a social problem and managing hybrids certainly requires taking account of 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.

Wolves and dogs: ancestors and descendants

According to archaeological data, hominids and grey wolves have had a relatively close relationship for at least 300,000 years (Olsen 1985). This close relationship probably 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; Larson and Fuller 2014). However, the debate remains open about when, where, and how the process of domestication happened. Some fossils dated from ca. 30,000 years BP or even earlier have been morphologically identified as dog remains (Germonpré et al. 2009; Ovodov et al. 2011; Germonpré et al. 2012; Germonpré et al. 2013; see also Germonpré et al. in this volume), but this proposal has been seriously questioned (Pionnier-Capitan et al. 2011; Crockford and Kuzmin 2012; Boudadi-Maligne and Escarguel 2014; Perri 2016).

The combination of archaeological and genetic data has begun to provide a better understanding of the dog domestication process. According to Larson et al. (2012), 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. Palaeogenetic analysis has revealed the existence of at least two centres of dog domestication (Frantz et al. 2016). It also appears that interbreeding (backcrossing) between dogs and local wolf populations often occurred during the early stages of the domestication process (Vilà et al. 1997; Ardalan et al. 2011; vonHoldt et al. 2011; Wayne and vonHoldt 2012). This would reinforce the suggestion that dog domestication in its early stages was probably more a stochastic evolutionary process 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). The hypothesis of self-domestication is contested, notably by Germonpré et al. (in this volume), who suggest the widespread existence of wolf pup rearing in Upper Palaeolithic human groups. Nonetheless, wolf pup

rearing did not imply any human intention to domesticate. This is all the more probable as humans had no prior experience with domestication.

According to the most recent studies combining archaeology and genetic data, earliest livestock domestication events for other species (cattle, sheep, goats, pigs) all occurred in the Near East around the same period between 8,500 and 11,000 years BP (Vigne 2011; Zeder 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 implies 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), even though events of hybridization have been detected later during the neolithization process (Ollivier et al. 2013).

Dogs' and wolves' relationships with humans: antithetical trajectories?

Whatever the place(s) of origin, the nature of the process or the exact time of dog domestication, accompanying humans somehow appears as a good strategy for dogs from an evolutionary point of view. In a few thousand years, they spread across all the continents and in almost all islands in the world in the wake of human migrations. Dogs became capable of digesting starch as early as 7,000 years BP in Southeastern Europe, suggesting a biocultural coevolution of humans and dogs, allowing the latter to live on a rich starch diet paralleling the development of farming societies (Ollivier et al. 2016). Despite low genetic diversity mainly due to recent efforts to create purebred dogs (Frantz & Larson, this volume), dogs have reached a very high phenotypic diversity with around 400 different breeds (Galibert et al. 2011) adapted to very different purposes, from providing meat to herding flocks to various other uses such as hunting, following scents, guiding blind people, carrying burdens, protecting livestock against wolves, or just to be pets and run after balls and sticks. As a consequence the largest dog is more than 100 times heavier than the smallest one (Galibert et al. 2011). In addition, beyond these 400 breeds, there are a lot of crossbreeds as well as village dogs unrelated to any breeds (Boyko et al. 2009). 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 (60% of them in rural areas) and certainly growing (Gompper 2014), while their ancestor population is estimated at around 400,000 individuals (Mech and Boitani 2003).

Indeed, from the time dogs and later ungulates were domesticated, the history of humans and wolves has been rather complex and often conflictual. Humans and grey wolves (Canis lupus) have been sharing the same landscape, the same habitats and even some similarities in their hunter's way of life for a long time (Olsen 1985; Clutton-Brock 1995). However, it is quite probable that the domestication of ungulate species (cattle, sheep, and goats) which started around 11,500 BP and spread across Eurasia through the neolithization process (Tresset and Vigne 2011) led to keeping wolves at a distance from human settlements (Clutton-Brock 1995; Sablin and Khlopachev 2002; Verginelli et al. 2005). Indeed, from this period, wolves became a potential threat for livestock, and they still appear as one of the most conflictual species wherever their presence overlaps with herding activities. Conflicts between wolves and livestock breeding have probably been responsible for motivating the past reduction in the number and distribution of large carnivores on a worldwide level (Mech 2017). In the western world, animals used to be categorized either as useful or as harmful for human activities. As they killed livestock and even occasionally humans (Linnell et al. 2003; Moriceau 2007), there is no doubt that wolves were on the harmful side. However, despite the worldwide expansion of agriculture and livestock breeding, the wolf's adaptability combined with low human density allowed them to survive in most of their historical range until a relatively recent past. Except for the British Isles (Hickey 2011), only from the middle of the 19th century did the increase in human population, deforestation, and progress in hunting equipment and organization start to dramatically impact wolf populations,

leading to the worldwide reduction of the wolf's historical range by a third in the middle of the 20th century (Mech 1995; Boitani 2003).

However, the sociocultural context in North America and Western Europe also dramatically changed during this period. Faced with industrialization and the concentration of human populations in large cities, a romantic vision of nature and an attraction towards the wilderness developed in North America and Western Europe at the end of the 19th century (Descola 2013). The development of ecology also changed the perception of animals, displaying their ecological role beyond their usefulness or harmfulness for human activities. The combination of attraction towards nature and the wilderness and concerns about the ecological role of animal species drove some people to be concerned about endangered species. In the USA, this concern was translated into the Endangered Species Act (1966) and even extended to wolves, which were protected in 1973. In the same year was created the wolf specialist group in the International Union for Conservation of Nature (IUCN). Information about wolves in the wild was not extensive at that time and essentially based on studies made in Alaska and Minnesota in the 1940s and the 1970s (Mech 1970; Mech and Frenzel 1971; Murie 1985 [1944]). Studies on wolf ecology and behaviour then became more numerous. Their circulation in popularized versions contributed to positively change the wolf's image, but also propagated incomplete information or even misconceptions towards mainly urban populations without experience-based knowledge about wolves (Mech 1995, 2017). Thus, wolves started to be perceived as a symbol of the wilderness, a keystone species able to self-regulate, and which only attack livestock in the absence of wild prey. These campaigns also led to the idea that wolves could not stand intense human activity and avoided settling in such anthropized areas. This idealized vision of the wolf contributed to the multiplication of environmentalist associations defending and protecting wolves, in the USA and then in Europe, and permitted a kind of wolf rehabilitation campaign, as well as its protection in several European countries. Nowadays, in many countries, land abandonment, drastic changes in rural land occupation, and/or conservation legislation are leading to the recovery of wolf populations in multiple-use landscapes (Linnell et al. 2001; Falcucci et al. 2007; Chapron et al. 2014). Accordingly, many conflicts are currently appearing or increasing in several countries (Skogen et al. 2008; Dressel et al. 2015; Garde 2015; Mech 2017).

The construction of the wolf-dog hybrids problem

As a consequence of wolves and dogs being closely related, they can interbreed and produce fertile offspring. 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. 350 BC) and Pliny (77 AD), 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 centuries, 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[1].

Evidence of uncontrolled wolf-dog hybridizations

While humans have been, and still are, crossbreeding wolves and dogs, hybridization can also occur in uncontrolled situations. Thus, hybridization was certainly a reoccurring part of the early dog domestication process and was possible because humans and wolves were living in close contact and early dogs and wolves were certainly morphologically similar. Nowadays, uncontrolled hybridization between dogs and wolves still occurs. Hybridization has to go through two steps in order to have an impact on wolf populations. Firstly, 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).

Analyses based on mtDNA have not detected much introgression of dog mtDNA into wolf populations (Muñoz-Fuentes et al. 2010). Therefore, wolf-dog hybridization has long been considered a very rare

event, since it was considered that crossing between male dogs and female wolves was unlikely to be successful because male dogs do not assist females in pup rearing and care (Vilà and Wayne 1999). However, more recent genetic studies that include Y-chromosome analysis tend to show that crosses between male dogs and female wolves not only occur but 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). Evidence for modern day hybridization in the wild has been detected in numerous places including Bulgaria, Canada, Italy, Latvia, Spain, Portugal, and Scandinavia (Caniglia et al. 2013; Lescureux and Linnell 2014; Torres et al. 2017). 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; Hailer and Leonard 2008). 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). Nonetheless, wolf-dog hybridization remains relatively rare compared to wild/domestic species couples like wild boars (Sus scrofa) and pigs (Sus scrofa domesticus) (Frantz & Larson, this volume).

Wolf-dog hybridization: double pollution

In some parts of conservation scientific literature, while natural hybridization (between wild living forms) is seen as having a role in speciation, anthropogenic hybridization (between wild and domestic forms) is seen as a pollution potentially compromising the genetic integrity of existing taxa (cf. Lorenzini et al. 2014). 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). Purity is associated with the respect for boundaries, whereas pollution occurs when boundaries are crossed, i.e. when the social understanding of the contextualized environmental order is disturbed (Knight 2000).

In addition, wolf – dog hybridization and dog genetic introgression into wolf populations are perceived as a double pollution. Indeed, on the one side they cross the boundary between two species (Canis lupus and Canis familiaris) and on the other side they cross the boundary between wild and domestic, which reflects the boundary between natural processes and human processes as proposed by Milton (2000). The boundary between wild and domestic is well established in Western societies and in Western science (Descola 2004, 2013). In the view of some conservationists, dogs – as domestic animals – are already “polluted” by human processes. They no longer belong to nature. This could probably explain the previous lack of interest among biologists in studying dog ecology (cf. Vanak and Gompper 2009).

Therefore, when dogs become feral, they fall between two categories; they are no longer domestic without, however, belonging to wildlife. They are not in the “right” place and they “pollute” nature (Knight 2000). As a consequence, they are perceived as a conservation problem and an anthropogenic threat to nature. When these feral dogs 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. What is the result of this hybridization? Is it wild, or is it domestic? Is it Canis lupus, or Canis familiaris? These hybrids fall between categories and, as such, generate pollution. But one can question the relevance of these categories. Indeed, the boundaries generating this sense of pollution are not rigidly established once and for all.

Domestic, wild, Canis lupus, Canis familiaris: relevant categories?

The socially constructed concepts of nature as separated from humans, and wild separated from domestic, are increasingly being questioned in the anthropology of nature (Descola and Pálsson 1996; Ellen and Katsuyoshi 1996; Ingold 2000; Descola 2004, 2013) and the sociology of science (Latour 1993), notably because they do not appear to be universal and also because they generate numerous

conceptual “hybrids”, which are neither pure natural objects nor pure social subjects, as in the case of wolf-dog hybrids, which are neither wild animals nor owned domestic animals. In addition, these conceptual boundaries are quite frequently transgressed in conservation actions (Linnell et al. 2015) since reintroductions, translocations, and other forms of wildlife management are above all human processes, and domestic animals are even sometimes used to maintain “natural” landscapes. Finally, processes like climate change also question the mere existence of natural processes outside of any human influence.

The interspecies border between wolves and dogs can also be questioned, and it has been particularly obvious in the uncertain taxonomic status of the dingo in Australia, which has variously been viewed as either a wolf subspecies, Canis lupus dingo, or a feral dog, Canis familiaris dingo (Newsome et al. 1980; Newsome and Corbett 1982, 1985; Corbett 1995), even if it now clearly appears as Canis familiaris (Larson et al. 2012). 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 (Canis lupus vs Canis lycaon), the role of hybridization between coyotes and wolves in the origins of the red wolf (Canis rufus) (Nowak 1992; Nowak and Federoff 1998; Wayne et al. 1998; Wilson et al. 2000; Grewal et al. 2004; Mech 2010; Benson et al. 2013), the adaptive introgression of wolf and dog genes into coyote populations (Monzón et al. 2014), and the identity of the Great Lakes wolves (Leonard and Wayne 2008, 2009; Cronin and Mech 2009; Mech 2009). It has also been claimed that North African jackals could potentially be considered as African wolves Canis lupus lupaster (Rueness et al. 2011; Gaubert et al. 2012). It now appears that hybridization exists between golden jackals (Canis aureus) and dogs (Galov et al. 2015). This pattern of cryptic relationships 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.

Hybridization as a social problem

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), notably if hybrids reveal themselves as competitors to wolf populations (Bassi et al. 2017). On the other hand, it has been shown that introgression can also be adaptive (Castric et al. 2008; Hedrick 2013) and it is possible that hybridization with dogs could sometimes provide advantages for their descendants. For instance, under certain circumstances, black wolves[2] 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). Behind conservationists’ concerns about hybridization and introgression seen as pollution, there is no apparent attested impact of wolf-dog hybridization and dog genes introgression on wolf behavioural patterns or wolf conservation status. It appears that the main concerns result from culturally defined boundaries which are not always biologically relevant (the one between canid species) and not universal (the one between wild and domestic). Conservation biologists are probably facing contradictions between their concerns – as conservationists – about human negative impacts on the planet (anthropophobia), and their concerns – as scientists – about the influence of their own human normative values on the way they do science (autophobia). Indeed, the influence of normative values appears rather obvious on hybridization problems, and the contradictions resulting from the combination of anthropophobia and autophobia will probably generate what Robbins and Moore call “ecological anxiety disorder” (2012).

Our anthropological view on wolf-dog relationships does not de-legitimize conservationists’ concerns for hybridization as a potential threat for wolf populations. However, it 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/or of wolf-dog hybridization goes beyond being a biological problem and requires consideration of the perceptions of society.

Hybrids as unmanageable animals?

Whatever the consequences, hybridization between dogs and wolves emerges as a major challenge for wildlife managers and conservation biologists for a number of reasons. First, identification of wolf-dog hybrids remains complex even with the latest advances in genetic techniques (cf. notably Lorenzini et al. 2014). 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). Faced with the revelation of the relatively high percentage of hybridization in wolf populations in Europe, a similar recommendation to protect hybrids was made by the standing committee of the Convention on the Conservation of European Wildlife and Natural Habitats of the Council of Europe in 2014 (Trouwborst 2014). These issues raise a number of difficult questions that conservationists need to address about the management of hybrids.

The question has been raised if all black wolves or wolves with dewclaws (cf. Ciucci et al. 2003) should be removed from the wild in Italy because there was an introgression of dog genes in their karyotype at some point in their history. Introgression of dog genes into wolf populations can be the result of ancient hybridizations. Robbins and Moore (2013) suggested that conservation sciences are edenic sciences in the sense they always refer to a previous point in history as a reference point, an a priori baseline when things were better or more natural. In that case, would an ancient hybridization be more acceptable than a more recent one? Were dogs more natural 300 or 3,000 years ago than they are now? Were wolves “pure” at that time? This also leads to further technical questions about what is an acceptable level of introgression. What percentage of dog genes introgression would make the wolf a dog? How can this percentage be quantified objectively? What would be an acceptable level of “pollution”? Finally, a wide range of ethical questions about the acceptability of various management interventions are apparent. Blurry boundaries and the impact of human society on wolf-dog relationships are 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 considerable variation between countries, from the shoot-on-sight policy for loose dogs in the Baltics to the full protection provided for them in Italy, 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 about hybrid management take place in highly emotional debates, and there are no widely accepted best practice management protocols for their management.

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 little data on the behaviour and ecology of wolf-dog hybrids under free-ranging conditions.

Conclusion

Human relationships with wolves and dogs definitely disrupt established categories and boundaries. In a part of conservation literature, intro-gression is perceived as a trans-gression, the pollution of the wild by the domestic world, associated with degeneration. Such a view of domestication as degeneration is also present in the theory of neoteny. Even if now contested (Drake and Klingenberg 2010), this theory postulates that domestic animal morphology and behaviour can be associated with different developmental stages of their wild counterparts, only the wild animal reaching the last stage (Coppinger and Coppinger 2001).

The huge variability in human relationships with both wolves and dogs brings into question the relevance of interspecific and wild-domestic boundaries, which are rather status and static boundaries. A more relational approach could appear more relevant, considering that a reasonable proportion of dogs are free-ranging and do not have close relationships with humans, while some wolves are closely tracked with GPS, trapped, captured, identified, and released, and others are selected according to their behaviour when dangerous or harmful individuals are shot. Some wolves also feed on refuse in cities, while free-ranging dogs hunt roe deer or wild boars in forests. We could almost say that there are now wild dogs and domestic wolves.

Both archaeology and genetics define differences between wild and domestic animals based on morphology, morphometry, phenotype, and genotype. However, the domestication process could rather be seen as an intensification of human-animal relationships (Vigne 2011, 2015) and appears to be very species specific (Frantz & Larson, this volume). It should also be noted that intense relationships can exist without domestication, notably in the case of pet keeping in hunter societies (see e.g. Erikson 2000). Nonetheless, numerous debates have arisen about measures and variability in order to determine if a particular skull is closer to the dog or wolf type. Of course, such differences can probably tell us if at one point in the ancestry of the individual there was enough human influence to modify its genotype and/or phenotype. However, it doesn't tell us if this animal was domestic or wild in the sense it had a particular relationship with humans. The dingo is not a wolf, but is it a domestic animal? Beyond the selection that operates at the species level and on an intergenerational scale, it appears that domestication is also an action that has to be repeated, a relation that has to be (re)constructed each generation in order to rebuild the special bond that exists between humans and animals in a domestic context.

Notes

1 E.g. the Saarloos wolf dog, the Czechoslovakian wolf dog, the Lupo Italiano, the Kunming wolf dog.

2 The black coat colour in wolves is probably the result of the introgression of a mutation resulting from hybridization with dogs (see Ollivier *et al* . 2013).

References

Adams, J. R., Leonard, J. A. and Waits, L. P. 2003. Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes. Molecular Ecology, 12, 541–546.

Allendorf, F. W., Luikart, G. and Aitken, S. N. 2013. Conservation and the genetics of populations. Oxford, UK: Wiley-Blackwell.

Anderson, T. M., et al. 2009. Molecular and evolutionary history of melanism in North American Gray Wolves. Science, 6(323), 1339–1343.

Ardalan, A., et al. 2011. Comprehensive study of mtDNA among Southwest Asian dogs contradicts independent domestication of wolf, but implies dog-wolf hybridization. Ecology and Evolution, 1(3), 373–385.

Bassi, E., et al. 2017. Trophic overlap between wolves and free-ranging wolf × dog hybrids in the Apennine Mountains, Italy. Global Ecology and Conservation, 9, 39–49.

Benson, J. F., et al. 2013. Genetic and environmental influences on pup mortality risk for wolves and coyotes within a Canis hybrid zone. Biological Conservation, 166, 133–141.

Boitani, L. 2003. Wolf conservation and recovery. In: Mech, L. D. and Boitani, L. eds. Wolves: Behavior, ecology, and conservation. Chicago, IL: The University of Chicago Press, 317–344.

Boudadi-Maligne, M. and Escarguel, G. 2014. A biometric re-evaluation of recent claims for Early Upper Palaeolithic wolf domestication in Eurasia. Journal of Archaeological Science, 45, 80–89.

Boyko, A. R., et al. 2009. Complex population structure in African village dogs and its implications for inferring dog domestication history. Proceedings of the National Academy of Science, 106(33), 13093–13908.

Caniglia, R., et al. 2013. Black coats in an admixed wolf x dog pack is melanism an indicator of hybridization in wolves? European Journal of Wildlife Research, 59, 543–555.

Castric, V., et al. 2008. Repeated adaptative introgression at a gene under multiallelic balancing selection. PLoS Genetics, 4(8), e1000168. doi:1000110.1001371/journal.pgen.1000168.

Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346(6216), 1517–1519.

Ciucci, P., et al. 2003. Dewclaws in wolves as evidence of admixed ancestry with dogs. Canadian Journal of Zoology, 81, 2077–2081.

Clutton-Brock, J. 1995. Origins of the dog: Domestication and early history. In: Serpell, J. ed. The domestic dog: Its evolution, behaviour and interactions with people. James Serpell ed. Cambridge: Cambridge University Press, 7–20.

Coppinger, R. and Coppinger, L. 2001. Dogs: A startling new understanding of canine origin, behavior and evolution. New York, NY: Scribner.

Corbett, L. K. 1995. The Dingo in Australia and Asia. Ithaca, NY: Cornell University Press.

Coulson, T., et al. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. Science, 334, 1275–1278.

Crockford, S. J. and Kuzmin, Y. V. 2012. Comments on Germonpré et al., Journal of Archaeological Science 36, 2009 'Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes', and Germonpré, Lázničková-Galetová, and Sablin,

Journal of Archaeological Science 39, 2012 'Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic'. Journal of Archaeological Science, 39, 2797–2801.

Cronin, M. A. and Mech, L. D. 2009. Problems with the claim of ecotype and taxon status of the wolf in the Great Lakes region. Molecular Ecology, 18, 4991–4993.

Daniels, M. J. and Corbett, L. K. 2003. Redefining introgressed protected mammals: When is a wildcat a wild cat and a dingo a wild dog? Wildlife Research, 30(3), 213–218.

Dayan, T. 1994. Early domesticated dogs of the near East. Journal of Archaeological Science, 21, 633–640.

Descola, P. 2004. Le sauvage et le domestique. Communications, 76(1), 17–39.

Descola, P. 2013. Beyond nature and culture. Chicago, IL: University of Chicago Press.

Descola, P. and Pálsson, G. 1996. Nature and society: Anthropological perspectives. London, UK: Routledge.

Douglas, M. 1966. Purity and danger: An analysis of the concepts of pollution and taboo. London and New York, NY: Ark Paperbacks.

Drake, A. G. and Klingenberg, C. P. 2010. Large-scale diversification of skull shape in domestic dogs: Disparity and modularity. The American Naturalist, 175(3), 289–301.

Dressel, S., Sandström, C. and Ericsson, G. 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. Conservation Biology, 29(2), 565–574.

Ellen, R. and Katsuyoshi, F. 1996. Redefining nature: Ecology, culture and domestication. Oxford, UK: Berg.

Erikson, P. 2000. The social significance of pet-keeping among Amazonian Indians. In: Podberscek, A. L., Paul, E. S. and Serpell, J. A. eds. Companion animals and us: Exploring the relationships between people and pets. Cambridge: Cambridge University Press, 7–26.

Falcucci, A., Maiorano, L. and Boitani, L. 2007. Changes in land-use/land-cover patterns in Italy and their implication for biodiversity conservation. Landscape Ecology, 22, 617–631.

Forsyth, T. 2003. Critical politcal ecology: The politics of environmental science. London and New York, NY: Routledge.

Frantz, L. A. F., et al. 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. Science, 352(6290), 1228–1231.

Galibert, F., et al. 2011. Toward understanding dog evolutionary and domestication history. Comptes Rendus Biologies, 334, 190–196.

Galov, A., et al. 2015. First evidence of hybridization between golden jackal (Canis aureus) and domestic dog (Canis familiaris) as revealed by genetic markers. Royal Society Open Science, 2(12).

Garde, L. 2015. Sheep farming in France: Facing the return of the wolf. Carnivore Damage Prevention News, 11, 17–27.

Gaubert, P., et al. 2012. Reviving the African Wolf Canis lupus lupaster in North and West Africa: A mitochondrial lineage ranging more than 6,000 km wide. PLoS ONE, 7(8), e42740.

Germonpré, M., et al. 2009. Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. Journal of Archaeological Science, 36(2), 473–490.

Germonpré, M., et al. 2013. Palaeolithic dogs and the early domestication of the wolf: A reply to the comments of Crockford and Kuzmin (2012). Journal of Archaeological Science, 40, 786–792.

Germonpré, M., Lázničková-Galetová, M. and Sablin, M. V. 2012. Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. Journal of Archaeological Science, 39(2012), 184–202.

Godinho, R., et al. 2011. Genetic evidence for multiple events of hybridization between wolves and domestic dogs in the Iberian Peninsula. Molecular Ecology, 20, 5154–5166.

Gompper, M. E. 2014. The dog-human-wildlife interface: Assessing the scope of the problem. In: Gompper, M. E. ed. Free-ranging dogs and wildlife conservation. Oxford, UK: Oxford University Press, 9–54.

Gottelli, D., et al. 1994. Molecular genetics of the most endangered canid: The Ethiopian wolf Canis Simensis. Molecular Ecology, 3, 301–312.

Grewal, S. K., et al. 2004. A genetic assessment of the Eastern Wolf (Canis lycaon) in Algonquin Provincial Park. Journal of Mammalogy, 85(4), 625–632.

Hailer, F. and Leonard, J. A. 2008. Hybridization among three native North American Canis species in a region of natural sympatry. PLoS ONE, 3(10), e3333.

Hedrick, P. W. 2009. Wolf of a different colour. Heredity, 103, 435–436.

Hedrick, P. W. 2013. Adaptive introgression in animals: Examples and comparison to new mutation and standing variation as sources of adaptive variation. Molecular Ecology, 22(18), 4606–4618.

Hickey, K. 2011. Wolves in Ireland. Dublin: Open Air.

Hindrikson, M., et al. 2012. Bucking the trend in wolf-dog hybridization: First evidence from Europe of hybridization between female dogs and male wolves. PLoS ONE, 7(10), e46465.

Iacolina, L., et al. 2010. Y-chromosome microsatellite variation in Italian wolves: A contribution to the study of wolf-do hybridization patterns. Mammalian Biology, 75, 341–347.

Iljin, N. A. 1941. Wolf-dog genetics. Journal of Genetics, 42(3), 359–414.

Ingold, T. 2000. The perception of the environment: Essays in Livelihood, dwelling and skill. London, UK: Routledge.

Knight, J. 2000. Introduction. In: Knight, J. ed. Natural enemies: People-wildlife conflicts in anthropological perspective. London, UK: Routledge, 1–36.

Larson, G. and Fuller, D. Q. 2014. The evolution of animal domestication. Annual Review of Ecology, Evolution, and Systematics, 45(1), 115–136.

Larson, G., et al. 2012. Rethinking dog domestication by integrating genetics, archaeology, and biogeography. Proceedings of the National Academy of Science, 109(23), 8878–8883.

Latour, B. 1993. We have never been modern. Cambridge, MA: Harvard University Press.

Leonard, J. A. and Wayne, R. K. 2008. Native Great Lakes wolves were not restored. Biology Letters, 4, 95–98.

Leonard, J. A. and Wayne, R. K. 2009. Wishful thinking: Imagining that the current Great Lakes wolf is the same entity that existed historically (invited reply). Biology Letters, 5, 67–68.

Lescureux, N. and Linnell, J. D. C. 2014. Warring brothers: The complex interactions between wolves (Canis lupus) and dogs (Canis familiaris) in a conservation context. Biological Conservation, 171, 232–245.

Linnell, J. D. C., et al. 2003. Is the fear of wolves justified? A Fennoscandian perspective. Acta Zoologica Lituanica, 13, 34–40.

Linnell, J. D. C., et al. 2015. Framing the relationship between people and nature in the context of European conservation. Conservation Biology, 29, 978–985.

Linnell, J. D. C., Swenson, J. E. and Andersen, R. 2001. Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation, 4, 345–349.

Lorenzini, R., et al. 2014. Wolf-dog crossbreeding: 'Smelling' a hybrid may not be easy. Mammalian Biology, 79, 149–156.

Mech, L. D. 1970. The wolf the ecology and behavior of an endangered species. Minneapolis, MN: University of Minnesota Press.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology, 9, 270–278.

Mech, L. D. 2009. Crying wolf: Concluding that wolves were not restored (comment). Biology Letters, 5, 65–66.

Mech, L. D. 2010. What is the taxonomic identity of Minnesota wolves? Canadian Journal of Zoology, 88, 129–138.

Mech, L. D. 2017. Where can wolves live and how can we live with them? Biological Conservation, 210, Part A, 310–317.

Mech, L. D. and Boitani, L. 2003. Wolves: Behavior, ecology, and conservation. Chicago, IL: The University of Chicago Press.

Mech, L. D. and Frenzel, L. D. 1971. Ecological studies of the timber wolf in Northeastern Minnesota. St Paul, MN: U.S. North Central Forest Experiment Station, Research Paper NC-52.

Milton, K. 2000. Ducks out of water: Nature conservation as boundary maintenance. In: Knight, J. ed. Natural enemies. New York, NY: Routledge, 229–248.

Monzón, J., Kays, R. and Dykhuizen, D. E. 2014. Assessment of coyote-wolf-dog admixture using ancestry-informative diagnostic SNPs. Molecular Ecology, 23(1), 182–197.

Morey, D. F. 1994. The early evolution of the domestic dog. American Scientist, 82(4), 336–347.

Moriceau, J.-M. 2007. Histoire du méchant loup. 3 000 attaques sur l'homme en France. Paris: Fayard.

Muñoz-Fuentes, V., et al. 2010. The genetic legacy of extirpation and re-colonization in Vancouver Island wolves. Conservation Genetics, 11, 547–556.

Murie, A. 1985 (1944). The wolves of Mount McKinley. Seattle, WA: University of Washington Press.

Newsome, A. E. and Corbett, L. K. 1982. The identity of the Dingo II. Hybridization with domestic dogs in captivity and in the wild. Australian Journal of Zoology, 30(2), 365–374.

Newsome, A. E. and Corbett, L. K. 1985. The identity of the Dingo III. The incidence of dingoes, dogs and hybrids and their coat colours in remote and settled regions of Australia. Australian Journal of Zoology, 33(3), 363–375.

Newsome, A. E., Corbett, L. K. and Carpenter, S. M. 1980. The identity of the Dingo I. Morphological discriminants of dingo and dog skulls. Australian Journal of Zoology, 28(4), 615–625.

Nowak, R. M. 1992. The red wolf is not a hybrid. Conservation Biology, 6(4), 593–595.

Nowak, R. M. and Federoff, N. E. 1998. Validity of the red wolf: Response to Roy et al. Conservation Biology, 12(3), 722–725.

Ollivier, M., et al. 2013. Evidence of coat color variation sheds new light on ancient canids. PLoS ONE, 8(10), e75110.

Ollivier, M., et al. 2016. Amy2B copy number variation reveals starch diet adaptations in ancient European dogs. Royal Society Open Science, 3(11).

Olsen, S. J. 1985. Origins of the domestic dog: The fossil record. Tucson, AZ: The University of Arizona Press.

Ovodov, N. D., et al. 2011. A 33,000-year-old incipient dog from the Altai Mountains of Siberia: Evidence of the earliest domestication disrupted by the last Glacian Maximum. PLoS ONE, 6(7), e22821.

Perri, A. 2016. A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. Journal of Archaeological Science, 68, 1–4.

Pionnier-Capitan, M., et al. 2011. New evidence for Upper Palaeolithic small domestic dogs in South-Western Europe. Journal of Archaeological Science, 38, 2123–2140.

Randi, E. 2008. Detecting hybridization between wild species and their domesticated relatives. Molecular Ecology, 17, 285–293.

Randi, E. 2011. Genetics and conservation of wolves Canis lupus in Europe. Mammal Review, 41(2), 99–111.

Randi, E., et al. 2000. Mitochondrial DNA Variability in Italian and East European Wolves: Detecting the consequences of small population size and hybridization. Conservation Biology, 14(2), 464–473.

Robbins, P. and Moore, S. A. 2013. Ecological anxiety disorder: Diagnosing the politics of the Anthropocene. Cultural Geographies, 20(1), 3–19.

Rueness, E. K., et al. 2011. The cryptic African wolf: Canis aureus lupaster is not a golden jackal and is not endemic to Egypt. PLoS ONE, 6(1), e16385.

Sablin, M. V. and Khlopachev, G. A. 2002. The earliest ice age dogs: Evidence from Eliseevichi 1. Current Anthropology, 43, 795–799.

Simberloff, D. 1996. Hybridization between native and introduced wildlife species: Importance for conservation. Wildlife Biology, 2, 143–150.

Skogen, K., Mauz, I. and Krange, O. 2008. Cry wolf!: Narratives of wolf recovery in France and Norway. Rural Sociology, 73, 105–133.

Torres, R. T., et al. 2017. Hybridization between wolf and domestic dog: First evidence from an endangered population in central Portugal. Mammalian Biology – Zeitschrift für Säugetierkunde, 86, 70–74.

Tresset, A. and Vigne, J.-D. 2011. Last hunter-gatherers and first farmers of Europe. Comptes Rendus Biologies, 334(3), 182–189.

Trouwborst, A. 2014. Applying the Bern Convention on the Conservation of European Wildlife and Natural Habitats to the Problem of Hybridisation Between Wolves (Canis Lupus) and Domestic Dogs – Document T-PVS/Inf (2014) 15. Council of Europe – Standing Committee of Convention on the Conservation of European Wildlife and Natural Habitats of the Council of Europe.

Vanak, A. T. and Gompper, M. E. 2009. Dogs Canis familiaris as carnivores: Their role and function in intraguild competition. Mammal Review, 39(4), 265–283.

Verginelli, F., et al. 2005. Mitochondrial DNA from prehistoric canid highlights relationships between dogs and South-East european wolves. Molecular Biology and Evolution, 22(12), 2541–2551.

Vigne, J.-D. 2011. The origins of animal domestication and husbandry: A major change in the history of humanity and the biosphere. Comptes Rendus Biologies, 334(3), 171–181.

Vigne, J.-D. 2015. Early domestication and farming: What should we know or do for a better understanding? Anthropozoologica, 50(2), 123–150.

Vilà, C., et al. 1997. Multiple and ancient origins of the domestic dogs. Science, 276(5319), 1687–1689.

Vilà, C., et al. 2003. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. Heredity, 90, 17–24.

Vilà, C. and Wayne, R. K. 1999. Hybridization between wolves and dogs. Conservation Biology, 13(1), 195–198.

vonHoldt, B. M., et al. 2010. Genowe-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. Nature, 464, 898–902.

vonHoldt, B. M., et al. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Research, 21, 1294–1305.

Wayne, R. K., Roy, M. S. and Gittleman, J. L. 1998. Origin of the red wolf: Response to nowak and federoff and gardener. Conservation Biology, 12(3), 726–729.

Wayne, R. K. and vonHoldt, B. M. 2012. Evolutionary genomics of dog domestication. Mammalian Genome, 23, 3–18.

Wilson, P. J., et al. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. Canadian Journal of Zoology, 78, 2156–2166.

Zeder, M. A. 2011. The origins of agriculture in the Near East. Current Anthropology, 52(4), S221–S235.