AARHUS UNIVERSITY

Coversheet

This is the accepted manuscript (post-print version) of the article.

Contentwise, the accepted manuscript version is identical to the final published version, but there may be differences in typography and layout.

How to cite this publication

Please cite the final published version:

Root-Bernstein, Meredith and Svenning, Jens-Christian. 2016. "Prospects for rewilding with camelids", *Journal of Arid Environments*, vol. 130, pp. 54-61, <https://doi.org/10.1016/j.jaridenv.2016.03.011>

Publication metadata

Title:	Prospects for rewilding with camelids
Author(s):	Root-Bernstein, Meredith and Svenning, Jens-Christian
Journal:	<i>Journal of Arid Environments</i>
DOI/Link:	https://doi.org/10.1016/j.jaridenv.2016.03.011
Document version:	Accepted manuscript (post-print)

© 2016. This manuscript version is made available under the CC-BY-NC-ND 4.0 license

<http://creativecommons.org/licenses/by-nc-nd/4.0/>

General Rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognize and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

If the document is published under a Creative Commons license, this applies instead of the general rights.

1 Prospects for rewilding with camelids

2 Meredith Root-Bernstein^{1,2}, Jens-Christian Svenning¹

3 1. Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus

4 University, Aarhus, Denmark

5 2. Institute for Ecology and Biodiversity, Santiago, Chile

6 keywords: Camelids, camel, guanaco, llama, rewilding, vicuña

7

8 Abstract

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

24

25

26 Introduction

27

28 Camelids were among the first species recommended for Pleistocene rewilding in
29 North America (Donlan et al. 2005; 2006). Rewilding is an emerging conservation
30 paradigm without a single definition, but most authors highlight that it aims to
31 reintroduce species or their functional proxies in order to restore lost ecological
32 processes (Naundrup & Svenning 2015; Sandom *et al.* 2012; Donlan *et al.* 2005). In
33 many cases such (re-)introductions are associated with passive conservation
34 management, an emphasis on large protected areas, and a cultural mythology of
35 wilderness (REF). Camelids are attractive candidates for rewilding because both
36 extant species and their extinct relatives used to be much more widespread and
37 abundant, suggesting that many current ecosystems around the world may lack
38 camelid ecological functions. They are adapted to marginal habitats where rewilding
39 could be carried out with relatively minor socio-economic and human-wildlife
40 conflicts, and are rarely perceived to be inherently dangerous animals. Finally, while
41 wild camelid species require active conservation efforts to ensure their futures, there
42 is no shortage of proxy species in the form of the four domestic species. Thus, both
43 proxy and non-proxy rewilding proposals may be considered.

44 There are currently three wild camelid species and four domestic ones. Of the
45 wild species, the vicuña *Vicugna vicugna* and the guanaco *Lama guanicoe* can be
46 found in the Andes and southern cone of South America. Both the vicuña and the
47 guanaco are listed as Least Concern by the IUCN Red List (accessed 2015). The
48 vicuña is protected by the Vicuña Convention in Peru, Bolivia, Chile and Argentina.
49 Both species are listed in CITES and are subject to conservation protections in Chile ,
50 Argentina, Peru (where the guanaco is considered Endangered) and Bolivia (where

51 the guanaco is considered Critically Endangered) (IUCN Red List accessed 2015;
52 Iriarte 2000; Nugent et al. 2006; Grimberg Pardo 2010) After many decades of
53 poaching vicuña conservation can be considered a success story (Arzamendia et al.
54 2006; Bonacic et al. 2002). *Camelus ferus*, the wild Bactrian camel, by contrast is
55 listed as Critically Endangered (IUCN Red List accessed 2015) due to its small and
56 declining population, estimated at around 350-500 in 1997 (Hare 1997), 1000 in 1999
57 (Reading et al. 1999) and 950 in 2004 (IUCN Red List accessed 2015). *Camelus*
58 *ferus* is found in the Gobi desert in China and Mongolia (Kaczensky et al. 2013). The
59 four domestic species, the llama *Lama glama*, the alpaca *Vicugna pacos*, the
60 dromedary *Camelus dromedarius* and the Bactrian camel *Camelus bactrianus*, as a
61 group can be found on every continent except Antarctica, with a large feral population
62 of dromedary in Australia. The ancestral wild form of the dromedary is extinct
63 (Churcher et al 1999; Lovei 2007), whereas the probable ancestors of the other three
64 are extant.

65 All extant camelids share adaptations to marginal habitats. The cameline
66 (subfamily Camelinae: *Camelus* spp.) species are notably adapted to arid desert
67 conditions: they can survive for many days without access to water by maintaining
68 hyperglycaemia, allowing for a very low metabolic rate, maintaining a high level of
69 salt in their blood by eating salty plants and drinking brackish water, and raising their
70 body temperature (Soliman 2015; Wu et al. 2015). They also have morphological
71 adaptations for preventing damage from dust, for walking on sand, for cooling the
72 brain, and for extracting a maximum amount of water from ingested food (Soliman
73 2015). Domestic camels predominantly browse woody, including spiny, plants, but
74 also graze (Sato 1980; Migongo-Bake & Hansen 1987). Both cameline and lamine
75 (subfamily Lamelinae: *Lama* and *Vicugna* spp.) species 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; Wurstten 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 & Rindel 2008; Wurstten 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 & Pereira 2012), although it can also be applied to densely populated landscapes (REF). 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.

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 *Pseudolabis* (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 & Churcher 1996; Feranec 2003; Semprebon & Rivals 2010; Kita et al. 2014).

Continental drift allowed this large diversity of camelids to spread beyond North America. 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). This accounts for the lack of early camelids outside 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 & 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 Franca et al. 2015). Other lamine species were primarily grazers (MacFadden & 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 (which ends around 5.3 Ma). 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, the dromedary and the guanaco 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 & Garrard 1983; Titov & 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), the Bactrian camel is present from the end of the Miocene and the dromedary 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 (Figure 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 (Sandom 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 & Stanford 1984; Frison 1998; Prado et al. 2015; Waters et al. 2015). This may be because camelids require water less than other large herbivores, and are thus found more often in marginal habitats and less often at waterholes where they may be surrounded by hunters (Frison et al. 1978). However, a more likely explanation is that the absence of evidence of extensive human hunting of camelids is due to taphonomic bias (Surovell & Grund 2012). During this period, North American camelids were mainly mixed browsers and grazers (Kohn et al. 2005; Semprebon & Rivals 2010). At the Pleistocene-Holocene transition in the Pampas, guanaco and

Paleolama spp. coexisted with *Macrauchenia*, horses, *Toxodon*, and a range of ground sloths such as *Megatherium*, *Eutatus*, and *Glossotherium* as well as large armadillos and their glyptodont relatives, e.g., *Glyptodon*, as well as various deer and rhea, and there is evidence that both horses and guanaco were hunted by humans (Borrero et al. 1998). With the onset of a more humid environment in the Pampas around 10,500 ya, the responses of humans are unclear, but their low population has been hypothesized to have impeded overhunting of camelids (Borrero et al. 1998). One hypothesis for the megafaunal extinctions in the Pampas is that increased cooling 14,000 ya followed by warming at the beginning of Holocene may have favored generalists, including the surviving guanaco and vicuña (Prado et al. 2015). One unsatisfactory thing about such local explanations is that they ignore that the megafaunal extinction constitute a global-scale event that is unique for the Cenozoic in its size-selective nature. In addition, humans are the only novel feature in the environment differentiating that climate change from previous ones, and must have played a major role in extinction despite lack of direct evidence for extensive hunting (Surovell & Grund 2012; Sandom et al. 2014). Further, other species that went extinct throughout South America were as generalist as the surviving camelids, demonstrating that generalist diets alone do not convey extinction survivalship (Dantas et al. 2013; Franca et al. 2015). *Vicugna vicugna* is proposed to be a surviving subpopulation of *Lama gracilis* (Weinstock et al. 2009). In any case, all camelid species in North America went extinct by the Holocene, leaving only the currently extant camelines and lamines in Eurasia and South America, respectively.

As in all pastoralist systems, human hunting of camelids is thought to have evolved into domestication and a pastoralist system, often involving transhumance to track environmental variability along altitudinal and other gradients (Alvard &

Kuznar 2001; FAO 2001). The process of domestication has been studied extensively in South America and almost entirely ignored in Eurasia. In the Andes and Pampas, wild guanacos and vicuñas were hunted or exploited for their fiber (wool) continuously alongside the domestication of several species or breeds in addition to the alpaca and llama (Gasco & Marsh 2013; Belardi & Rindel 2008; Westreicher et al. 2007; Jackson S. et al. 2005; Yacobaccio 2004; Lynch 1983). Camelids were the only domestic large herbivore species of South America. Andean cultures relied in multiple ways on llama breeds, collecting their feces to fertilize staple potato crops, using their fiber for cloth and rope, and transporting trade goods across empires on their backs (Lynch 1983). Interestingly, unlike in Eurasia and Africa, in South American cultures the milk of camelids has apparently never been a food resource. With the arrival of European colonists and their livestock, several varieties of domestic camelid went extinct, including for example the chilihueque, a somewhat mysterious domestic guanaco or llama breed from central Chile (Miller 1980). Overhunting of guanaco starting in the colonial period led to the disappearance of the guanaco from parts of its range, including the heavily colonized central zone of Chile (Miller 1980, Westreicher et al. 2007).

In Eurasia, domestic camel pastoralist cultures are found continuously from Mongolia to the Sahel. The wild Bactrian camel (*Camelus ferus*) may be the ancestor of the domestic Bactrian camel, which is found in northern Asia (Tulgat & Schaler 1992; Potts 2004) or a congener (Ji et al. 2009). Bactrian camels are thought to have been domesticated in China, Mongolia or Kazakhstan, and subsequently introduced into Iran and Turkmenistan (Peters & von den Driesch 1997). Bactrian camels provide essential resources to nomadic pastoralists, including feces collected for use as fuel, hair for rope and cloth, milk, and transport, although sheep, goats, horses and

cattle have increasingly been adopted since the 1800s (Chuluunbat et al. 2014; Berger et al. 2013; Peters & von den Driesch 1997; Krader 1955). Throughout Central Asia and the Near East since antiquity, Bactrian and dromedaries have been crossed, yielding a fertile and hardy hybrid that was highly valued in the region (Potts 2004). However, it was not allowed to breed as the offspring were aggressive. Observing “camel wrestling” contests between hybrid males is a traditional social activity that continues in Turkey (Çakırlar & Berthon 2014). Camel racing is additionally an important traditional sport both with Bactrian camels in Central Asia and dromedaries, in the Gulf States.

The dromedary appears to have been domesticated around 5000 ya in central Arabia from *Camelus thomasi* (Grigson et al. 1989; Spassov & Stoytchev 2004; but see Gautier 1966). *Camelus thomasi* occurred in northern Africa, and perhaps the Levant, into the Holocene (Grigson 1983; Chercher et al 1999). Its extinction is attributed to the increasingly arid conditions of the Sahara after a moist period ended around 4000-5000 ya; some large animals survived in the Maghreb, but *Camelus thomasi*, along with the Atlantic gazelle and North African buffalo, disappeared (Lovei 2007). However, it is more likely to have been incorporated into domestic herds or exterminated to prevent competition with dromedaries than to have gone extinct due to climate change alone. Subsequently dromedaries became integral parts of pastoralist cultures throughout arid and semi-arid parts of northern Africa, the Levant and India (Raziq et al. 2011; Farah et al. 2004; Mehta et al. 2007; Raziq et al. 2011; Volpato & Puri 2014). There are many local breeds across this range, often complementary, such that one breed in a particular area is preferred for transport of goods, while another is a good source of milk and fiber (e.g. Raziq et al. 2011; Mehta et al. 2007). Transhumance in camel pastoralists systems is threatened by economic

and political pressures toward sedentarization throughout Africa and Eurasia, despite recognition that camel transhumance is a robust and adaptive system in marginal areas (Farah et al. 2004; Volpato & Puri 2014). Thus, millennia of domestic camelid socio-ecologies are at risk of disappearance across Eurasia and Africa.

Bactrian camels are feral or free-ranging in some areas. In some Gulf States, high densities of free-ranging dromedaries result in land degradation by overgrazing (Gallacher & Hill 2006a, b). In Australia, a small number of dromedaries that were imported during the 1800s to provide transportation across the desert, was eventually abandoned and formed a feral population that appears to have slowly increased in population to an estimated size of 1,000,000 (Spenser et al. 2012; Crowley 2014). (While Spenser et al. (2012) notes that dromedaries have no history of being invasive species outside Australia, camelids are clearly able to migrate into suitable habitat and establish new populations). Australian dromedaries are blamed for soil degradation and reduction in water quality at watering holes (Crowley 2014; McBurnie et al. 2015). Others argue that dromedaries are an acceptable part of modern Australian fauna, carrying out proxy functions (Crowly 2014; Gibbs et al. 2015). Dromedary and Bactrian camels were imported to the western United States during the mid-1800s as military transport, and small feral populations existed for several years, but were eradicated before the turn of the century (Young 1892). Llamas and alpacas, although popular as livestock and even as pets in North America and elsewhere, seem to rarely form feral populations. One exception is the Lago Peñuelas National Reserve in Chile, where feral llamas have crossed with guanacos to form “guallamas” or “llamacos,” a fertile hybrid with intermediate appearance and behaviors (pers. comm. L. Gutiérrez, pers. obs. MR-B). Guanaco were experimentally introduced as part of a naturalistic grazing scheme in sown swards in Scotland, with the conclusion that they

275 did not compete with goats and red deer and could be raised for their fiber along with
276 these species (Fraser & Gordon 1997).

277
278 Potential ecological roles of camelids within rewilding projects
279 Reintroductions of camelids are already taking place in some areas and can provide
280 insight into the challenges of camelid rewilding. The Wild Camel Protection
281 Foundation NGO is breeding and reintroducing *Camelus ferus* in Mongolia
282 (www.wildcamels.com accessed May 2015). Here, the main challenges are the low
283 population of *Camelus ferus*, its avoidance of human presence, and the increase in
284 anthropogenic activities in its habitat, including mining, poaching, and goat herding
285 for cashmere production (Hare 1997; Berger et al. 2013). In South America,
286 reintroductions of vicuña from captive breeding facilities have been declared
287 successful (Arzamendia et al. 2006; Bonacic et al. 2002). Guanaco are still being
288 reintroduced sporadically into some parts of their former range, primarily in protected
289 areas, while in other areas they are managed for sustainable harvests (Sarno et al.
290 1999). The main challenges to these programs include ongoing poaching, and
291 uncontrolled feral dog populations in Chile (Donadio & Buskirk 2006; C. Bonacic,
292 pers. comm.).

293 This last challenge underscores the important role that Pleistocene history can
294 have on reintroductions or rewilding. Since the Pleistocene, southern South American
295 ecosystems appear have not included group-hunting pursuit predators. Group-hunting
296 pursuit canids are only known from further north, although it is not clear what would
297 have restricted their expansion further south: *Procyon* spp. are known from Brazil,
298 Ecuador and northern Argentina (Prevosti et al. 2005), while the dire wolf (*Canis*
299 *dirus*) ranged from North America as far south as Bolivia (Dundas 1999). Borhyenas,

large marsupial carnivores that went extinct in the Pliocene, had limited cursiality and were primarily ambush predators (Argot 2004). The sabertoothed cat *Smilodon populator*, although likely social, was probably primarily an ambush predator, like modern lions (McCall et al. 2003; Carbone et al. 2009). *Dusicyon avus*, a large fox, and *Arctotherium tarijense*, a bear, were omnivorous, are likely to have been solitary, and may have scavenged camelids more than they hunted them (Prevosti & Vizcaíno 2006; Prevosti & Martin 2013). After the end-Pleistocene/early Holocene megafauna extinction in South America, the remaining camelid species in South America were those existing south of these canids' historical range, in the Pampas, Tierra del Fuego and the Andes. The predator defense strategies most appropriate for ambush as opposed to pursuit, and solitary vs. group predators are different, and it is likely that South American camelids would have evolved appropriate defense mechanisms against social and solitary ambush hunters, such as *Smilodon*, pumas, jaguars, and humans. This strategy, present in guanacos (Darwin 2015 (1839); MR-B pers. obs.), consists of “predator inspection,” in which the predator loses the advantage of surprise (FitzGibbon 1994). At the same time, surviving camelid populations may have lost components of defense strategies suitable for group-hunting pursuit predators (e.g. Walther 1969; Blumstein & Daniel 2005), which could explain their vulnerability to feral dogs.

Rewilding introductions are distinguished from classical reintroductions by a motivation to restore ecological functions rather than populations *per se* (Svenning *et al.* 2015). A stumbling block in the use of camelids for rewilding is the relative lack of research on camelid functions in ecosystems. As camels drink brackish water and eat salty plants, they may act to redistribute salts, as well as other nutrients, over the landscape (Doughty et al. 2013a,b; Wolf et al. 2013). As both browsers and grazers,

camelids may participate in functions such as stimulating tree growth (McNoughton 1983; Gowda 1997) and affecting N and P cycling rates (Schmitz 2008; Metcalfe et al. 2014). Guanacos in particular make latrines, forming large mounds, which are likely to have ecological engineering effects. Camelids' role in transporting seeds via endo- and exo-zoochory is largely unexamined. Guanacos are reported to stimulate the germination of *Acacia caven* and *Prosopis* seeds via endozoochory (Fuentes et al. 1989). Guanacos also form trails, which could have intermediate disturbance effects or act as corridors for seed dispersal. Camelid interactions with animal species other than livestock are seemingly not researched. However, as highly selective foragers, they rarely or weakly compete with other grazers even when sharing territory with them (Migongo-Bake & Hansen 1987; Fraser & Gordon 1997; Borgnia et al. 2008; Acebes et al. 2012; Berger et al. 2013; Iranzo et al. 2013; Wurstten et al. 2013; O'Connor et al. 2015). Thus they may either increase or decrease plant species evenness by targeting specific plants (rare or common) not eaten by other grazers in the system. They also act as prey species for large carnivores (Donadio et al. 2010). Unfortunately, many of these ecological functions are not well understood. Thus, a great deal of ecological research remains to be carried out, and rewilding may provide opportunities to do so (Svenning *et al.* 2015).

Here, we consider the potential costs and benefits of rewilding with camelids in deserts, semi-arid grasslands and semi-arid savannas and thorn woodlands on a global scale. Such habitats correspond to the current habitats of extant camelids as well as the past habitats of extinct camelids.

Deserts around the world hold a relatively small fraction of global biodiversity. However, their conservation is nonetheless important because deserts have many species that are uniquely adapted to extreme conditions, including for

example many EDGE (Evolutionarily Distinct and Globally Endangered) species (www.edgeofexistence.org; Olson & Dinerstein 1998). While desertification is often a threat to other habitats, deserts themselves can also be threatened by increasing aridity and soil degradation or erosion, invasive species, shrub encroachment, and loss of plant diversity, and loss of pollinators and seed dispersers (Puigdefabregas & Mendizabal 1998; Eldridge et al. 2011; Maestre et al. 2012). Camels are the obvious choice for rewilding in the most arid regions, and the introduction histories in Australia and the western US suggest that dromedaries and Bactrian camels are both able to find suitable forage in unfamiliar habitats dominated by spiny and woody plants. Camels could probably be used to combat shrub encroachment and reduce the risk of fire. However, camels are able to eat very spiny and thorny plants, and their generalist foraging habitats combined with selective bite capacity mean that they may be prone to destroy plants that are not adapted to intensive grazing or browsing.

Semi-arid grasslands such as the Pampas, the North American prairies, or the Eurasian steppe, are important ecosystems for many large grazers including species that are endangered or that used to be much more numerous, such as the saiga *Saiga tatarica* and the American bison *Bison bison*. Grasslands can also be important habitats for migratory birds, as well as providing migratory corridors for large herbivores (Berger 2004; Brennan & Kuvlesky 2005). Shrub encroachment, overgrazing by livestock in pastoralist systems, desertification, and land conversion to agriculture are common conservation problems in grasslands (Bond & Parr 2010; Henwood 2010). All extant camelids are well suited to grassland habitats. From a compositionalist perspective, reintroducing camelids to parts of their historical range or as proxies for extinct camelids can serve to recreate the high richness of grazers typical of most grasslands. From the functionalist perspective, this can provide

greater prey for large predators and assist in nutrient cycling. In addition, as camelids rarely compete directly with other grazers, they are expected to perform slightly different grazing functions, which may be unexpectedly beneficial or harmful. A likely benefit is that they can avoid competing with livestock and may thus be compatible with rewilding in areas and projects where removal of pastoralism is neither feasible nor desirable. However, using the same camelid species or breed for rewilding that is used for pastoralism in a given area is likely to create problems related to the mixing of feral and domestic populations. Where camel pastoralism is declining, wild camelids could maintain ecological benefits of camel movements over the landscape.

Finally, savannas and thorn woodlands include many different kinds of open and generally thorny woodlands around the world, such as the acacia savannas of sub-Saharan Africa, seasonally dry tropical forests and thorn woodlands (Pennington et al. 2000; van Bloem et al. 2004). Although diverse in form, these habitats in general have many endemic plant species, and a relatively high species richness (van Bloem et al. 2004). They are often threatened by strong anthropogenic influences including pasturing animals, gathering firewood, setting fires, hunting game, gathering food resources, or conversion to agriculture (van Bloem et al. 2004; Leal et al. 2005; Syampungani et al. 2009; Root-Bernstein & Jaksic in press). These influences can lead to fragmentation, degradation and defaunation. This is the kind of habitat in which camelids evolved during the Miocene- Pleistocene, and thus they can be expected to have important ecological functions in such habitats, although unfortunately these are among the least known of camelid- environment interactions since they are currently only relevant to small populations of guanaco in the Chaco (semi-tropical seasonally dry forest) in Bolivia. Camelids could be reintroduced as

seed dispersers, to provide browsing on thorny trees, or as prey for large predators. For example, a pilot rewilding project in central Chile, Proyecto REGenera (run by MR-B) aims to reintroduce the guanaco to restore browsing and seed dispersal functions with the goal of restoring the “espinal” savanna silvopastoral system (Root-Bernstein & Jaksic 2013; Lindon & Root-Bernstein 2015; Root-Bernstein et al. submitted). Conflicts with such models of rewilding are likely to include issues surrounding wild animals in highly anthropogenic habitats, such as human-wildlife conflict and poaching.

Although this review focuses on the functional ecology and paleoecology of camelids, a thorough consideration of rewilding prospects must also consider human social and cultural interactions with the reintroduced species or proxy species. Opportunities exist to rewild camelids in areas with low densities of humans and human uses. However, many camelid reintroduction and conservation projects in South America, as well as discussions of African and Eurasian camel pastoralism, take for granted that sustainable use is part and parcel of conservation of camelid landscapes (Meta et al. 2007; Westreicher et al. 2007; Çakırlar & Berthon 2014; Volpato & Puri 2014). For example, sustainable and high-welfare practices of shearing wild vicuña for their extra-fine fiber have been a focus of vicuña conservation research (Bonacic et al. 2006). Since rewilding already often blurs the line between domestic species and wild ones, e.g., by rewilding cattle and horses as proxies for aurochs and tarpan (e.g. at Oostvaardersplassen, NL; Lorimer & Driessen 2013), camelid rewilding projects may find it pragmatic to do so as well, in the opposite direction. For example, domestic camelids could be managed in ways that allow them to carry out more ecosystem functions. This might mean reviving

transhumance, mixing camelids with other grazers and browsers, or allowing a percentage of their feces to remain uncollected, for example.

Conclusions

Camelids were once highly species-rich and abundant, co-existing in savannas with a wide variety of large fauna, now mostly extinct. Along with horses, camelids were among the most successful of the large fauna that originated in North America, but went completely extinct there at the end of the Pleistocene. They are mixed browser/grazer generalists adapted to marginal habitats with an evolutionary history of spreading into new areas and coexisting alongside many other grazers and browsers. These characteristics make them potentially attractive species for rewilding for a number of purposes. We suggest that evaluations of the suitability of the various extant camelid species for rewilding be carried out on a site-by-site basis, considering the functions to be restored, the potential biotic and abiotic interactions and side-effects, and potential for social conflicts or benefits (cf. the general trophic rewilding priorities outlined by Svenning *et al.* 2015). Further ecological research on contributions to ecological processes would contribute to their conservation and management as well as the conservation and management of arid and semi-arid habitats around the world.

Acknowledgements

Thanks to Søren Faurby for producing Figure 1. MR-B is funded by FONDECYT Post Doctoral Fellowship No. 3130336 and Danish National Research Foundation Niels Bohr professorship project Aarhus University Research on the Anthropocene (AURA). JCS was supported by the European Research Council (ERC-2012-StG-

449 310886-HISTFUNC).

450

451 References

- 452 Acebes, P., Traba J., Malo, J.E. (2012) Co-occurrence and potential for competition
453 between wild and domestic large herbivores in a South American
454 desert. *Journal of Arid Environments*, **77**, 3944.
455
- 456 Alvard MS., Kuznar L. (2001) Deferred harvests: The transition from hunting to
457 animal husbandry. *American Anthropology*, **103**(2), 295-311.
458
- 459 Argot, C. (2004) Evolution of South American mammalian predators
460 (Borhyaenoidea): anatomical and palaeobiological implications. *Zoological*
461 *Journal of the Linnean Society*, **140**, 487–521.
462
- 463 Arzamendia, Y., Cassini, M. & Vilá, B. (2006) Habitat use by vicuña *Vicugna*
464 *vicugna* in Laguna Pozuelos Reserve, Jujuy, Argentina. *Oryx*, **40**, 198
465
- 466 Bacon, C., Silvestro, D., Jaramillo, C., Smith, B., Chakrabarty, P. & Antonelli, A.
467 (2015) Biological evidence supports an early and complex emergence of the
468 Isthmus of Panama. *Proceedings of the National Academy of Sciences*, **112**,
469 6110–6115
470
- 471 Belardi, J. & Rindel, D. (2008) Taphonomic and archeological aspects of massive
472 mortality processes in guanaco (*Lama guanicoe*) caused by winter stress in
473 Southern Patagonia. *Quaternary International*, **180**, 3851.
474
- 475 Berger, J., Buuveibaatar, B. & Mishra, C. (2013) Globalization of the Cashmere
476 Market and the Decline of Large Mammals in Central Asia. *Conservation*
477 *Biology*, **27**, 679–689.
478
- 479 Blumstein, DT., & Daniel JC. 2005. The loss of anti-predator behavior following
480 isolation on islands. *Proceedings of the Royal Society B*, **272**, 1663-1668.
481
- 482 Bonacic, C., Macdonald, D., Galaz, J. & Sibly, R. (2002) Density dependence in the
483 camelid *Vicugna vicugna*: the recovery of a protected population in
484 Chile. *Oryx*, **36**.
485
- 486 Bonacic, C., Feber, R. & Macdonald, D. (2006) Capture of the vicuña (*Vicugna*
487 *vicugna*) for sustainable use: Animal welfare implications. *Biological*
488 *Conservation*, **129**, 543550.
489
- 490 Bond, W. & Parr, C. (2010) Beyond the forest edge: Ecology, diversity and
491 conservation of the grassy biomes. *Biological Conservation*, **143**, 23952404.
492
- 493 Borgnia, M., Vilá, B. & Cassini, M. (2008) Interaction between wild camelids and
494 livestock in an Andean semi-desert. *Journal of Arid Environments*, **72**,
495 21502158.
496

- Borrero, L. A., Zárata, M., Miotti, L., & Massone, M. (1998) The Pleistocene–Holocene transition and human occupations in the southern cone of South America. *Quaternary International*, **49**, 191-199.
- Bowman, D. (2012) Conservation: Bring elephants to Australia? *Nature*, **482**, 30.
- Brennan, L.A., & Kuvlesky Jr., W.P. (2005) North American grassland birds: An unfolding conservation crisis? *The Journal of Wildlife Management*, **69**(1), 1-13.
- Carbone, C., Maddox, T., Funston, P., Mills, M., Grether, G. & Valkenburgh, B. (2009) Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat, *Smilodon*. *Biology Letters*, **5**, 81-85.
- Chuluunbat B., Charruau P., Silbermayr K., Khorloojav T. & Burger PA. (2014) Genetic diversity and population structure of Mongolian domestic Bactrian camels (*Camelus bactrianus*). *Animal Genetics*, **45**, 550–558.
- Churcher, C., Kleindienst, M. & Schwarcz, H. (1999) Faunal remains from a Middle Pleistocene lacustrine marl in Dakhleh Oasis, Egypt: palaeoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **154**, 301-312.
- Crowley, S. (2014) Camels out of place and time: The Dromedary *Camelus dromedarius* in Australia. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, **27**, 191-203.
- Cui, P., Ji, R., Ding, F., Qi, D., Gao, H., Meng, H., Yu, J., Hu, S., & Zhang, H. (2007) A complete mitochondrial genome sequence of the wild two-humped camel (*Camelus bactrianus ferus*): an evolutionary history of camelidae. *BMC Genomics*, **8**, 241.
- Çakırlar, C. & Berthon, R. (2014) Caravans, camel wrestling and cowrie shells: towards a social zooarchaeology of camel hybridization in anatolia and adjacent eegions. *Anthropozoologica*, **49**.
- Dantas, MAT., Dutra, RP., Cherkinsky, A., Fortier, DC., Kamino, LHY., Cozzuol, MA. *et al.* (2013) Paleoecology and radiocarbon dating of the Pleistocene megafauna of the Brazilian Intertropical Region. *Quaternary Research*, **79**, 61-65.
- Darwin, C. (2015; 1839) *It was snowing butterflies*. Penguin Classics, London.
- Dittmann, M., Hummel, J., Runge, U., Galeffi, C., Kreuzer, M. & Clauss, M. (2014) Characterising an artiodactyl family inhabiting arid habitats by its metabolism: Low metabolism and maintenance requirements in camelids. *Journal of Arid Environments*, **107**, 41-48.

545 Dompierre, H & Churcher, CS. (1996) Premaxillary shape as an indicator of the diet
546 of seven extinct late Cenozoic New World camels. *Journal of Vertebrate*
547 *Paleontology*. **16**(1), 141-148.
548

549 Donadio, E. & Buskirk, S. (2006) Flight behavior in guanacos and vicuñas in areas
550 with and without poaching in western Argentina. *Biological*
551 *Conservation*, **127**, 139-145.
552

553 Donadio, E., Novaro, A., Buskirk, S., Wurstten, A., Vitali, M. & Monteverde, M.
554 (2010) Evaluating a potentially strong trophic interaction: pumas and wild
555 camelids in protected areas of Argentina. *Journal of Zoology*, **280**, 33–40.
556

557 Donlan, J., Green, HW., Berger, J., Bock, C.E., Bock, JH., Burney, DA., Estes, JA.,
558 Foreman, D., Martin, PS., Roemer, GW., Smith, FA., Soulé, ME. (2005)
559 Rewilding North America. *Nature*, **436**, 913-914.
560

561 Donlan, J., Berger, J., Bock, CE., Bock, JH., Burney, DA., Estes, JA., Foreman, D.,
562 Martin, PS., Roemer, GW., Smith, FA., Soulé, ME. & Greene, HW. 2006.
563 Pleistocene Rewilding: An optimistic agenda for twenty-first century
564 conservation. *The American Naturalist*, **168**(5), 660-681.
565

566 Doughty, C., Wolf, A. & Malhi, Y. (2013a) The impact of large animal extinctions on
567 nutrient fluxes in early river valley civilizations. *Ecosphere*, **4**, 148.
568

569 Dundas, R. (1999) Quaternary records of the dire wolf, *Canis dirus*, in North and
570 South America. *Boreas*, **28**, 375–385.
571

572 Doughty, C., Wolf, A. & Malhi, Y. (2013b) The legacy of the Pleistocene megafauna
573 extinctions on nutrient availability in Amazonia. *Nature Geoscience*, **6**, 761–
574 764.
575

576 Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford,
577 W.G. (2011). Impacts of shrub encroachment on ecosystem structure and
578 functioning: towards a global synthesis. *Ecology Letters*, **14**, 709-722.
579

580 FAO (Food and Agriculture Organization of the United Nations) (2001) Pastoralism
581 in the New Millenium. *FAO Animal Production and Health Paper* **150**,
582 Rome, Italy.
583

584 Farah, K.O., Nyariki, D.M., Ngugi, R.K., Noor, I.M., Guliye, A.Y. (2004) The Somali
585 and the camel: Ecology, management and economics. *Anthropologist*, **6**(1),
586 45-55.
587

588 Faurby, S. & Svenning, J.-C. 2015. Historic and prehistoric human-driven extinctions
589 have reshaped global mammal diversity patterns. *Diversity & Distributions*,
590 **21**, 1155–1166
591

592 Feranec, R. (2003) Stable isotopes, hypsodonty, and the paleodiet of Hemiauchenia
593 (Mammalia: Camelidae): a morphological specialization creating ecological
594 generalization. *Paleobiology*, **40**.

- FitzGibbon, CD. (1994) The costs and benefits of predator inspection behaviour in Thomson's gazelles. *Behavioral Ecology and Sociobiology*, **34**(2), 139-148.
- França, LdM., de Asevedo, L., Dantas, MAT., Bocchiglieri, A., Avilla, LdS., Lopes, RP. *et al.* (2015) Review of feeding ecology data of Late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. *Earth-Science Reviews*, **140**, 158-165.
- Fraser, MD & Gordon, IJ. (1997) The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *Journal of Applied Ecology*, **34**(3), 668-686.
- Frison, G. (1998) Paleoindian large mammal hunters on the plains of North America. *Proceedings of the National Academy of Sciences USA*, **95**, 14576–14583.
- Frison, G.C., Walker, D.N. Webb, S.D., & Ziemens, G.M. (1978) Paleo-Indian procurement of *Camelops* on the Northern Plains. *Quaternary Research*, **10**, 385-400.
- Fuentes ER, Avilés R, & Segura A (1989) Landscape change under indirect effects of human use: the Savanna of Central Chile. *Landscape Ecology*, **2**(2), 73-80.
- Gallacher, DJ & Hill, JP. (2006b) Effects of camel vs oryx and gazelle grazing on the plant ecology of the Dubai Desert Conservation Reserve. *Reclaiming the Desert: Towards a Sustainable Environment in Arid Lands. Proceedings of the Third Joint UAE-Japan Symposium on Sustainable GCC Environment and Water Resources*. Taylor & Francis. Abu Dhabi, UAE.
- Gallacher, D. & Hill, J. (2006a) Effects of camel grazing on the ecology of small perennial plants in the Dubai (UAE) inland desert. *Journal of Arid Environments*, **66**, 738-750.
- Gautier, A. (1966) *Camelus thomasi* from the northern Sudan and its bearing on the relationship *C. thomasi*: *C. bactrianus*. *Journal of Paleontology*, 40(6), 1368-1372.
- Gautier, A., Makowiecki, D., Paner, H. & Neer, W. (2012) Palaeolithic Big Game Hunting at HP766 in Wadi Umm Rahau, Northern Sudan. *Journal of African Archaeology*, **10**, 165-174.
- Gasco, A.V., Marsh, E.J. (2013) Hunting, Herding, and Caravanning: Osteometric Identifications of Camelid Morphotypes at Khonkho Wankane, Bolivia. *International Journal of Osteoarchaeology*, **0**.
- Geraads, D. (2014) *Camelus grattardi*, sp. nov., a new camel from the Shungura Formation, Omo Valley, Ethiopia, and the relationships of African fossil Camelidae (Mammalia). *Journal of Vertebrate Paleontology*, **34**, 1481-1485.

645 Gibbs, L., Atchinson, J., Macfarlane, I. (2015) Camel country: Assemblage,
646 belonging and scale in invasive species geographies. *Geoforum* **58**, 56-67.
647

648 González, B., Orozco-terWengel, P., Borries, R., Johnson, W., Franklin, W. & Marín,
649 J. (2014) Maintenance of Genetic Diversity in an Introduced Island Population
650 of Guanacos after Seven Decades and Two Severe Demographic Bottlenecks:
651 Implications for Camelid Conservation. *PLoS ONE*, **9**, e91714.
652

653 Gowda, JH. (1997) Physical and chemical response of juvenile *Acacia tortilis* trees to
654 browsing. Experimental evidence. *Functional Ecology*, **11**, 106-111.
655

656 Grigson, C. (1983) A very large camel from the Upper Pleistocene of the Negev
657 Desert. *Journal of archaeological science*, **10**, 311-316.
658

659 Grigson, C., Gowlett, J. & Zarins, J. (1989) The Camel in Arabia—A direct
660 radiocarbon date, calibrated to about 7000 BC. *Journal of Archaeological*
661 *Science*, **16**, 355-362.
662

663 Grimberg Pardo, M.P. 2010. *Plan Nacional de Conservación del Guanaco (Lama*
664 *guanicoe) en Chile 2010–2015, Macrozona Norte y Centro*. Chile: CONAF.

665 Hare, J. (1997) The wild Bactrian camel *Camelus bactrianus* ferus in China: the need
666 for urgent action. *Oryx*, **31**, 45–48.
667

668 Haynes, G. & Stanford, D. (1984) On the possible utilization of *Camelops* by early
669 man in North America. *Quaternary Research*, **22**, 216-230.
670

671 Henwood, W.D. (2010) Toward A Strategy For The Conservation And Protection Of
672 The World's Temperate Grasslands. *Great Plains Research: A Journal of*
673 *Natural and Social Sciences*. Paper 1074.
674

675 Hubbe, A., Hubbe, M., & Neves, W.A. (2013). The Brazilian megamastofauna of the
676 Pleistocene/Holocene transition and its relationship with the early human
677 settlement of the continent. *Earth-Science Reviews*, **118**, 1-10.
678

679 Iranzo, E., Traba, J., Acebes, P., González, B., Mata, C., Estades, C. & Malo, J.
680 (2013) Niche Segregation between Wild and Domestic Herbivores in Chilean
681 Patagonia. *PLoS ONE*, **8**, e59326.
682

683 Iriarte, A. 2000. Normativa legal sobre conservación y uso sustentable de vicuña y
684 guanaco en Chile. In *Manejo Sustentable de la Vicuña y el Guanaco*, ed. B.
685 González, F. Bas, C. Tala, and A. Iriarte, 209–221. Santiago: SAG, PUC, FIA

686 Jackson S., D., Méndez M., C., López M., P., Jackson S., D., Seguel Q., R. 2005.
687 Evaluación de un asentamiento arqueológico en el semiárido de Chile:
688 procesos de formación, fauna extinta y componentes culturales.
689 *Intersecciones en Antropología* **6**, 139-151.

690 Janis, C., Damuth, J., Thoeodor, J.M. (2004) The species richness of Miocene
691 browsers, and implications for habitat type and primary productivity in the

692 North American grassland biome. *Palaeogeography, Palaeoclimatology,*
693 *Palaeoecology*, **207**, 371–398.
694

695 Ji, R., Cui, P., Ding, F., Geng, J., Gao, H., Zhang, H., Yu, J., Hu, S. & Meng, H.
696 (2009) Monophyletic origin of domestic bactrian camel (*Camelus bactrianus*)
697 and its evolutionary relationship with the extant wild camel (*Camelus*
698 *bactrianus ferus*). *Animal Genetics*, **40**, 377–382.
699

700 Kaczensky, P., Adiya, Y., Wehrden, H., Mijiddorj, B., Walzer, C., Güthlin, D.,
701 Enkhbileg, D. & Reading, R. (2013) Space and habitat use by wild Bactrian
702 camels in the Transaltai Gobi of southern Mongolia. *Biological*
703 *Conservation*, **169**, 311–318.
704

705 Kita, Z., Secord, R. & Boardman, G. (2014) A new stable isotope record of Neogene
706 paleoenvironments and mammalian paleoecologies in the western Great Plains
707 during the expansion of C4 grasslands. *Palaeogeography, Palaeoclimatology,*
708 *Palaeoecology*, **399**, 160–172.
709

710 Kohn, M., McKay, M. & Knight, J. (2005) Dining in the Pleistocene—Who’s on the
711 menu? *Geology*, **33**, 649–652.
712

713 Krader, L. (1955) Ecology of Central Asian Pastoralism. *Southwestern Journal of*
714 *Anthropology*, **11(4)**, 301–326.
715

716 Leal, IR., Cardoso da Silva, JM., Tabarelli, M., & Lacher Jr., T.E. (2005) Changing
717 the course of biodiversity conservation in the Caatinga of Northeastern Brazil.
718 *Conservation Biology*, **19(3)**, 701–706.
719

720 Le Roux, J. (2012) A review of Tertiary climate changes in southern South America
721 and the Antarctic Peninsula. Part 2: continental conditions. *Sedimentary*
722 *Geology*, **247–248**, 21–38.
723

724 Lindon, A., & Root-Bernstein, M. (2015) Phoenix flagships: Conservation values and
725 guanaco reintroduction in an anthropogenic landscape. *Ambio*, **44**, 458–471.
726

727 Lorimer, J. & Driessen, C. (2013) Bovine biopolitics and the promise of monsters in
728 the rewilding of Heck cattle. *Geoforum*, **48**, 249–259.
729

730 Lövei, G. (2007) Extinctions, modern examples of. *Encyclopedia of Biodiversity*.
731 Ed. S. Levin. Academic Press.
732

733 Lucherini, M. (1996) Group size, spatial segregation and activity of wild sympatric
734 vicuñas, *Vicugna vicugna* and guanacos *Lama guanicoe*. *Small Ruminant*
735 *Research* **20**, 193–198.
736

737 Lynch, TF. (1983) Camelid pastoralism and the emergence of Tiwanaku civilization
738 in the South-Central Andes. *World archaeology*, **15(1)**, 1–14.
739

- MacFadden, BJ & Shockey, BJ. (1997) Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology*, **22**(1), 77-100.
- Maestre, FT, Quero, JL, Gotelli, NJ, Escudero, A & Ochoa, V. et al. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**, 214-218.
- McBurnie, G., Davis, J., Thompson, R., Nano, C. & Brim-Box, J. (2015) The impacts of an invasive herbivore (*Camelus dromedaries*) on arid zone freshwater pools: An experimental investigation of the effects of dung on macroinvertebrate colonisation. *Journal of Arid Environments*, **113**, 69-76.
- McCall, S., Naples, V. & Martin, L. (2003) Assessing Behavior in Extinct Animals: Was Smilodon Social? *Brain, Behavior and Evolution*, **61**, 159–164.
- McKenna, MC. (1966) Synopsis of Whitneyan and Arikareean camelid phylogeny. *American Museum Novitates*, **2253**, 1-11.
- McNaughton, SJ. (1983) Compensatory plant growth as a response to herbivory. *Oikos*, **40**, 329-336.
- de Melo França, L., Asevedo, L., Dantas, M., Bocchiglieri, A., Avilla, L., Lopes, R. & Silva, J. (2015) Review of feeding ecology data of Late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. *Earth-Science Reviews*, **140**, 158-165.
- Mehta, SC, Bhardwaj, B & Sahani, MS. (2007) Status and conservation of Mewari and Jaisalmeri camels in India. *Animal Genetic Resources*, **40**, 87-102.
- Mendoza, M., Janis, C. & Palmqvist, P. (2006) Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology*, **270**, 90–101.
- Metcalf, D., Asner, G., Martin, R., Espejo, J., Huasco, W., Amézquita, F., Carranza-Jimenez, L., Cabrera, D., Baca, L., Sinca, F., Quispe, L., Taype, I., Mora, L., Dávila, A., Solórzano, M., Vilca, B., Román, J., Bustios, P., Revilla, N., Tupayachi, R., Girardin, C., Doughty, C. & Malhi, Y. (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, **17**, 324–332.
- Migongo-Bake, W & Hansen, RM. (1987) Seasonal diets of camels, cattle, sheep, and goats in a common range in eastern Africa. *Journal of Range Management*.
- Miller, S. (1980) *Human influence on the distribution and abundance of wild Chilean mammals: Prehistoric—Present*. PhD thesis, University of Washington.
- Naundrup, P.J. & Svenning, J.-C. (2015). A geographic assessment of the global scope for rewilding with wild-living horses (*Equus ferus*). *PLoS ONE*, **10**, e0132359.

- Navarro, L.M., and H.M. Pereira. (2012) Rewilding abandoned landscapes in Europe. *Ecosystems* **15**, 900–912.
- Nugent, P., Baldi, R., Carmanchahi, P., De Lamo, D., Failla, M., Ferrando, P., Funes, M., Puig, S., Rivero, S., & von Thungen, J. (2006) Conservación del guanaco en la Argentina. In Bolkovic, M. L. y D. Ramadori (eds.). *Manejo de Fauna Silvestre en la Argentina. Programas de uso sustentable*. Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires.
- O'Connor, D., Butt, B. & Foufopoulos, J. (2015) Foraging ecologies of giraffe (*Giraffa camelopardalis reticulata*) and camels (*Camelus dromedarius*) in northern Kenya: effects of habitat structure and possibilities for competition? *African Journal of Ecology*, **53**, 183–193.
- Olson, D. & Dinerstein, E. (1998) The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology*, **12**, 502–515.
- Owen-Smith, RN. (1988) *Megaherbivores: The influence of very large body size on ecology*. Cambridge, University of Cambridge Press.
- Payne, S., & Garrard, A. *Camelus* from the Upper Pleistocene of Mount Carmel, Israel. (1983) *Journal of Archaeological Science*, **10**, 243–247.
- Pennington, T.R. Prado, D.E., & Pendry C.A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, **27**, 261–273.
- Peters, J & Driesch, A. (1997) The two-humped camel (*Camelus bactrianus*): New light on its distribution, management and medical treatment in the past. *Journal of Zoology*, **242**, 651–679.
- Potts, DT. (2004) Camel hybridization and the role of *Camelus bactrianus* in the ancient Near East. *Journal of the Economic and Social History of the Orient*, **47(2)**, 143–165.
- Prado, J., Martinez-Maza, C. & Alberdi, M. (2015) Megafauna extinction in South America: A new chronology for the Argentine Pampas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **425**, 4149.
- Prevosti, F. & Martin, F. (2013) Paleoecology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: Ecomorphology, stable isotopes, and taphonomy. *Quaternary International*, **305**, 74–84.
- Prevosti, FJ & Vizcaíno, SF. (2006) Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. *Acta Palaeontologica Polonica*, **51(3)**, 407–422.

- Prevosti, F., Zurita, A. & Carlini, A. (2005) Biostratigraphy, systematics, and paleoecology of *Procyon* Giebel, 1855 (Carnivora, Canidae) in South America. *Journal of South American Earth Sciences*, **20**, 5-12.
- Puigdefábregas, J., & Mendizabal, T. (1998) Perspectives on desertification: western Mediterranean. *Journal of Arid Environments*, **39**(2), 209-224.
- Raziq, A., Verdier, K. & Younas, M. (2011) Rapid change of strategy is necessary for development of dromedary camel pastoralism in the Cholistan desert of Pakistan. *Pastoralism: Research, Policy and Practice*, **1**, 3.
- Reading, R.P., Mix, H., Lhagvasuren, B., & Blumer, E.S. (1999) Status of wild Bactrian camels and other large ungulates in south-western Mongolia. *Oryx*, **33**(3), 247-255.
- Root-Bernstein, M., & Jaksic, F. In press. Oportunidades y desafíos para cambios adaptivos en el sistema silvopastoral de Chile central [Opportunities and challenges for adaptive change in the silvopastoral system of central Chile]. In Postigo, J.C., & Young, K.R. Eds. *Perspectivas socio-ecológicas, actividades productivas y cambios globales en América Latina*.
- Root-Bernstein, M., & Jaksic, F. 2013. The Chilean espinal: Restoration for a sustainable silvopastoral system. *Restoration Ecology*. **21**(4), 409-414.
- Rybczynski, N., Gosse, J., Harington, C., Wogelius, R., Hidy, A. & Buckley, M. (2013) Mid-Pliocene warm-period deposits in the High Arctic yield insight into camel evolution. *Nature Communications*, **4**, 1-9.
- Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. (2014) Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133254.
- Sarno, R., Clark, W., Bank, M., Prexl, W., Behl, M., Johnson, W. & Franklin, W. (1999) Juvenile guanaco survival: management and conservation implications. *Journal of Applied Ecology*, **36**, 937-945.
- Sato, S. (1980) Pastoral movements and the subsistence unit of the Rendille of northern Kenya: With special reference to camel ecology. *Senri Ethnological Studies Osaka*, **6**, 1-78.
- Semprebon, G. & Rivals, F. (2010) Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **295**, 131-145.
- Sandom, C.J., Hughes, J. & Macdonald, D.W. (2012) Rewilding the Scottish highlands: Do wild boar, *sus scrofa*, use a suitable foraging strategy to be effective ecosystem engineers? *Restoration Ecology* **21**(3): 336-343.
- Schmitz, O. (2008) Herbivory from Individuals to Ecosystems. *Ecology, Evolution, and Systematics*, **39**, 133-152.

- 886
887 Skidmore, J., Billah, M., Binns, M., Short, R. & Allen, W. (1999) Hybridizing Old
888 and New World camelids: *Camelus dromedarius* x *Lama*
889 *guanicoe*. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 649-
890 656.
- 891
892 Schroeder, N.M., Ovejero, R., Moreno, P.G., Gregorio, P., Taraborelli, P., Matteucci,
893 S.D., & Carmanchahi, P.D. (2013) Including species interactions in resource
894 selection of guanacos and livestock in Northern Patagonia. *Journal of*
895 *Zoology*, **291**, 213–225.
- 896
897 Soliman, M.K. 2015. Anatomical adaptations of dromedary (*Camelus dromedaries*)
898 and Ecological Evolutionary Impacts in KSA. *Proceedings, International*
899 *Conference on Plant, Marine and Enviromental Sciences, Jan. 1-2, 2015*
900 Kuala Lumpur, Malasia.
- 901
902 Surovell, T. & Grund, B. (2012) The Associational Critique of Quaternary Overkill
903 and Why It is Largely Irrelevant to the Extinction Debate. *American*
904 *Antiquity*, **77**, 672-687.
- 905
906 Spencer, P., Giustiniano, D., Hampton, J. O., Gee, P., Burrows, N., Rose, K., Martin,
907 G.R., & Woolnough, A. P. (2012) Identification and management of a single
908 large population of wild dromedary camels. *The journal of wildlife*
909 *management*, **76(6)**, 1254-1263.
- 910
911 Syampungani, S., Chirwa, P., Akinnifesi, F., Sileshi, G. & Ajayi, O. (2009) The
912 miombo woodlands at the cross roads: Potential threats, sustainable
913 livelihoods, policy gaps and challenges. *Natural Resources Forum*, **33**, 150–
914 159.
- 915
916 Titov, V. & Logvynenko, V. (2006) Early *Paracamelus* (Mammalia, Tylopoda) in
917 Eastern Europe. *Acta Zoologica Cracoviensia - Series A: Vertebrata*, **49**, 163-
918 178.
- 919
920 Tulgat, R., & Schaller, GB. (1992) Status and distribution of wild Bactrian camels
921 *Camelus bactrianus ferus*. *Biological Conservation* 62, 11-19.
- 922
923 Volpato, G & Puri, RK. (2014) Dormancy and Revitalization: The fate of
924 ethnobotanical knowledge of camel forage among Sahrawi nomads and
925 refugees of Western Sahara. *Ethnobotany Research and Applications*, **12**, 183-
926 210.
- 927
928 van Bloem, SJ., Murphy, PG., & Lugo, AE. 2004. Tropical Dry Forests. In
929 *Encyclopedia of Forest Sciences*. Academic Press, Boston, 1767-1775.
- 930
931 Waters, M., Stafford, T., Kooyman, B. & Hills, L. (2015) Late Pleistocene horse and
932 camel hunting at the southern margin of the ice-free corridor: Reassessing the
933 age of Wally's Beach, Canada. *Proceedings of the National Academy of*
934 *Sciences*, **112**, 4263–4267.
- 935

- Weinstock, J., Shapiro, B., Prieto, A., Marín, J., González, B., Gilbert, M. & Willerslev, E. (2009) The Late Pleistocene distribution of vicuñas (*Vicugna vicugna*) and the “extinction” of the gracile llama (“*Lama gracilis*”): New molecular data. *Quaternary Science Reviews*, **28**, 1369-1373.
- Westreicher, CA, Mérega, JL & Palmili, G. (2007) The economics of pastoralism: Study on current practices in South America. *Nomadic Peoples*, **11(2)**, 87-105.
- Wolf, A., Doughty, C. & Malhi, Y. (2013) Lateral Diffusion of Nutrients by Mammalian Herbivores in Terrestrial Ecosystems. *PLoS ONE*, **8**, e71352.
- Wu, H., Guang, X., Al-Fageeh, M., Cao, J., Pan, S., Zhou, H., Zhang, L., Abutarboush, M., Xing, Y., Xie, Z., Alshanqeeti, A., Zhang, Y., Yao, Q., Al-Shomrani, B., Zhang, D., Li, J., Manee, M., Yang, Z., Yang, L., Liu, Y., Zhang, J., Altammami, M., Wang, S., Yu, L., Zhang, W., Liu, S., Ba, L., Liu, C., Yang, X., Meng, F., Wang, S., Li, L., Li, E., Li, X., Wu, K., Zhang, S., Wang, J., Yin, Y., Yang, H., Al-Swailem, A. & Wang, J. (2015) Camelid genomes reveal evolution and adaptation to desert environments. *Nature Communications*, **5**, 5188.
- Walther, FR. (1969) Flight behaviour and avoidance of predators in Thomson’s gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, **34(3)**, 184-221.
- Wurstten, A., Novaro, A. & Walker, R. (2014) Habitat use and preference by guanacos, vicuñas, and livestock in an altitudinal gradient in northwest Argentina. *European Journal of Wildlife Research*, **60**, 35–43.
- Yacobaccio, HD. (2004) Social dimensions of camelid domestication in the southern Andes. *Anthropozoologica*, 39(1), 237-247.
- Young, J. (1982) Camels on the Western Range. *Rangelands*, 4(6), 248-251.
- Zazula, G., Turner, D., Ward, B. & Bond, J. (2011) Last interglacial western camel (*Camelops hesternus*) from eastern Beringia. *Quaternary Science Reviews*, **30**, 2355-2360.

Range of extant Camelids

Natural range of extinct Camelids

Figure 1. Top, the current and historical ranges of extant wild camelid species. Domestic species are not shown. Bottom, potential ranges under current climate of seven camelid species that have gone globally extinct in the Late Pleistocene or Holocene (or now only survive in domesticated form). Data from Faurby & Svenning (2015).