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What should we do with wild dogs? Taxonomic tangles and the management of dingo-dog hybridisation

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ABSTRACT

Taxonomy plays an important role in defining biodiversity and shaping conservation efforts. However, the biological species concept is a human construct and organisms that do not abide by the rules do not fit easily into conservation and policy frameworks. Organisms that are hybrids are one such example. Indeed, hybridisation can result in both the protection and persecution of wild organisms, especially if the hybrid status is uncertain. Here, we outline the issue of hybridisation between dingoes and dogs in Australia, revealing the multidimensional problems that arise when defining and addressing the issue. Before we can decide if and how we should manage hybridisation, we must define the issue and our management goals. For the dingo (and other hybridising species), any resolution of the hybridisation dilemma must consider not only genetics, but also biology, ecology, social values, and ethics. In order to progress dingo management in Australia, we provide a new framework that aims to assist rather than jeopardise dingo conservation.

Key words: Wildlife management, *Canis,* taxonomy, introgression, conservation

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Introduction

Almost everything about the dingo is controversial. Having arrived in Australia sometime between 4600 and 18,300 years ago, possibly via multiple arrival events (Cairns and Wilton 2016; Oskarsson *et al.* 2011), its status as a native species is debated. There is disagreement on whether the dingo plays a role as a top predator in Australian ecosystems (Allen *et al.* 2013; Letnic *et al.* 2012; Newsome *et al.* 2015). As a consequence of these uncertainties – and the fact that the dingo attacks livestock – its position in Australian policy is contradictory, being considered both a protected native species and a declared pest (Hytten 2009). Adding to the issue is the dingo's ambiguous taxonomic status (Crowther *et al.* 2014; Jackson *et al.* 2017) and the fact it can hybridise with domestic dogs (that were introduced into Australia after European settlement in 1788 and subsequently spread into the wild).

Conservation is closely linked with our ability to name things (Mace 2004). The concept of taxonomy fundamentally shapes our contemporary scientific research, but it is a continually evolving idea. The philosophical foundations of taxonomy began with Plato and Aristotle more than 2000 years ago, but it was not until the 1700s that our modern taxonomic system was developed by Carl Linnaeus, who considered that species were unchangeable entities created by God (Wilkins 2009). Since then, recognition of the plasticity of species led to evolutionary theory, and some have suggested that Charles Darwin himself "*considered species as something purely arbitrary and invented merely for the convenience of taxonomists*" (Mayr 1982 p. 268).

Today, more than 30 different species concepts exist (Mayden 1997; Zachos 2016), providing a clear indication of the difficulty of defining rules by which all organisms abide. Taxonomy is a useful framework, but we sometimes fail to recognise that it is at least partly a philosophical, and not necessarily only a biological, construct. Speciation, for instance, occurs naturally along a continuum and grey zones exist between clearly established and emerging (or disappearing) species (Roux *et al.* 2016). This becomes problematic when it limits our ability to conserve or manage organisms that don't fit within our policy or cognitive frameworks.

Recognising that taxonomy is partly a human construct requires us to acknowledge that this discipline is shaped by human values. Debate about whether a population should be considered distinct, which is a delineation inherently linked to conservation status, has played out differently for a range of plant and animal species with some arguing that 'unworthy' populations have maintained species or variant status because revised nomenclature could result in delisting of their populations from threatened species lists (see review by Morrison *et al.* 2009). This debate

occurs in Australia for the dingo, which has been variously described as *Canis antarticus, C. dingo, C. familiaris dingo,* and *C. lupus dingo*, among others (Crowther *et al.* 2014; Smith *et al.* in press). As with other species, the debate about dingo taxonomy (Crowther *et al.* 2014; Jackson *et al.* 2017) is arguably value-laden, and the definition that different stakeholders align with is influenced ultimately by their view of dingoes (Clutton-Brock 2015).

For example, *C. dingo* defines the dingo as a separate taxon from both grey wolves (*C. lupus*) and domestic dogs (*C. familiaris*), and might be used by those who consider the dingo a native Australian animal worthy of conservation. In contrast, *C. familiaris dingo* defines dingoes as a subspecies of dog by those who are more likely to consider it an invasive pest. It has even been suggested that dingoes do not warrant subspecies status and are simply domestic dogs (*Canis familiaris*, Jackson *et al.* 2017). We intentionally do not commit to any specific nomenclature for dingoes in this particular article because it is not a necessity for the arguments and proposals that we posit.

Hybridisation and introgression

A process that challenges taxonomic conventions is hybridisation. This phenomenon occurs naturally, resulting in possible introgression, in at least 25% of plant species and 10% of animal species (Mallet 2005) but is considered to be increasing due to human impacts causing environmental homogeneity (Seehausen *et al.* 2007). Hybridisation occurs between species with common ancestors, including between wild species and their domestic relatives. It can result in genetic swamping and potential extinction of 'pure' populations. Anthropogenic (human-caused) hybridisation (Allendorf *et al.* 2001) threatens several taxa with extinction. Considering hybridisation between wild mammals and their domestic relatives alone, this includes European and Scottish wildcats (*Felis silvestris*, Beaumont *et al.* 2001), Przewalski's horses (*Equus ferus przewalskii*, King *et al.* 2015), bison (*Bison bison*, Hedrick 2009), and several species of Asian wild pig (*Sus* spp., Groves 1997). Interbreeding among wild canid species and between wild canids and domestic dogs can potentially occur between all canid species (Wayne and Ostrander 1999), and is considered a major threat to Ethiopian wolves (*C. simensis*, Gottelli *et al.* 1994), red wolves (*C. rufus*, Wayne and Jenks 1991), and dingoes (Stephens *et al.* 2015).

Like the dingo's debated nomenclature, hybridisation influences dingo management. Hybridisation with domestic dogs is considered by some to be the greatest threat to the dingo's long-term survival (Daniels and Corbett 2003), and recent analysis observed hybridisation across much of mainland Australia, with particularly high levels of hybridisation detected in eastern States (Stephens *et al.* 2015). For this reason, dingoes are listed as Vulnerable under the International Union for Conservation of Nature's Red List (Corbett 2008), hybridisation between dingoes and feral dogs is listed as a key threatening process in New South Wales (NSW Scientific Committee 2009), and dingoes are listed as threatened under the Victorian Flora and Fauna Guarantee Act 1988 (and subsequently protected under the Wildlife Act 1975). Dingoes are protected in some conservation areas in other States, for example, under the Northern Territory's Territory Parks and Wildlife Conservation Act 2014, Queensland's Nature Conservation Act 1992, and in New South Wales they are protected within National Parks and Nature Reserves, which are managed under the NSW Biodiversity Conservation Act 2016, while in other areas and other States, dingoes are regarded as unprotected wildlife, declared pests (Smith and Appleby 2015), or not defined as native wildlife (e.g. South Australia's Natural Resources Management Act 2004).

But at the same time as being considered a threat, hybridisation is used as justification for control programmes by claiming that hybrids do not qualify as dingoes because of their mixed ancestry. The difficulty in defining what is a dingo, a domestic dog, or a hybrid, and the fact that it is difficult to identify hybrids based on phenotype (Crowther *et al.* 2014; Elledge *et al.* 2008; Newsome and Corbett 1982), has resulted in no subtlety in canid management – all forms are persecuted throughout much of their range. Indeed, meat baits laced with the poison sodium fluoroacetate (commonly referred to as '1080') are commonly used in broad-scale cross-tenure control programmes (up to 40 baits/km in some areas; e.g., Fleming and Ballard 2014). These baits are lethal to dingoes, domestic dogs, and hybrids. Such management is broadly referred to under the all-inclusive term "wild dog control". Use of this term has been described as intentionally obscuring public knowledge about dingo management practices (Hytten 2009), demonstrating the possible influence that ambiguous canid definitions can have on dingo conservation and management.

If hybridisation is considered a management priority, there is no silver bullet response and any policy needs to be adapted to suit context-specific objectives (Allendorf *et al.* 2001; vonHoldt *et al.* 2018, Figure 1). Thus, any management framework must be developed by defining what the problem is and the objectives of such management. Given that taxonomy is not black and white (Zachos 2016), we will likely never agree what is a dingo from a taxonomic perspective. We may therefore need to consider other questions that define how we view and manage dingoes and their interbreeding with domestic dogs.

As a first step, we have developed a decision tree to help address this quandary (Figure 1). The tree considers three main levels: first, whether we should protect dingoes, based on their ecological and cultural value; second, whether we should manage hybridisation, which may depend on location-specific management objectives

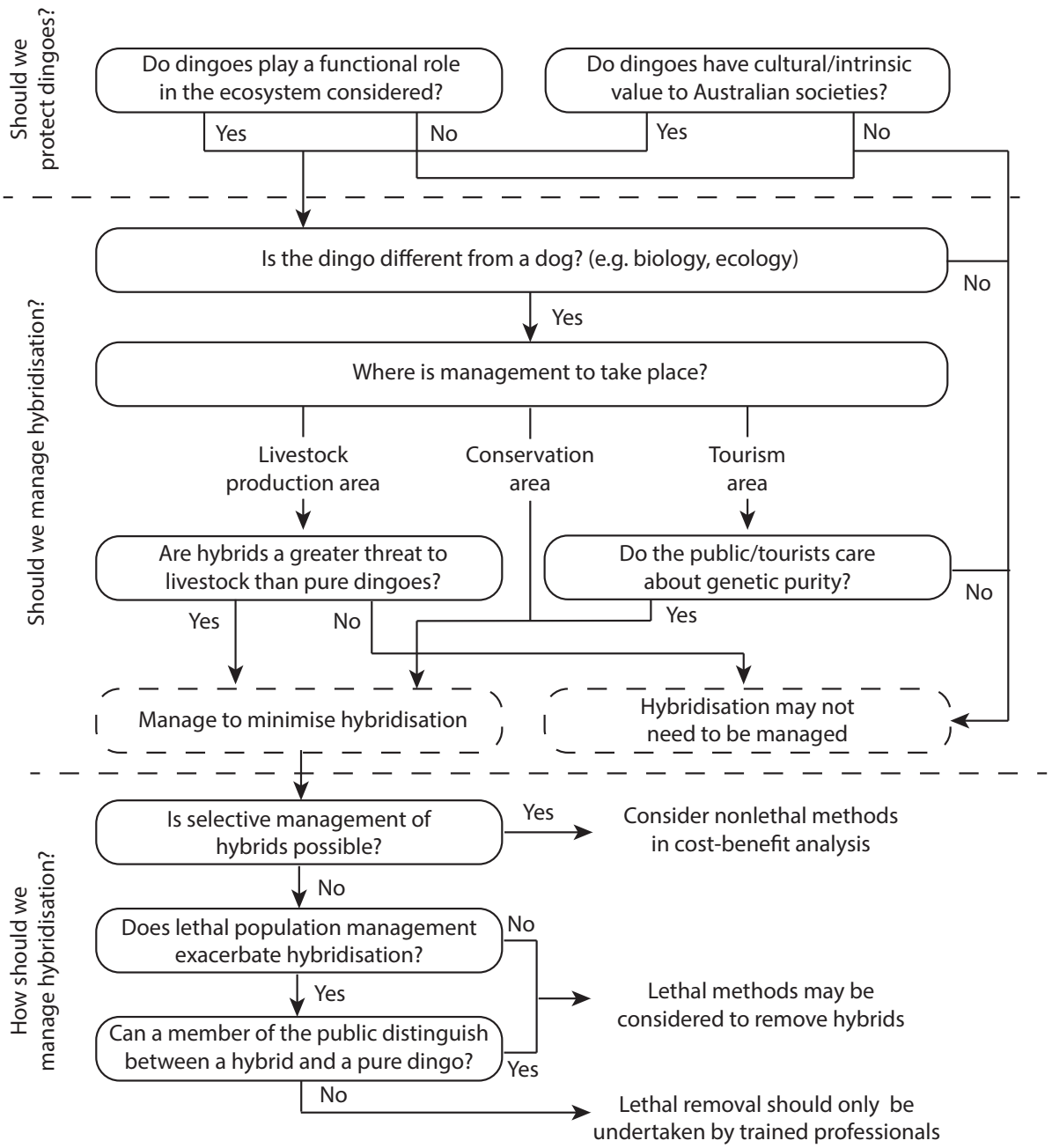

Figure 1 Decision tree highlighting knowledge gaps, lack of consensus about the factors that shape dingo management, and how filling these gaps might result in targeted management.

shaped by social and economic factors; and third, if we are to manage hybridisation, we should consider what is achievable and appropriate given dingo biology and landscape contexts. This approach stands in contrast to Allen *et al.* (2017) who recently outlined a "roadmap" to dingo conservation. Specifically, their proposal did not incorporate the social, ecological, and economic factors that influence the aims of dingo conservation and management in different contexts, despite discussing the importance of socio-ecological factors in parts of their paper. In addition, they did not address how their proposed management goals could actually be achieved, which limits their appeal.

Genetics, biology, and ecology: what defines an acceptable dingo?

Totally eradicating domestic dog genes from dingo populations is likely an impossible task, so we must accept some level of hybridisation where this has already occurred. Hybridisation is common in other canid populations and in some instances there has been a long history of it occurring. For example, analysis of Eurasian grey wolves indicated that introgression of dog genes is not a recent phenomenon, with most wolves showing some level of historic admixture (Pilot *et al.* 2018). Similarly, a long history of interbreeding events

between wolves (*C. lupus* and subspecies), coyotes (*C. latrans*) and domestic dogs across North America means there are areas where wolf subspecies are defined based on whether they are more or less coyote-like, and that individual wolves and coyotes may contain small amounts of genetic material representative of domestic dogs (vonHoldt *et al.* 2011). In these cases, introgression of dog genes into wolf and coyote populations is not considered a major conservation issue because the extent of introgression is limited compared with, for example, wolf-coyote hybridisation, which may have greater ecological consequences.

For dingoes, recent mapping of the extent of hybridisation between dingoes and dogs suggests the highest degree of introgression has occurred within the eastern States, where up to 99% of dingoes may have hybridised with domestic dogs (Stephens *et al.* 2015). Higher levels of introgression in these areas may be due to a combination of greater lethal control efforts and proximity to urban areas where dingoes and dogs may be more likely to interact. However, recent analyses of the mitochondrial DNA genome and nuclear genes suggest that there are two distinct dingo clades, a 'south-eastern' Australian and a 'north-western' Australian clade (Cairns *et al.* 2017; Cairns and Wilton 2016). Hence attempts to discriminate dingoes from hybrids using molecular markers may have been confounded by using animals from the south-eastern clade as controls representative of 'pure' dingoes in the north-western clade distribution (and vice versa). Stephens *et al.* (2015) also used inappropriate spatial over-smoothing to estimate the extent of hybridisation in south-eastern Australia. There were relatively few animals from south-eastern Australia (95 animals from NSW and the Australian Capital Territory) compared to Western Australia (228 samples), and hence the extent of hybridisation was estimated through geographical biases in the density of samples and through interpolating over large geographical distances (e.g., Hofstra *et al.* 2010). The maps by Stephens *et al.* (2015) were uncritically accepted by Allen *et al.* (2017) when defining the distribution of hybridisation in Australia, despite the potential for erroneous conclusions.

Furthermore, there is still disagreement or uncertainty about the genetic identity of a 'pure' dingo. Allen *et al.* (2017) used a definition of 'pure dingoes' of 93%, based on Stephens *et al.* (2015). There are proposals to sequence the dingo genome, which, in addition to improved technologies for genetic sequencing (Cairns *et al.* 2011), may assist in clarifying what individuals we perceive to be undesirable hybrids. But at present, we still do not fully understand the link between genotype and phenotype in dingo/hybrid populations (Elledge *et al.* 2006). Thus, while we could define an acceptable proportion of admixture (e.g., <0 %, 5%, 25%, Allendorf *et al.* 2001) the usefulness of doing so may be hindered by our ability to measure this accurately and feasibly with current technology.

So if we cannot agree on a definition for what a 'desirable' dingo is based on genetics, we might instead consider its biology and ecological role (see also Figure 1). Most free-roaming dogs in Australia are generally observed to be more dingo-like in appearance and behaviour due to the dominance of wild-type phenotypes (Parr *et al.* 2016) and possibly natural selection imposed by the prevailing environmental conditions. Furthermore, much of our current evidence for the ecological role of the dingo as a top predator has been conducted in areas that Stephens *et al.* (2015) considered to have highly hybridised populations (Claridge and Hunt 2008; Letnic *et al.* 2012). This might suggest that if our management goal is to preserve the dingo's ecological role, then hybridisation is not a threatening process. In addition, it suggests that dingo-dog hybridisation may not reduce the fitness of the overall population; a concern that has been raised in other cases (vonHoldt *et al.* 2018).

Additionally, it has been proposed that hybrids breed more frequently than dingoes and therefore pose a greater threat to wildlife and livestock (Fleming *et al.* 2001). However, recent evidence suggests that hybrids behave more like dingoes in their breeding patterns (Cursino *et al.* 2017). Similarly, it has been suggested that hybrids have higher body mass and may pose a greater risk to ecological systems and livestock due to their higher metabolic needs (Claridge *et al.* 2014) but again, there is no consensus that this is occurring at a large scale.

Cultural value and ethical considerations

We are not the first to suggest that further research is needed to understand how a dingo differs from a dog or a hybrid (e.g., Claridge and Hunt 2008); however, such studies are very difficult to undertake experimentally. So, we propose that further questions need to be asked relating to cultural and social perceptions of dingoes and hybrids. We currently have little idea of the Australian public's view of the dingo, and regardless of its origin and taxonomy, it is likely perceived as an iconic Australian species. Furthermore, we do not know whether awareness about hybridisation would affect the public's perception of individuals or populations of dingoes. Dingoes are an important tourist attraction at K'gari (Fraser Island), and yet tourists seem unaware and unperturbed that these dingoes may be up to 30% hybridised with domestic dogs (Queensland Parks and Wildlife Service unpublished data in Department of Environment and Heritage Protection 2014). Phenotype is thus potentially more important than genotype to the public.

The significance of dingoes for Aboriginal societies has also largely been ignored in dingo management. The dingo, like most long established wild animals in Australia, has deep cultural significance to many Aboriginal communities (Parker 2006; Smith and Litchfield 2009). When dingoes arrived in Australia, some may have

become part of Aboriginal communities as hunting dogs and companion animals (Hamilton 1972; Kolig 1978; Smith and Litchfield 2009). In some Aboriginal societies, dingoes feature in dreaming stories, falling somewhere between human and nonhuman animal, and are regarded as members of the community (Maddock 1982) with taboos against killing them (Kolig 1978). That said, after European settlement, Aboriginal Australians sometimes killed dingoes to claim bounties (Meggitt 1965). There was also a shift towards keeping European domestic dog breeds as pets because they were easier to acquire and control (Kolig 1978). The values that indigenous groups assign to non-native species do not always align with Eurocentric ideas of species identity (Gibbs *et al.* 2015; Trigger *et al.* 2008) so we cannot be certain whether a distinction is made between dingoes, dogs, and their hybrids. Some Aboriginal societies assign different words for dingoes (or dogs) based on whether they were tame or wild (e.g., camp dogs versus wild dingoes), while others do not (e.g., Hamilton 1972; Ryan 1964), but any distinctions may not consider the phenotype—let alone genotype—of the animals.

There are also ethical factors to consider where lethal control or breeding manipulation occurs, especially when humans drive processes that facilitate hybridisation. The differences in our approach to management of different organisms have been likened to racism among humans (Simberloff 2003). For dingoes, parallels are drawn with colonial Australians' fear of race-mixing between Aboriginal and European Australians (Carter *et al.* 2017; Probyn-Rapsey 2015). Mixed race people were deemed "no longer authentically indigenous" and thus denied a claim to belong (Probyn-Rapsey 2015 p. 70). We now recognise the atrocities against human rights that occurred as a result of assimilation policies such as removal of Aboriginal children from their families and female trafficking (Probyn-Rapsey 2015), but speciesism (and associated culling practices) remains prevalent in our attitudes towards non-human organisms (Singer 2009). Philosophical debate rightly occurs about the right of humans to shape future evolutionary trajectories (Jackiw *et al.* 2015) and whether we should deny an individual animal the right to exist because it has mixed genetics (that resulted from human activities) is a question fraught with ethical dilemmas that are largely ignored in our current practices.

Management and policy

Currently, our management of dingoes and other wild canids in Australia is focused on lethal control and there is very limited evidence of management actions that effectively prevent further introgression between dingoes and domestic dogs (Smith and Appleby 2015). Unfortunately, we don't fully understand the processes that contribute to dingo-dog hybridisation, but as with other wild canids (Moura *et al.* 2014; Rutledge *et al.* 2011), it is possible that lethal control may increase opportunities for hybridisation by destabilising dingo pack structures (Wallach *et al.* 2009). Otherwise, behavioural differences between canid species in the wild limit interbreeding (Andersone *et al.* 2002; Lehman *et al.* 1991), even in canids that may have related hybrid ancestry (e.g., red wolves and coyotes, Hinton *et al.* 2018). Because dingoes are both protected and culled, the resulting management likely exacerbates the hybridisation situation (Figure 2). To break this cycle, we can at least learn something from the experiences of managing hybridising canids elsewhere.

European policy, for example, has been amended (Directorate of Democratic Governance 2014) to give wolf-dog hybrids protection. This occurred out of concern that allowing members of the public to kill what they perceived to be hybrids could be counterproductive to wolf conservation as it was likely to result in accidental or intentional killing of pure wolves and hinder prosecution for illegal wolf-culling (Trouwborst 2014). These changes mean that any removal of wild hybrids must be government controlled (Directorate of Democratic Governance 2014). Similarly, in the USA, while there is currently no legal protection for hybrids, there has been a proposal to protect hybrids under certain circumstances where the last remaining genetic material of a canid species exists, but also by promoting protection of "hybrid individuals that more closely resemble a parent belonging to a listed species" (Fish & Wildlife Service 1996). Twenty years after its proposal, this amendment has neither been accepted nor rejected and so management of hybrids in the US remains ambiguous, with only 16% of North American conservation policies

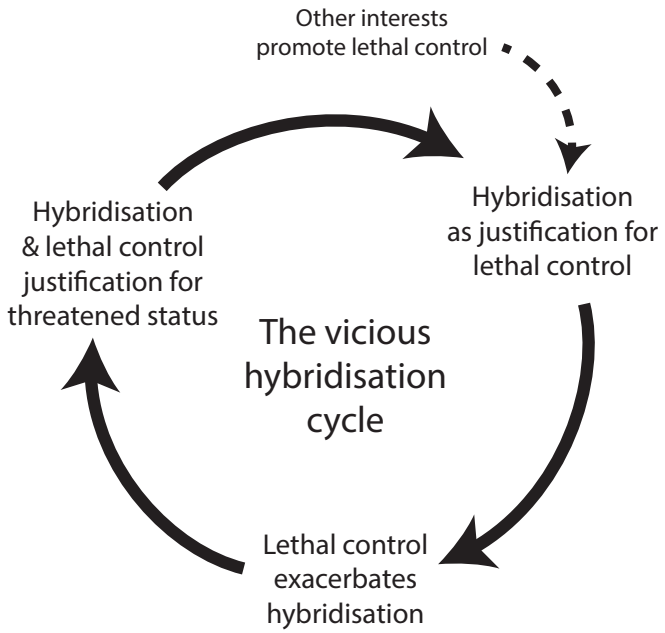

Figure 2 Ambiguity caused by hybridisation between dingoes and dogs is influenced by human values, resulting in a vicious cycle of ineffective management.

incorporating hybrid management guidelines (Jackiw *et al.* 2015). Nonetheless, the protection of hybrids, or suggestion to protect them, in other countries is a far cry from dingo management in Australia, where landholders are required by law to actively seek and destroy dingoes and their hybrids throughout large parts of their range (Smith and Appleby 2015).

Currently, while pure dingoes are listed as protected in some areas, it is unclear whether hybrids could also be afforded protection under current legislation. While the federal Australian Environment Protection and Biodiversity Conservation Act 1999 makes no mention of hybrids, some states do include hybrids under their definition of wildlife. For example, the Territory Parks and Wildlife Conservation Act 2000 gives dingoes full legal protection (although control takes place where permitted), and also defines wildlife as including "a hybrid or variant race of a species of wildlife." Given the difficulty of distinguishing between hybrids and dingoes, it is likely that in practice the protection or persecution of dingoes extends to their hybrids where legislation applies.

In order to progress dingo management in Australia, we need to consider what is achievable for managing hybridisation in order to determine what path is appropriate at a local and broad scale (Figure 1). Management of hybridisation for some species with restricted ranges has been possible, as with Ethiopian wolves (which have hybridised with domestic dogs, Sillero-Zubiri and Marino 2004), red wolves (which hybridise with coyotes, Stoskopf *et al.* 2005), and Scottish wildcats (which hybridise with domestic cats, *Felis catus*, Hetherington and Campbell 2013). In these situations, selective removal or sterilisation of hybrids (or individuals that may contribute genetic material perceived to be undesirable by managers) has been conducted. Importantly, incorporating sterilisation rather than culling into management recognises that the removal of unwanted individuals is likely to result in migration of new individuals which may be considered equally undesirable. However, there is debate about how recently red wolves became isolated from their grey wolf and coyote ancestors (Hohenlohe *et al.* 2017; vonHoldt *et al.* 2016), although recognition of their hybrid ancestry does not appear to affect their protected status (Morrison *et al.* 2009), whether such intensive management to prevent hybridisation should continue (Murray *et al.* 2015), as well as some concern that the current extant red wolf population, which is founded entirely from a captive bred population, has been shaped by artificially selecting for wild individuals that appeared more like grey wolves than coyotes (vonHoldt *et al.* 2011).

Currently, it is not possible to reliably and consistently detect whether a dingo is pure or hybridised in the field, so if we were to manage hybridisation, we might expect a similar selective process that favours "postcard" tan-coloured dingoes regardless of genotype. Culling obvious hybrids (e.g., with patchy coat colours) might slow the process of hybridisation (Elledge *et al.* 2008), but effective management may not currently be achievable over large areas. With advances in technology, it could be possible to undertake similar targeted management in localised areas to prevent further introgression between dingoes and dogs where considered desirable. Reducing attacks on livestock is currently a priority over any actions to prevent further introgression. As such, perhaps predator-friendly farming could be used to protect livestock (e.g., livestock guardian animals, appropriate animal husbandry), as a reduction in lethal control may reduce further opportunities for introgression (Johnson and Wallach 2016). Selective removal might also be undertaken to prevent further attacks on livestock by problem individuals (Swan *et al.* 2017) which may have a lesser impact on disrupting pack structures and exacerbating hybridisation than localised eradication attempts.

At the very least, humans in both urban and rural areas should restrain (or control the movements) of any domestic dogs kept as working animals or as pets, and even more preferably, all dogs should be de-sexed unless they are owned by a registered breeder. In some areas such as National Parks, domestic dogs are prohibited. Such policies could be rolled out further to other designated areas managed by the States, Territories or Local Councils. Indeed, such actions should be implemented in conjunction with lethal control, in case it disrupts stable pack structures and enhances the likelihood of hybridisation occurring. Claridge *et al.* (2014) suggest it may be possible to develop a dog-specific toxin that dingoes are resistant to, but in most places where lethal dingo/dog control is undertaken, pressures from the agriculture industry to protect livestock will likely prevent adoption of management techniques that selectively cull some wild canids and protect others. These conflicting interests and values are a significant barrier to dingo conservation and must be considered in any local management, but this should not be at the cost of ignoring the perspectives and values of other stakeholders.

Conclusion

The case of the dingo reveals how species identity, and the values associated with it, have implications for conservation. The concept of a taxonomic system has been debated for centuries, with species concepts criticised as "names standing for nothing but the ideas that are in men's minds" (Locke 1999 p. 362). While biology plays a stronger role in taxonomy than it did when this statement was made in 1690, these words maintain relevance in debate about dingo management and taxonomy today. Some continue to recognise species as merely tools fashioned to help us to understand biodiversity, "to make sense out of nonsense and put the world into some

perspective which has order and harmony" (Levin 1979 p. 382). This is useful when this harmony can be found, but ambiguity (like that caused by hybridisation) means that such constructs can become dangerous, allowing values to play an overwhelming role in shaping management.

For dingo conservation, we must decide (and ideally agree upon) what it is we wish to achieve. There remain unanswered questions that prevent us from defining an acceptable dingo, including its genetic profile, ecological role, and how it is perceived by society, some of which may never be agreed upon, that will decide whether we manage hybridisation at all. Our framework provides a platform to begin filling these knowledge gaps so that we can define how best to approach this dingo-dog dilemma. These are ultimately ethical questions that are difficult to answer, but addressing them is essential to begin conserving the dingo in earnest.

References

Allen, B.L., Allen, L.R., Ballard, G., Jackson, S.M., and Fleming, P.J.S. 2017. A roadmap to meaningful dingo conservation. *Canid Biology & Conservation* **20**(11): 45–56.

Allen, B.L., Fleming, P.J.S., Allen, L.R., Engeman, R.M., Ballard, G., and Leung, L.K.P. 2013. As clear as mud: a critical review of evidence for the ecological roles of Australian dingoes. *Biological Conservation* **159**: 158–174. http://doi.org/10.1016/j.biocon.2012.12.004

Allendorf, F.W., Leary, R.F., Spruell, P., and Wenburg, J.K. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* **16**(11): 613–622. http://doi.org/10.1016/S0169-5347(01)02290-X

Andersone, Ž., Lucchini, V., and Ozoliņš, J. 2002. Hybridisation between wolves and dogs in Latvia as documented using mitochondrial and microsatellite DNA markers. *Mammalian Biology - Zeitschrift Für Säugetierkunde* **67**(2): 79–90. http://doi.org/10.1078/1616-5047-00012

Beaumont, M., Barratt, E.M., Gottelli, D., Kitchener, A.C., Daniels, M.J., Pritchard, J.K., and Bruford, M.W. 2001. Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology* **10**(2): 319–336. http://doi.org/10.1046/j.1365-294X.2001.01196.x

Cairns, K.M., Brown, S.K., Sacks, B.N., and Ballard, J.W.O. 2017. Conservation implications for dingoes from the maternal and paternal genome: Multiple populations, dog introgression, and demography. *Ecology and Evolution* 9787–9807. http://doi.org/10.1002/ece3.3487

Cairns, K.M., and Wilton, A.N. 2016. New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica* **144**(5): 553–565. http://doi.org/10.1007/s10709-016-9924-z

Cairns, K.M., Wilton, A.N., and Ballard, J.W.O. 2011. The identification of dingoes in a background of hybrids. In K.V. Urbano (Ed.), *Advances in genetics research* (pp. 309–327). Nova Science Publishers, New York.

Carter, J., Wardell-Johnson, A., and Archer-Lean, C. 2017. Butchulla perspectives on dingo displacement and agency at K'gari-Fraser Island, Australia. *Geoforum* **85**: 197–205. http://doi.org/10.1016/j.geoforum.2017.08.001

Claridge, A. W., and Hunt, R. 2008. Evaluating the role of the dingo as a trophic regulator: additional practical suggestions. *Ecological Management & Restoration* **9**: 116–119. http://doi.org/10.1111/j.1442-8903.2008.00402.x

Claridge, Andrew W., Spencer, R.J., Wilton, A.N., Jenkins, D.J., and Lapidge, S.J. 2014. When is a dingo not a dingo? Hybridisation with domestic dogs. In A.S. Glen and C.R. Dickman (Eds.), *Carnivores of Australia: past, present and future* (pp. 151–172). CSIRO Publishing, Collingwood, Victoria.

Clutton-Brock, J. 2015. Naming the scale of nature. In A.M. Behie and M.F. Oxenham (Eds.), *Taxonomic tapestries: the threads of evolutionary behavioural and conservation research* (pp. 172–182). Australian National University Press, Canberra, Australia.

Corbett, L.K. 2008. *Canis lupus* spp. *dingo*. *The IUCN Red List of Threatened Species* (**e.T41585A10484199**). http://doi.org/10.2305/IUCN.UK.2008.RLTS.T41585A10484199.en

Crowther, M.S., Fillios, M., Colman, N., and Letnic, M. 2014. An updated description of the Australian dingo (*Canis dingo* Meyer, 1793). *Journal of Zoology* **293**(3): 192–203. http://doi.org/10.1111/jzo.12134

Cursino, M.S., Harriott, L., Allen, B.L., Gentle, M., and Leung, L.K.-P. 2017. Do female dingo–dog hybrids breed like dingoes or dogs? *Australian Journal of Zoology* **65**(2): 112–119. http://doi.org/10.1071/ZO17005

Daniels, M.J., and Corbett, L. 2003. Redefining introgressed protected mammals: when is a wildcat a wild cat and a dingo a wild dog? *Wildlife Research* **30**(3): 213–218. http://doi.org/10.1071/WR02045

Department of Environment and Heritage Protection. 2014. Fraser Island Dingo Strategic Research Program. Biodiversity Strategy Team, Biodiversity Implementation Unit, Ecosystems Outcomes Branch, Department of Environment and Heritage Protection, State of Queensland. Retrieved from https://www.ehp.qld.gov.au/wildlife/livingwith/dingoes/pdf/fraser-island-dingo-research.pdf

Directorate of Democratic Governance. Recommendation No. 173 (2014) on Hybridisation between wild grey wolves (*Canis lupus*) and domestic dogs (*Canis lupus familiaris*), Convention on the Conservation of European Wildlife and Natural Habitats, Standing Committee (2014). Council of Europe/Conseil de L'Europe, Strasbourg. Retrieved from https://wcd.coe.int/com.instranet.InstraServlet?command=com.instranet.CmdBlobGet&InstranetImage=2654095&SecMode=1&DocId=2196762&Usage=2

Elledge, A.E., Allen, L.R., Carlsson, B.-L., Wilton, A.N., and Leung, L.K.-P. 2008. An evaluation of genetic analyses, skull morphology and visual appearance for assessing dingo purity: implications for dingo conservation. *Wildlife Research* **35**(8): 812–820. http://doi.org/10.1071/WR07056

Elledge, A.E., Leung, L.K., Allen, L.R., Firestone, K., and Wilton, A.N. 2006. Assessing the taxonomic status of dingoes *Canis familiaris dingo* for conservation. *Mammal Review* **36**(2): 142–156. http://doi.org/10.1071/WR07056

Fish & Wildlife Service. Proposed policy on the treatment of intercrosses and intercross progeny (the issue of "hybridization"), Pub. L. No. Propose Rule, 50 CFR Part 424 (1996).

Fleming, P., and Ballard, G. 2014. An investigation or aerial baiting rates for strategic control of wild dogs: final report to Biosecurity NSW, Local Land Services and the Australian Pesticides and Veterinary Medicines Authority. NSW Department of Primary Industries. Retrieved from https://www.pestsmart.org.au/wp-content/uploads/2015/04/FlemingBallard_AerialBaitingRept_APVMA.pdf

Fleming, P.J.S., Corbett, L., Harden, R., and Thomson, P. 2001. Managing the impacts of dingoes and other wild dogs (p. 198). Canberra: Bureau of Rural Sciences.

Gibbs, L., Atchison, J., and Macfarlane, I. 2015. Camel country: assemblage, belonging and scale in invasive species geographies. *Geoforum* **58**: 56–67. http://doi.org/10.1016/j.geoforum.2014.10.013

Gottelli, D., Sillero-Zubiri, C., Applebaum, G.D., Roy, M.S., Girman, D.J., Garcia-Moreno, J., Ostrander, E.A., and Wayne, R.K. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf *Canis simensis*. *Molecular Ecology* **3**(4): 301–312. http://doi.org/10.1111/j.1365-294X.1994.tb00070.x

Groves, C.P. 1997. Taxonomy of wild pigs (*Sus*) of the Philippines. *Zoological Journal of the Linnean Society* **120**(2): 163–191. http://doi.org/10.1111/j.1096-3642.1997.tb01277.x

Hamilton, A. 1972. Aboriginal man's best friend? *Mankind* **8**: 287–95. http://doi.org/10.1111/j.1835-9310.1972.tb00449.x

Hedrick, P.W. 2009. Conservation genetics and North American Bison (*Bison bison*). *Journal of Heredity* **100**(4): 411–420. http://doi.org/10.1093/jhered/esp024

Hetherington, D., and Campbell, R. 2013. The Cairngorms Wildcat Project: final report. Report to Cairngorms National Park Authority, Scottish Natural Heritage, Royal Zoological Society of Scotland, Scottish Gamekeepers Association and Forestry Commission Scotland. Retrieved from https://www.nature.scot/sites/default/files/2017-07/A1697327%20-%20The%20Cairngorms%20Wildcat%20Project%20-%20final%20report.pdf

Hinton, J.W., Gittleman, J.L., van Manen, F.T., and Chamberlain, M.J. 2018. Size-assortative choice and mate availability influences hybridization between red wolves (*Canis rufus*) and coyotes (*Canis latrans*). *Ecology and Evolution* **8**(8): 3927–3940. http://doi.org/10.1002/ece3.3950

Hofstra, N., New, M., and McSweeney, C. 2010. The influence of interpolation and station network density on the distribution and trends of climate variables in gridded daily data. *Climate Dynamics* **35**: 841–858. http://doi.org/10.1007/s00382-009-0698-1

Hohenlohe, P.A., Rutledge, L.Y., Waits, L.P., Andrews, K.R., Adams, J.R., Hinton, J.W., Nowak, R.M., Patterson, B.R., Wydeven, A.P., Wilson, P.A., and White, B.N. 2017. Comment on "Whole-genome sequence analysis shows two endemic species of North American wolf are admixtures of the coyote and gray wolf." *Science Advances* **3**(6). http://doi.org/10.1126/sciadv.1602250

Hytten, K.F. 2009. Dingo dualisms: exploring the ambiguous identity of Australian dingoes. *Australian Zoologist* **35**(1): 18–27. http://doi.org/10.7882/AZ.2009.003

Jackiw, R.N., Mandil, G., and Hager, H.A. 2015. A framework to guide the conservation of species hybrids based on ethical and ecological considerations. *Conservation Biology* 1040–1051. http://doi.org/10.1111/cobi.12526

Jackson, S.M., Groves, C.P., Fleming, P.J.S., Aplin, K.P., Eldridge, M.D.B., Gonzalez, A., and Helgen, K.M. 2017. The wayward dog: is the Australian native dog or dingo a distinct species? *Zootaxa* **4317**(2): 201–224. http://doi.org/10.11646/zootaxa.4317.2.1

Johnson, C.N., and Wallach, A.D. 2016. The virtuous circle: predator-friendly farming and ecological restoration in Australia. *Restoration Ecology* **24**(6): 821–826. http://doi.org/10.1111/rec.12396

King, S.R.B., Boyd, L., Zimmermann, W., and Kendall, B.E. 2015. *Equus ferus* ssp. *przewalskii*. *The IUCN Red List of Threatened Species* (**e.T7961A97205530**). http://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T7961A45172099.en

Kolig, E. 1978. Aboriginal dogmatics: canines in theory, myth and dogma. *Journal of the Humanities and Social Sciences of Southeast Asia* **134**(1): 84–115. http://doi.org/10.1163/22134379-90002597

Lehman, N., Eisenhawer, A., Hansen, K., Mech, L.D., Peterson, R.O., Gogan, P.J.P., and Wayne, R.K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution* **45**(1): 104–119. http://doi.org/10.1111/j.1558-5646.1991.tb05270.x

Letnic, M., Ritchie, E.G., and Dickman, C.R. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* **87**(2): 390–413. http://doi.org/10.1111/j.1469-185X.2011.00203.x

Levin, D.A. 1979. The nature of plant species. *Science* **204**(**4391**): 381–384. http://doi.org/10.1126/science.204.4391.381

Locke, J. 1999. An essay concerning human understanding. The Pennsylvania State University. Retrieved from ftp://ftp.dca.fee.unicamp.br/pub/docs/ia005/humanund.pdf

Mace, G.M. 2004. The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London B* **359**: 711–719. http://doi.org/10.1098/rstb.2003.1454

Maddock, K. 1982. The Australian Aborigines: a portrait of their society. Penguin Australia, Ringwood, Victoria.

Mallet, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology & Evolution* **20**(**5**): 229–237.

Mayden, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In M.F. Claridge, H.A. Dawah, and M.R. Wilson (Eds.), *Species: the units of biodiversity* (pp. 381–424). Chapman & Hall, New York.

Mayr, E. 1982. The grown of biological thought: diversity, evolution, and inheritance. Belknap Press of Harvard University Press, Cambridge, MA.

Meggitt, M. 1965. Australian aborigines and dingoes. In A. Leeds and P. Vayda (Eds.), *Man, culture and animals* (pp. 7–26). American Association for the Advancement of Science Symposium Publication.

Morrison, W.R., Lohr, J.L., Duchen, P., Wilches, R., Trujillo, D., Mair, M., and Renner, S.S. 2009. The impact of taxonomic change on conservation: Does it kill, can it save, or is it just irrelevant? *Biological Conservation* **142**(12): 3201–3206. http://doi.org/10.1016/j.biocon.2009.07.019

Moura, A.E., Tsingarska, E., Dąbrowski, M.J., Czarnomska, S.D., Jędrzejewska, B., and Pilot, M. 2014. Unregulated hunting and genetic recovery from a severe population decline: the cautionary case of Bulgarian wolves. *Conservation Genetics* **15**(2): 405–417. http://doi.org/10.1007/s10592-013-0547-y

Murray, D.L., Bastille-Rousseau, G., Adams, J.R. and Waits, L.P. The challenges of red wolf conservation and the fate of an endangered species recovery program.. *Conservation Letters* **8**(5): 338–344. http://doi.org/10.1111/conl.12157

Newsome, A.E., and Corbett, L. 1982. The identity of the dingo II. Hybridization with domestic dogs in captivity and in the wild. *Australian Journal of Zoology* **30**: 365–374. http://doi.org/10.1071/ZO9820365

Newsome, T.M., Ballard, G.-A., Crowther, M.S., Dellinger, J.A., Fleming, P.J.S., Glen, A.S., Greenville, A.C., Johnson, C.N., Letnic, M., Moseby, K.E., Read, J.L., Ripple, W.J., Ritchie, E.G., Shores, C.R., Wallach, A.D., Wirsing, A.J., and Dickman, C.R. 2015. Resolving the value of dingoes in ecological restoration. *Restoration Ecology* **23**(3): 201–208. http://doi.org/10.1111/rec.12186

NSW Scientific Committee. 2011. Predation and hybridisation by feral dogs (*Canis lupus familiaris*) - key threatening process listing. NSW Government, Office of Environment & Heritage. Retrieved from http://www.environment.nsw.gov.au/determinations/feraldogsFD.htm

Oskarsson, M.C.R., Klutsch, C.F.C., Boonyaprakob, U., Wilton, A., Tanaabe, Y., and Savolainen, P. 2011. Mitochondrial DNA data indicate an introduction through mainland southeast Asia for Australian dingoes and Polynesian domestic dogs. *Proceedings of the Royal Society B: Biological Scienes* **279**(1730): 967–974.

Parker, M. 2006. Bringing the dingo home: discursive representations of the dingo by Aboriginal, colonial and contemporary Australians. University of Tasmania, Australia.

Parr, W.C.H., Wilson, L.A.B., Wroe, S., Colman, N.J., Crowther, M.S., and Letnic, M. 2016. Cranial shape and the modularity of hybridization in dingoes and dogs; hybridization does not spell the end for native morphology. *Evolutionary Biology* **43**(2): 171–187. http://doi.org/http://dx.doi.org/10.1007/s11692-016-9371-x

Pilot, M., Greco, C., vonHoldt, B.M., Randi, E., Jędrzejewski, Sidorovich, V.E., Konopiński, M.K., Ostrander, E.A., and Wayne, R.K. 2018. Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. *Evolutionary Applications* **11**(5): 662-680. http://doi.org/10.1111/eva.12595

Probyn-Rapsey, F. 2015. Dingoes and dog-whistling: a cultural politics of race and species in Australia. *Animal Studies Journal* **4**(2): 55–77.

Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N., and Bierne, N. 2016. Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLOS Biology* **14**(12): e2000234. http://doi.org/10.1371/journal.pbio.2000234

Rutledge, L.Y., White, B.N., Row, J.R., and Patterson, B.R. 2011. Intense harvesting of eastern wolves facilitated hybridization with coyotes. *Ecology and Evolution* **2**(1): 19–33. http://doi.org/10.1002/ece3.61

Ryan, J.S. 1964. Plotting an isogloss—the location and types of Aboriginal names for native dog in New South Wales. *Oceania* **35**(2): 111–123. http://doi.org/10.1002/j.1834-4461.1964.tb00837.x

Seehausen, O., Takimoto, G., Roy, D., and Jokela, J. 2007. Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Molecular Ecology* **17**(1): 30–44. http://doi.org/10.1111/j.1365-294X.2007.03529.x

Sillero-Zubiri, C., and Marino, J. 2004. Ethiopian wolf (*Canis simensis*). In C. Sillero-Zubiri, M. Hoffmann, and D.W. Macdonald (Eds.), *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan* (pp. 167–173). IUCN/SSC Canid Specialist Group, Gland, Switzerland.

Simberloff, D. 2003. Confronting introduced species: a form of xenophobia? *Biological Invasions* **5**(3): 179–192. http://doi.org/10.1023/A:1026164419010

Singer, P. 2009. Speciesism and moral status. *Metaphilosophy* **40**(3–4): 567–581. http://doi.org/10.1111/j.1467-9973.2009.01608.x

Smith, B., and Appleby, R. 2015. Forging a new future for the Australian dingo. In B. Smith (Ed.), *The dingo debate: origins, behaviour and conservation* (pp. 301–316). CSIRO Publishing, Clayton South.

Smith, B.P., Cairns, K.M., Adams, J.W., Newsome, T.M., Filios, M., Déaux, E.C., Parr, W.C.H., Letnic, M., van Eeden, L.M., Appleby, R.G., Bradshaw, C.J.A., Savolainen, P., Ritchie, E.G., Nimmo, D.G., Archer-Lean, C., Greenville, A.C., Dickman, C.R., … Crowther, M.S. in press. Taxonomic status of the Australian dingo: the case for *Canis dingo* Meyer, 1793. *Zootaxa*.

Smith, B.P., and Litchfield, C.A. 2009. A review of the relationship between indigenous Australians, dingoes (*Canis dingo*) and domestic dogs (*Canis familiaris*). *Anthrozoös* **22**(2): 111–129. http://doi.org/10.2752/175303709X434149

Stephens, D., Wilton, A.N., Fleming, P.J.S., and Berry, O. 2015. Death by sex in an Australian icon: a continent-wide survey reveals extensive hybridization between dingoes and domestic dogs. *Molecular Ecology* **24**(22): 5643–5656. http://doi.org/10.1111/mec.13416

Stoskopf, M.K., Beck, K., Fazio, B.B., Fuller, T.K., and Gese, E.M. 2005. Implementing recovery of the red wolf - integrating research scientists and managers. *Wildlife Society Bulletin* **33**(3): 1145–1152. http://doi.org/10.2193/0091-7648(2005)33[1145:FTFIRO]2.0.CO;2

Swan, G.J.F., Redpath, S.M., Bearhop, S., and McDonald, R.A. 2017. Ecology of problem individuals and the efficacy of selective wildlife management. *Trends in Ecology & Evolution* **32**(7): 518–530. http://doi.org/10.1016/j.tree.2017.03.011

Trigger, D., Mulcock, J., Gaynor, A., and Toussaint, Y. 2008. Ecological restoration, cultural preferences and the negotiation of 'nativeness' in Australia. *Geoforum* **39**(3): 1273–1283. http://doi.org/10.1016/j.geoforum.2007.05.010

Trouwborst, A. 2014. Exploring the legal status of wolf-dog hybrids and other dubious animals: international and EU law and the wildlife conservation problem of hybridization with domestic and alien species. *Review of European Community & International Environmental Law* **23**(1): 111–124. http://doi.org/10.1111/reel.12052

vonHoldt, B.M., Brzeski, K.E., Wilcove, D.S., and Rutledge, L.Y. 2018. Redefining the role of admixture and genomics in species conservation. *Conservation Letters* **11**: e12371. http://doi.org/10.1111/conl.12371

vonHoldt, B.M., Cahill, J.A., Fan, Z., Gronau, I., Robinson, J., Pollinger, J.P., Shapiro, B., Wall, J., and Wayne, R.K. 2016. Whole-genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf. *Science Advances* **2**(7). http://doi.org/10.1126/sciadv.1501714

vonHoldt, B.M., Pollinger, J.P., Earl, D.A., Knowles, J.C., Boyko, A.R., Parker, H., Geffen, E., Pilot, M., Jedrzejewski, W., Jedrzejewski, B., Sidorovich, V., Greco, C., Randi, E., Musiani, M., Kays, R., Bustamante, C.D., Ostrander, E.E., … Wayne, R.K. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. *Genome Research* **21**: 1294–1305. http://doi.org/10.1101/gr.116301.110

Wallach, A.D., Ritchie, E.G., Read, J., and O'Neill, A.J. 2009. More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLOS ONE* **4**(9): e6861. http://doi.org/10.1371/journal.pone.0006861

Wayne, R. K., and Jenks, S.M. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf Canis rufus. *Nature* **351**(6327): 565–568. http://doi.org/10.1038/351565a0

Wayne, Robert K., and Ostrander, E.A. 1999. Origin, genetic diversity, and genome structure of the domestic dog. *BioEssays* **21**(3): 247–257. http://doi.org/10.1002/(SICI)1521-1878(199903)21:3<247::AID-BIES9>3.0.CO;2-Z

Wilkins, J.S. 2009. Species: a history of the idea. University of California Press, Berkeley and Los Angeles.

Zachos, F.E. 2016. Species concepts in biology: historical development, theoretical foundations and practical relevance. Springer, Charm, Switzerland.