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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).

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 antarcticus, 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
What should we do with wild dogs?

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

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.

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 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.
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
The vicious cycle that we are currently facing with dingoes and dogs is a result of the hybridisation between wild and domestic canids. Hybridisation is a process that occurs naturally and can be accelerated by human activities. Hybridisation has serious ecological and social implications, and it is essential to understand the processes that contribute to it in order to develop effective management strategies.

The hybridisation cycle is a result of the interaction between wild and domestic canids. The cycle begins with the introduction of domestic dogs into new environments, where they interbreed with wild canids. This hybridisation process leads to the creation of a new population that is distinct from both the wild and domestic canids. The hybrid population then becomes a breeding stock, and the cycle continues.

Management and policy

Currently, our management of dingoes and other wild canids in Australia is focused on lethal control and breeding manipulation. While these methods are effective in controlling the population, they do not address the underlying issues that contribute to hybridisation. There are ethical factors to consider when deciding on the management of wild canids, and we need to consider the rights of all non-human organisms.

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 giving 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 giving wolf-dog hybrids protection.
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.

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