

The wild ancestors of domestic animals as a neglected and threatened component of biodiversity

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Abstract

Domestic animals have immense economic, cultural and practical value, and have played pivotal roles in the development of human civilization. Many domesticates have, among their wild relatives, undomesticated forms representative of their ancestors. Resurgent interest in these ancestral forms has highlighted the unclear genetic status of many, with some threatened with extinction by hybridization with domestic conspecifics. Our aim is to focus attention on the contemporary status of these ancestral forms, by first discussing their scientific, practical and ecological importance; second, outlining the varied impacts of wild-domestic hybridization; and third discussing the challenges and potential resolutions involved in conservation efforts. We highlight the complexity of identifying and conserving ancestral forms, particularly with respect to disentangling patterns of gene flow from domesticates. Comparative behavioural, ecological and genetic studies of ancestral-type, feral and domestic animals should be prioritized to establish the contemporary status of the former. Such baseline information will be fundamental in ensuring successful conservation efforts.

Introduction

Among animals, domesticated species have developed an unparalleled relationship with humanity, playing fundamental economic and sociocultural roles (Zeder, 1982). They hold a unique position in our collective culture, with many having central roles in human mythologies and major world religions (Lodrick, 2005). As well as this cultural importance,

there is growing recognition of their ecological role (Doherty et al., 2017). The current global biomass of mammalian domestic livestock and chickens surpasses that of all wild mammals and birds respectively, resulting in significant climatic and ecological impacts (Bar-On et al., 2018). In addition, predation, competition and disease transmission occur at the wild-domestic interface – the latter being of particular interest in the context of emerging zoonotic disease threats (White & Razgour, 2020). Despite the importance of domestic animals, many of their undomesticated forms are relatively poorly understood. This lack of knowledge is a major problem because many undomesticated forms are at risk of extinction, and the failure of these entities to persist represents a loss of scientific, socio-economic and ecological opportunity (Taberlet et al., 2008).

The origin of domestic animals is often obscure. Most are presumed to originate from a primary ancestor with genetic contributions from closely related species (Thakur et al., 2018). Domestication can be considered a process rather than an outcome, and porous reproductive boundaries frequently allow extensive gene flow with related wild populations (McHugo et al., 2019). Currently, the status of undomesticated forms of many domestic animals is uncertain due to a lack of clear phenotypic demarcations between them and their relatives of domestic origin, which is often exacerbated by hybridization between the forms (Redford & Dudley, 2018) (Fig. 1, Table 1, Appendix S1). In this essay, we use the term ‘undomesticated forms’ to refer to the variously labelled ‘truly-wild’ or ‘ancestral’ populations thought to be the closest extant wild relatives of a domesticate, descending from the wild populations from which related lineages were originally domesticated. This definition is used to prevent confusion when discussing feral entities, where both domestic and the original wild populations are ‘ancestral’. Our use of the term ‘undomesticated forms’ excludes other wild relatives. For example, we do not consider the speckled pigeon (*Columba guinea*), and grey junglefowl (*Gallus sonneratii*), which made small genetic contributions to domestic

pigeons (*Columba livia*) (Vickrey et al., 2018) and chickens (*Gallus gallus*) (Lawal et al., 2020) respectively, as undomesticated forms. Our focus is specifically on the extant representatives of the primary wild ancestors of domestic animals and the issues associated with their conservation. Whilst extant grey wolves (*Canis lupus*) and European wildcats (*Felis silvestris*) are not the ancestral lineages of domestic dogs (*Canis familiaris*) and cats (*Felis catus*) (these being an extinct wolf population and the African wildcat (*Felis lybica*) respectively), we discuss them where appropriate given their ecological and cultural importance, and parallel conservation issues.

One of the main applied benefits of maintaining wild relatives is as a source of genetic variation for domestic forms. There has been a particular focus on wild crop relatives, given their potential contribution of beneficial genetic variation to modern crops (Zhang et al., 2016). The extinction of the undomesticated forms of domestic animals may similarly lead to the loss of genetic variation for potential introduction into domestic populations – and therefore a reduction in our ability to assure the resilience of domestic populations to disease and environmental threats (Redford & Dudley, 2018). Yet, they receive far less attention despite the importance of domestic animals as food sources, major ecological players and model organisms. Here our aim is to increase awareness of the importance of conserving the undomesticated forms of domestic animals. We expand on the multiple practical and scientific benefits of their protection, before highlighting the threat to undomesticated lineages particularly with respect to hybridization with feral and domestic relatives. Finally, we explore the challenges of their conservation, propose potential resolutions, and highlight priorities for research in these systems.

Importance of Maintaining Wild Ancestors

Scientific opportunity

The undomesticated forms of domestic animals provide multiple avenues of scientific opportunity. Teasing apart the complexity of gene flow at the wild-domestic interface will be valuable in elucidating the evolutionary role of hybridization. Due to the often-cosmopolitan presence of feral animals, there are usually multiple contact zones with undomesticated populations, providing the opportunity to study geographic variation in patterns of introgression across the genome. For example, different populations of the European wildcat (*Felis silvestris*) (Senn et al., 2019), wild greylag goose (*Anser anser*) (Heikkinen et al., 2020) and wild mallard (*Anas platyrhynchos*) (Söderquist et al., 2017) experience varying extents of gene flow with their domestic counterparts. Studies of such scenarios contribute to our understanding of the homogenizing effect of hybridization, which could in turn improve our understanding of diversification and the evolution of novel lineages (Taylor & Larson, 2019). Genomic regions of very low introgression may represent ‘barrier loci’ which are important in the development of reproductive isolation (Liu et al., 2020). Therefore, studying introgression in wild-domestic systems could also advance our understanding of the speciation process.

Characterization of undomesticated lineages informs our understanding of the processes of domestication and feralization, both important processes in an increasingly anthropogenic world (Gering et al., 2019). Feralization in particular is understudied, and cannot be seen as a reverse of domestication, given that it involves novel selective pressures and evolutionary trajectories. Studies of feral chickens in Kauai have shown that feralization and domestication target different genomic loci (Johnsson et al., 2016). Such an understanding will enhance our ability to comprehend the biology of economically and practically important domestic animals, as well as economically and ecologically important feral pests (Henriksen

et al., 2018). Furthermore, domestic animals are important model organisms in biomedical and zoological research (Bähr & Wolf, 2012). Characterization of the genetics, behaviour and physiology of undomesticated lineages would allow investigation of trait evolution and selection in a wild setting. This context will increase the relevance of conclusions drawn from experiments carried out using model organisms. For example, studies using domestic pigeons to understand collective behaviour (Sasaki & Biro, 2017) could benefit from parallel information in wild rock doves, allowing inferences about the evolution of the observed traits and their adaptive roles in a natural setting. Whilst it is important to recognize that extant undomesticated forms are not perfectly representative of the original ancestral populations (Bosse, 2019), such comparative studies of undomesticated, domestic and feral forms will allow us to identify traits of scientific, practical and economic interest in understudied wild populations.

Reservoir of genetic diversity

Many domestic animals, including our most economically important livestock species such as cattle and sheep, are genetically impoverished following many generations under artificial selection. Consequently, many livestock species could be considered to be 'genetically endangered' due to their low adaptive potential and concomitant vulnerability to developing climatic and disease threats (Taberlet et al., 2008). Undomesticated populations may act as reservoirs of genetic diversity and harbor useful traits that could be introduced into domestic stock. This has been well-recognized with respect to plants (Zhang et al., 2016). For example, a lack of genetic diversity in the apple (*Malus pumila*) and barley (*Hordeum vulgare*) gene pools led to suggestions that wild relatives could alleviate this threat (Dempewolf et al., 2017). Animal ancestors have similar utility in terms of harboring useful genetic diversity. For example, introgression of genes from wild sheep into domestic breeds

such as Soay sheep (*Ovis aries*) has been argued to have enhanced innate immunity (Barbato et al., 2017). Similarly, it is thought that introgression from (now-extinct) aurochs (*Bos primigenius*) conveyed parasite resistance to domestic cattle (Decker et al., 2014). The loss of distinct undomesticated lineages would mean a missed opportunity to introduce favorable traits into domestic stocks, though some ancestral genomic variation may be recoverable from older domestic lineages. For example, Highland cattle have been shown to have a greater genetic contribution from the ancestral aurochs than many extant breeds (Park et al., 2015). Nevertheless, the maintenance of genetically diverse populations of extant undomesticated lineages would be the optimal strategy to ensure that adaptive introgression remains an option for domestic animals.

Ecological function

The ecological repercussions of the loss of wild ancestors, and the extent to which hybrid or domestic forms could replace them, is an important topic of discussion. In the wildcat system, it has been proposed that hybrid cats of mixed domestic-wild ancestry could approximate the ecological role of 'true' wildcats in Scotland, as a predominantly solitary mesopredator of forested regions (Fredriksen, 2015). However, individuals of mixed ancestry may have an ecological role intermediate between their feral and wild forms. Feral domestic cats are known to be ecologically damaging due to predation of birds and small mammals (Trouwborst et al., 2020), whereas wildcats have more specific habitat and dietary requirements (Széles et al., 2018). Hence, it would be an undesirable outcome if hybrid individuals behave more like feral cats than wildcats. Where there is no other option, domestic animals have been used as ecological proxies for their extinct ancestors to apparent success in landscape-level conservation efforts. An example of this is the substitution of domestic cattle for extinct aurochs (Marris, 2011). It is likely that aurochs

played a broadly similar ecosystem engineering role, grazing and fertilizing grassland, though extent of overlap with the ecological functionality of domestic cattle is unknown. The degree to which individuals of mixed ancestry, or domesticates, are adequate ecological replacements for undomesticated forms will depend on the domestic animal involved and requires species-specific research. It would seem wise to adhere to the precautionary principle with respect to ecological function, without good evidence for the ecological utility of hybrid or domestic forms.

Outcomes of hybridization between domestic animals and their undomesticated forms

The outcomes of hybridization, whether homogenizing or diversifying, have attracted significant attention from conservationists. With respect to hybridization between domestic animals and their undomesticated forms, it is likely that spatially and temporally varying gene flow has occurred since domestication began (Lawal et al., 2020). To explore the varying impacts of wild-domestic hybridization, we outline two gene flow scenarios, which need not be mutually exclusive across the range of a species. In the first, the distinction between the lineages breaks down. In the second, the two lineages remain distinct despite transfer of genetic material. Both scenarios are of conservation relevance.

1) Extensive gene flow leading to the formation of a hybrid swarm

Extensive gene flow between undomesticated and domestic forms can lead to the formation of a 'hybrid swarm', as seen in Scotland's European wildcats (Senn et al., 2019). Hybrid swarms are populations where most or all individuals are of mixed-ancestry individuals (Beninde et al., 2018). As the undomesticated population is often less populous than its

domestic relative, the formation of hybrid swarms can lead to the eventual ‘extinction by hybridization’ of the former (Senn et al., 2019). This process can be defined as the genetic replacement of a distinct population or species with a relative following introgression. When it occurs ‘naturally’, without either human introductions of species or anthropogenic habitat alteration leading to range-shifts, this breakdown in the distinctiveness of different lineages has been referred to as ‘reverse speciation’ (Kearns et al., 2018). It is possible that extinction by hybridization is of particular interest to conservationists following population reductions driven by various demographic threats. For example, there is evidence that domestic cattle and horses hybridized with their respective undomesticated forms (now extinct, primarily due to habitat loss and overhunting), when those undomesticated forms were geographically restricted and demographically imperilled (Decker et al., 2014).

The process of extinction by hybridization can proceed in a geographically restricted manner, as appears to be the case for the polecat (*Mustela putorius*) (Croose et al., 2018) and wild boar (*Sus scrofa*) (Iacolina et al., 2018), and can also be common across the entire range of the undomesticated form, as is the case for the Atlantic salmon (*Salmo salar*) (Solberg et al., 2020) and red junglefowl (Thakur et al., 2018). For species in the latter category, which also includes the rock dove (Baldaccini, 2020) and wild water buffalo (*Bubalus arnee*) (Flamand et al., 2003), there is often uncertainty regarding the continued persistence of ‘pure’ undomesticated populations. Even in the absence of data on genomic-level introgression, the geographic arrangements of populations strongly suggest that introgression is occurring. For example, it is known that African wild ass (*Equus africanus*) populations are very small, fragmented, and in sympatry with domestic populations (Tesfai et al., 2019). In such situations, individuals making up the undomesticated populations may have more difficulty finding mating partners, becoming less choosy and increasing their likelihood of mating with a domestic individual (the ‘desperation hypothesis’) (Hubbs, 1955).

Such demographic imbalances and mate choice opportunities are also relevant for expanding undomesticated populations. In the Swiss Jura, European wildcats are undergoing a spatial demographic recovery following conservation efforts, and are at much lower density than feral cats at the expanding front. Here, wildcats are more likely to mate with their domestic counterparts, resulting in extensive introgression (Quilodrán et al., 2019). This highlights that any conservation efforts for undomesticated populations should give special attention to the potential for introgression from domestic relatives upon range expansion (Quilodrán et al., 2020), and should survey the extent to which introgression is geographically and temporally limited to the expansion front.

The evolutionary consequences of hybrid swarm formation can vary depending on the fitness of hybrid individuals in the local environment. In many situations, hybrids may be at a selective advantage. Such 'hybrid vigor' has been noted in non-domestic situations. For example, hybrid individuals of the medium tree finch (*Camarhynchus pauper*) and small tree finch (*C. pauper*) had fewer parasites in their nests compared to their parental species (Peters et al., 2019). This could accelerate hybrid swarm formation and the genetic replacement of the rarer parental lineage. Conversely, hybrid populations may also be maladapted compared to their parental lineages. Whilst this should limit introgression and therefore the formation of hybrid swarms, in many cases the population imbalance between undomesticated and domestic forms is so great that extensive introgression still occurs. For example, in Atlantic salmon (*Salmo salar*), domestic escapees often far outnumber undomesticated populations (Sylvester et al., 2019). Selection for increased growth rate (and perhaps relaxed selection in a captive context) in domestic populations has been hypothesized to have reduced their environmental sensitivity, rendering wild-domestic hybrids more prone to risk-taking behavior. This can cause increased predation of wild-

domestic hybrids in natural settings (Solberg et al., 2020). Such unwitting introduction of maladaptive traits may pose a risk, especially to small and disjunct wild populations.

2.) Low levels of introgression with maintenance of distinct lineages

The formation of hybrid swarms is not inevitable, and in many cases hybridization is limited spatially and temporally (Iacolina et al., 2018). In such situations, introgression can introduce traits of interest without complete admixture of the entire genome and a subsequent breakdown in the genomic distinctiveness of the two lineages involved. Multiple conditions could foster such a limitation. Firstly, if both populations are large enough, then heterospecific mating will be rare, especially if assortative mating occurs (Hubbs, 1955). Assortative mating could be reinforced when wild populations and those of domestic origin have different social systems. Wolves exhibit a level of social complexity and cooperation that is not seen in wildcats (Cordoni & Palagi, 2019). It is possible that feral dogs are therefore less able to interbreed with wolves than feral cats are with wildcats, and this may help to explain why the latter has been more prone to hybrid swarm formation. The risk of hybrid swarm formation may also be reduced when hybrids are less fit than parental lineages, and undomesticated population sizes are substantial. However, the production of less-fit hybrids is not always sufficient to maintain lineage distinction, especially when there are large disparities in population sizes (as in the salmon example above). Even when the overall level of hybridization is insufficient for formation of hybrid swarms and the genetic replacement of the undomesticated lineage, traits that have been introgressed into undomesticated populations can still be of evolutionary and conservation significance. For example, it has been hypothesized that genes providing immunological benefits to North American wolves were introduced via introgression from domestic dogs (Coulson et al.,

2011; Smith et al., 2020). This highlights the potential of hybridization with the domestic form to have some positive outcomes for undomesticated forms.

Challenges of Studying and Conserving the Ancestors of Domestic Animals

Quantifying mixed ancestry

All domestic animals examined have been in contact with their undomesticated forms to some extent since their initial divergence (Larson & Fuller, 2014). In this respect, they differ from examples of the process of extinction by hybridization not involving a domestic entity, such as the Lesser Antillian iguana (*Iguana delicatissima*), threatened by the green iguana (*Iguana iguana*) (Vuillaume et al., 2015). In such cases, prior to secondary contact, populations have often diverged in isolation (Schield et al., 2019). Reproductive barriers are therefore likely to be less permeable on average than at the wild-domestic interface. For the latter situation, this means that there is sometimes no useful baseline for non-introgressed ('pure') individuals, making it difficult to quantify the degree of mixed ancestry. This situation occurs for Scottish European wildcats, where introgression with domestic cats has been so extensive that a breakdown in the linkage disequilibrium between genes used in genetic hybrid indices developed by conservation biologists to estimate wildcat 'purity', and those coding for traits used in phenotypic hybrid indices (that mostly relate to pelage patterning), means there is no identifiable 'pure' wildcat to use as a baseline for hybrid identification (Senn et al., 2019). In this case, further debate identifying an acceptable cut-off level of introgression to be considered a 'wildcat' should be coupled with research efforts establishing how to maintain demographically viable and genetically diverse 'wild' populations, mediating wild-domestic hybridization where feasible. More generally, conservation aims must be coupled with strategies to manage both the undomesticated and

domestic populations, and must accept that some level of introgression is inevitable. This has relevance to legislative issues regarding whether individuals of hybrid ancestry receive protection or not. In many cases they do not, and this risks the loss of important ancestral variation, especially in situations where hybrid swarms predominate (Trouwborst, 2014).

Unbalanced population sizes and genetic diversity

In contrast to feral and semi-captive domestic animals, which can sustain superabundant and globally distributed populations due to their commensal relationships with humans, undomesticated lineages often suffer from habitat change and other demographic pressures acting in their natural environments, resulting in numerically small and geographically restricted populations. For example, the wild banteng (*Bos javanicus*) in Vietnam is the endangered wild ancestor of domesticated Bali cattle, existing in disjunct populations that have experienced significant declines in their geographic range following poaching, disease and habitat loss (Pedrono et al., 2009). Small populations often harbor less genetic diversity than large ones, limiting their evolutionary potential (Hoffmann et al., 2017). Conservation of undomesticated lineages in the face of such an imbalance in population size and low genetic diversity is challenging. Where logistically possible, demographic and genetic reinforcement of undomesticated populations could alleviate the risk of population imbalance. For instance, the banteng was introduced to Australia in 1849, and this non-native population could potentially be used for reintroduction projects back in its native range (Bradshaw et al., 2006). Such approaches must be informed by an appreciation of the factors affecting the populations of both the domestic and undomesticated lineages, including disease, persecution and habitat change. For example, reintroductions into regions where feral populations have not been removed would lead to massive introgression (Nussberger et al., 2018). Overall, a greater understanding of demography and genetic diversity via

comparative studies at different spatial scales should allow for a more holistic approach to conservation of undomesticated lineages.

Ancient feral populations

Feral populations of some previously domesticated animals, for example the Australian dingo (*Canis familiaris*) and New Guinea singing dog (*Canis familiaris*), have existed for thousands of years (Zhang et al., 2020). These forms are often far less dependent on close association with humans than other feral animals, and we term them ‘ancient feral’ populations. Their existence can make it difficult to identify ‘true’ undomesticated populations because older feral populations are often phenotypically convergent with their ancestors (Johnston, 1992). Although we have long been aware that canid lineages mentioned above are of domestic origin, other cases have only recently been revealed or are contentious. For example, it is likely that European mouflon (*Ovis aries musimon*) descended from early domestic sheep (Barbato et al., 2017). Przewalski’s horse (*Equus ferus przewalskii*), long thought to be the last undomesticated horse, was identified as an ancient feral population using genomic approaches (Gaunitz et al., 2018), but a recent zooarchaeological study disputed this conclusion on the basis of osteological traits (Taylor & Barrón-Ortiz, 2021). Using ancient DNA could further elucidate the origins of such populations, and indeed it is probable that no wild-living populations of any domesticated species are fully representative of the original undomesticated populations. In many examples, the ancient ferals are among the earliest diverging extant groups in their species’ phylogenies (Stephens et al., 2015). Hence, we argue that from a conservation perspective, the existence of ancient feral populations is best viewed as an opportunity for conservation biologists studying the ancestors of domestic animals, in that they may represent among the closest extant analogues to the ancestor in situations where undomesticated forms have become extinct.

More genomic research is needed to quantify the extent to which they harbour ancestral genetic variation originating from undomesticated populations, that has been lost in contemporary domestic populations. This could involve identifying 'ghost' introgression, where admixture is detected from a now-extinct species or population (Ottenburghs, 2020).

Conclusion

Extinction by hybridization of the undomesticated forms of domestic animals poses unique conservation challenges. Recent divergence, population imbalances and longstanding contact make undomesticated forms vulnerable to extinction by hybridization. The complex spatial and temporal variation in the level of introgression within and between wild-domestic systems can make it difficult to resolve their status. Despite these challenges, we argue that the importance of undomesticated forms, socio-economically and via the contribution they can make to science, cannot be overstated. Preventing their extinction will provide the opportunity for a greater understanding of processes such as extinction by hybridization, adaptation, domestication and feralization. This research will also provide valuable context allowing for a better understanding of some of our most important model organisms, and enhancing our ability to protect valuable sources of genetic diversity that could be introduced to domestic populations. Although there are many outstanding questions to be addressed, a priority should be to compare the genetics and behaviour of undomesticated, ancient feral, contemporary feral, domestic and hybrid forms. This variation underpins the evolutionary, scientific, socioeconomic and practical opportunities that these animals provide, allowing us to identify valuable traits and design efficient conservation strategies.

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Supporting Information

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Table 1. Examples of domestic animals and their IUCN status in an undomesticated form.

<u>Domestic form</u>	<u>Undomesticated form</u>	<u>Contemporary feral status</u>	<u>Conservation status of the undomesticated form</u>	<u>References</u>
Animals primarily used as companions				
Dog <i>Canis familiaris</i>	An extinct population of wolves	Globally distributed and abundant. There are two ancient feral populations of note (the dingo and the New Guinea singing dog).	Generally accepted to be an extinct population of wolves. Domestic hybridization does however locally threaten extant populations of the grey wolf, which is widely distributed across Eurasia and North America and has seen recoveries in its range in some regions (e.g. in Europe) in recent years.	(Bergström et al., 2020; Freedman et al., 2014; Perri et al., 2021)
Cat <i>Felis catus</i>	Wildcat <i>Felis lybica</i> (<i>Felis silvestris</i> is the sister species)	Globally distributed and abundant.	Least Concern, and widely distributed across Afro-Eurasia. Threatened with extinction by hybridization with feral and domestic cats. Many wildcat populations, particularly in Europe, have now experienced extensive introgression, and some (e.g. in Scotland) have become extinct as a separate phylogenetic entity and replaced by hybrids and feral cats.	(Beugin et al., 2020; Quilodrán et al., 2019; Senn et al., 2019)
Animals primarily used as a food source (including those originally domesticated for food but now mostly kept for recreation)				
Cattle <i>Bos taurus</i>	Aurochs <i>Bos primigenius</i>	Globally distributed and abundant.	Extinct. Originally present across Asia, Europe and North Africa.	(Decker et al., 2014; Mona et al., 2010; Upadhyay et al., 2017)
Sheep <i>Ovis aries</i>	Mouflon <i>Ovis gmelini</i>	Globally distributed and abundant. A famous example is the Soay sheep on St Kilda, Scotland, used by biologists to study evolution. European mouflon represent a feral population of early domestic sheep.	Near Threatened and distributed in the Near East and Middle East. The most significant conservation issue is poaching. No genomic studies have yet assessed global variation in the extent of domestic introgression in the various wild populations.	(Barbato et al., 2017; Bleyhl et al., 2019; Ciani et al., 2020; Eydivandi et al., 2020)
Goat <i>Capra aegagrus</i> or <i>Capra hircus</i>	Probably the bezoar ibex <i>Capra aegagrus</i>	Globally distributed and abundant.	Near Threatened and distributed from the Near East to south Asia. Threatened by habitat change, hunting and competition with livestock. No genomic studies have yet assessed global variation in the extent of domestic introgression in the various	(Alberto et al., 2018; Dong et al., 2015; Kuemmerle et al., 2020)

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Water buffalo <i>Bubalus bubalis</i>	Wild water buffalo <i>Bubalus arnee</i>	Regionally common in southeast Asia and Oceania, including Australia. Also present elsewhere including South America.	wild populations. Endangered. Now very restricted in range and almost completely found in India. Threatened by habitat change, competition and disease transmission from domestic livestock, hunting and domestic introgression.	(Flamand et al., 2003; Kierstein et al., 2004; Zhang et al., 2020)
Bali cattle <i>Bos javanicus</i>	Banteng <i>Bos javanicus</i>	Locally common within the region where the domestic form is kept.	Endangered. Native to southeast Asia. Threatened by poaching, habitat change and disease transmission from domestic livestock. Also experiences hybridization with domestic bovids. An introduced population in Australia is potentially of conservation significance, being more isolated from these risks.	(Corey et al., 2006)
Gayal <i>Bos frontalis</i>	Gaur <i>Bos gaurus</i>	Relatively rare and limited to the regions in which gayal are commonly kept.	Vulnerable. Native to Southeast Asia and south Asia. Threatened by habitat loss and poaching. There is little data regarding hybridization between gaur and domestic bovids.	(Choudhury, 2002; Nguyen et al., 2007)
Pig <i>Sus scrofa</i>	Wild boar <i>Sus scrofa</i>	Globally distributed and abundant.	Least Concern. Widely distributed throughout Afro-Eurasia. Experiencing gene flow from feral domestic pigs.	(Giuffra et al., 2000; Iacolina et al., 2018)
Chicken <i>Gallus gallus</i>	Red junglefowl <i>Gallus gallus</i>	Globally distributed and abundant. Common in the United States, but also elsewhere including throughout the range of the ancestral junglefowl.	Least Concern. Widely distributed throughout Southeast Asia and South Asia. Threatened with extinction by hybridization with feral and domestic chickens. Most populations have now experienced extensive introgression.	(Lawal et al., 2020; Thakur et al., 2018; Wu et al., 2020)
Domestic pigeon <i>Columba livia</i>	Rock dove <i>Columba livia</i>	Cosmopolitan distribution (in suitable habitats globally) and superabundant.	Least Concern. Originally present across Afro-Eurasia in suitable habitat. Threatened with extinction by hybridization with feral and domestic pigeons. Appears to be restricted to relict populations in more remote regions, and most of these populations have now experienced extensive introgression. It is unclear if any population exist that haven't been extensively influenced by gene flow from domestic pigeons.	(Johnston et al., 1988; Johnston & Janiga, 1995)
Domestic goose <i>Anser anser</i>	Greylag goose <i>Anser anser</i>	Globally distributed and abundant, including within the native range of the Greylag Goose.	Least Concern. Distributed across Eurasia. Very widespread and abundant. Evidence of bidirectional gene flow with the domestic goose.	(Heikkinen et al., 2020)
Guinea pig <i>Cavia porcellus</i>	Montane guinea pig <i>Cavia tshcudii</i>	Little evidence of substantial self-sustaining feral populations.	Least Concern. Native to the Andes. IUCN considers there to be no major threats to the species.	(Lord et al., 2020)
'Domestic' Atlantic salmon	Atlantic salmon <i>Salmo salar</i>	Substantial escaped populations from fish farms.	Least Concern. Native to the North Atlantic. Widespread domestic introgression in existing wild populations leading to negative demographic impacts.	(Glover et al., 2020; McGinnity et al., 2003; Solberg et al.,

Western honey bee <i>Apis mellifera</i>	Wild honey bee <i>Apis mellifera</i>	Feral colonies can occur and indeed are the dominant form of the species in the wild in many regions.	Populations lacking domestic influence are now rare.	2020)
Animals primarily used for practical utility				
Horse <i>Equus ferus</i>	Possibly the tarpan <i>Equus ferus</i>	Globally distributed and abundant. Famous examples are the mustangs of the Western United States, and semi-feral 'mountain and moorland' breeds of pony in the British Isles. There is also a potential ancient feral population (Przewalski's horse, see discussion).	Extinct, or represented by Przewalski's horse which is restricted to the steppes of Central Asia (see discussion).	(Gaunitz et al., 2018; Kavar & Dovč, 2008; Librado et al., 2016)
Donkey <i>Equus africanus</i>	African wild ass <i>Equus africanus</i>	Globally distributed and abundant. Famous examples are the burros of North America and the albinistic Asinara donkeys of Sardinia.	Critically Endangered, and currently found on the Horn of Africa. Threatened by hunting, habitat change and competition with domestic livestock. Some putative subspecies such as the Atlas wild ass are now extinct. The extent of domestic introgression in surviving populations is unclear.	(Tesfai et al., 2019; Utzeri et al., 2016)
Domestic yak <i>Bos grunniens</i>	Wild yak <i>Bos mutus</i>	Relatively rare and almost completely limited to the regions in which domestic yaks are commonly kept, although domestic yaks are often kept in a manner allowing contact with wild yaks.	Vulnerable, and found in the Himalayas. Threatened by poaching. Some evidence of interbreeding with domestic yaks suggests introgression may be an issue.	(Chen et al., 2018; Wang et al., 2016)
Domestic Bactrian camel <i>Camelus bactrianus</i>	Direct ancestor is extinct, but a closely related species (the wild Bactrian camel <i>Camelus ferus</i>) exists	Relatively rare. There were once populations of feral domestic Bactrian camels in the deserts of the United States.	Critically Endangered and restricted to the steppes of Central Asia. Threatened by poaching and genetic introgression from domestic Bactrian camels.	(Fitak et al., 2020; Kaczensky et al., 2014)
Dromedary <i>Camelus dromedarius</i>	Ancestral dromedary	Patchy global distribution. Notably there is a significant population in Australia.	Extinct.	(Almathen et al., 2016; Orlando, 2016)
Llama <i>Lama glama</i>	Guanaco <i>Lama guanicoe</i>	Rare and localized.	Least Concern, and common in southern South America. Abundant, with an introduced population in the Falkland Islands. Unclear to what extent hybridization with llamas occurs.	(Bustamante et al., 2002; González et al., 2014)
Alpaca <i>Vicugna pacos</i>	Vicuña <i>Vicugna vicugna</i>	Rare and localized.	Least Concern, and common in the central Andes. Abundant, although some subpopulations are at risk from poaching and habitat loss. Unclear to what extent	(Marín et al., 2007; Wakild, 2020)

Domestic ferret <i>Mustela putorius</i>	European polecat <i>Mustela putorius</i>	Patchy global distribution. Often occurs on islands, including New Zealand and Guernsey.	Least Concern. Widely distributed throughout western Eurasia. Locally and regionally threatened by persecution and also domestic introgression from feral ferrets.	(Croose et al., 2018)
Domestic silk moth <i>Bombyx mori</i>	Wild silk moth <i>Bombyx mandarina</i>	Survival of domestic silk moths outside of captivity is apparently poor.	Not assessed by IUCN. Occurs over a wide range in Asia. Extent of domestic introgression to the wild moth is unclear, although the two forms are known to be able to hybridize.	(Sun et al., 2012; Xiang et al., 2018)

Figure 1. The undomesticated (and ancient feral) forms of domestic animals are globally distributed.

The undomesticated forms of domestic animals include the (a) vicuña (*Vicugna vicugna*) (Thomas Quine, [CC BY 2.0](#)), (b) Atlantic salmon (*Salmo salar*) (Greg Thompson/USFWS, Public domain), (c) rock dove (*Columba livia*) (Mike Pennington, [CC BY-SA 2.0](#)), (d) wildcat (*Felis silvestris*) (Peter Trimming, [CC BY 2.0](#)), (e) African wild ass (*Equus africanus*) (Greg Goebel, [CC BY 2.0](#)), (f) red junglefowl (*Gallus gallus*) (Francesco Veronesi, [CC BY-SA 2.0](#)), (g) gaur (*Bos gaurus*) (Mahbob Yusof, [CC BY 2.0](#)) and (h) banteng (*Bos javanicus*) (Rochmad Setyadi, [CC BY-SA 2.0](#)). These examples have extant populations, many of which are of conservation concern. Some lineages such as (i) aurochs (*Bos primigenius*) (Charles Hamilton Smith, Public domain) and (j) tarpan (*Equus ferus ferus*) (Public domain) are globally extinct. In addition, there are ancient feral populations such as the (k) European mouflon (*Ovis aries*) (Andrea Schieber, [CC BY-NC-ND 2.0](#)), (l) dingo (*Canis familiaris*) (Jarrod Amore, [CC BY 2.0](#)) and (m) New Guinea singing dog (*Canis familiaris*) (Patti McNeal, [CC BY 2.0](#)). Note that the undomesticated or ancient feral status of (n) Przewalski's horse (*Equus ferus przewalski*) (Lawrence Schaefer, [CC BY 2.0](#)) is disputed. Photographs are credited to the photographers in parentheses.

