



Prospects for rewilding with camelids



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ABSTRACT

The wild camelids wild Bactrian camel (*Camelus ferus*), guanaco (*Lama guanicoe*), and vicuña (*Vicugna vicugna*) as well as their domestic relatives llama (*Lama glama*), alpaca (*Vicugna pacos*), dromedary (*Camelus dromedarius*) and domestic Bactrian camel (*Camelus bactrianus*) may be good candidates for rewilding, either as proxy species for extinct camelids or other herbivores, or as reintroductions to their former ranges. Camels were among the first species recommended for Pleistocene rewilding. Camelids have been abundant and widely distributed since the mid-Cenozoic and were among the first species recommended for Pleistocene rewilding. They show a range of adaptations to dry and marginal habitats, and have been found in deserts, grasslands and savannas throughout paleohistory. Camelids have also developed close relationships with pastoralist and farming cultures wherever they occur. We review the evolutionary and paleoecological history of extinct and extant camelids, and then discuss their potential ecological roles within rewilding projects for deserts, grasslands and savannas. The functional ecosystem ecology of camelids has not been well researched, and we highlight functions that camelids are likely to have, but which require further study. We also discuss alternative rewilding-inspired land-use models given the close relationships between humans and some camelid species.

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1. Introduction

Camelids were among the first species recommended for Pleistocene rewilding in North America (Donlan et al., 2005, 2006). Trophic rewilding is an emerging conservation paradigm that has recently been defined as “species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems” (Svenning et al., 2015; see also Naundrup and Svenning, 2015; Sandom et al., 2012; Donlan et al., 2005). In many cases such (re-)introductions are associated with passive conservation management, an emphasis on large protected areas, and a cultural mythology of wilderness (Lorimer et al., 2015). Here, we examine how camelids could be used in both proxy and non-proxy trophic rewilding.

There are currently three wild camelid species and four domestic ones. Of the wild species, vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe* can be found in the Andes and southern cone of South America. Both vicuñas and guanacos are listed as Least Concern by the IUCN Red List (accessed 2015). Vicuñas is

protected by vicuñas Convention in Peru, Bolivia, Chile and Argentina. Both species are listed in CITES and are subject to conservation protections in Chile, Argentina, Peru (where guanacos is considered Endangered) and Bolivia (where guanacos is considered Critically Endangered) (IUCN Red List accessed 2015; Iriarte, 2000; Nugent et al., 2006; Grimberg Pardo, 2010). After many decades of poaching vicuña conservation can be considered a success story (Arzamendia et al., 2006; Bonacic et al., 2002). *Camelus ferus*, the wild Bactrian camel, by contrast is listed as Critically Endangered (IUCN Red List accessed 2015) due to its small and declining population, estimated at around 350–500 in 1997 (Hare, 1997), 1000 in 1999 (Reading et al., 1999) and 950 in 2004 (IUCN Red List accessed 2015). *Camelus ferus* is found in the Gobi desert in China and Mongolia (Kaczensky et al., 2013). The four domestic species, llamas *Lama glama*, alpacas *Vicugna pacos*, dromedaries *Camelus dromedarius* and Bactrian camels *Camelus bactrianus*, as a group can be found on every continent except Antarctica, with a large feral population of dromedary in Australia. The ancestral wild form of dromedary is extinct (Churcher et al., 1999; Lövei, 2007), whereas the probable ancestors of the other three are extant.

All extant camelids share adaptations to marginal habitats. The cameline (subfamily Camelinae: *Camelus* spp.) species are notably adapted to arid desert conditions: they can survive for many days

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without access to water by maintaining hyperglycaemia, allowing for a very low metabolic rate, maintaining a high level of salt in their blood by eating salty plants and drinking brackish water, and raising their body temperature (Soliman, 2015; Wu et al., 2015). They also have morphological adaptations for preventing damage from dust, for walking on sand, for cooling the brain, and for extracting a maximum amount of water from ingested food (Soliman, 2015). Domestic camels predominantly browse woody, including spiny, plants, but it must be noted that they also graze (Sato, 1980; Migongo-Bake and Hansen, 1987). Both cameline and lamine (subfamily Lamelinae: *Lama* and *Vicugna* spp.) species are both grazers and browsers, and have lower metabolic rates than other large grazers and browsers, an adaptation that can be advantageous in arid and semi-arid environments with sparse and low quality forage (Dittmann et al., 2014). Vicuña specialize in high altitudes and predominantly graze (Lucherini, 1996; Wursten et al., 2014). Guanacos by contrast are able to survive in isolated populations in marginal and stressful habitats due to generalist feeding strategies (browsing and grazing), flexible social structure and timing of birth to coincide with rainfall (González et al., 2014; Belardi and Rindel, 2008; Wursten et al., 2014).

Rewilding is most likely to be successful when large fauna can be reintroduced onto large, continuous tracts of land with low likelihood of human-wildlife conflict (Navarro and Pereira, 2012), although it can also be applied to densely populated landscapes (Jepson, 2015). Such wild, abandoned or marginal lands in the Americas, Eurasia and North Africa, East Africa and the Sahel are, in general, likely to have once had at least one camelid species sometime between the Miocene and the present. Australian drylands, although not native habitat for camelids (since they evolved in what became North America after the split between Laurasia and Gondwana), have lost most of their marsupial large herbivores, and thus could be assessed for proxy rewilding (cf. Bowman, 2012). Although the Pleistocene occurrence patterns is usually taken as the earliest reasonable baseline for rewilding, we emphasize that camelids are generalists and their pre-Quaternary as well as Pleistocene and Holocene niches might point to ways in which they can serve as proxy (or ecological analogue) species. The biota in different regions are a product of evolution over millions of years, and shaped by biotic interactions across these time frames and not just between extant species, with large mammal species most having had large continental-to hemisphere-scale range dynamics. Hence, there is no strong biological reason to focus solely on extant species that have occurred in the focal region within the last few hundreds years.

1.1. Camelids from the Miocene to the Holocene

Camelids emerged in the Oligocene (around 34–23 Ma) in North America, with three main branches including the *Poebrotherium*, *Stenomylus* and *Pseudorabis* (McKenna, 1966). They were small, such as *Stenomylus hitchcocki* at just 30 kg around 30 Ma (Mendoza et al., 2006), but later during the Miocene, Pliocene and Pleistocene the camelids radiated into large forms, even megaherbivores (≥ 1000 kg, Owen-Smith, 1988), such as *Gigantocamelus* spp. During the Miocene camelids such as *Gigantocamelus spatulus*, *Megatylopus* spp., *Megacamelus merriami*, *Camelops* spp., *Aepycamelus* spp., *Procamelus* spp., *Paramiolabis* spp., *Protolabis* spp., *Miolabis* spp., *Michenia* spp., *Hemiauchenia* spp., and *Pliauchenia* spp., coexisted with a high diversity of other browsers and grazers, such as rhinoceros, proboscideans, horses, and numerous genera of ruminants, in the savanna woodlands of North America (Janis et al., 2004). These camelids were predominantly browsers and mixed browsers (Dompierre and Churcher, 1996; Feranec, 2003; Semperebón and Rivals, 2010; Kita et al., 2014).

North America had already broken away from Gondwana as part of Laurasia around 175 Ma. Gondwana then broke into South America, Antarctica, and Australia (184–40 Ma). A number of land-bridges sporadically connected Eurasia and North America, all before the emergence of camelids (Brikatis, 2014). This accounts for the lack of early camelids outside North America. Continental drift then allowed this large diversity of camelids to spread beyond North America. However, the formation of the Isthmus of Panama allowed the Great American Biotic Interchange of species, peaking around 3 Ma, towards the end of the Pliocene (Bacon et al., 2015). Among the species from North America that extended their ranges into South America were camelids. The camelids that were present or evolved in South America by the Pleistocene include *Hemiauchenia* spp., and the lamine camelids, *Paleolama* spp., *Lama* spp., *Provicugna* spp. and *Vicugna* spp., which coexisted throughout South America with large grazers and browsers such as the locally evolved toxodonts, *Macrauchenia*, capybaras, and giant sloths as well as other immigrant herbivores such as gomphotheres, horses, deer, tapirs, and peccaries (MacFadden and Shockey, 1997; Hubbe et al., 2013). *Paleolama*, for example, was a browser of the Brazilian tropical dry forests, which are likely to have been much more extensive during the Pleistocene (Pennington et al., 2000), and further south inhabited more open habitats (de Melo França et al., 2015). Other lamine species were primarily grazers (MacFadden and Shockey, 1997). While the rise of the Andes had contributed to increased aridity on the west coast of South America around 14 Ma (Le Roux, 2012), cooling and/or increased aridity are associated with the Ice Age (beginning 10.5–7 Ma) in South America (Pennington et al., 2000). These conditions would have favored camelids.

Meanwhile, a land bridge formed across the Bering Strait linking Eurasia to North America in the late Miocene, allowing faunal interchange throughout the late Miocene until its opening around 5.5 Ma (Rybczynski et al., 2013). The Camelini tribe diverged from the Lamini camelids earlier, around 17 Ma (cited in Rybczynski et al., 2013), 8 Ma (cited in Cui et al., 2007) or 25 Ma (Cui et al., 2007). Notably, dromedaries and guanacos are able to form hybrids despite what is referred to as 11 Ma of reproductive isolation by Skidmore et al. (1999). Either a so-called High Arctic giant camel (*Paracamelus* spp.) and/or *Camelops hesternus* are thought to be the ancestor of Eurasian camels (Zazula et al., 2011; Rybczynski et al., 2013). *Paracamelus* has been found in Spain and China by 6 Ma (late Miocene) and in Eastern Europe, the Levant and North Africa between the late Miocene and early Pliocene (Payne and Garrard, 1983; Titov and Logvynenko, 2006; Gautier et al., 2012; Rybczynski et al., 2013). Geraads (2014) suggests that dromedaries and Bactrian camels are more closely related to one other than to either *Camelus thomasi*, *Camelus grattardi*, or any other African Pliocene and Pleistocene camelid species, based on archaeological morphological evidence. Further, confusing the evidence, the split between the Bactrian and dromedary species is dated at around 8 Ma, apparently while still in North America, by Cui et al. (2007) based on mtDNA analysis. According to population size estimates by Wu et al. (2015), Bactrian camels are present from the end of the Miocene and dromedaries since the end of the Pliocene. On the whole, the evolution and paleoecology of the Eurasian camelines has been studied far less than that of the South American lamines, and appears to be somewhat unresolved.

The modern camelid species are many fewer than their ancestors (Fig. 1). Humans crossed the Bering Strait land bridge from Asia, and have been implicated in the late Late Pleistocene/early Holocene megafaunal extinctions in the Americas (Sandorn et al., 2014). However, evidence that they hunted camelid species in North and South America more than sporadically is lacking (Frison et al., 1978; Haynes and Stanford, 1984; Frison, 1998; Prado et al., 2015; Waters

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