

Understanding Introduced Megafauna in the Anthropocene: Wild Burros as Ecosystem

Engineers in the Sonoran Desert

by

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## ABSTRACT

Megafauna species worldwide have undergone dramatic declines since the end of the Pleistocene, twelve thousand years ago. In response, there have been numerous calls to increase conservation attention to these ecologically important species. However, introduced megafauna continue to be treated as pests. This thesis evaluates the extent of this conservation paradox in relation to changing megafauna diversity from the Pleistocene to the Anthropocene and finds that introductions have provided refuge for a substantial number threatened and endangered megafaunal species and has restored generic diversity levels per continent to levels closer to the Pleistocene than the Holocene. Furthermore, this thesis describes a previously unstudied behavior of wild burros (*Equus asinus*), an introduced megafauna whose pre-domestic ancestors are Critically Endangered. Wild burros dig wells to access groundwater and in doing so substantially increase water availability on several scales, create sites that are visited by numerous species and are comparable to natural water sources in terms of species richness, and provide germination nurseries for important riparian pioneer plant species. My results suggest that relaxing concepts of nativity in an age of extinction will provide new understandings of ecological function and can help focus attention on broader conservation goals.



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## CHAPTER 1: INTRODUCTION

Introduced species are conventionally viewed as drivers of ecological instability because they lack coevolutionary history with the communities to which they are introduced. However, growing evidence has shown that introduced species respond to ecological contexts as any species does (Wallach et al. 2015), that native and introduced species undergo rapid reciprocal evolution (Carroll et al. 2005), that introduced species provide ecosystem services in their introduced ranges (Schlaepfer et al. 2011, Mascaro et al. 2012), and that introduced species are likely passengers of change not drivers of change (MacDougall and Turkington 2005). It has been further argued that branding introduced species with ‘invasion’ narratives creates a myopic tales of good and evil, which reduces our ability to understand the complexity of natural systems and to find creative and ethical responses to environmental problems (Prevot-Julliard et al. 2011, Chew 2015, Lidström et al. 2015).

It has also recently come to light that certain introduced species are threatened or extinct in their native ranges, or have no known native range, which presents a ‘conservation paradox’ (Marchetti and Engstrom 2015). These conservation paradoxes put to question the practice of attempting to cause local extinctions of introduced organisms in an age of global extinction. New perspectives on how introduced species function in their new homes are necessary and help inform our valuation of introduced organisms.

The wild burro (*Equus asinus*) of the North American deserts is a contentious introduced species. Many studies suggest that wild burros compete with native wildlife

(Seegmiller and Ohmart 1981, Marshal et al. 2008) and exert strong grazing pressure. However, as documented by Abella (2008), evidence of overgrazing is inconsistent and suffers from weak methodology and the majority of studies do not account for the ecological context of predator persecution.

Regardless, the prerogative to manage this species is predicated on the premise that wild burros as introduced species are fundamentally detrimental to local ecologies and are not regulated by native predators such as mountain lions. New perspectives not founded on *a priori* notions of harm may provide new insights, new management strategies, and deepen understandings of the novel ecosystems of the Anthropocene.

In this thesis I evaluate the conservation paradox of introduced megafauna species and investigate well digging, a unique and ecologically important behavior of wild burros in the Sonoran Desert of Arizona.

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## CHAPTER 2

**TITLE:** Introduced megafauna are rewilding the Anthropocene

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### **INTRODUCTION**

Terrestrial megafauna are undergoing severe declines around the world: of 74 extant species of large herbivorous mammals with body masses  $\geq 100$  kg, 44 (~60%) are threatened with extinction (Ripple et al. 2015). The decline of this functional group began 10,000-50,000 years ago, most likely due to overhunting by humans during the late Pleistocene (Barnosky et al. 2004, Bartlett et al. 2015). While this long-term trend is alarming, many species in this functional group have also found opportunities through introduction to new landscapes, a fact overlooked when only native ranges are considered.

Megafauna perform significant roles that contribute to the functioning of ecological systems by causing physical disturbance, dispersing seeds great distances, consuming fibrous vegetation which can benefit smaller herbivores and reduce fire-risk,

and by accelerating rates of nutrient cycling. The considerable loss of this functionality at the end of the Pleistocene had dramatic effects on fire regimes, nutrient cycling, food web complexity, and plant community structure (Gill et al. 2009, Bakker et al. 2016, Doughty et al. 2016). Modern declines in megafauna have similar consequences for terrestrial ecosystems and community dynamics, and are of conservation concern (Ripple et al. 2015).

Introductions of megafauna worldwide may be inadvertently restoring some of these processes. Acknowledgement of this possibility is being fostered by the burgeoning concept of ‘rewilding’, which seeks to proactively introduce megafauna in order to provide refuge for these species and to restore lost ecological processes (Svenning et al. 2016). While ‘rewilding’ often argues for intentional introductions of taxon substitutes (Donlan et al. 2006), much remains unknown about the contribution of already introduced populations to global conservation goals.

Given that introduced populations are often unwanted and considered symptomatic of ecological imbalance, the existence of populations that are simultaneously introduced and threatened or extinct in their native ranges has been highlighted as a conservation paradox (Marchetti and Engstrom 2015). Indeed, the considerable redistribution of biota that characterizes the Anthropocene may be a countercurrent to the extinction crisis by providing refuge and new opportunities for threatened species. However, comprehensive analyses of threatened species with introduced populations have not been conducted.

To determine the potential conservation values of introduced megafauna, we compiled current information on introduced populations, their threat statuses and

population trends in their native ranges, their relative population sizes in and out of their native ranges, and their contribution to continental assemblages in the Anthropocene relative to large herbivore diversity during the Pleistocene and Holocene epochs.

## **METHODS**

We searched for all large herbivores with masses  $\geq 100\text{kg}$  (following Ripple et al. 2015) with introduced populations using Long (2003) and supplemented with online searches (Google) using the terms “feral”, “introduced”, “invasive”, “exotic” and “non-native” (Data collection concluded in October 2015).

We calculated the percentage of species with introduced populations within each taxonomic family, their IUCN threat statuses and trends in their historic ranges, and the proportion of their populations that are currently outside of their native ranges (Appendix A). Wild post-domestic species were assigned the threat status of their pre-domestic ancestor. For example, wild cattle (*Bos taurus* or *Bos primigenius taurus*), are the domesticated form of the extinct Aurochs (*Bos primigenius*), and are therefore considered “Extinct” as well.

To understand the importance of introduced large herbivores in continent-scale assemblages, the numbers of native, recently extinct, and introduced large herbivore species on each continent were tabulated and compared. Holocene extinctions included all species that were lost in the last 10,000 years. Europe and Asia were counted as separate continents for this comparison.

We further assessed how Anthropocene large herbivore assemblages compare to those of past geological epochs. For each continent, we compared terrestrial megafauna

richness, persistence and status between the late Pleistocene, Holocene, and Anthropocene epochs. The choice to compare genera-richness instead of species-richness was due to poor resolution in the fossil record and uncertain species-level taxonomy. Unlike the previous comparison, Europe and Asia were grouped together as Eurasia, following the convention of most paleontological literature.

Pleistocene genera were classified as ‘extinct’ or ‘survived’ based on their fate through the late-Pleistocene extinction, which occurred at different times on different continents. For North America and South America, Pleistocene taxa were only included if their most recent remains were dated after 50,000 years ago (Barnosky et al. 2004), which excluded a number of taxa commonly described in relation to the late-Pleistocene overkill extinctions. We counted extinct taxa found within the last 100 thousand years for Eurasia, Africa, and Australia, given the earlier onset of the late-Pleistocene extinctions on these continents (Barnosky et al. 2004). The Holocene included genera from the end of the Pleistocene until the Anthropocene, which we define here as beginning 1650 CE.

Taxa with unknown body masses were excluded. Extinct genera included taxa with surviving species of body masses less than 100kg (e.g. *Macropus*—the kangaroos). Holocene genera included ‘survived’ taxa, natural immigrants, and Holocene extinct species, while Anthropocene genera included ‘survived’, ‘survived’ threatened (if more than 50% of species are threatened on continent), introduced, and introduced threatened genera (Appendix B).

## RESULTS

Eighteen (~24%) of the 76 extant megafauna species have established wild populations outside their native ranges (Appendix A). By including post-domesticates of extinct heritage, an additional two species (the dromedary camel, *Camelus dromedarius* and the cow, *Bos taurus*) are added to the 74 remaining native megafauna. Eleven additional species were excluded from analysis: three species because they appear to be confined to game ranches, five because introductions are within their native continent, one because introduced populations are described as semi-wild, and two because of uncertain taxonomic relation to already included species.

Six (55%) of the eleven families containing herbivorous megafauna have introduced populations outside their native ranges. Introduced species represent between ~24% (Bovidae) and 55% (Cervidae) of the large ( $\geq 100$  kg) herbivore species within their families (Fig. 1). Furthermore, at the genus level, introduced populations represent between 41% (Bovidae) and 100% (Equidae) of the genera within their families.

Of the 18 species with introduced populations, ten (~56%) are threatened or extinct in their native ranges (Fig. 1). This includes two Vulnerable and one Endangered species, three post-domestic species whose wild progenitors are Extinct, one post-domestic whose progenitor is Critically Endangered, and two post-domestics whose progenitors are Endangered. All six post-domestic species are extinct or endangered in their native ranges. The remaining seven introduced large herbivores are currently ranked as Least Concern in their native ranges. Of the 16 introduced species with surviving native populations, eight (50%) are declining in their native ranges, six (~36%) are stable, and two (~13.5%) are increasing (Appendix A).

On average, over 38% (ranging between <1% and 100%) of large herbivore populations are outside of their native ranges. Whereas two species have relatively small (possibly ~100) populations (hippopotamus, *Hippopotamus amphibius*, and Asian elephant, *Elephas maximus*), twelve populations are estimated in the thousands and up to over 1 million individuals (Fig. 2, Appendix A).

Introduced large herbivores constitute a substantial proportion of megafauna assemblages around the globe: 100% of Australia's megafaunal species richness (N = 8 of 8 species), 54% of North America's (N = 7 of 13), 55% of South America's (N = 6 of 11), 36% of Europe's (N = 4 of 11), 9% of Africa's (N = 3 of 35), and 3% of Asia's (N = 1 of 36). Australia has no surviving Pleistocene large herbivores yet is now home to eight introduced species in the Anthropocene, including the Endangered Banteng, the world's only population of wild dromedary camel (*Camelus dromedarius*), the Vulnerable sambar (*Rusa unicolor*), and the water buffalo (*Bubalus bubalis*), the descendant of the Endangered water buffalo (*Bubalus arnee*). Wild donkeys (*Equus asinus*), whose progenitor, the African wild ass (*E. africanus*) is Critically Endangered, and horses (*E. ferus caballus*), have also found refuge in Australia, as well as in North America, South America, and Europe.

Pleistocene losses of megafauna genera (100% for Australia, 86% for South America, 80% for North America, 24% for Eurasia, and 19% for Africa) and Holocene losses (9% for Africa) have been counteracted by gains from introduced megafauna in the Anthropocene, so that there are currently more megafauna genera per continent than during the Holocene. Introduced megafauna have numerically replaced 44% of North America's, 38% of Australia's, 32% of South America's, 29% of Africa's, and 14% of

Eurasia's extinct genera (Fig. 3). North American genera richness increased, from 4 to 6, at the end of the Pleistocene due to immigration of *Cervus* (red deer) and *Alces* (moose) from Eurasia concurrent with the arrival of the first humans to the continent (Meiri *et al.* 2014, Hundertmark *et al.*, 2002).

## **DISCUSSION**

Our results indicate that introduced megafauna represent a significant proportion of the remaining taxonomic diversity of their functional group and are themselves significantly threatened in their historic ranges. This raises the question of how to assign conservation value in an era of extinction. Conservation biology is a field driven by a plurality of values, which offer different visions at different scales (Sandbrook *et al.* 2011). Many of these schools of thought prioritize the conservation of native species at the local and regional scale. However, given the ongoing global extinction threat, more research and dialogue is needed to understand when these values may be counterproductive to other important conservation goals.

While many introduced populations were formerly domesticated, they may still effectively represent their wild relatives; introduced populations of endangered Banteng (*Bos javanicus*) in northern Australia have maintained high genetic fidelity to their pre-domestic ancestors and are valued by some as conservation assets (Bradshaw *et al.* 2005). Likewise, domesticated horses retain a substantial component of the genetic diversity of extinct Holarctic horse lineages (Lippold *et al.* 2011). Given that the closest wild relatives of all six post-domestic introduced megafauna are endangered or extinct, our results suggest that domestication may have been a bridge for certain species from the pre-



pastoral wild landscapes of the early Holocene to the post-industrial wild landscapes of the Anthropocene.

Evolutionary and ecological change has also been witnessed in post-domestic populations: post-domestic goats (*Capra aegragus*) on Aldabra Atoll regularly drink saltwater when freshwater is absent (Burke 1990); wild post-domestic sheep (*Ovis aries*) show higher resistance to local parasites than sympatric domestic sheep; wild Oossabaw island pigs (*Sus scrofa*) have unique lipid structures that have been used in biomedical research (Van Vuren and Hedrick 1989); wild cattle in Mexico do not linger in riparian areas like their sympatric domestic cousins due to altered predation threats (Hernandez et al. 1999); and native Torresian crows (*Corvus orru*) appear to have developed a mutualistic grooming behavior on introduced Banteng in Australia, a behavior not seen otherwise within the species (Bradshaw and White 2006)

Like all herbivores, introduced megafauna can exert strong grazing pressure to the detriment of other species, most notably where apex predators are extirpated or continue to be persecuted (Wallach et al. 2010). Unfortunately, much of the research to document these effects has ignored the ecological context of predator control, which is to ignore an important explanatory variable for the density-dependent effects of all herbivores. Indeed, certain wild horse populations in the United States are limited by mountain lions (Turner and Morrison 2001) and dingoes appear to suppress populations of wild donkeys in Australia (Wallach et al. 2010). The potential to manage irruptive introduced megafauna by protecting or restoring large predators is an important topic for further research.

In the Pleistocene, the ecological influences of large herbivorous megafauna on disturbance regimes, seed dispersal, nutrient cycling, and community structure were

ubiquitous. Introduced megafauna have potentially augmented this lost functional and taxonomic diversity across most continents, particularly in those regions most depleted: Australia, North America, and South America (Fig. 3). Eurasia and Africa have retained many Pleistocene megafauna and have few introduced species. Several of these introductions restore taxonomic analogues to extinct Pleistocene species: introduced donkeys are morphologically similar to congeneric extinct North and South American stilt-legged horses, and the modern wild horse is the same species as the horse of the Holarctic Pleistocene (Weinstock et al. 2005). Determining if introductions of taxonomically dissimilar species restore functionality within insular ecosystems (there are no existing taxonomic analogues to Australia's Pleistocene marsupial megafauna) requires further research into the relative importance of co-evolutionary history versus ecological context (e.g. predator presence) in determining species coexistence and ecosystem function (Wallach et al. 2010).

While most studies are conducted on the premise that introduced species are harmful, substantial evidence suggests that they can perform significant ecological functions (Schlaepfer et al. 2011). Bighorn sheep forage more efficiently, with less time invested in vigilance behaviors in mixed herds with introduced wild horses (Coates and Schemnitz 1994); giant tortoises introduced onto oceanic islands as substitutes for extinct species are dispersing large-seeded endemic plants and shaping plant communities through grazing (Hansen et al. 2010); intentional introductions of horses and cattle in the Oostvaardersplassen nature reserve in the Netherlands have created Pleistocene-like savanna conditions in a temperate deciduous forest environment (Vera 2009); and in North American and Australia, the drying and constriction of desert springs and the

extinction of several endemic fish populations was linked to the removal of wild introduced megafauna whose grazing appeared to maintain open-water habitat (Kodric-Brown and Brown 2007).

Likewise, our own ongoing research is yielding similarly surprising observations. For example, in the Sonoran Desert of North America, wild burros (*E. asinus*) dig groundwater wells of more than a meter in depth (Appendix C). These wells are common wherever groundwater approaches the surface, are used by many other species, and in certain conditions become nurseries for riparian trees (Fig. 4).

It is possible that by creating new water sources across the landscape, maintaining access to receding water-tables during droughts, and providing conditions ideal for the germination of riparian trees, burros play a facilitative role—one that may improve the resilience of these arid ecosystems to climate change. Furthermore, given the ubiquity of taxa whose contemporaries dig wells, such as Proboscideans (Ramey et al. 2013) and other Equids (P. Kaczensky, personal communication, 2015) in the North American Pleistocene, it is likely that introduced burros have restored a functionality recently lost from these landscapes.

The introduced megafauna of the world have numerically restored generic richness across many continents to levels approaching the Pleistocene epoch, and may be an important refuge for their functional group. We propose that further research and dialogue on how introduced megafauna, and their predators, interact in the novel ecosystems of the Anthropocene will be essential in reconciling the concerns of local managers with global conservation efforts and will bring a new attention to the emerging eco-evolutionary trajectories of these populations.

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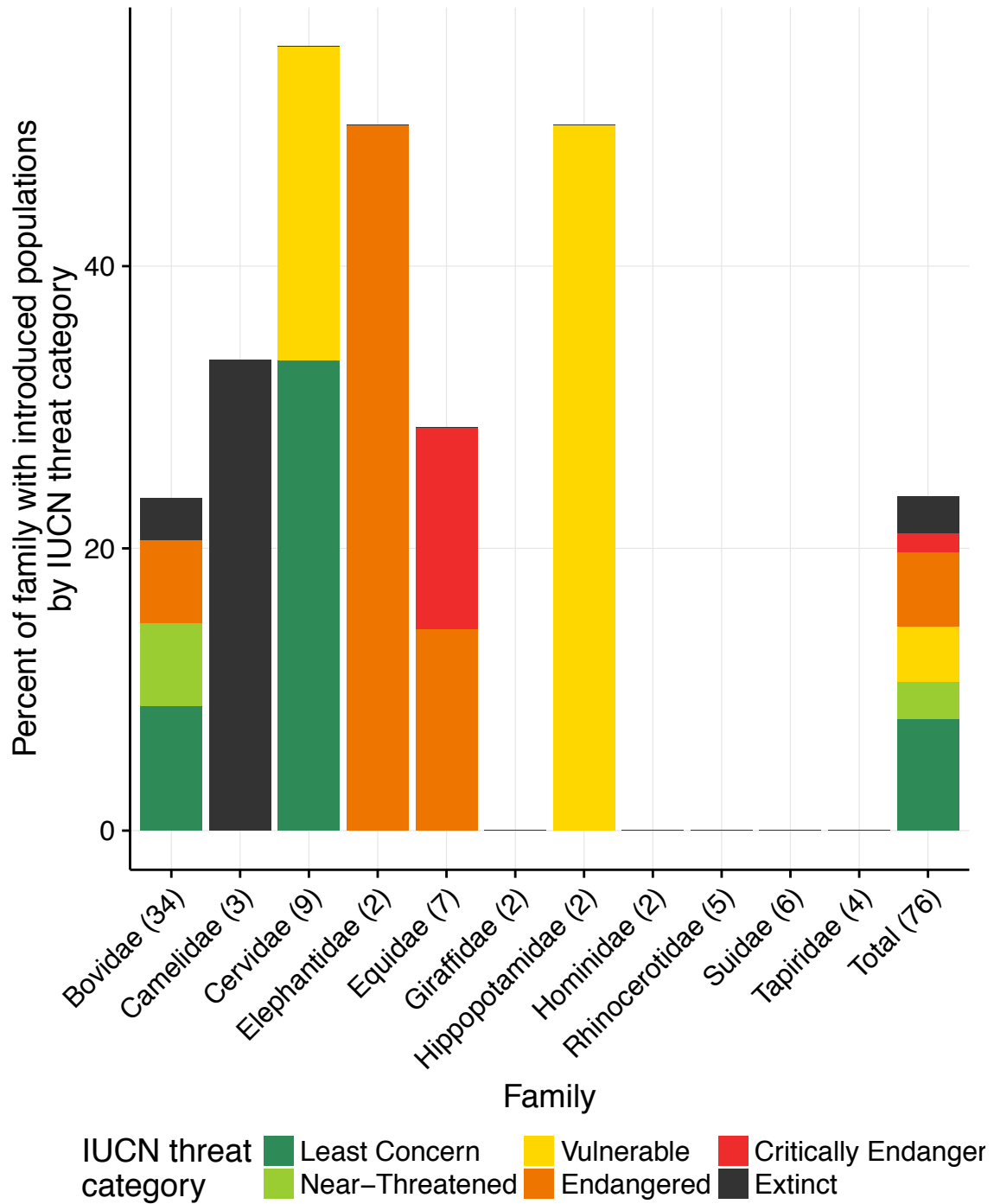


Fig 1. Threatened large herbivore species are finding refuge outside their native ranges. Percent of megafauna ( $\geq 100\text{kg}$  body mass) in each family with introduced populations, colored by IUCN threat categories in their native ranges.



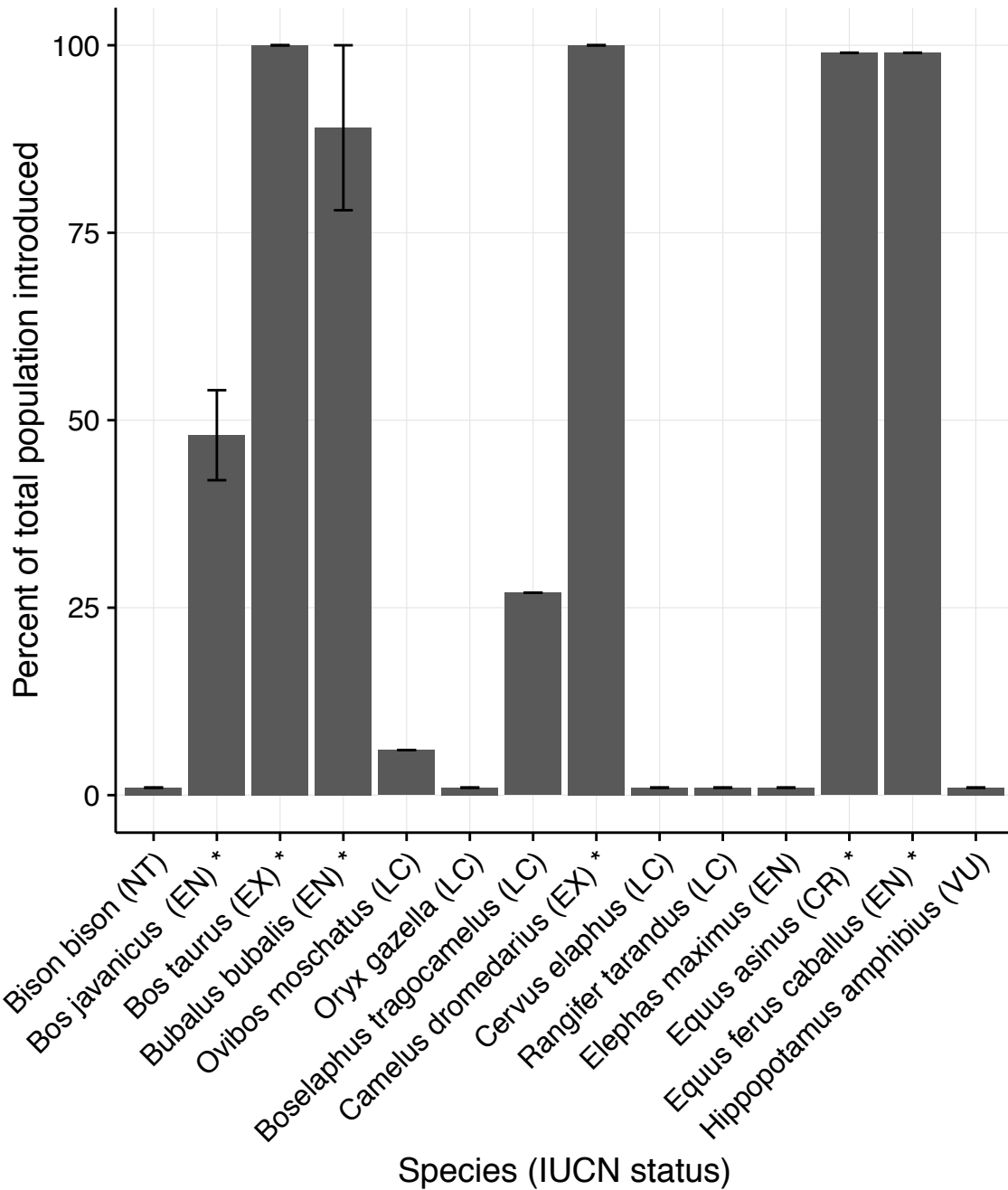


Fig 2. Percent of global populations of megafauna that are introduced. Bars indicate high and low estimates, if multiple estimates were found. Includes only species with known population sizes in native and non-native ranges and thus excludes *Rusa unicolor* (VU), *Rucervus duvaucelii* (VU), *Alces americanus* (LC), and *Ovis ammon* (NT).

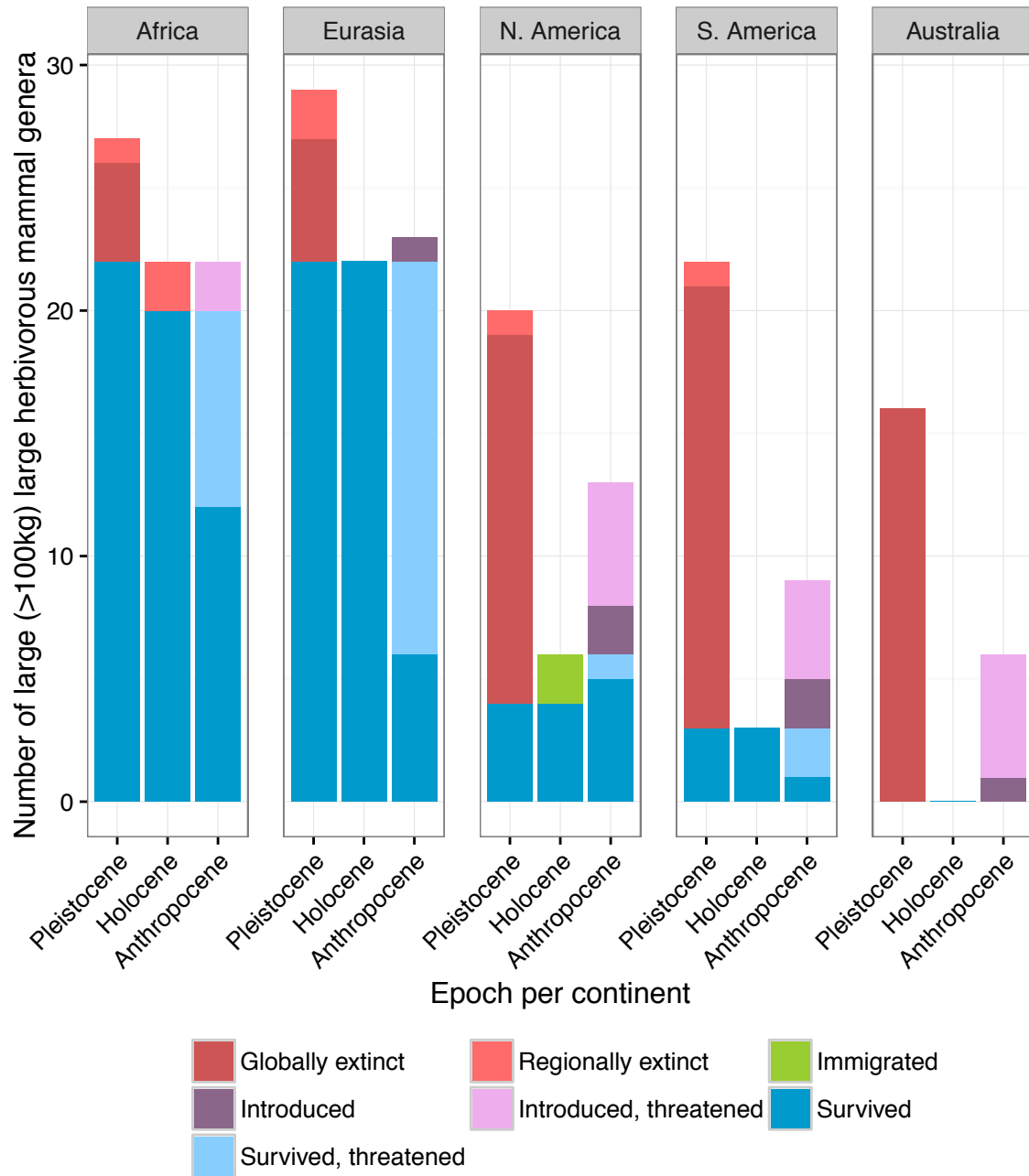


Fig 3. Large herbivore genera-richness per continent and per epoch. ‘Globally extinct’ indicates genera that went extinct on all continents by the end of the Pleistocene; ‘Regionally extinct’ are genera that survived elsewhere; ‘Immigrated’ are genera that immigrated without human intervention; ‘Introduced’ indicates genera introduced by humans; ‘Introduced, threatened’ are introduced genera threatened in their native ranges; ‘Survived’ indicates genera that were still present into the following epoch; ‘Survived, threatened’ are threatened native genera. Genera are counted as threatened if 50% or more of the species are threatened (Appendix B).

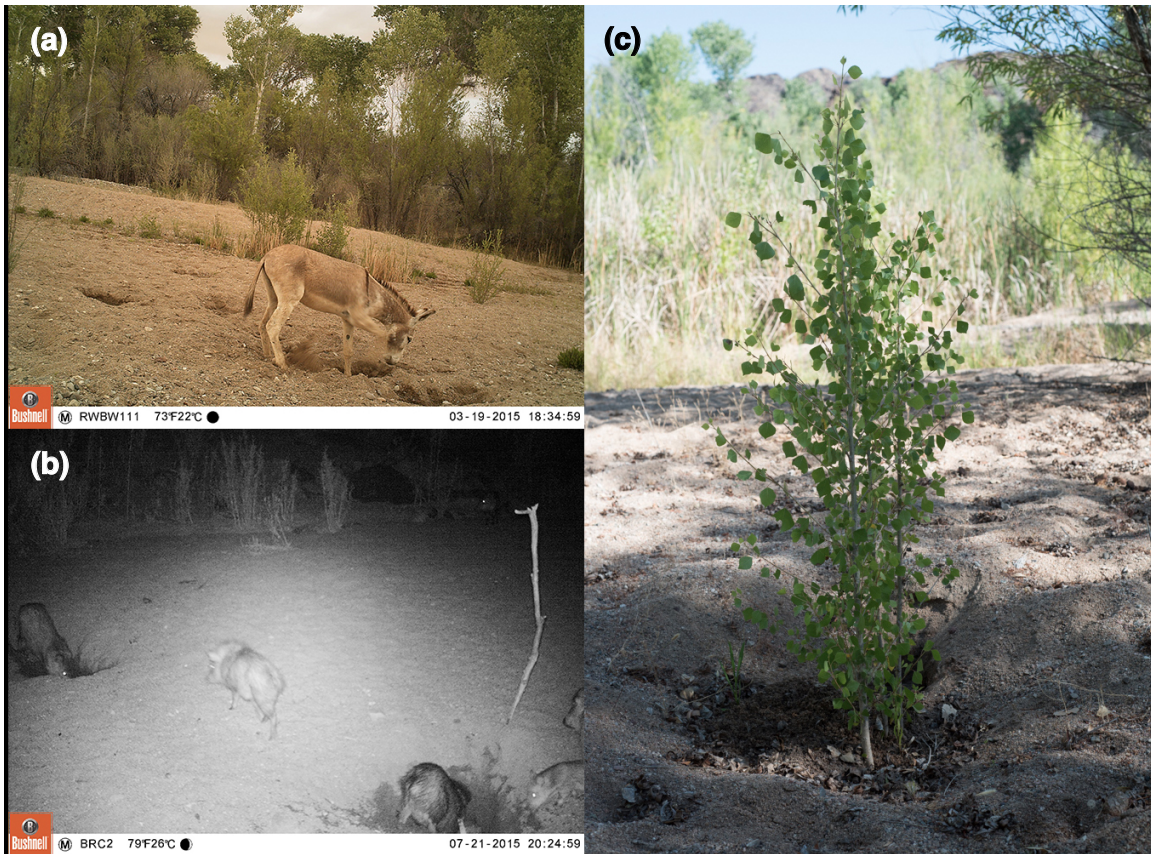


Fig 4. Wild burros increase surface water availability in the Sonoran Desert. (a) Burro digging well to water table, (b) troop of javelina (*Pecari tajacu*) bathing and drinking in burro-wells, and (c) several-year-old Fremont's cottonwoods (*Populus fremontii*) growing in an abandoned burro-well on a high channel bar.

## CHAPTER 3

**TITLE:** Well-digging by wild burros increases water availability through the dry season in the Sonoran Desert of Arizona

### INTRODUCTION

Like most non-native species, the introduced wild burro (*Equus asinus*) of the North American deserts is considered ecologically destructive. Many studies indicate that wild burros compete with native wildlife (Seegmiller and Ohmart 1981, Marshal et al. 2008) and exert strong grazing pressure. However, as documented by Abella (2008) evidence of overgrazing is inconsistent and suffers from weak methodology, and the majority of studies do not account for the ecological context of predator persecution (Lundgren, unpublished data).

In native systems, herbivorous megafauna are known to play critical ecological roles by consuming coarse and unpalatable vegetation to the benefit of smaller herbivores, increasing nutrient cycling rates by orders of magnitude, dispersing nutrients and seeds, and engineering systems through ecological disturbance (Ripple et al. 2015). North America once possessed numerous megafauna species, including several members of the genus *Equus*, the majority of which went extinct at the end of the Pleistocene epoch due to overhunting by early humans (Barnosky et al. 2004). Today, burros are the largest extant megafauna in the deserts of North America, leading some to view the introduction of burros to North America as an inadvertent case of Pleistocene rewilding (Donlan et al. 2006). Studying introduced burros as megafauna, rather than as introduced ‘invasive’ species—an emotional metaphor many times indicted for oversimplifying

ecological processes (Davis et al. 2011, Lidström et al. 2015)—may provide an alternative lens to understand the ecology of these organisms in the novel ecosystems of the Anthropocene.

This article describes a previously unstudied behavior of introduced wild burros. In the Sonoran Desert of Arizona, wild burros dig groundwater wells of more than a meter in depth. These wells are common wherever groundwater approaches the surface, are utilized by other species, and in certain situations become nurseries for riparian trees (Lundgren, Chapter 4). Burro-wells are common on the floodplains of perennial streams, within the channels of intermittent streams, and in ephemeral desert systems. In intermittent systems, well digging is common year-round, including when there is natural adjacent surface water.

Burro-wells are generally a square meter in area and occur in clusters of as few as three and as many as 30 wells in areas ranging from 25m<sup>2</sup> to 500m<sup>2</sup>. Well clusters are generally located in areas with little to no vegetative cover, and are generally located proximal to clear entrance and exit trails. While I have personally found burro-wells of just over a meter in depth, McKnight (1958), in the only publication to mention burro-wells, described burros digging as deep as five feet (1.5m) to reach groundwater.

Worldwide, well digging is relatively common among large desert-dwelling species, and is known in African elephants *Loxodonta* (Haynes 2012), gemsbok *Oryx gazella* (Hamilton et al. 1977), and the Khula *Equus hemionus* (Feh et al. 2002). The effects of well-digging in these native systems have been described as ecosystem engineering (Haynes 2012), as they maintain access to water through dry seasons (Hamilton et al. 1977), are relied upon by many other species (Payne 1999) and increase

the heterogeneity of riparian systems (Naiman and Rogers 1997). However, no published studies have quantified the effects of this behavior on the availability and spatial distribution of water resources.

In the Sonoran Desert, coyotes (*Canis latrans*) also dig to access groundwater, although this behavior appears casually only in non-scientific literature, and was only observed in one location during the study period. Regardless, it is likely that this behavior is not entirely unique to wild burros in North America, but that wild burros dig more readily (even in the presence of other sources of water), more efficiently, and to greater depths than other species.

#### *Potential effects of well-digging on other species*

Several desert animals, particularly large-bodied species such as mule deer and bighorn sheep, are semi-dependent upon free-water, or surface water, to survive, especially through the summer and if forage quality is poor (Krausman et al. 2006). Epps et al. (2004) determined that the third greatest threat after elevation and precipitation to the persistence of desert bighorn sheep was the disappearance of springs and other water sources due to climate change and continued groundwater depletion. For this reason, land managers for decades have invested significant effort installing artificial water features to augment wildlife populations across the Southwest (Rosenstock et al. 2004). However, this practice is not without controversy, as disease outbreaks have been linked to wildlife water tanks, as have mortalities from drowning (Swift et al. 2000). Others have expressed concern that artificial water sources create scenarios of hyper-predation and intensified competition (Broyles 1995).

Although modeling efforts have demonstrated the importance of surface water in the resource selection habits of both mule deer and bighorn sheep (Rautenstrauch and Krausman 1989, Bleich et al. 2010), surprisingly few empirical studies have unequivocally demonstrated an effect of increasing water resources on wildlife populations. Burkett and Thompson (1994) found negligible effects of artificial water sources on small mammal, invertebrate, and herpetofauna richness or composition, and Broyles and Cutler (1999) found no difference in bighorn sheep population structures between ranges with and without surface water in the Cabeza Prieta, Arizona. However, survivorship of endangered Sonoran pronghorn, especially fawns, is strongly affected by the absence of free-water, even if forage succulence is above average (Beale and Holmgren 1975). Moreover, the movement patterns and abundances of African ungulates are largely controlled by water availability (Western 1975).

Decreasing the distance between water sources in dryland systems increases available habitat for water-dependent species. Bleich et al. (2010), using a resource selection function (RSF) developed from bighorn sheep telemetry data, predicted that decreasing distance to water from 3033m to an average of 2000m would yield a 92% increase in high quality habitat for bighorn sheep in the deserts of western Arizona. Longshore et al. (2009) showed that drought and groundwater mining reduced the number of permanent summer-dependable natural water sources in Joshua Tree National Park from 19 in 1950 to 5 in 2004, which, based on RSF predictions, reduced available summer habitat for desert bighorn sheep from an estimated 584 km<sup>2</sup> to 171 km<sup>2</sup> within the park.

Movement patterns of mule deer (*Odocoileus virginianus*) in the Sonoran Desert pivot around water sources with substantial range contraction during the summer dry season (Rautenstrauch and Krausman 1989). Similarly, as the number of distinct water sources increases, elephant (*Loxodonta africana*) home range sizes decrease (de Beer and van Aarde 2008). Activity patterns of predators at water sources has also been shown to be driven primarily by time since last rainfall and nearest-neighbor distance to other water sources (Atwood et al. 2011).

Isolated water sources are likely to be intense areas of competition (Perry et al. 2016), disease transmission (owing to animal congregation) (Barlow 1996), and herbivory (Thrash et al. 1993). Increasing the number of water sources likely moderates these interactions. For example, the use of densely vegetated watering holes by Sonoran pronghorn during summer droughts is related to increased fawn predation (Bright and Hervert 2005), and congregation in riparian areas increases exposure and transmission between bighorn sheep and gastropod hosts of lungworm (Rogerson et al. 2008, Whiting et al. 2009). Increasing the number of water sources and reducing their isolation likely moderates these effects.

Some desert species can extract sufficient moisture from food (pre-formed water), and are thus independent of free-water for survival. Yet by obtaining water from food, these species' food requirements change when free-water is absent: as free-water availability decreases, water replaces nutrients and energy as the driving trophic currency in food webs, which can increase interaction strengths and destabilize food web dynamics (McCluney and Sabo 2009, Allen et al. 2014). Therefore, water availability likely has



strong effects on the dynamics of desert food webs, even of potentially water-independent organisms.

Alterations in spatial patterning of water resources due to the digging of wells likely influences both free-water independent and dependent species. Reducing nearest-neighbor distance and average distance between water sources is likely to increase available habitat for free-water dependent species, reduce the energy spent accessing water, decrease competition and the risk of predation, and reduce interaction strengths by decoupling water from trophic interactions.

I wished to identify the geographic extent of well digging by wild burros and describe how this behavior increases water availability and alters the spatial patterning of water resources. I predicted that burro wells would sustain water access when natural sources of water were absent; would increase the amount of water available and the number of water sources available per km of intermittent stream; and would decrease average distance, nearest-neighbor distance, and consecutive distances between water sources.

## **METHODS**

### *Regional surveys*

Regional surveys throughout the deserts of Arizona, Nevada, and northwestern Mexico were undertaken between 2015 and 2016 to identify areas with burro wells. Sites were investigated based on evidence of riparian vegetation in Google Earth or prior knowledge of water availability. Sites were evaluated for the presence of burros in the area, the type of hydrologic system (perennial, intermittent, ephemeral), soil substrate,

and for the presence of burro wells. Only a subset of these sites with burro wells was selected for repeat surveys.

### *Study Sites*

Two sites, Black Canyon and Hackberry Wash, were selected for repeat surveys in 2015, based on presence of burro wells and accessibility. These two sites plus a third site, Greenwood Spring, were monitored in 2016 as well. All sites were located in the Arizona Upland subdivision of the Sonoran desert (Brown 1994). Upland vegetation was dominated by foothills palo verde (*Parkinsonia microphylla*), creosote bush (*Larrea tridentata*), saguaro (*Carnegiea gigantea*), and triangle-leaf bursage (*Ambrosia deltoidea*), with scattered presence of crucifixion thorn (*Canotia holacantha*) and juniper (*Juniperus californica*) at Black Canyon and Greenwood Springs, and Joshua tree (*Yucca brevifolia*) at Hackberry Wash. Riparian vegetation consisted of tamarisk (*Tamarix chinensis*), Goodding willow (*Salix gooddingii*), Fremont cottonwood (*Populus fremontii*), seepwillow (*Baccharis salicifolia*), burrobrush (*Hymenoclea monogyra*), and mesquite (*Prosopis juliflora*), with a lesser presence of velvet ash (*Fraxinus velutina*) at Black Canyon.

The entirety of each sites' riparian zone was surveyed, with the exception of the terminus of Hackberry wash, which drains into the Santa Maria River. This section was surveyed 200m upstream and 200m downstream from the confluence with Hackberry. This stretch was representative of the Santa Maria River's water levels until its own confluence with the Big Sandy River upstream of Lake Alamo and the consequent surfacing of groundwater. In addition to this section, the Hackberry Wash survey was

1280m (total survey of 1680m). The Black Canyon survey was 1817m long and encompassed the extent of the intermittent riparian zone of the drainage. The Greenwood Spring survey, encompassing the intermittent riparian section of this drainage, was only 400m long.

Additional reconnaissance, using satellite photography and on-foot, identified the nearest external perennial water features to each survey site for sites with less than two perennial water features. For Hackberry Wash, this was a perched mountain spring in the nearby Black Mountains (1600m away); and for Greenwood Spring, it was Burro Creek (6192m away) and a cattle stock tank (3477m away).

#### *Water availability*

The effect of well-digging by wild burros on water availability was quantified in several ways. Sites were surveyed as frequently as possible, approximately every two weeks, during the summer of 2015 and 2016. During 2015 and the first survey of 2016 (May), the upstream end of water locations were recorded with GPS technology. For each location the number of active, wet wells was recorded and in a modified (finer-scale) version of the Nature Conservancy's wet/dry mapping protocol, all water sources within channel, and the distances between were mapped in relation to distance from beginning of water location (Turner and Richter 2011). From this, the linear dimension (parallel to river channel) and location of water sources water was determined. Only the length was measured because measuring perimeter accurately was impractical, and most water sources were rarely more than 1.5m wide; likewise water depth was not estimated because depth was generally shallow but could vary drastically across water sources and

is likely not as biologically significant for terrestrial water-using species. After the first survey of 2016, the linear dimension of burro wells were measured as well.

At Hackberry Wash in 2015 and 2016, several shallow wells were found that appeared to have been dug by other species; the digging marks of the wells were evident of small clawed or cloven-hoofed feet. This was further supported by two weeks of camera monitoring on one well cluster; no burros visited the wells and coyotes were seen excavating fresh wells. These wells, unlike burro-wells, were shallow (<30cm) and occurred in dense dried mud.

To estimate the linear dimension of wells from 2015 and survey one of 2016, the average well length (.4m) and standard deviation (.16) was calculated from the remaining 2016 surveys (n = 34), after high outliers (>.8m, n = 6) were removed. Since the distribution of well lengths was normally distributed and had a low standard deviation and range (.1-.8), randomized estimates of well lengths were applied post-hoc to the 2015 and survey one well lengths using the R package 'truncnorm' (version 1.0-7).

To compare the effect of burro wells on water quantity at sites, the number of linear meters of water were summed for each water origin class: natural, modified by human, burro-dug, and dug by other species.

To understand the relative effect of different water origins on the spatial distribution of water, the locations of each distinct water-feature were mapped with GIS tools (R packages: 'sp' v1.2.3, 'rgdal' v1.1.10, and QGIS v2.14.0). Water classes were treated additively because the effect of burro wells on water distribution patterns is dependent upon background distribution patterns of natural and modified water. Therefore, only natural water was included in the 'natural' class; natural and modified

were included in the ‘modified’ class; natural, modified, and burro-dug were included in the ‘burro’ class; and natural, modified, and other species’ wells were included in the ‘other species’ class.

Distance between water sources and nearest neighbor distance was calculated (R package ‘rgeos’ v0.3.20) for each additive water class. Calculating these statistics for the natural water class was impossible when there was only one (or zero) water source(s) present, therefore the nearest external perennial source was included. External water features to Black Canyon were not included in the spatial analysis of Black Canyon water resources due to the year-round persistence of water at the site in the two modified springs (which allowed calculation of distance metrics).

The ecological relevance of the spatial patterning of water resources likely varies depending on the biology of the water-user; therefore approaching these patterns from different scales was necessary. For example, trail camera observations of burro wells showed frequent and consistent use of background wells by rodents and amphibians concurrent with the use of foreground wells by larger species, but concurrent use by similar sized species was rare. Therefore, both of these comparisons, as well as density of water per km were conducted on a feature scale (including every distinct water source) and a patch scale—where water sources within 5m of each other were lumped.

To understand how different water origins affected the linear distribution of water along the stream channel, water features were snapped to a stream channel polyline in R (package ‘maptools’ v.8.39 and ‘geosphere’ v1.5.5). Maximum and average distance between consecutive water sources was calculated to understand how various water

origins alter the linear distribution of water in intermittent streams. External features were excluded from this analysis.

## **RESULTS**

### *Regional surveys*

Of 25 sites surveyed in 2015 and 2016, 15 had evidence of burro presence. Of these, 11 had burro wells. Six of these 15 systems were perennial, two were intermittent, and two were ephemeral, the rest had undeterminable hydrology.

Of the four sites with burros but without burro wells, two were in drainages with fine, clay soils, or heavily compacted clay and gravel soils (Fig. 1). All sites with burro wells had sediments composed of sand, gravel, or cobbles. The other two sites with burros but without wells had recently experienced floods, which likely removed any evidence of well digging.

The 10 sites where burros were absent were often in close geographic proximity to areas with burros and had similar abiotic conditions: all had sand, gravel or cobble sediments and were located in similar topography and vegetation as sites with burros. Four of these sites were perennial streams, one was a perennial seep, and five had undeterminable hydrology. Burro absence may reflect seasonal shifts in landscape use, as there was no evidence that absence was due to site characteristics.

### *Repeat surveys – Black Canyon*

At Black Canyon, surface water was available throughout both 2015 and 2016 in two densely vegetated, human-modified springs, which retained water with concrete

walls. Without these modifications, it is unclear how much surface water would be available. These springs contained an average of 1m and 6m linear meters of water over the course of the survey periods (and were between 20cm and 1m in width). Additionally, a *tinaja* (or natural water tank) was present at the upstream edge of the survey area, which contained water on 7/17/15, 8/16/15, and 9/3/16 (Fig. 2). Burro wells were present throughout both survey years in two main clusters.

At Black Canyon, burro wells substantially augmented the linear meters of available water by between 16% and 74% (Fig. 3), increased total number of water sources by 175% - 1450% in the fine scale analysis and 67% - 200% in the patch scale analysis (Fig. 4); reduced average distance between consecutive water features by 70% - 97% (Fig. 5); changed average distance by -4% - 52% in the fine scale analysis and -3% - 20% in the patch scale analysis; and reduced nearest-neighbor distance by 76% - 99% in the fine scale analysis and 27% - 84% in the patch scale analysis; Fig. 6) (Table 1). The increases in average distance at both scales were due to the digging of burro wells outside the former extent of natural/modified surface water.

### *Greenwood Spring*

Burro wells were common at Greenwood Spring in March 2016 during a reconnaissance visit, downstream from a small natural spring. However, burro wells were abandoned and dried before the second survey period starting 6/25/16. For the rest of the monitoring period, water availability was limited to a small (2-3m long) seep (Fig. 2). External water sources consisted of Burro Creek (6192m away) and a cattle stock tank (3477m away).

At Greenwood Spring, burro wells when present augmented the linear meters of available water by 73% (Fig. 3), increased total number of water sources by 1400% in the fine scale analysis, 1300% in the patch scale analysis (Fig. 4); changed average distance by 69% in the fine scale analysis, 68% in the patch scale analysis; and reduced nearest-neighbor distance by 91% in the fine scale analysis, and 90% in the patch scale analysis (Fig. 6). Calculating reduction in distance between consecutive water sources was not possible since there was only one natural water source (Table 1).

### *Hackberry Wash*

In late spring, 2015, and 2016, spring-fed surface water was present at the upstream portion of this site during the first survey, however by 8/15/15 and 6/25/16, this water receded to subsurface. Additionally, several stone *tinajas* store water runoff at this site, but only for limited periods of time. During the 8/15/15 10/2/15, 6/25/16 and 7/10/16 survey periods the only water available was from burro wells or wells dug by other species. The wells dug by coyotes at this site occurred in the thick mud of the now dry *tinajas* (Fig. 2).

Hackberry Wash drains into the Santa Maria River, a large intermittent stream. The Santa Maria River retained natural water after Hackberry Wash had already dried, but eventually dried up as well. There was no water in the Santa Maria River survey segment on 7/4/15, 6/25/16 and 7/10/16. Floods added intermittent moisture to Hackberry Wash, refilled *tinajas*, washed out wells and caused surface stream flow in the Santa Maria on 7/4/15, 8/4/16, 8/9/16, 8/10/16, 8/27/16.



At the intermittent site (Hackberry Wash), burro wells and wells dug by coyotes provided the only water when natural surface water dried (on the 6/25/16 and 7/10/16 survey periods). When water was still present at Hackberry Wash, burro wells substantially augmented the linear meters of available water by between .3% and 73% (Fig. 3); increased total number of water sources by 25% -1300% at the fine scale and 33% -300% at the patch scale (Fig. 4); reduced average distance between consecutive water features by 11% - 93% (Fig. 5); reduced average distance by 8% - 65% at the fine scale and 7% - 43% at the patch scale analysis; and reduced nearest-neighbor distance by 20%- 93% at the fine scale and 24% -77% at the patch scale (Fig 6, Table 1).

Wells dug by coyotes were present during three survey periods (10/2/15, 6/25/16 and 7/10/16). During the 2016 survey periods, these wells provided 40% to 50% of the linear meters of water at that time (the rest were provided by burro wells) (Fig. 3); and produced between 1.19 and .59 sources/km when no natural water sources were available (burros provided between .59 and 2.38 sources/km at that time). In both 2015 and 2016 there were one or zero natural sources of background water other than other species' wells and burro wells, making calculating the effect of other species' wells on water arrangement impossible.

## **DISCUSSION**

Water is a critical limiting resource in aridlands worldwide. The distribution of water in deserts has strong effects on animal communities and associated ecosystem processes; therefore modification of surface water availability by animal activity is a topic of a great interest. The effects of well-digging on water availability has gone

unstudied but likely has strong implications on how ecological communities respond to increasing risk of drought (McCluney et al. 2012). Modifications of water availability by native organisms, such as the maintenance of surface water in drought-prone streams by beaver dams (Magoulick and Kobza 2003, Hood and Bayley 2008), have been referred to as ecological engineering. Burros likewise substantially increased the number of water sources and the linear meters of water available, and reduced consecutive distance, average distance, and nearest neighbor distance between water sources at the sites monitored. These alterations of the abiotic environment suggest that, in certain contexts, wild introduced burros act as ecosystem engineers (Jones et al. 1994) in the Sonoran Desert.

At Hackberry Wash, the study's one true intermittent site, burro wells and wells dug by coyotes sustained water access when no natural water was available. While natural water was present, burro wells substantially increased water availability and altered spatial patterning of water at this site. Likewise, at Black Canyon, burro wells substantially augmented water availability and reduced the distance between water sources. At both sites, burros likely increased the ability of organisms to find water and avoid competition and predation threat.

The limited availability of wells at Greenwood Spring, which were only present on the first survey, is likely due to substantial declines in the water table downstream from the perennial seep. When wells were absent, I dug in the bottom of old wells and found water within a meter and a half of the surface. I suspect that if there had been no perennial water at this site, the burros would have dug deep enough to reach the water table. It is likely that the penchant to dig is driven by landscape scale patterns of

background water availability—that the effort invested in digging may be proportional to desperation.

Unfortunately, despite the strong effects of burro wells on water availability at the sites monitored, this study suffers from its small sample size. Accessing additional sites, which were found in remote, mountainous and road-less terrain through the hot summer dry season was impractical and dangerous. However, regional surveys undertaken in the winter and spring of 2016 did indicate the ubiquity of this behavioral phenomenon across the burros' range in the Sonoran Desert. High resolution remote sensing or drone-based aerial photography of intermittent and riparian desert systems would be essential for further research on the importance of this behavior on larger temporal and spatial scales.

Through both survey years, other species dug only 7 wells at one monitored site, while burros dug 184 wells between the three sites. It is likely that well digging by other species can also play significant roles in the aridlands of North America. However, during regional surveys wells were only found in areas with clear burro sign, and all wells showed clear evidence that burros dug them. The other species' wells at Hackberry Wash were limited to two survey periods and to fine clay soil, which only occurred in the main *tinaja* of the site. The near absence of burro wells in systems with fine clay or silt sediments, and observations of burro slip-marks in fine sediments, suggest that substrate type may constrain well-digging animals. Future monitoring of areas with and without burros, or burro-specific enclosure experiments in areas with wells, would help decipher how different species contribute to accessing water in these arid landscapes.

By digging wells to access groundwater, burros appear to be a type of ecological engineer referred to as 'critical-link species' (Westman 1990), which are species that link

resources between resource-rich and resource-poor systems. For example, greenfall from phreatophytic (groundwater reliant) trees supplies water to terrestrial arthropod herbivores in arid systems (Sabo et al. 2008), water excretions from cicada nymphs feeding on phreatophytic trees may provide as much as 12% of yearly precipitation to upper soil layers on the hyper-arid Lower Colorado River (Andersen 1994), and mistletoes, which, as parasites, live in nutrient-unlimited environments, produce nutrient-rich leaf litter that appears to hypercharge soil food webs and sustain high avian diversity and abundance (Watson 2009). These influences are functionally similar to well digging by burros and other species.

In addition to increasing potential habitat for water-dependent species, further research on how burro wells alter food web dynamics of free water-independent species will provide a fascinating lens into the role these linkage species can play in engineering ecosystems, particularly in the face of ongoing climate change and drought risk (McCluney et al. 2012). It is likely that by increasing water availability, burro wells decouple water from trophic interactions: Golightly and Ohmart (1984) found that kitfoxes and coyotes in the Sonoran desert consume fewer rodents in the presence of free-water, McCluney and Sabo (2009) found that both crickets and wolf spiders interaction strengths weakened in response to increased free-water availability in experimental treatments on the San Pedro River in Arizona; likewise, the Nubian ibex requires more green foliage in the absence of surface water (Hochman and Kotler 2006), as do crickets which can lead to potentially severe herbivory (Sabo et al. 2008). Increasing free-water availability decouples energy and water in food-web dynamics, and can lead to more commensal interactions (Sabo et al. 2008). If burro wells play a similar role, which seems

likely, then the effects of this behavior are likely to cascade through food webs by increasing water availability for burros and other species.

The evidence that burros substantially increase the availability of water in quantity, linear size, and spatial pattern strongly suggests that, in certain contexts, introduced wild burros act as ecosystem engineers in the Sonoran Desert. Given that the North American landscape once possessed numerous Equid species as well as other megafauna known to dig wells (e.g. elephants), it now seems likely, as others have suggested (Donlan et al. 2006), that burros have restored a functionality recently lost from these landscapes.

As introduced species, burros are conventionally thought of as ‘pests.’ However, judging species based on their historic origins says little about their present ecology: if the effect of a species is judged *a priori*, then evidence can easily be sought to fit the claim. The fact that burro wells are common across North American desert landscapes but have never been studied is evidence of this self-fulfilling prophecy and suggests that many other species may be playing important ecological roles that have been ignored because we did not expect them. Relaxing the concept of nativity may allow us to better address concerns with the ecological effects of introduced species by finding synergy with broader goals, such as the protection of movement corridors and promoting tolerance for predators (Wallach et al. 2015). More importantly, doing so may help us become more aware of the thriving, persistent wildness of the Anthropocene.

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Table 1. Results from analyses, comparing linear meters of water, number of water sources/km, and spatial metrics with and without burro wells at fine scale and patch scale (all water sources within five meters, lumped).

Metric	Perennial springs				Intermittent stream	
	Black Canyon		Greenwood Spring	Hackberry Wash	Hackberry Wash	
	2015	2016	2016	2015	2015	2016
Increase in linear meters water	12% - 32% (1.6m of 12.8m; 5.2 of 16.5m)	16% - 74% (2.1 of 12.7m and 5.8m of 7.8m)	73% (6.7m of 9.2m)	3% - 73% (2.8m of 80m; 1.3m of 1.8m)	3% - 60% (.7m of 219m; 3.5m of 5.8m)	
Reduction in average consecutive distance	75% - 93% (1338m to 335m; 1338m to 97m)	70% - 97% (448m to 136m; 1339m to 45m)	N/A	22% - 93% (186m to 145m; 984m to 71m)	11% - 84% (150m to 133m; 264m to 43m)	
Increase in number of water features / km	150% - 650% (1.1 to 2.75; 1.1 to 8.25)	175% - 1450% (2.2 to 6.05; 1.1 to 17.06)	1400% (2.5 to 37.5)	350% - 1300% (1.19 to 5.36; 49 to 8.3)	25% - 500% (4.76 to 5.9; 2.97 to 17.85)	
Reduction in average distance	24% - 41% (625m to 481m; 625m to 372m)	4% - 52% (477m to 496m; 631m to 304m)	69% (3549m to 1090m)	35% - 65% (819m to 530m; 1199m to 415m)	8% - 52% (621m to 571m; 839m to 403m)	
Reduction in nearest neighbor distance	80% - 98% (1269m to 251m; 1269m to 31.7m)	76% - 99% (564m to 135m; 1261m to 15m)	91% (4320m to 570m)	62% - 93% (666m to 252m; 2398m to 158m)	20% - 82% (260m to 208m; 321m to 59m)	
Increase in number of water features / km	67% - 150% (1.65 to 2.75; 1.1 to 2.75)	67% - 200% (1.65 to 2.75; 1.1 to 3.3)	1300% (2.5 to 35)	100% - 300% (1.19 to 2.38; 59 to 2.38)	33% - 220% (3.57 to 4.76; 2.97 to 9.52)	
Reduction in average distance	-3 - 16% (624m to 641m; 634m to 532m)	13% - 20% (631m to 546m; 630m to 504m)	68% (3548 to 1144)	7% - 43% (818m to 757m; 1106m to 632m)	10% - 39% (734m to 660m; 838m to 513m)	
Reduction in nearest neighbor distance	64% - 80% (509m to 181m; 1268m to 251m)	27% - 84% (652m to 410m; 1260m to 203m)	90% (6152 to 605m)	34% - 77% (664m to 440m; 2396m to 548m)	24%-66% (333m to 254m; 319m to 117m)	
	<b>Fine scale</b>			<b>Patch scale</b>		

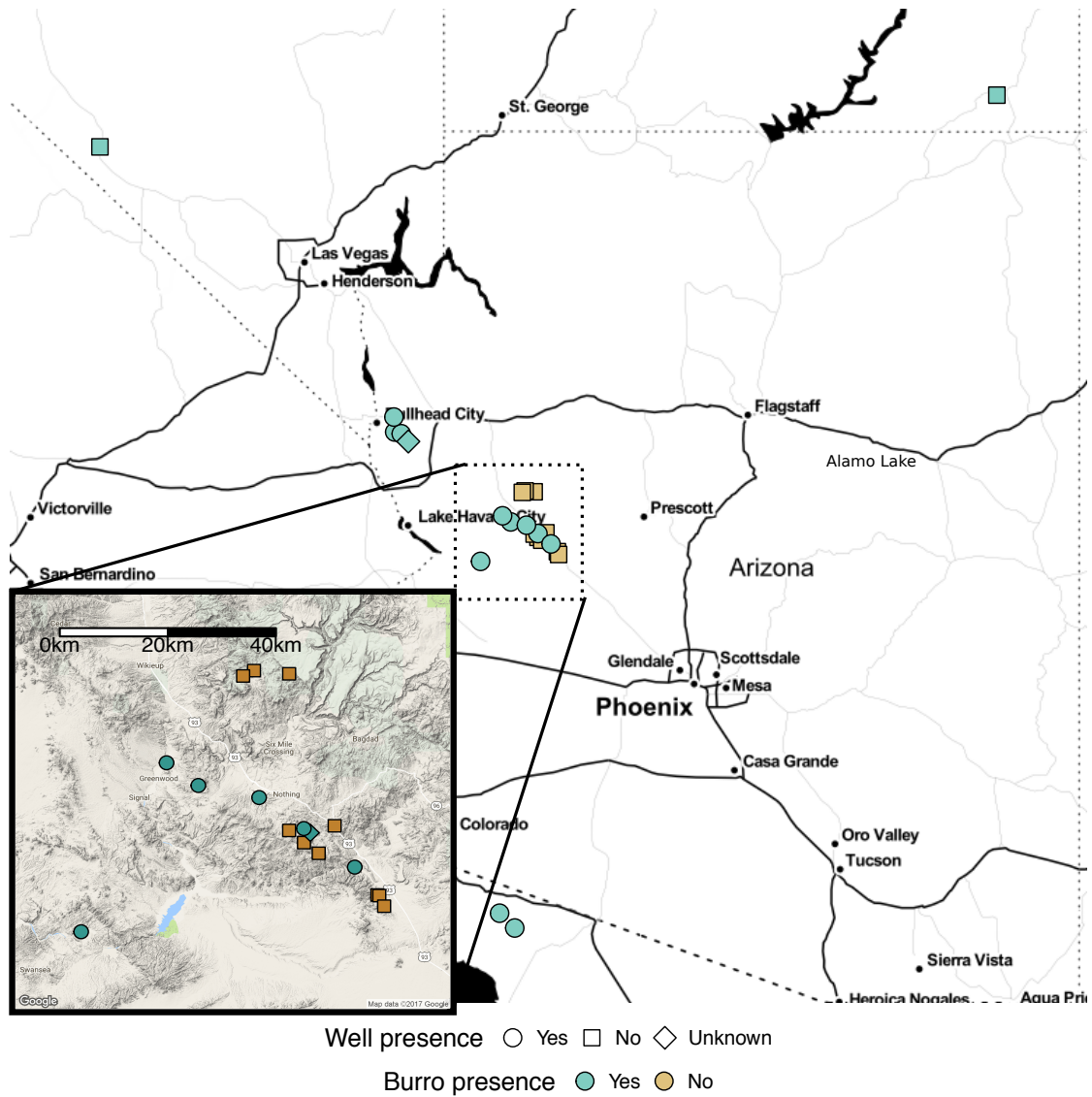


Fig 1. Regional surveys of burro well locations, indicating presence of wells and presence of burros. All surveys were conducted in 2015 and 2016. Map made in R, 'ggmap', version 2.6.1 (Kahle and Wickham).

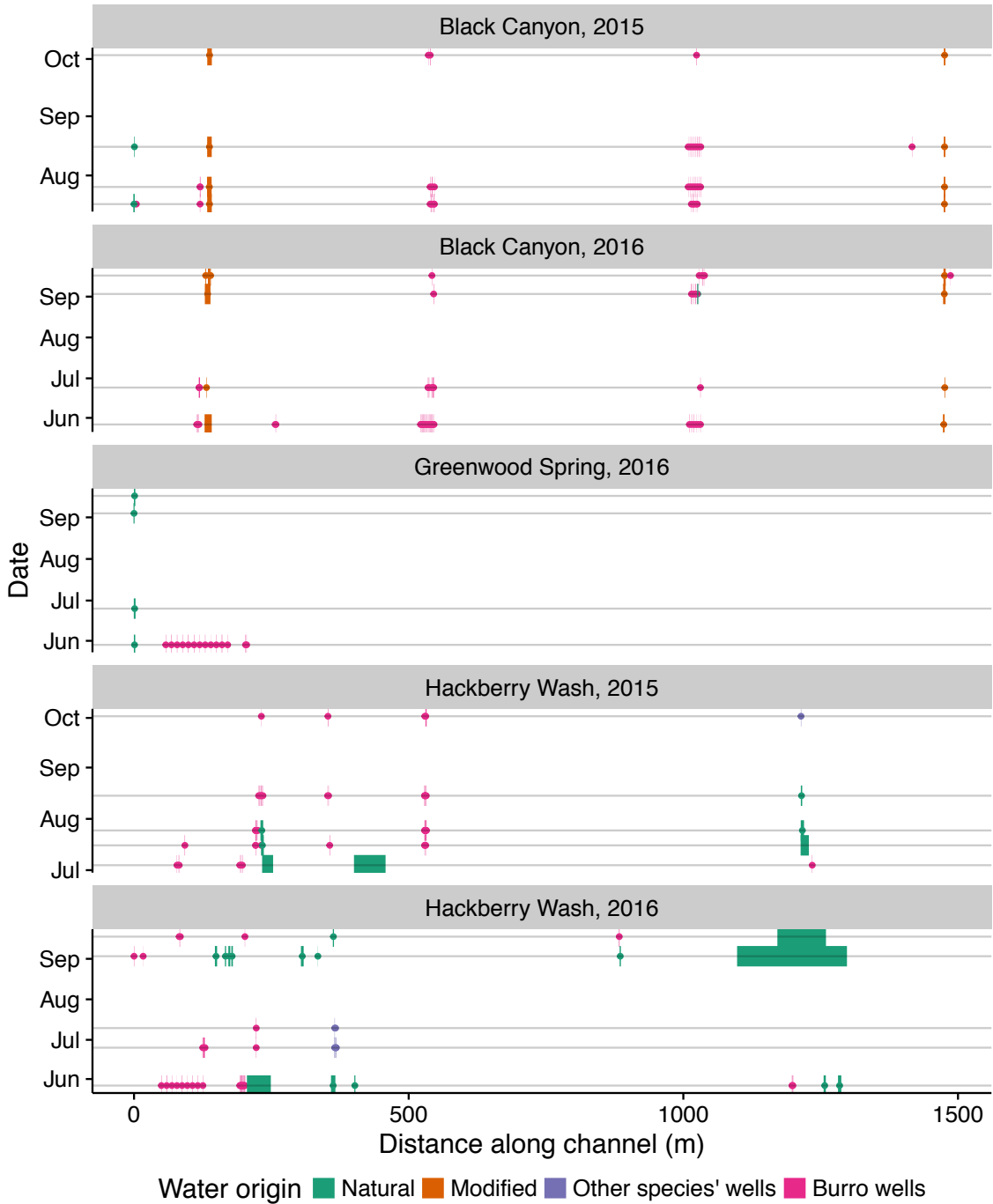


Fig 2. Distribution of water sources along stream surveys from upstream end to downstream terminus of survey. Horizontal lines indicate sampling period. Width of vertical bars indicate actual linear dimension of water. Natural water sources include groundwater fed springs, and surface water from precipitation runoff; modified water sources are water sources retained by dams or weirs; other species' wells are wells dug by coyotes or other species; burro wells are wells definitively dug by burros. Hackberry Wash includes the Santa Maria River at the downstream end.

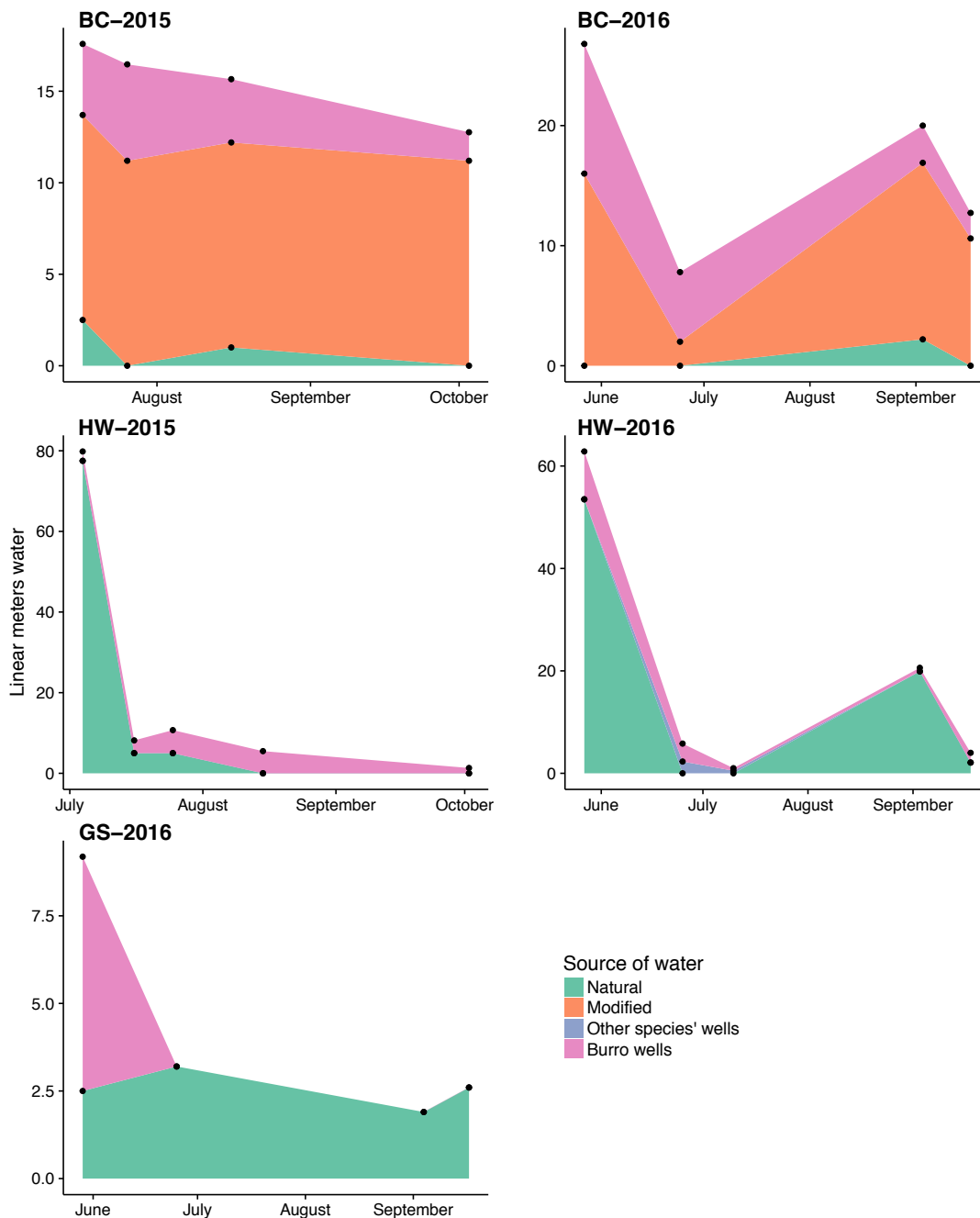


Fig 3. Linear meters water available through 2015 and 2016 survey season. Ribbons are stacked additively on background sources of water. Dots indicate measurements at survey periods. Site abbreviations: 'BC' is Black Canyon, 'HW' is Hackberry Wash, and 'GS' is Greenwood Spring. The Santa Maria River was excluded graphically from the HW graphs because the 400m extent of it, which was in flood during one sampling period, swamped the patterns occurring through the rest of the surveys.

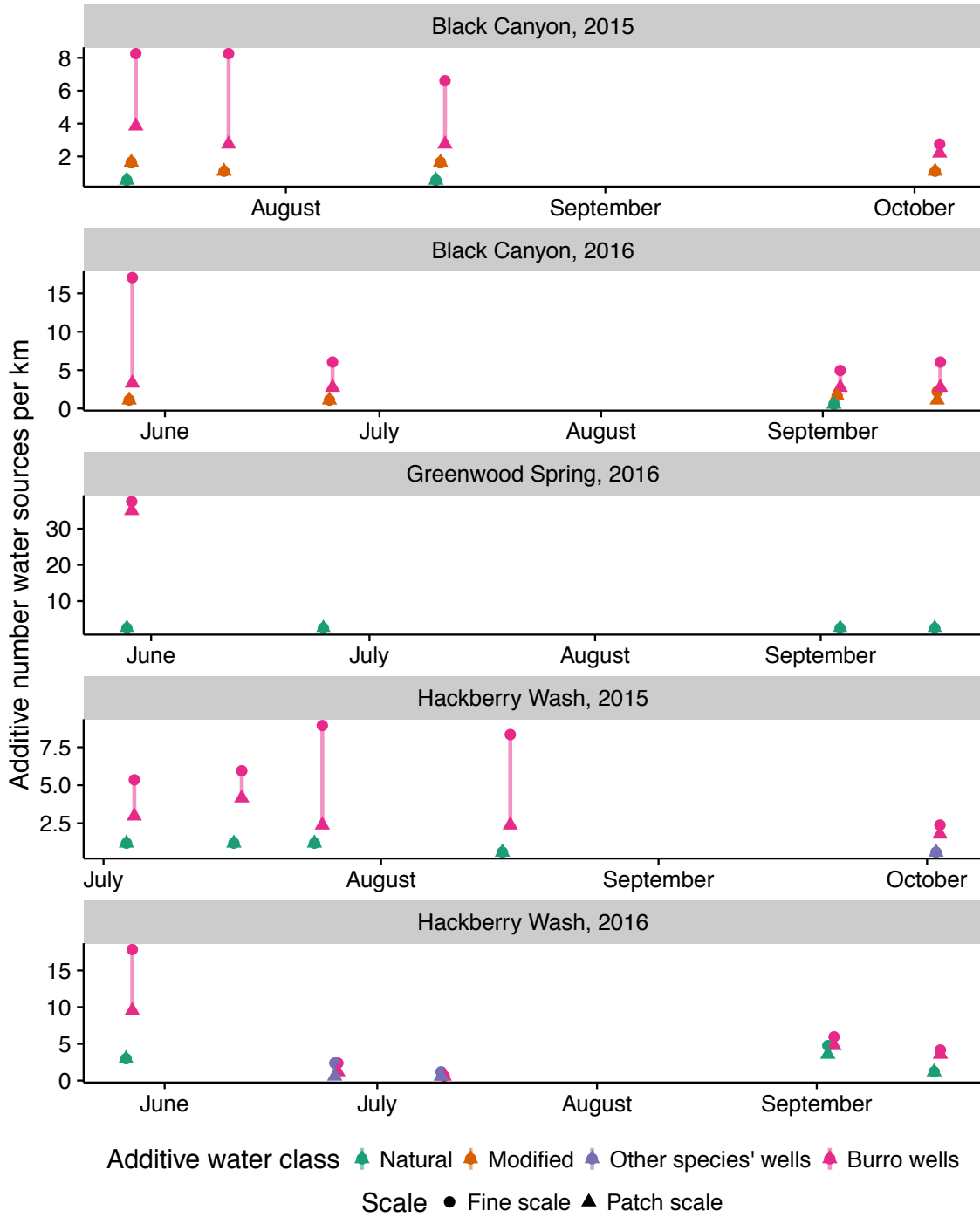


Fig 4. Number of water sources per km at two scales. Fine-scale water sources are every distinct water source. For patch-scale water sources, all water sources within 5m have been lumped. Additive water classes were calculated from base levels of water availability: natural water was calculated from only natural sources of water; modified water was calculated from natural and modified sources of water; the burro well class was calculated from natural, modified water and burro wells; and the other species' wells class was calculated from natural, modified, and other species' wells.

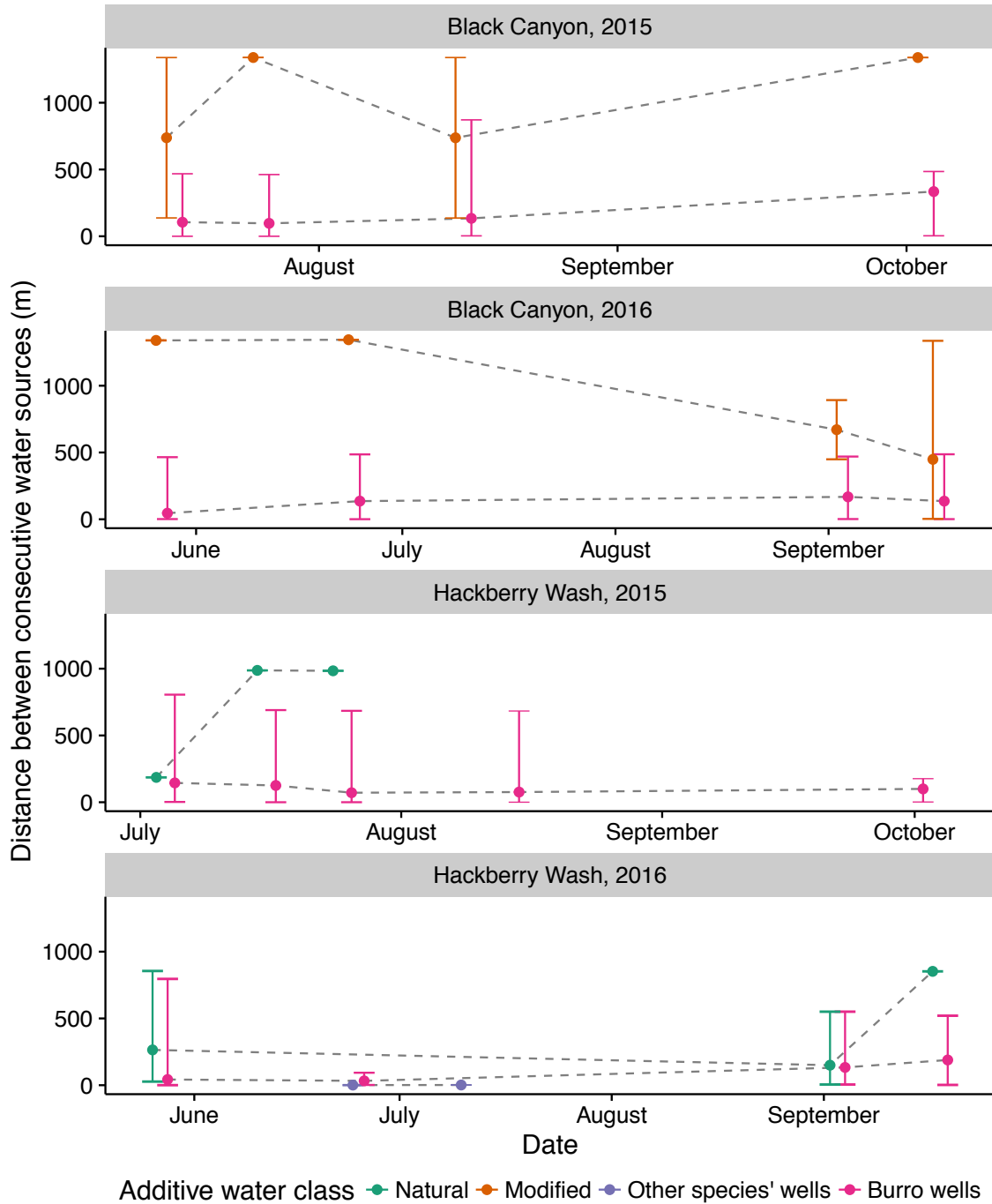


Fig 5. Consecutive distance between water features along stream channel. Points are average consecutive distance, and error bars indicate minimum and maximum consecutive distances. Additive water classes were calculated from base levels of water availability: natural water was calculated from only natural sources of water; modified water was calculated from natural and modified sources of water; the burro well class was calculated from natural, modified water and burro wells; and the other species' wells class was calculated from natural, modified, and other species' wells.

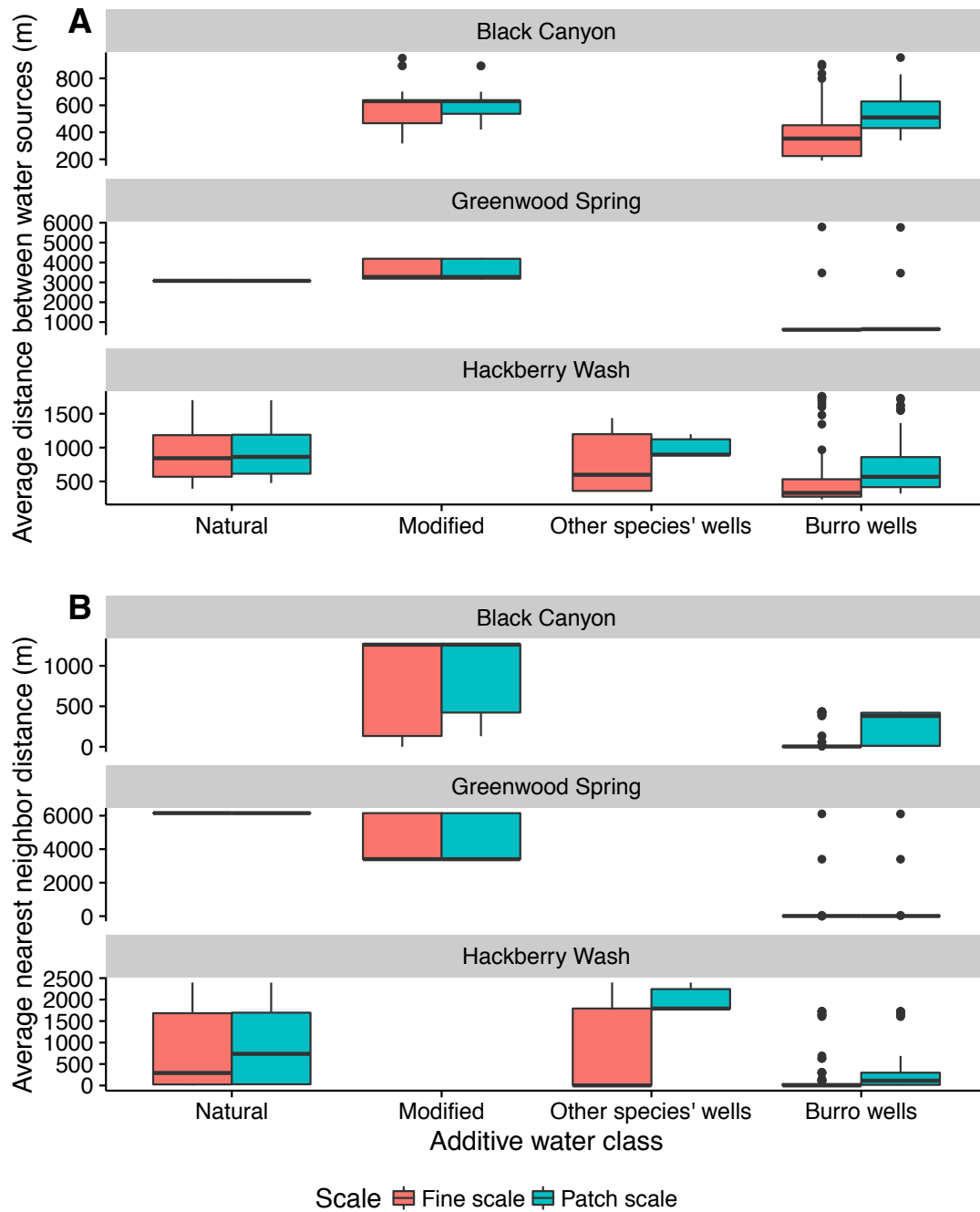


Fig 6. Distance metrics at two scales, for 2015/2016 survey periods. A. Average distance between water sources at fine-scale (all distinct water sources) and patch-scale (water sources within 5m lumped). B. Average nearest-neighbor distance at fine scale and path scale. Additive water classes were calculated from base levels of water availability: natural water was calculated from only natural sources of water; modified water was calculated from natural and modified sources of water; the burro well class was calculated from natural, modified water and burro wells; and the other species' wells class was calculated from natural, modified, and other species' wells



## CHAPTER 4

**TITLE:** Well digging by wild burros and other species increases species richness and animal activity in the Sonoran Desert.

### INTRODUCTION

The increase in water availability caused by wild burros, as described in Chapter 2 of the present thesis, likely has strong effects on species other than burros (*Equus asinus*), both by extending available habitat for water-dependent species (Longshore et al. 2009) and by altering food web dynamics by decoupling energy from water (McCluney and Sabo 2009). However, there is also the possibility that interference competition by wild burros restricts usage of well sites by other species. Interference competition at isolated water sources has been shown between introduced wild horses (*Equus caballus*) and pronghorn (*Antilocapra americana*) (Gooch et al. 2017) and elk (*Cervus canadensis*) (Perry et al. 2016). Thus, the question remains as to whether the wells dug by wild burros are used by other species.

Interspecies dominance hierarchies at water sources are also known from native systems, with patterns of dominance corresponding to body size (Valeix et al. 2007). The existence of dominance hierarchies does not preclude water use by sub-dominant species as the need to forage away from water sites by dominant species likely provides windows for subdominant species, allowing temporal partitioning of these shared resources (Carothers and Jaksić 1984, Atwood et al. 2011).

Burros dig wells even in the presence of perennial sources of water. This suggests that well-digging itself is a response to predation threat, interference competition, or is conducted in order to access higher quality water, as is the case in African elephants

(*Loxodonta africana*) (Ramey et al. 2013). Burro well clusters are dynamic as they require frequent re-digging and are washed away by floods, and are generally located in open areas with clear lines of sight. These characteristics differ from perennial, natural and manmade water sources, which are often densely vegetated, especially in systems with low-power flood regimes. It is likely that species have differential affinities for vegetation cover based on predator avoidance strategies (Kotler 1984) which may be reflected in the differential use of burro wells compared to other water sources.

I was interested in describing how vertebrate species composition and activity differed between natural water, well clusters, and dry control sites. Specifically, I wished to test two hypotheses: Visit frequency, activity duration, species richness, and species diversity (1) would be significantly greater at burro well sites than at dry controls and (2) would not be significantly different between burro wells and natural water sites.

## **METHODS**

Two sites, Black Canyon and Hackberry Wash, were selected for study in 2015, based on the presence of burro wells and on accessibility. These two sites, in addition to a third site, Greenwood Spring, were monitored throughout 2016. All sites were located in the Arizona Upland subdivision of the Sonoran desert (Brown 1994). Upland vegetation was dominated by foothills palo verde (*Parkinsonia microphylla*), creosote bush (*Larrea tridentata*), saguaro (*Carnegiea gigantea*), triangle-leaf bursage (*Ambrosia deltoidea*), with scattered presence of crucifixion thorn (*Canotia holacantha*) and juniper (*Juniperus californica*) at Black Canyon and Greenwood Springs, and Joshua tree (*Yucca brevifolia*) at Hackberry Wash. Riparian vegetation consisted of tamarisk (*Tamarix chinensis*),

Goodding willow (*Salix gooddingii*), Fremont cottonwood (*Populus fremontii*), seepwillow (*Baccharis salicifolia*), burrobrush (*Hymenoclea monogyra*), and mesquite (*Prosopis juliflora*), with a lesser presence of velvet ash (*Fraxinus velutina*) at Black Canyon.

To evaluate how burro wells affected the local abundance and diversity of animal species at sites, trail cameras were employed during the summers of 2015 and 2016. In the summer of 2015, Bushnell Trophy Cam HD (Bushnell Outdoor Products, Overland Park, Kansas, USA) trail cameras were installed on burro-well clusters and were checked approximately every fourteen days. In the summer of 2016, trail cameras (same model) were installed on burro-wells, other natural water sources, and adjacent dry areas, which were placed 150m upstream or downstream from well clusters and were matched based on similarity in vegetation type, which reflects depth to groundwater and has strong controls over animal movement patterns and community composition (Kluever et al. 2016). At each site, cameras were installed at consistent distances from water sources.

Organisms captured in trail camera images were identified to species. ‘Events’ were classified based on any contiguous activity by the same species, with no more than a fifteen-minute gap between images. The total duration of events was calculated and used to determine the duration of time spent by species at sites. To account for evenness of use, a modified version of the Shannon Diversity Index was used, wherein the sum of the ratio of each species’ number of visits to total visits multiplied by the natural log of the same was calculated for each site and water type.

Data from 2015 and 2016 was used to calculate species composition of sites and water types. When comparing all three treatments, only 2016 data was included and was

relativized by dividing each of the above dependent variables (duration, number of visits, richness, and diversity) by total sampling effort at a particular station. Observations from each water type were lumped within each site. Differences between water types were tested with ANOVA omnibus tests if data could be transformed to meet assumptions of normality and equal variance, or with Kruskal-Wallis non-parametric ANOVAs Tukey HSD or non-parametric Conover post-hoc tests (Conover 1999), in R package ‘PMCMR’ (v4.1), were conducted depending on satisfaction of assumptions. With the exception of the Conover post-hoc tests, all other tests were conducted in R package ‘stats’ v3.3.2. In some cases, omnibus tests were insignificant, but post-hoc tests were conducted to provide some insight into differences between treatments as justified by (Hsu 1999) and (Maxwell and Delaney 2013).

## **RESULTS**

In 2016, across all sites, burro wells were monitored for 2234 hours, dry sites were monitored for 16,873 hours, modified water sources were monitored for 2219 hours, natural sources for 3419 hours, and wells dug by other species for 478 hours. The disproportionate monitoring of dry sites was caused by battery failure and exhaustion of memory card capacity at wells and natural water sites.

Trail cameras recorded 36 species at burro well sites over the course of 2015 and 2016 monitoring periods. Of these, 30 were recorded drinking from burro wells (Appendix D). Three species were detected at burro wells but not at other habitat types. Nineteen species were detected at other species wells, including one species that was not detected elsewhere. Fifty-one species were detected at natural or modified waters, of

which 41 were recorded drinking. Twenty-six species were recorded at dry controls, one of which was not recorded at burro well sites.

Burros were the most active users and most frequent visitors to burro wells at Black Canyon and Greenwood Spring, followed by Common Ravens (*Corvus corax*), cattle (*Bos taurus*), and Gambel's Quail (*Callipepla gambelii*). At Hackberry Wash, cattle were the most active and most frequent visitors to burro wells, followed by burros and javelina (*Pecari tajacu*). Interestingly, burros were infrequent users of natural or modified water sources relative to the other common users (Fig. 1 & 2). Natural and modified sources were dominated by Mourning Doves (*Zenaida macroura*), gray foxes (*Urocyon cinereoargenteus*) and cattle at Black Canyon; by cattle, wild horses (*Equus ferus caballus*), and Gambel's Quail at Greenwood Spring; and by cattle and mule deer (*Odocoileus hemionus*) at Hackberry Wash (Fig. 1 & 2). Well and natural/modified water sites were only documented in use an average of 4% and 8% of total sampling effort respectively, and dry sites only .5% of sampling effort.

After transformation with recommendations from the boxCox function in R package 'car' (v2.1-3), parametric one-way ANOVA showed that relative species richness was significantly different between water types monitored ( $F_3 = 15.87$ ,  $p = .003$ ). Parametric Tukey's post-hoc test showed significant differences between dry sites and burro wells ( $p = .005$ ), natural sites ( $p = .006$ ), and other species' wells ( $p = .014$ ), with no significant difference between any combination of natural sites, burro wells, and other species' wells ( $p = .98$ ).

There was a significant difference in relative visit frequency in the omnibus test (untransformed, parametric:  $F_3 = 4.99 = .045$ ), but a following Tukey post-hoc test

showed no difference between treatment groups. Relative duration of visits was not significantly different using a non-parametric Kruskal-Wallis ANOVA ( $\chi^2 = 6.3$ ,  $df = 3$ ,  $p = .1$ ), nor with consecutive nonparametric post-hoc tests. Finally, nonparametric Kruskal-Wallis test showed no significance in diversity between sites ( $\chi^2 = 4.7$ ,  $df = 3$ ,  $p = .19$ ), nor did post-hoc tests reveal any significant difference (Fig. 3).

These tests were conducted a second time with burros excluded to remove burro activity from the response variables and to test the effect of wells solely on other species. Relative richness was significantly different between monitored areas (transformed with boxCox function as above:  $F_3 = 15.49$ ,  $p = .003$ ), with significant differences between dry sites and burro wells ( $p = .005$ ), natural sites ( $p = .006$ ), and other species' wells ( $p = .014$ ), but not between natural, burro wells, or other species' wells. Relative visit frequency, as when burros were included, was significant ( $F_3 = 6.27$ ,  $p = .03$ ), with significant differences between other species' wells and dry ( $p = .03$ ) but not between any other treatment types. Relative visit duration, transformed with boxCox was significant ( $F_3 = 5.38$ ,  $p = .04$ ), with post-hoc tests revealing significant differences only between natural and dry sites ( $p = .04$ ). Kruskal-Wallis ANOVA did not find significant differences in relative Shannon Diversity between treatments ( $\chi^2 = 3.8$ ,  $df = 3$ ,  $p = .28$ ), nor did post-hoc tests reveal significance (Fig. 3).

## **DISCUSSION**

Our results indicate that by digging wells, burros and other species increase species richness relative to adjacent dry areas and are not significantly different than

natural water sources, and this result remained significant after the removal of burros from the analysis.

Burros were the dominant users of burro wells, but were only present at well sites from 1%-3% of total monitoring time. It is likely, given our field observations, that use of burro wells by smaller-bodied species is more common but significantly under recorded by our trail cameras. It is highly likely that the use of water sites by smaller, less detectable species was more frequent than the data suggests. During fieldwork, Yellow Warblers (*Setophaga petechia*), rock squirrels (*Otospermophilus variegatus*), and Common Ravens (*Corvus corax*) were observed using burro wells in the immediate vicinity, but were not detected by trail cameras.

It also appears that wells are of comparable quality with respect to animal communities as natural or modified water sources. Differences in total species richness between natural/modified sources and wells (36 versus 51) do suggest, however, that natural water sources may be preferred to burro wells. This may be due to differences in vegetation cover between well sites and natural/modified sites. Burro well clusters are generally located in areas with little vegetation cover, whereas natural, perennial water sources often support dense vegetation, which may alter predation risk for certain species (Kotler 1984). Further research comparing vegetation cover between burro well clusters and natural water sources may determine how differences in species composition between these water sources reflect habitat affinities of burros or other species. It is possible that burro wells are a particularly high quality water resource for species averse to dense vegetative cover.

The relative scarcity of burros at natural and modified water sources suggests that burros may in fact dig wells in order to avoid predation risk at natural water sources. Predators have been shown to strongly affect ungulate use of vegetated riparian areas (Ripple and Beschta 2004), as predator abundance attenuates with distance from perennial water, while herbivore abundance increases (DeStefano et al. 2000). Interactions between burros and predators in the Sonoran Desert are largely unstudied but evidence does suggest that mountain lions (*Puma concolor*) can exert profound influences on wild horse (*Equus ferus*) population dynamics (Turner and Morrison 2001), and trail camera footage from sites with consistent mountain lion presence indicate common and severe injuries in wild burros.

This study suffered from small sample size, although it is visually apparent (Fig. 3) that well digging by burros and other species, in addition to dramatically increasing water availability (Chapter 2, thesis) provides resources used by many other species and affects the local composition of the animal community in a way that is comparable to natural water sources. Further research, at additional sites, it would be necessary to further document how animal-made water sources affect animal communities.

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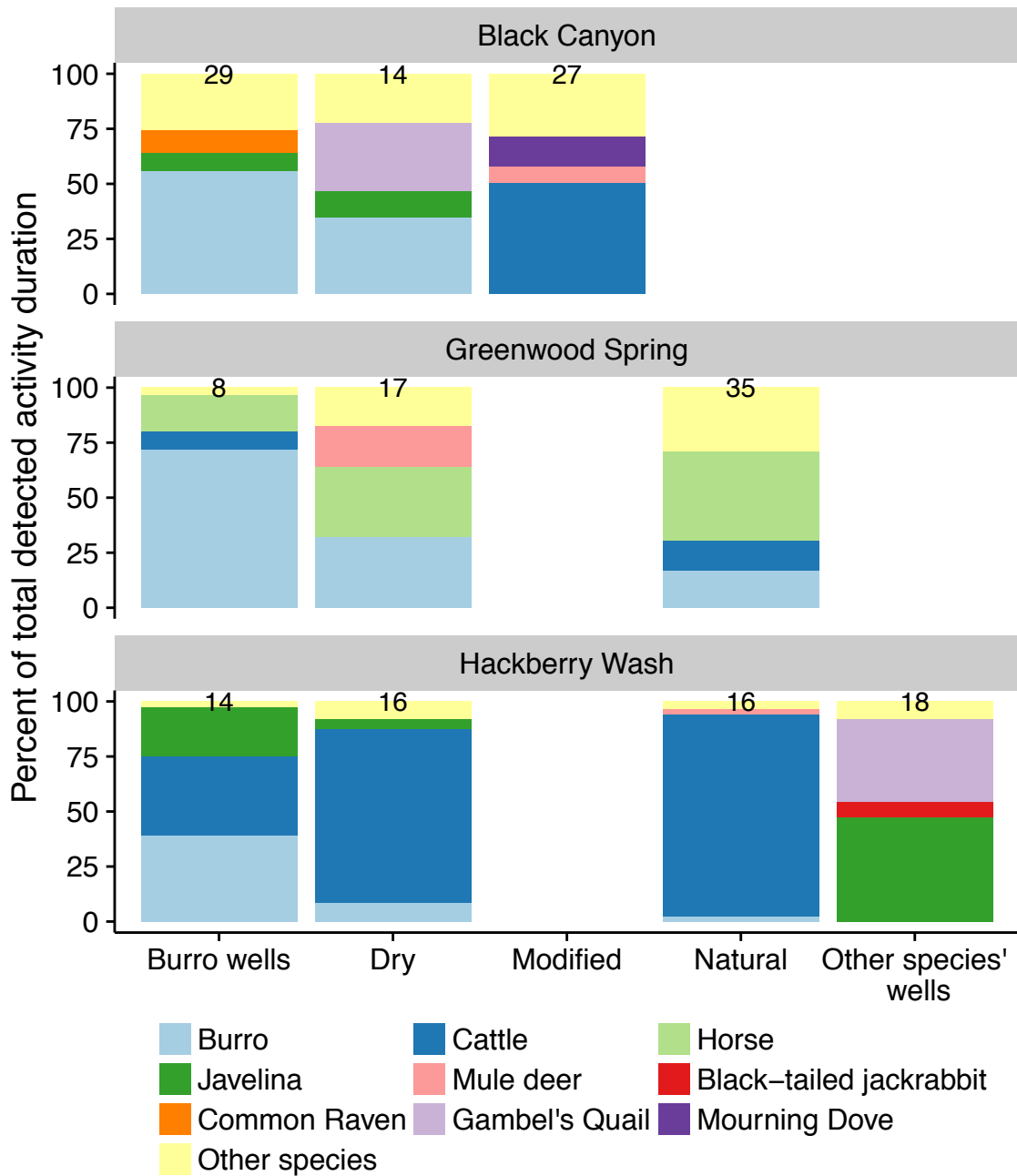


Fig 1. Percent of total detected site use calculated from duration of activity divided by total activity duration for all species. The three most active species from each water type at each site are indicated with color; the number of other species is annotated on each bar.

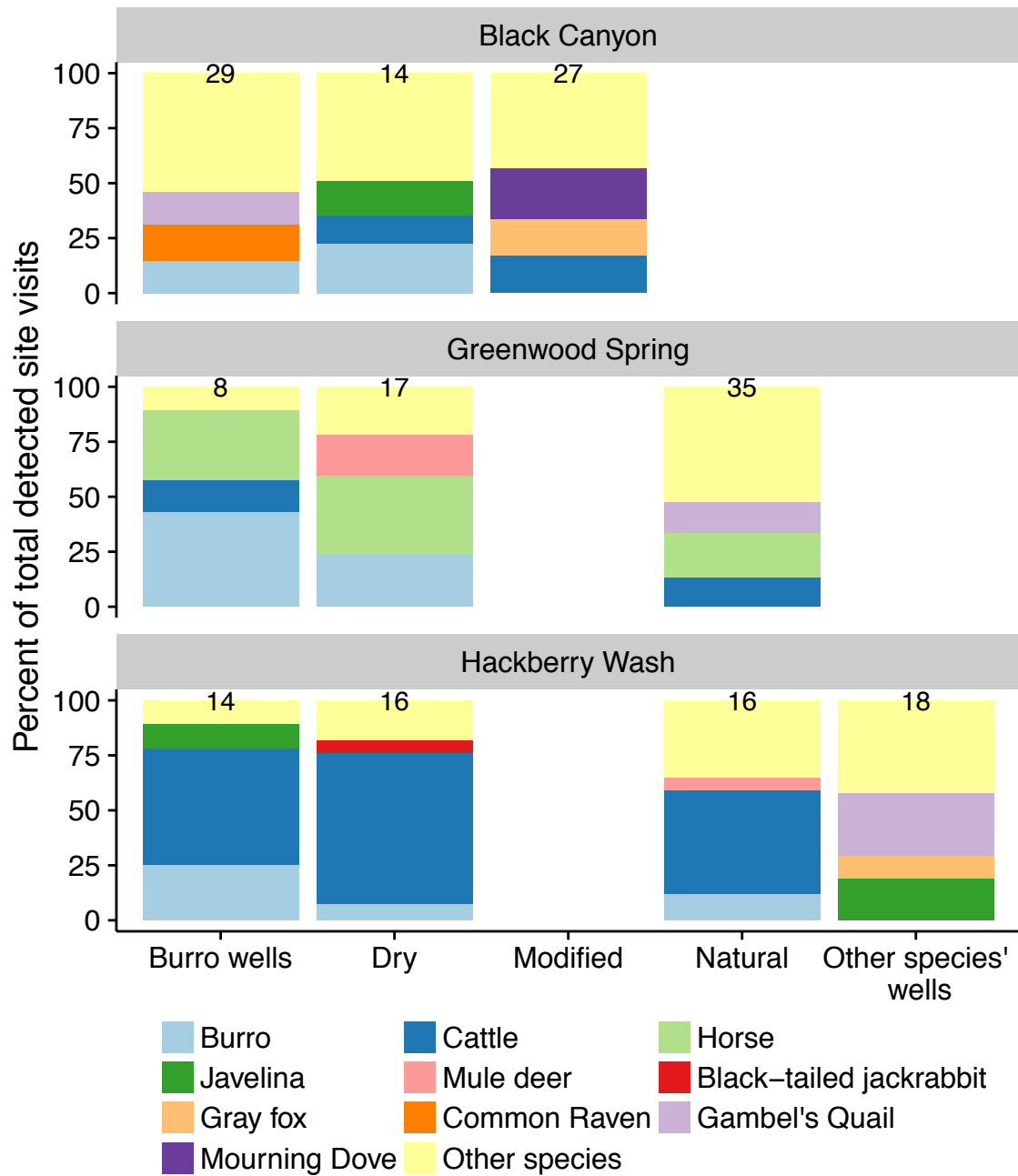


Fig 2. Percent of total detected visits by species calculated from total number of visits at each water type per site. The three most active species from each water type at each site are indicated with color; the number of other species is annotated on each bar.

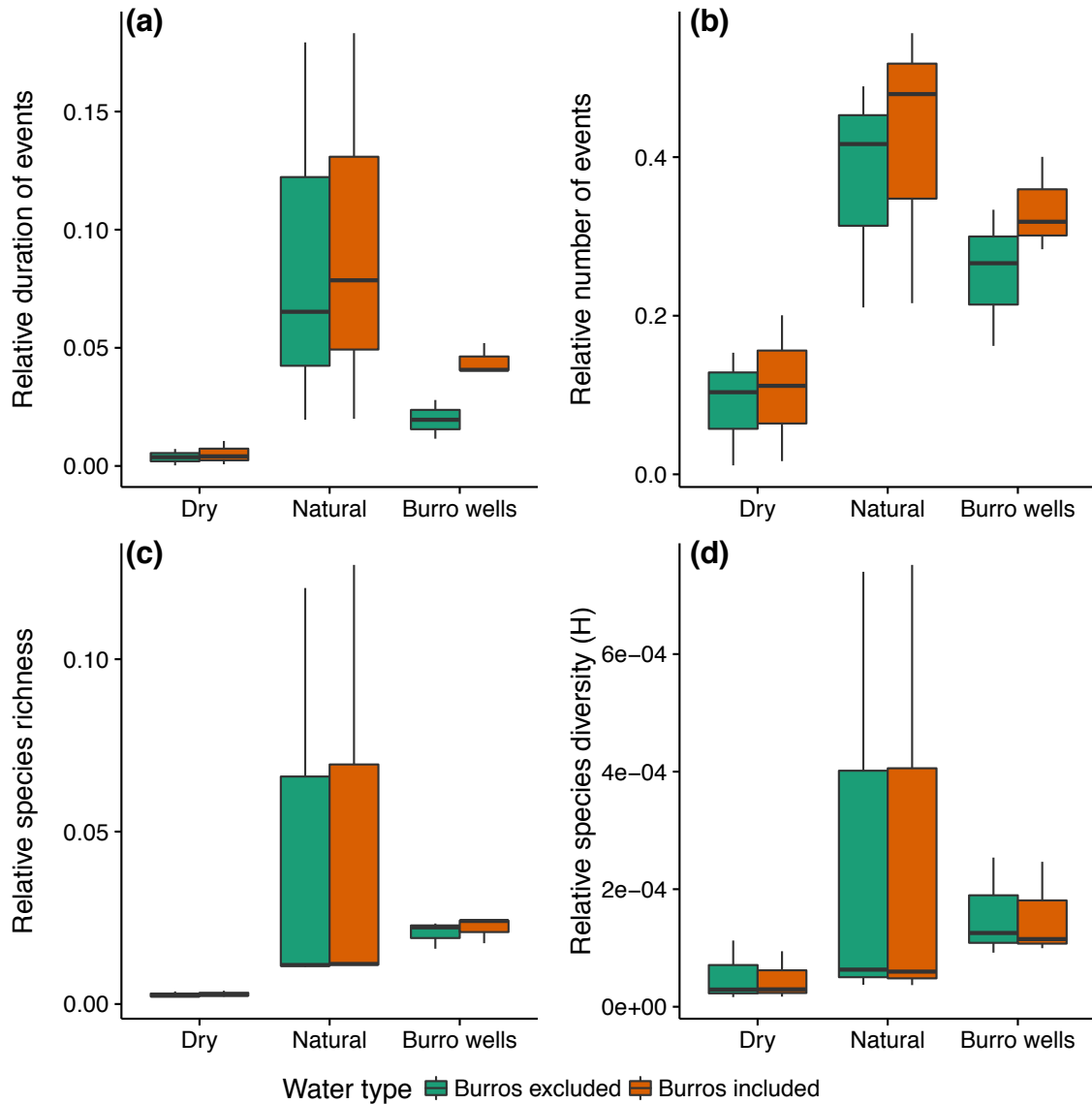


Fig 3. Comparisons of animal community metrics, relativized by sampling effort, with burros included and excluded, between dry, well and natural water locations. **(a)** Relative duration of site use in seconds, **(b)** Relative number of distinct visits (with at least five minute interval between visits), **(c)** Relative species richness, and **(d)** Relative Shannon diversity index (calculated from the ratio of each species' visit frequency to total visit frequency for all species multiplied by the natural log of this ratio).

## CHAPTER 5

**TITLE:** Introduced wild burros (*Equus asinus*) increase germination of Fremont cottonwood (*Populus fremontii*) on a Sonoran Desert River.

### INTRODUCTION

Like many non-native species, the introduced wild burro (*Equus asinus*) of the North American deserts is generally considered ecologically destructive. Numerous studies indicate that wild burros can compete with native species (Marshall et al. 2008) and exert strong grazing pressure, although evidence of overgrazing is inconsistent and suffers from weak methodology (Abella 2008).

In native systems, herbivorous megafauna are known to play critical ecological roles by consuming coarse, unpalatable vegetation which can release less fibrous plant species from competition to the benefit of smaller herbivores; by increasing nutrient cycling rates by orders of magnitude; by dispersing nutrients and seeds; and by engineering ecosystems (Ripple et al. 2015). North America once possessed numerous megafauna species, including several *Equus* species, the majority of which went extinct at the end of the Pleistocene epoch due to overhunting by early humans (Barnosky et al. 2004).

Today, burros are the largest extant herbivorous megafauna in the deserts of North America, which has led some to view the introduction of burros to North America as an inadvertent case of Pleistocene rewilding (Donlan et al. 2006), a proposal which suggests that reintroducing proxies for extinct Pleistocene megafauna could restore lost ecological functions and provide refuge for highly endangered megafauna (Estes et al. 2011, Ripple et al. 2015). Indeed, *Equus africanus*, the wild ancestor of burros, is Critically

Endangered (Moehlman et al. 2015), as are large herbivore species worldwide (Ripple et al. 2015).

Animals influence river geomorphology, hydrology, and plant communities through multiple means, including wallowing, dam building and well digging. Their behaviors create novel water sources and influence the distribution and patterning of this resource, which in turn can influence abundance and dynamics of invertebrates, amphibians, and plants (Naiman and Rogers 1997). In both the United States and Australia, burros and other wild post-domestic megafauna have been credited with the maintenance of desert springs: removal of these herbivores led to prolific emergent vegetation growth, hypoxia, disappearance of surface waters, and extinction of several endemic fish populations (Kodric-Brown and Brown 2007).

In the Sonoran Desert of Arizona, wild burros dig wells to access groundwater. Numerous abandoned wells contain pioneer riparian vegetation including Fremont's cottonwood (*Populus fremontii*) and Goodding's willow (*Salix gooddingii*). These fast growing, productive, disturbance-adapted pioneer trees provide habitat for many riparian birds and insects (Hinojosa-Huerta et al. 2013) and are foundational species within threatened riparian forest ecosystems (Rood et al. 2005).

These pioneer tree species are tightly coupled to flood regimes. Their germination and establishment requirements include the removal of competing vegetation (Stromberg et al. 1991, Cooper et al. 1999, Stromberg and Merritt 2015) and the creation of bare, moist mineral seedbeds by floods (Cooper and Andersen 2012) in concurrence with seed production (Stella et al. 2006). Following germination, seedling root elongation must match soil moisture recession rates for establishment to occur, therefore elevation from

the water table is a critical determinant of seedling establishment; depths to the water table beneath a threshold of ca. 2m make establishment highly unlikely (Lite and Stromberg 2005). Disruption of flood disturbance regimes from river damming, flow regulation, and groundwater declines from pumping has resulted in widespread replacement of these pioneer species with other plant functional types (Stromberg et al. 2007). The microhabitats produced by the well digging disturbances of wild burros may satisfy the requirements of these woody pioneer species by removing competing vegetation, as well as by providing year-round, bare, moist substrate at a low elevation relative to surrounding surfaces.

In addition to these establishment requirements, riparian pioneer seedling survivorship can also be affected by herbivory (Stromberg 1997). Burros, who have cecal digestive systems, are capable of consuming very coarse high fiber vegetation, more so than any other sympatric herbivore including cattle (Duncan et al. 1990). The effect of this herbivory on riparian species is unknown, but has been observed in the past (personal observation, Juliet Stromberg).

This study sought to determine whether pioneer woody tree species germinate at higher densities in burro wells than in adjacent germination zones on the Bill Williams River. It was hypothesized that by satisfying the germination requirements of *P. fremontii* and *S. gooddingi*, burro wells enable germination at higher densities than in adjacent riverbank zones or on adjacent undisturbed surfaces. We further noted the presence of herbivory to assess causes of seedling mortality over the summer of 2015.

## METHODS

The Bill Williams is a western Arizona river with a managed flood regime within the lower Colorado subdivision of the Sonoran Desert (Brown 1994). Floods are released when excess water has accumulated in Alamo Lake upstream, which has not occurred since 2010 (Shafroth, personal communication, 2017). Floods are timed to maximize the recruitment of pioneer tree species, in particular of *P. fremontii* and *S. gooddingii*. Continual base-level releases are maintained to provide surface water through several reaches and to sustain tree survivorship (Shafroth et al. 2002). This unique system, therefore, has a relatively stable water table in several reaches, to which burro-wells access, and retains open bars of flood-deposited sediment, in which burros dig.

Burro-wells are generally a square meter in area and occur in clusters of between 3 and 20 wells in areas ranging from 25m<sup>2</sup> to 500m<sup>2</sup>. Five burro-well clusters were randomly selected, with each cluster being an anchor of a site (Fig. 1). Within each site 10-15 1m<sup>2</sup> plots were distributed among 2-3 treatments: randomly selected abandoned wells, adjacent undisturbed surfaces, and nearest natural riverbank germination zones. In April 2016 we sampled only abandoned wells and riverbank zones; the undisturbed surface treatment was included in November 2016. All woody tree species were counted in each plot and assigned to the following height classes: <1cm, 1-10cm, 10.1-50cm, 50.1-100cm, 100.1-200cm, >200.1cm. Percent cover of each herbaceous plant species was also recorded. In November, to determine how significant browsing/grazing was for seedlings, the presence/absence of browsing were recorded by species per plot.

The effect of plot type (burro-well, natural riverbank, and adjacent surface) were analyzed on the following variables: total seedling density, density of Fremont's



cottonwood (*Populus fremontii*), Goodding's willow (*Salix gooddingii*), ditch-willow (*Baccharis salicifolia*), and tamarisk (*Tamarix ramosissima*) seedling stems, and total % cover herbaceous. Data was tested for normality and homoscedascity of variance. Data was transformed with recommendations from the boxCox function in the R package 'car' (v2.1-3), April data was tested with two-tailed t-tests if successfully transformed, otherwise it was tested with Wilcox's signed rank tests. The November data was analyzed with one-way mixed effect ANOVAs, nesting plot within site as a random effect on seedling density; if data could not be transformed it was tested with Kruskal Wallis non-parametric tests. In April, first year seedlings were defined as being the two lowest height classes, <1 and 1-10cm, based on field observations that these height classes were in their first year given the lack of growth scars, the November analysis treated seedlings as anything less than 50cm.

## RESULTS

Significantly more woody seedlings were present in burro wells than in adjacent riverbank germination zones in April ( $W = 98.5$ ,  $p < .0001$ ) (Fig. 2). *P. fremontii*, which constituted 3730 of the 3776 woody seedlings, likewise was significantly more common in burro-wells than in adjacent riverbank zones ( $W = 107.5$ ,  $p < .0001$ ). The effect of germination zone on *T. chinensis*, which had only 9 seedlings in 2 plots, and *S. gooddingii*, which had 18 seedlings in 3 plots, were insignificant (respectively,  $W = 264$ ,  $p = 0.49$ ;  $W = 276$ ,  $p = 0.74$ ), (Fig. 2). The effect of germination zone on percent herbaceous cover, including grasses and sedges, was significant ( $W = 516$ ,  $p < .0001$ ),

with greater cover in riverbank zones than in burro-wells (Fig. 2). Eighty-nine percent of the 3779 seedlings counted in April germinated in burro-wells.

By November, the total number of seedlings (including plants up to 50 cm) had decreased by 95%, from 3779 in April to 201; this decrease was symmetrical for riverbank zones (96%) and burro well zones (94%). Given the lack of normality and heteroscedascity, which could not be improved by transformation, the November data was analyzed with Kruskal-Wallis nonparametric ANOVAs, but all comparisons were insignificant (all seedlings:  $\chi^2 = 2.82$ ,  $df = 2$ ,  $p = 0.24$ , *P. fremontii*:  $\chi^2 = 4.84$ ,  $df = 2$ ,  $p = .09$ , *S. gooddingii*:  $\chi^2 = 4.13$ ,  $df = 2$ ,  $p = 1.13$ ; and *Tamarix*:  $\chi^2 = 2.04$ ,  $df = 2$ ,  $p = .36$ ) (Fig. 3).

Despite the lack of significance in seedling density between zones in November, of 201 surviving seedlings, 72% were found in burro wells, opposed to 11% in riverbank zones and 16% on floodplain surfaces adjacent to burro wells. There was a significant difference in herbaceous cover between treatments when tested with Kruskal-Wallis non-parametric ANOVA ( $\chi^2 = 7.53$ ,  $df = 2$ ,  $p = .02$ ), and a successive Kruskal-Wallis Dunn's nonparametric post-hoc test with Bonferroni correction (R package 'PMCMR' v 4.1) revealed that the undisturbed surface germination zone had significantly less herbaceous cover than the riverbank ( $z = 2.61$ ,  $p = .027$ ) but not burro wells ( $z = 2.04$ ,  $p = .12$ ), and there was no significant difference between the burro-wells and riverbank ( $z = .57$ ,  $p = 1$ ) at this point (Fig. 3).

In November 2015, 25% of screwbean mesquite (*Prosopis pubescens*) occurrences (n = 1 of 4) showed evidence of browsing, 28% of cattail (*Typha*) occurrences (n = 6 of 21) in plots were grazed, 100% of an unidentified grass species (n =

7) were grazed, and 33% of an unidentified sedge species (n = 5 of 15) were grazed. No grazing was observed on *P. fremontii* or *S. gooddingii* in plots—but young *P. fremontii* were observed uprooted by javelina in unmonitored burro wells.

## DISCUSSION

Our data indicates that woody riparian species germinate abundantly in abandoned burro wells, more so than in adjacent riverbank zones or adjacent undisturbed surfaces along the flow-regulated Bill Williams River in the Sonoran Desert of Arizona. Survival through the summer of 2015 was low in all zones, as is typical for these riparian species (Stromberg 1997). Observations of several year-old cottonwoods in old burro wells suggest that survival past seedling stage occurs frequently (Fig. 4), although it is likely to be dependent upon distance to groundwater and reach. Many wells that formerly hosted numerous seedlings had turned into pools of water by November as the water-table rose, drowning all seedlings. Higher surfaces still retained successful germination nurseries, but many of the abandoned wells closer to the channel saw little to no survivorship. Furthermore, two sites in a lower reach of the study area completely dried out—eliminating all seedlings from all plots.

Herbivory was not observed on riparian trees with the exception of screwbean mesquite seedlings. Javelina (*Pecari tajacu*), were observed digging up cattail tubers in both wells and riverbank zones during field work, and several young cottonwood trees in burro-wells outside of study plots appear to have been uprooted as a result. This suggests that herbivory by burros was not a significant cause of seedling mortality, although rooting by javelina contributed to mortality in certain wells. However, it is likely that the

degree of herbivory in the riparian zone, and of woody pioneer species, is dependent upon range conditions in the surrounding landscape. The majority of burro herbivory observed was of cattails (*Typha*) and sedges (Cyperaceae). The grazing of these species produces low-cut grazing meadows and may actually release pioneer woody species from competition, thus contributing to riverbank germination rates.

The increased herbaceous cover in riverbank germination zones compared to burro wells supports our hypothesis that removal of competing vegetation would facilitate the germination and establishment of these seedlings in burro well plots. However, by November, herbaceous cover in burro wells was not significantly different from cover in riverbank zones—it appears that the lag time in the growth of herbaceous plants enabled the establishment of *P. fremontii* through the summer of 2015.

Unfortunately, burro wells are unstable geomorphic phenomena and identifying burro well-born mature plants was not possible. Understanding the extent of burro well-germinated vegetation's contribution to forest stand dynamics will require long-term studies that track seedling cohort survivorship through time.

Surveys of undammed intermittent streams in Arizona, including the Santa Maria River (surveyed June 2015) and the Big Sandy River (June 2015), have found uncommon germination of riparian woody tree species in burro wells and no establishment, likely due to the vulnerability of these wells to scouring floods given their placement in the thalweg closest to the water table. Also, in intermittent streams where burro wells provide a significant amount of total available water (Lundgren, Chapter 2) the frequency of well use by burros and other animals is extremely high, producing a level of disturbance which likely suppresses seedling survivorship.

It may be that burro well germination nurseries are an isolated phenomena resulting from the interaction of burro behavior with flood management on the Bill Williams River. This study was conducted five years after any flood pulses, due to limited water levels in the upstream Alamo Lake dam. The importance of burro wells ecologically, in terms of pool creation and tree recruitment, may only be pronounced during drought years between flood releases. To determine if this phenomenon has a more generalizable effect in other systems will require additional surveys of river systems varying in intermittency and flood magnitude and frequency across the burros' range.

Disturbance from burro well digging activity may also be important for the maintenance of abiotic spatial heterogeneity, particularly on regulated rivers where flood disturbances have become rare. Large floods create scour pools and other transient geomorphic features that subsequently fill in with sediment and become habitat for various specialized organisms (Pardo and Armitage 1997). Some burro well clusters, as the water table rose in the fall and winter, became large shallow pools outside the main channel that may mimic scour-pools. These burro-dug features may offer important microhabitats for amphibians, invertebrates, and wetland plants (Effenberger et al. 2008); indeed, amphibian larvae were common to these pools and may find refuge from predators in the main channel (Hecnar and M'Closkey 1997).

Twelve thousand years ago there were numerous megafauna species in North America whose modern relatives are known to dig wells, such as elephants (*Loxodonta africana*) (Haynes 2012) and other Equids (*Equus hemionus*) (Kaczensky, personal communication, 2015). The return of this function to the North American landscape by the inadvertent reintroduction of the family Equidae presents an opportunity for further

research into the ecological influences of megafauna and to better understand the importance of nativity in determining ecological function and value. It appears that burro wells compensate in multiple ways for the reduction in the frequency of floods capable of structuring and sculpting riparian ecosystems and landforms on the Bill Williams River. Further research is necessary to elucidate the spatial and temporal scale of this phenomenon, and how burro well-born woody vegetation contributes to forest stand characteristics in this novel ecosystem.

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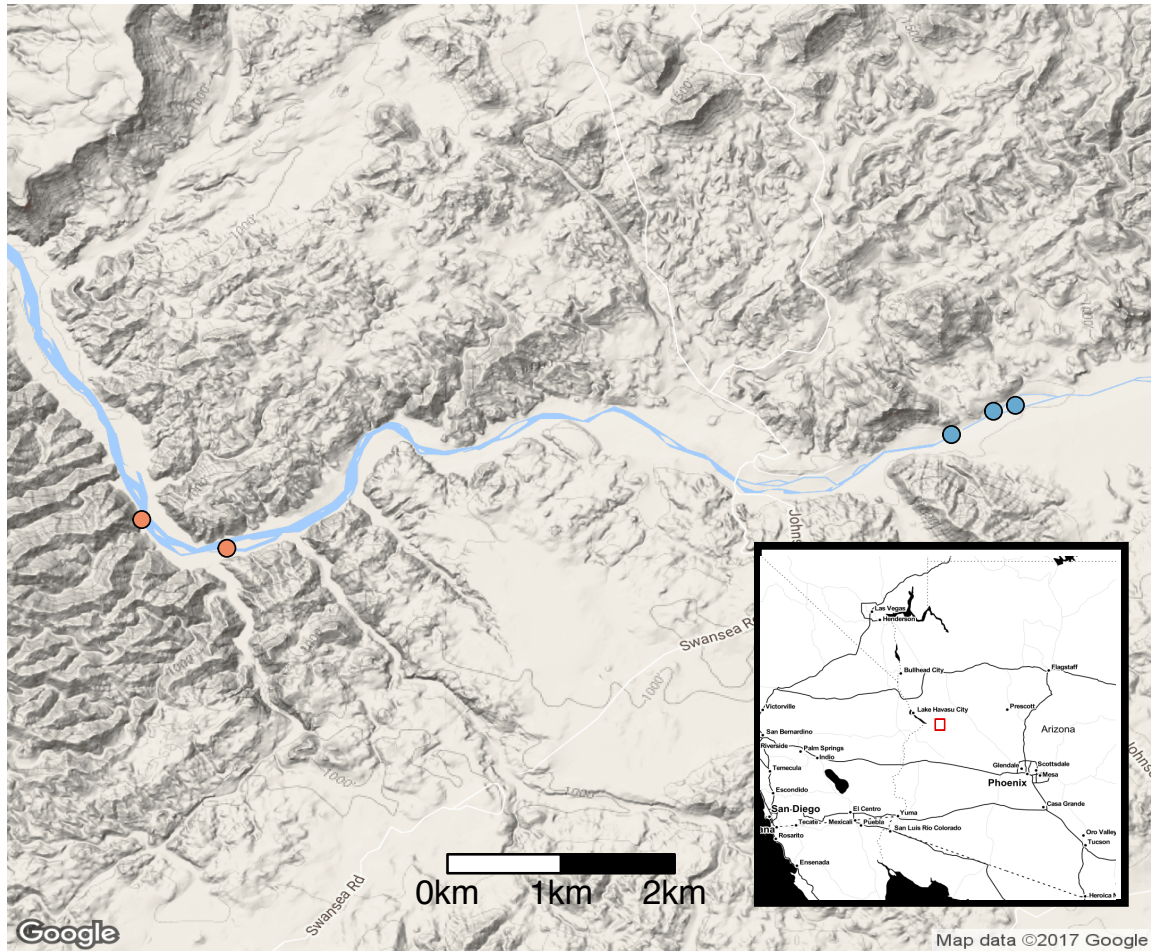
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● Dried out ● Survived

Fig 1. Map of the Bill Williams River study sites. The lower reach desiccated over the summer of 2015, causing widespread mortality of phreatophytic plants and all monitored seedlings.

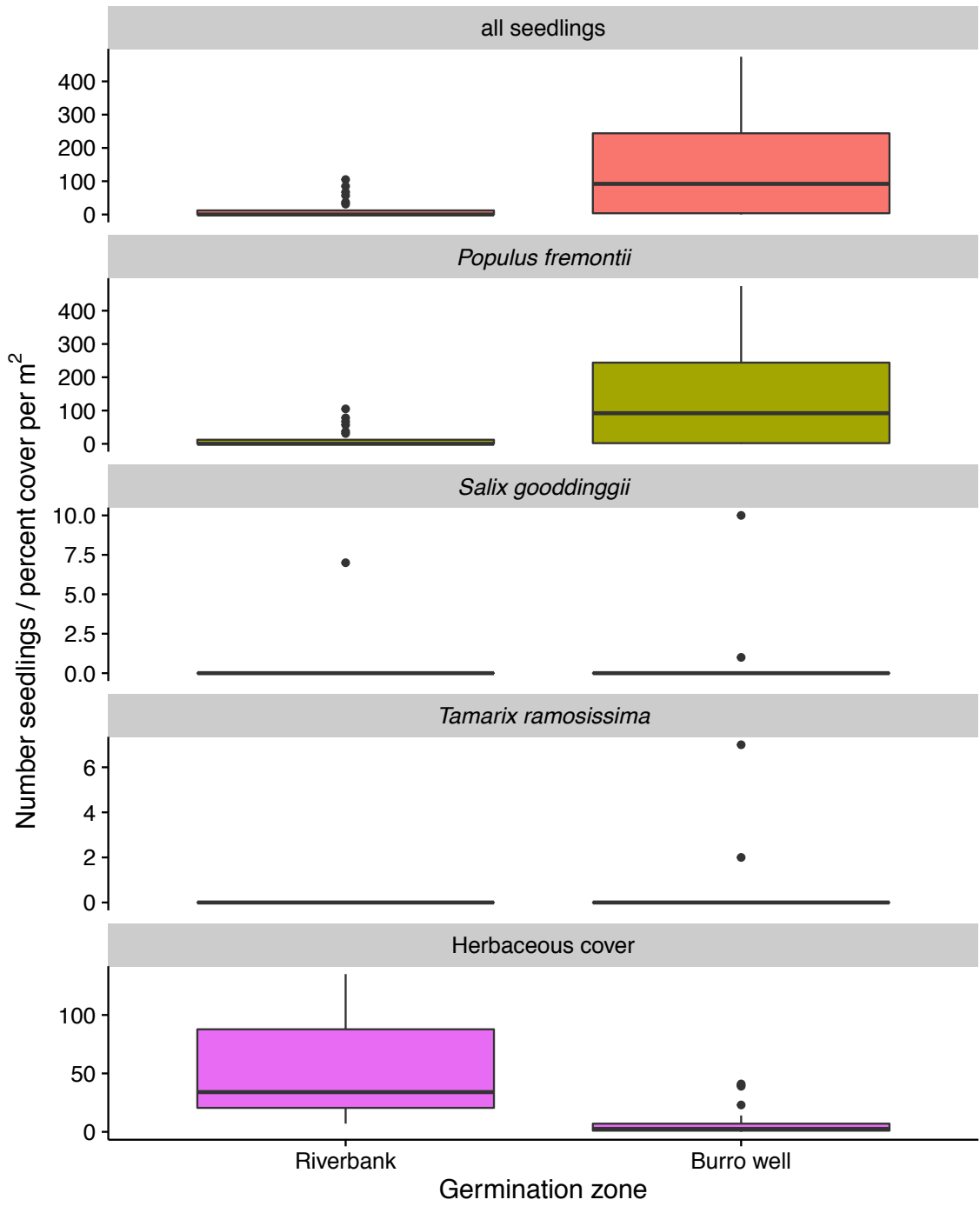


Fig 2. Woody seedling germination (stems per m<sup>2</sup>) and percent cover herbaceous (per m<sup>2</sup>) between riverbank zones and burro well plots in April 2015.







Fig 4. Several year old *P. fremontii* in burro well on the Bill Williams River. Photograph by Michael Lundgren, 2015.

## CHAPTER 6: CONCLUSION

Well digging by wild burros (*Equus asinus*) increases water availability and has facilitative effects on plant and animal communities. This behavior has many potential implications and may be contingent upon numerous other interactions, which offer areas for future research. In this section I will briefly summarize additional research questions and observations relating to well-digging and general wild burro ecology.

Burro wells appear to differ significantly from natural water sources in water quality (Fig. 1), as do the wells dug by African elephants (*Loxodonta africana*) (Ramey et al. 2013), which have lower concentrations of fecal coliforms than other adjacent water sources. Natural water sources frequently accumulate high loads of organic matter, including leaf litter, dung from cattle (no burro dung was observed in natural water sources), and carcasses. Burro wells, however, access groundwater and do not accumulate similar levels of organic matter because they rapidly erode and must be redug. If burro wells differ in quality in ecologically relevant ways, then this behavior may have implications for disease dynamics in addition to water availability.

In addition to the larger vertebrate species detected at burro wells, observations indicate that burro wells are significant resources for arthropods: numerous Hymenopterans and Lepidopterans aggregate at burro wells (Appendix E), which potentially has effects on the community structure of these important groups. Likewise, amphibians and various rodent species were visible at high densities in and around burro wells in nighttime camera trap images when cameras were triggered by larger-bodied organisms. Population dynamics of amphibians, many of which are threatened, are strongly affected by the presence of surface water (Zylstra et al. 2015) and are thus likely

influenced by burro wells. Population studies of these species would give additional insight on how burro wells affect the larger community.

I conducted experimental tests of the effects of burro wells on interaction strengths modeled after Sabo et al. (2008), Allen et al. (2014), and McCluney and Sabo (2009). In these studies, leaf buffets of fresh and dried leaves were provided near and distal to surface water; in all cases arthropod herbivores consumed fresh leaves when distal to surface water and no leaves when water was present. Over the summer of 2016 I attempted to repeat these methods at Black Canyon and Hackberry Wash. However, no herbivory of any kind was observed at any site despite repeated trials; I suspect that the densities of these herbivores at these arid sites were too low to support this experimental design. Additional efforts with alternative food offerings or an increased number of offerings would be an interesting future study: if a megafauna species indirectly alters food web topologies by increasing resource availability would be a unique finding.

Additional avenues of research are presented by the interactions between beavers (*Castor canadensis*) and burros on the Bill Williams River. The Bill Williams River is heavily occupied by beavers, who have transformed the river into a series of lentic pools (Andersen et al. 2011), which may raise the water table and contribute to the persistence of dense emergent vegetation such as cattails (*Typha* spp.) on the riverbanks (Pollock et al. 2014). The density of emergent vegetation may drive wild burros to dig wells to access water and avoid dense potentially predator-harboring vegetation, and by raising the water table, beavers may facilitate burros by decreasing water table depth on the distal flood plain. However, continued dam-construction by beavers may eventually flood

burro well germination nurseries, thus reducing the effect of burro well nurseries on riparian tree recruitment.

An additional interesting interaction was observed on the Bill Williams River in 2015 and on the lower Santa Maria River in 2016 (N. Goodman personal communication 2017). In the early season burros dug wells in distal surfaces on the floodplain. The channel in these reaches desiccated over the course of the dry season and water became initially reserved to small pools in the bottoms of beaver ponds, which then subsequently dried. As these pools dried, burros began to dig wells in the deepest portions of beaver ponds. Eventually, as the recession continued (to likely more than a meter and a half in depth to groundwater), even these wells became dry, but were further excavated by some fossorial species, most likely badgers (*Taxidea taxus*). In this way, a trio of species maintained water access as surface water receded in these Sonoran Desert systems. This interaction is reminiscent of the observations of Hamilton et al. (1977) who observed that baboons (*Papio ursinus*) continue to excavate the wells initially dug by gemsbok (*Oryx gazella*).

Additional questions remain concerning the sociality of wild burros in regard to well digging. Unlike in gemsbok, the males of which exclude females from using their wells (Hamilton et al. 1977), there was no evidence of territoriality at burro well clusters. Multiple males and females were recorded at well clusters at the same time and with limited conflict. Frequently, well digging appeared to be conducted by one primary individual, while a group of one to seven watched. Young burros were often recorded trying to dig next to the primary digger, which suggests this behavior might be learned. If well digging is a learned behavior or a behavior stratified in some way through social

structures, then disrupting the social stability of burros may disrupt this important ecological function. As is, herd management approaches in the United States involve the rounding up of substantial portions of burro populations; individuals are removed regardless of age and sex. Studying how these round-ups affect the ecological function of wild burros would be an interesting and relevant area for research.

Likewise, preliminary evidence suggests that interspecific dominance hierarchies may influence the use of burro wells by burros and other species. Cattle were the dominant users of natural water sources and were observed on numerous occasions competitively excluding burros from burro wells (Fig. 2). This suggests that well digging could be a response of burros to competition with cattle at natural water sources. Furthermore, qualitative assessments of cattle density during regional surveys (discussed in Chapter 2) showed that all sites lacking burros had abundant cattle sign. If this is the case, perspectives on how wild burros compete with livestock may need to be reassessed.

Burros were also observed to dig depressions on high silty surfaces, which appeared to provide a mineral salt. An early camera trap monitoring effort on one of these in January 2012, showed use of this feature by javelina, bobcats, and badgers, in addition to burros. It is unclear what these minerals are, why they must be dug to, and their value to vertebrate species. By June 2012, the base of the salt excavation monitored had become the entrance to a badger burrow; suggesting again that badgers may use burro excavations as a head start.

Burros possess a cecal hindgut digestive system, making them capable of consuming extremely coarse fibrous biomass. These influences are generally viewed as negative. However, herbivory at these scales of fiber have been lost from the North



American landscape since the Pleistocene. The return of this functional trait may have important consequences for nutrient cycling, community structure, and on smaller herbivores.

Decomposition in dryland systems is largely driven by abiotic photodegradation due to the limited availability of moisture (Barnes et al. 2015). However, the conversion of coarse woody biomass to moist pre-digested and bacterially enriched dung by wild burros may alter decomposition pathways in desert systems. Furthermore, male equids mark territories with dung middens (Feist and McCullough 1975). These middens can be quite large and may thus be able to retain moisture, which could lead to increased rates of microbial decomposition, with influences on carbon cycling, carbon sequestration, and the dynamics of other nutrients (Moorhead and Reynolds 1991). Understanding how an introduced megafauna species may affect these cycles is an exciting research area, given that nutrient cycling worldwide was once strongly influenced by megafauna species (Doughty et al. 2016).

To date, little is known about how burros influence plant communities, since there have been no rigorous before-after or exclosure-based experimental studies (Abella 2008). Understanding how burros interact with the plant community is important to address concerns of land managers and to understand how an introduced megafauna species may alter vegetation communities, given that modern plant communities are radically different given the loss of Pleistocene herbivores (Bakker et al. 2016). The following anecdotes may provide handles for future research on these questions.

I did not observe browsing by burros on cottonwoods or willows on the Bill Williams River, although burros have been observed to strip bark from mature

cottonwood trees in the past (Stromberg, personal communication 2016). I did, however, observe browsing on mesquite (*Prosopis* spp.) seedlings in burro wells and elsewhere. Interestingly, many of these germinants originated from seeds likely deposited in burro dung, including the screwbean mesquite (*P. pubescens*), which is an important riparian species that has declined dramatically in the Southwestern United States for largely unknown reasons (Foldi 2014). The relative effect of seed dispersal versus herbivory by burros on *P. pubescens* is unknown but may be relevant to the conservation of this important plant species.

*Typha* and various sedges (Cyperaceae) were the primary observed food of burros in the riparian systems monitored. Burros were observed grazing this emergent vegetation to within 2 or 3 inches of the surface on the Amargosa River in Nevada and on the Bill Williams River in Arizona. Much as Kodric-Brown and Brown (2007) showed, the grazing of emergent vegetation appeared to maintain open water habitat at these sites. Similarly, this grazing may increase the establishment success of woody pioneer species like cottonwood and willow by freeing them from competition.

Another interesting feeding association of burros at my study sites was of hillside palo verde (*Parkinsonia microphylla*), an upland tree species. Burros tear lower branches from the trunk and then consume the lower, woody end, leaving the twigs at the base of the tree. These twig piles are common around the bases of these trees and may present an interesting microhabitat for reptiles and small mammals. Furthermore, the removal of these branches may stimulate regrowth of less fibrous shoots; if so, this regrowth could be palatable food for smaller herbivores and could be a starting point for research on possible feeding synergies between burros and species like bighorn sheep (*Ovis*

*canadensis*). Conversely, at certain burro densities, this feeding pattern may contribute to mortality in these trees.

The influences of wild burros are likely density-dependent and likely vary from facilitative to antagonistic as burro density increases. Factors influencing burro densities are largely unknown but may include the presence and age structure of apex predators, which in the majority of the burro's range are mountain lions (*Puma concolor*). Little is known about interactions between lions and burros, but lions are known to suppress wild horse (*Equus caballus*) population growth (Turner and Morrison 2001). Lions are killed in many areas of Arizona to protect bighorn sheep production and livestock. These lethal removals may reduce the ability of lions to hunt burros, regardless of the lion population size by disrupting social order and removing experienced individuals (Wallach et al. 2010).

Studies to investigate the influences of wild burros should quantify the presence and social stability of potential predators, as novel trophic cascades may explain the irruptive population dynamics of many introduced species and associated undesirable effects (Wallach et al. 2015). To ignore this possibility is to treat burros as density-independent and context-independent essences, a manifestation of essentialism that can lead to simplified and myopic understandings (Simberloff 1980).

Observations from trail camera monitoring suggest that lion attacks may be common on wild burros. At Greenwood Spring, the only site where mountain lions were regularly detected, burros commonly showed signs of injury including torn faces and hamstrings. Testing if lions alter burro population dynamics or behavioral patterns by altering the 'landscape of fear' would have profound implications for our understandings

of wild burros and of other introduced megafauna. This research may benefit from comparing the population dynamics, behavioral patterns, and ecological influences of wild burros in Arizona where lions are persecuted to nearby California where mountain lions are protected.

Studying introduced wild burros as organisms with value to global conservation goals and as members of an ecologically important functional group opens new trajectories in research and allows new understandings. If introduced burros were treated as conservation assets, conservation efforts to protect these populations would likely find synergy with other conservation goals such as the restoration of predators and the preservation of landscape connectivity. Ultimately, valuing the wildness of the world as it is offers a more compelling vision than working to beget local extinction in an age of global extinction.

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Fig. 1. Water quality differences between burro wells and natural water sources. (a) Natural water is often full of accumulated organic matter and growing algae, (b) Burro well water tends to be clear and lacks organic matter and algae.





Fig. 2. Typical encounter between burros and cattle at a burro well cluster. Sequence of event is (a) – (d).

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APPENDIX A

THE INTRODUCED LARGE ( $\geq 100\text{KG}$ ) HERBIVOROUS MAMMALS OF THE  
WORLD

The introduced large ( $\geq 100\text{kg}$ ) herbivorous mammals of the world. Data from Ripple et al. (2015), Long (2003), and the Large Herbivore Network (2015) unless otherwise noted.

Species	IUCN Status	Trend	Range		Approximate population size		Percent of pop. outside native range
			Native	Introduced	Native	Introduced	
<b>Family Bovidae</b>							
<i>Bison bison</i>	NT	Stable	NA	EU	11,300	>100?	~1%
<i>Boselaphus tragocamelus</i>	LC	Stable	IN	NA	100,000	37,000	27%
<i>Bubalus bubalis</i> *	EN <sup>1</sup>	Dec	IN, SEA	SA, AU, AF, SEA, IOI, POI	200-4,000 <i>Bubalis arnee</i>	>150,000	78%-99%
<i>Bos javanicus</i> *	EN	Dec	SEA	AU	<8,000 (but likely <5,000)	6000	42%-54%
<i>Bos taurus</i> *	EX <sup>2</sup>	N/A	EU	NA, SA, EU, AU, POI, AOI, IOI, CI	extinct	Common	100%
<i>Oryx gazella</i>	LC	Stable	AF	NA	373,000	3000-6000	~1%
<i>Ovibos moschatus</i>	LC	Stable	NA	EU, RU elsewhere in NA	132,000	>8000	6%
<i>Ovis ammon</i>	NT	Dec	EU, AS	EU, NA, SA, MI, POI	96,000-114,000	unknown	unknown
<b>Family Camelidae</b>							

<i>Camelus dromedarius</i> *	EX	N/A		AU	extinct	>300,000	100%
<b>Family Cervidae</b>							
<i>Cervus elaphus</i>	LC	Inc	EU, IN, CN, AS, NA, AF	AU, SA, AF, EU, POI, AOI	>1,000,000, with some endemic populations in sharp decline	>10,000	~1%
<i>Rangifer tarandus</i>	LC	Stable	NA, SI, EU	AOI, IOI	1,000,000, with some populations in sharp decline	>1000	<1%
<i>Rusa unicolor</i>	VU	Dec	IN, CN, SEA	AU, AF, NA, POI, CI	unknown: declining	100,000	Unknown, probably significant given declines
<i>Alces americanus</i>	LC	Stable	NA, EU, RU, CN	AOI	high: .1-1.1 moose per km <sup>2</sup>	150,000	Unknown
<i>Rucervus duvaucelii</i> (Blouch et al. 1998)	VU	Dec	IN	NA	4300	Unknown	Unknown
<b>Family Equidae</b>							
<i>Equus ferus caballus</i> *	EN <sup>3</sup>	Inc	RU	NA, SA, AU, AF, EU, AS, POI, IOI, AOI	310 Przewalski's horse, other horse varieties are extinct	>500,000	99%
<i>Equus asinus</i> *	CR <sup>4</sup>	Dec	AF	NA, AU, EU, AF, AS, IOI, POI,	No more than 200	>5,000,000	99%
<b>Family Hippopotamidae</b>							
<i>Hippopotamus amphibius</i> (Kremer 2014)	VU	Dec	AF	SA	125,000 and 148,000	~100	<1%

Family Proboscidea							
<i>Elephas maximus</i>	EN	Dec	AS, CN, IN, SEA	IOI	41,000–52,000	~100	<1%

### Regions

NA: North America, SA: South America and Central America, EU: Europe, AF: Africa, SEA: Southeast Asia, including islands such as Borneo, IN: India, CN: China, AS: the rest of Asia including Asia Minor, RU: Russia, Siberia and Mongolia, AU: Australia, POI: Pacific Ocean Islands, IOI: Indian Ocean Islands, AOI: Atlantic Ocean Islands, CI: Caribbean Islands, MI: Mediterranean Islands

\* indicates ex-domesticated origin.

<sup>1</sup> *Bubalus bubalis* is the domestic form of the endangered *Bubalis arnee*.

<sup>2</sup> *Bos taurus* is the domesticated form of the extinct European aurochs, *Bos taurus primigenius*.

<sup>3</sup> *Equus ferus caballus* is the domesticated form of the extinct *Equus ferus*, which is survived only by the endangered sister lineage, the Przewalskii horse, *Equus ferus ssp. przewalskii*.

<sup>1</sup> *Equus asinus* is the domesticated descendent of the critically endangered *Equus africanus*.

APPENDIX B

LARGE ( $\geq 100\text{KG}$ ) HERBIVORE GENERA STATUS BY CONTINENT AND BY

EPOCH

Large ( $\geq 100\text{kg}$ ) herbivore genera status by continent (Africa, Australia, Eurasia, North America, South America), by epoch (Pleistocene, Holocene, Anthropocene). Holocene genera were assumed to be present in the Pleistocene unless it could be verified that their Holocene presence was the result of immigration.

Family	Genera	Status	Presence Source	Mass source
<b>Epoch: Pleistocene</b>				
<b>Continent: Africa</b>				
Bovidae	Alcelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bos	Survived	(Ripple et al. 2015)	(Smith et al. 2003)
Bovidae	Capra	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Connochaetes	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Damaliscus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Hippotragus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Kobus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Oryx	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Syncerus	Survived	(Faith 2014)	(Smith et al. 2003)
Bovidae	Tragelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Megalotragus	Globally extinct	(Faith 2014)	(Smith et al. 2003)
Bovidae	Rusingoryx	Globally extinct	(Faith 2014)	(Smith et al. 2003)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Megaceroides	Globally extinct	(Faith 2014)	(Smith et al. 2003)
Camelidae	Camelus	Extant	(Burns 2010)	(Ripple et al. 2015)
Elephantidae	Loxodonta	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Elephantidae	Elephas	Regionally extinct	(Faith 2014)	(Smith et al. 2003)
Equidae	Equus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)



Giraffidae	Giraffa	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Giraffidae	Okapia	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Choeropsis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Hippopotamus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hominidae	Gorilla	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Ceratotherium	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Diceros	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Stephanorhinus	Globally extinct	(Faith 2014)	(Smith et al. 2003)
Suidae	Hylochoerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: Australia</b>				
Diprotodontidae	Diprotodon	Globally extinct	(Barnosky et al. 2004)	(Johnson and Prideaux 2004)
Diprotodontidae	Euowenia	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Diprotodontidae	Euryzygoma	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Diprotodontidae	Hulitherium	Globally extinct	(Johnson & Prideaux 2004)	(Johnson & Prideaux 2004)
Diprotodontidae	Kolopsis	Globally extinct	(Johnson & Prideaux 2004)	(Roberts et al. 2001)
Diprotodontidae	Maokopia	Globally extinct	(Johnson & Prideaux 2004)	(Roberts et al. 2001)
Diprotodontidae	Nototherium	Globally extinct	(Barnosky et al. 2004)	(Roberts et al. 2001)
Diprotodontidae	Palorchestes	Globally extinct	(Barnosky et al. 2004)	(Roberts et al. 2001)
Diprotodontidae	Zygomaturus	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Macropodidae	Macropus	Globally extinct	(Johnson & Prideaux 2004)	(Johnson & Prideaux 2004)

Macropodidae	Procoptodon	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Macropodidae	Protemnodon	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Macropodidae	Simosthenurus	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Macropodidae	Sthenurus	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Vombatidae	Phascolonus	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
Vombatidae	Ramsayia	Globally extinct	(Barnosky et al. 2004)	(Johnson & Prideaux 2004)
<b>Continent: Eurasia</b>				
Bovidae	Bison	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bos	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Boselaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bubalus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Budorcas	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capra	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capricornis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovibos	Regionally extinct	(Barnosky et al. 2004)	(Pushkina & Raia 2008)
Camelidae	Camelus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Alces	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Elaphurus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)

Cervidae	Przewalskium	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rangifer	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rucervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rusa	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Megaloceros	Globally extinct	(Barnosky et al. 2004)	(Pushkina and Raia 2008)
Elephantidae	Elephas	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Equidae	Equus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Hippopotamus	Regionally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Proboscidea	Mammuthus	Globally extinct	(Barnosky et al. 2004)	(Pushkina & Raia 2008)
Proboscidea	Palaeoloxodon	Globally extinct	(Barnosky et al. 2004)	(Pushkina & Raia 2008)
Rhinocerotidae	Dicerorhinus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Rhinoceros	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Coelodonta	Globally extinct	(Barnosky et al. 2004)	(Pushkina & Raia 2008)
Rhinocerotidae	Stephanorhinus	Globally extinct	(Pushkina & Raia 2008)	(Pushkina & Raia 2008)
Suidae	Sus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: North America</b>				
Bovidae	Bison	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovibos	Survived	(Campos et al. 2010)	(Ripple et al. 2015)
Bovidae	Euceratherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Camelidae	Camelops	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Camelidae	Hemiauchenia	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Camelidae	Palaeolama	Globally	(Barnosky et al.	(Smith et al.

		extinct	2004)	2003)
Cervidae	Rangifer	Survived	(Long and Yahnke 2011)	(Ripple et al. 2015)
Cervidae	Cervalces	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Elephantidae	Mammuthus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Equidae	Equus	Regionally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Gomphotheriidae	Cuvieronius	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Mammutidae	Mammut	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Megalonychidae	Megalonyx	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Megatheriidae	Nothrotheriops	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Mylodontidae	Glossotherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Pampatheriidae	Pampatherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Rodentia	Castoroides	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Tapiridae	Tapirus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Tayassuidae	Platygonus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Toxodontidae	Mixotoxodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
<b>Continent: South America</b>				
Camelidae	Lama	Survived	(Ripple et al. 2015)	(Smith et al. 2003)
Camelidae	Hemiauchenia	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Camelidae	Palaeolama	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Cervidae	Blastocerus	Survived	(Márquez et al. 2006)	(Ripple et al. 2015)
Equidae	Hippidion	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Equidae	Equus	Regionally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Glyptodontidae	Doedicurus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)

Glyptodontidae	Glyptodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Glyptodontidae	Hoplophorus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Glyptodontidae	Chlamydotherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Gomphotheriidae	Cuvieronius	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Gomphotheriidae	Haplomastodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al., 2003)
Gomphotheriidae	Stegomastodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Hydrochoeridae	Nechoerus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Megatheriidae	Eremotherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Megatheriidae	Megatherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Myodontidae	Glossotherium	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Myodontidae	Myodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Tapiridae	Tapirus	Survived	(Ruiz-Garcia et al. 2012)	(Smith et al. 2003)
Tayassuidae	Platygonus	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Toxodontidae	Mixotoxodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
Toxodontidae	Toxodon	Globally extinct	(Barnosky et al. 2004)	(Smith et al. 2003)
<b>Epoch: Holocene</b>				
<b>Continent: Africa</b>				
Bovidae	Alcelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capra	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Connochaetes	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Damaliscus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Hippotragus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Kobus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)

Bovidae	Oryx	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Syncerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Tragelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bos	Regionally extinct	(Ajmone-Marsan et al. 2010)	(Ripple et al. 2015)
Camelidae	Camelus	Regionally extinct	(Burns 2010)	(Ripple et al. 2015)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Elephantidae	Loxodonta	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Equidae	Equus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Giraffidae	Giraffa	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Giraffidae	Okapia	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Choeropsis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Hippopotamus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Hominidae	Gorilla	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Ceratotherium	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Diceros	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Suidae	Hylochoerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: Eurasia</b>				
Bovidae	Bison	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bos	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Boselaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bubalus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Budorcas	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)

Bovidae	Capra	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capricornis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Camelidae	Camelus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Alces	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Elaphurus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Przewalskium	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rangifer	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rucervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rusa	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Elephantidae	Elephas	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Equidae	Equus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Dicerorhinus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Rhinoceros	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Suidae	Sus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: North America</b>				
Bovidae	Bison	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovibos	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rangifer	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Alces	Immigrated	(Meiri et al. 2014)	(Ripple et al. 2015)
Cervidae	Cervus	Immigrated	(Hundertmark	(Ripple et al.

			et al. 2002)	2015)
Tapiridae	Tapirus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: South America</b>				
Camelidae	Lama	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Blastocerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Epoch: Anthropocene</b>				
<b>Continent: Africa</b>				
Bovidae	Alcelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Connochaetes	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Damaliscus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Hippotragus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Kobus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Syncerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Tragelaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bubalus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Bovidae	Capra	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Oryx	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rusa	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Elephantidae	Loxodonta	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Equidae	Equus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Giraffidae	Giraffa	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Giraffidae	Okapia	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)



			2015)	2015)
Hippopotamidae	Choeropsis	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Hippopotamidae	Hippopotamus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Hominidae	Gorilla	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Ceratotherium	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Diceros	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Suidae	Hylochoerus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: Australia</b>				
Bovidae	Bos	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Bovidae	Bubalus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Camelidae	Camelus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Cervidae	Cervus	Introduced	(Long 2003)	(Ripple et al. 2015)
Cervidae	Rusa	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Equidae	Equus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
<b>Continent: Eurasia</b>				
Bovidae	Boselaphus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capra	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovis	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovibos	Introduced	(Long 2003)	(Ripple et al. 2015)
Bovidae	Bison	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bos	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Bubalus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Budorcas	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Capricornis	Survived,	(Ripple et al. 2015)	(Ripple et al. 2015)

		threatened	2015)	2015)
Camelidae	Camelus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Alces	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rangifer	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Elaphurus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Przewalskium	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rucervus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rusa	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Elephantidae	Elephas	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Equidae	Equus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Dicerorhinus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Rhinocerotidae	Rhinoceros	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Suidae	Sus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: North America</b>				
Bovidae	Bison	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Ovibos	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Bovidae	Boselaphus	Introduced	(Long 2003)	(Ripple et al. 2015)
Bovidae	Ovis	Introduced	(Long 2003)	(Ripple et al. 2015)
Bovidae	Bos	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Bovidae	Oryx	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Cervidae	Alces	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)

Cervidae	Cervus	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rangifer	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Rucervus	Introduced, threatened	(Blouch et al. 1998)	(Ripple et al. 2015)
Cervidae	Rusa	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Equidae	Equus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)
<b>Continent: South America</b>				
Bovidae	Ovis	Introduced	(Long 2003)	(Ripple et al. 2015)
Bovidae	Bos	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Bovidae	Bubalus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Camelidae	Lama	Survived	(Ripple et al. 2015)	(Ripple et al. 2015)
Cervidae	Cervus	Introduced	(Long 2003)	(Ripple et al. 2015)
Cervidae	Blastocerus	Survived, threatened	(Márquez et al. 2006)	(Ripple et al. 2015)
Equidae	Equus	Introduced, threatened	(Long 2003)	(Ripple et al. 2015)
Hippopotamidae	Hippopotamus	Introduced, threatened	(Kremer 2014)	(Ripple et al. 2015)
Tapiridae	Tapirus	Survived, threatened	(Ripple et al. 2015)	(Ripple et al. 2015)

APPENDIX C

DIGGING BY WILD BURROS CREATES WATER SOURCES USED BY OTHER

SPECIES

[Consult Attached Files]

APPENDIX D

TRAIL CAMERA DATA SUMMARIZED BY SITE AND WATER TYPE FOR EACH  
SPECIES

Species detected from 2015 and 2016 monitoring periods, summarized by site and water type. Activity indicates if a species drank or was merely detected. Percent of total use and percent of total visits calculated from total use and visits for each site and water type. 'Unknown' species are species that could not be identified and were excluded from data analyses.

Common name	Scientific name	Activity	Use (hrs)	Percent of total use	Number of visits	Percent of total visits
Water type: Burro wells						
Site: Black Canyon; 2186 hours sampling effort, 63.5 hours in use, 463 distinct visits						
Common Raven	<i>Corvus corax</i>	Drank	6.67	10.50	76.00	16.41
Gambel's Quail	<i>Callipepla gambelii</i>	Drank	5.08	7.99	70.00	15.12
Burro	<i>Equus asinus</i>	Drank	35.41	55.72	68.00	14.69
Javelina	<i>Pecari tajacu</i>	Drank	5.37	8.45	38.00	8.21
Gray fox	<i>Urocyon cinereoargenteus</i>	Drank	0.47	0.74	34.00	7.34
Rock squirrel	<i>Otospermophilus variegatus</i>	Drank	0.81	1.27	28.00	6.05
Cattle	<i>Bos taurus</i>	Drank	2.51	3.95	18.00	3.89
Coyote	<i>Canis latrans</i>	Drank	0.33	0.52	18.00	3.89
Mourning Dove	<i>Zenaida macroura</i>	Drank	0.19	0.31	17.00	3.67
Bobcat	<i>Lynx rufus</i>	Drank	0.49	0.77	16.00	3.46
Gila Woodpecker	<i>Melanerpes uropygialis</i>	Drank	0.23	0.35	11.00	2.38
Mule deer	<i>Odocoileus hemionus</i>	Drank	2.97	4.68	10.00	2.16
White-winged Dove	<i>Zenaida asiatica</i>	Drank	0.02	0.04	10.00	2.16
Hooded Oriole	<i>Icterus cucullatus</i>	Drank	0.17	0.27	7.00	1.51
Myiarchus flycatcher	<i>Myiarchus spp.</i>	Drank	0.22	0.35	6.00	1.30
Black-tailed jackrabbit	<i>Lepus californicus</i>	Drank	0.03	0.04	5.00	1.08
Greater Roadrunner	<i>Geococcyx californianus</i>	Detected	0.02	0.04	5.00	1.08
American Badger	<i>Taxidea taxus</i>	Drank	0.01	0.02	4.00	0.86
Rodent sp	<i>Unknown</i>	Drank	2.45	3.85	3.00	0.65
Cottontail Rabbit	<i>Sylvilagus audubonii</i>	Detected	0.00	0.00	3.00	0.65
Unknown	Unknown	Detected	0.00	0.00	3.00	0.65
Ringtail cat	<i>Bassariscus astutus</i>	Drank	0.00	0.01	2.00	0.43
Curve-billed Thrasher	<i>Toxostoma curvirostre</i>	Drank	0.00	0.00	2.00	0.43
Unknown lizard	Unknown lizard	Detected	0.05	0.08	1.00	0.22
Turkey Vulture	<i>Cathartes aura</i>	Drank	0.02	0.03	1.00	0.22
Spotted skunk	<i>Spilogale gracilis</i>	Detected	0.01	0.01	1.00	0.22

Spiny lizard	<i>Sceloporus</i> spp.	Detecte d	0.00	0.00	1.00	0.22
Striped skunk	<i>Mephitis mephitis</i>	Drank	0.00	0.00	1.00	0.22
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Detecte d	0.00	0.00	1.00	0.22
Bell's Vireo	<i>Vireo bellii</i>	Drank	0.00	0.00	1.00	0.22
House Finch	<i>Haemorhous mexicanus</i>	Drank	0.00	0.00	1.00	0.22
Mountain lion	<i>Puma concolor</i>	Detecte d	0.00	0.00	1.00	0.22
<i>Water type: Dry</i>						
<i>Site: Black Canyon; 4236 hours sampling effort, 5.3 hours in use, 102 distinct visits</i>						
Burro	<i>Equus asinus</i>	Detecte d	1.86	34.90	23.00	22.55
Javelina	<i>Pecari tajacu</i>	Detecte d	0.64	11.94	16.00	15.69
Cattle	<i>Bos taurus</i>	Detecte d	0.60	11.26	13.00	12.75
Gambel's Quail	<i>Callipepla gambelii</i>	Detecte d	1.65	30.84	11.00	10.78
Cottontail Rabbit	<i>Sylvilagus audubonii</i>	Detecte d	0.02	0.41	9.00	8.82
Gray fox	<i>Urocyon cinereoargenteus</i>	Detecte d	0.00	0.06	8.00	7.84
White-winged Dove	<i>Zenaida asiatica</i>	Detecte d	0.30	5.70	4.00	3.92
Mule deer	<i>Odocoileus hemionus</i>	Detecte d	0.01	0.23	4.00	3.92
Mourning Dove	<i>Zenaida macroura</i>	Detecte d	0.24	4.51	3.00	2.94
Bobcat	<i>Lynx rufus</i>	Detecte d	0.01	0.13	3.00	2.94
Black-tailed jackrabbit	<i>Lepus californicus</i>	Detecte d	0.00	0.01	2.00	1.96
American Badger	<i>Taxidea taxus</i>	Detecte d	0.00	0.01	1.00	0.98
Unknown	Unknown	Detecte d	0.00	0.01	1.00	0.98
Coyote	<i>Canis latrans</i>	Detecte d	0.00	0.01	1.00	0.98
Mountain lion	<i>Puma concolor</i>	Detecte d	0.00	0.01	1.00	0.98
Spotted skunk	<i>Spilogale gracilis</i>	Detecte d	0.00	0.01	1.00	0.98
<i>Water type: Natural (modified) Spring</i>						
<i>Site: Black Canyon; 2939 hours sampling effort, 66.8 hours in use, 732 distinct visits</i>						
Mourning Dove	<i>Zenaida macroura</i>	Drank	9.17	13.72	169.00	23.09
Cattle	<i>Bos taurus</i>	Drank	33.82	50.61	127.00	17.35
Gray fox	<i>Urocyon cinereoargenteus</i>	Drank	3.83	5.72	120.00	16.39
Common Raven	<i>Corvus corax</i>	Drank	3.93	5.89	68.00	9.29

Javelina	<i>Pecari tajacu</i>	Drank	2.84	4.24	55.00	7.51
White-winged Dove	<i>Zenaida asiatica</i>	Drank	2.88	4.31	48.00	6.56
Mule deer	<i>Odocoileus hemionus</i>	Drank	4.88	7.30	37.00	5.05
Zone-tailed Hawk	<i>Buteo albonotatus</i>	Drank	0.94	1.40	18.00	2.46
Rock squirrel	<i>Otospermophilus variegatus</i>	Drank	0.24	0.35	17.00	2.32
Burro	<i>Equus asinus</i>	Drank	1.32	1.97	15.00	2.05
Cooper's Hawk	<i>Accipiter cooperii</i>	Drank	0.61	0.91	14.00	1.91
Gambel's Quail	<i>Callipepla gambelii</i>	Drank	1.73	2.59	11.00	1.50
Great-horned Owl	<i>Bubo virginianus</i>	Drank	0.13	0.19	4.00	0.55
Unknown	Unknown	Drank	0.00	0.01	4.00	0.55
Bobcat	<i>Lynx rufus</i>	Drank	0.13	0.19	3.00	0.41
Lesser Nighthawk	<i>Chordeiles acutipennis</i>	Detected	0.10	0.16	3.00	0.41
Spotted skunk	<i>Spilogale gracilis</i>	Drank	0.00	0.00	3.00	0.41
Black-throated sparrow	<i>Amphispiza bileata</i>	Drank	0.00	0.00	2.00	0.27
Rodent sp	Unknown	Detected	0.00	0.00	2.00	0.27
Hooded Oriole	<i>Icterus cucullatus</i>	Drank	0.00	0.00	2.00	0.27
North American porcupine	<i>Erethizon dorsatum</i>	Drank	0.06	0.09	1.00	0.14
Turkey Vulture	<i>Cathartes aura</i>	Detected	0.01	0.02	1.00	0.14
Barn Owl	<i>Tyto alba</i>	Drank	0.00	0.00	1.00	0.14
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Detected	0.00	0.00	1.00	0.14
House Finch	<i>Haemorhous mexicanus</i>	Drank	0.00	0.00	1.00	0.14
Lesser Goldfinch	<i>spinus psaltria</i>	Drank	0.00	0.00	1.00	0.14
Coyote	<i>Canis latrans</i>	Detected	0.00	0.00	1.00	0.14
Western Screech-owl	<i>Megascops kennicottii</i>	Detected	0.00	0.00	1.00	0.14
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	Drank	0.00	0.00	1.00	0.14
<i>Water type: Burro wells</i>						
<i>Site: Greenwood Spring; 624 hours sampling effort, 25.3 hours in use, 177 distinct visits</i>						
Burro	<i>Equus asinus</i>	Drank	18.17	71.65	76.00	42.94
Horse	<i>Equus ferus</i>	Drank	4.23	16.69	56.00	31.64
Cattle	<i>Bos taurus</i>	Drank	2.19	8.63	26.00	14.69
Mule deer	<i>Odocoileus hemionus</i>	Drank	0.76	3.01	8.00	4.52
Coyote	<i>Canis latrans</i>	Detected	0.00	0.00	3.00	1.69
Gray fox	<i>Urocyon cinereoargenteus</i>	Detected	0.00	0.00	2.00	1.13
Gambel's Quail	<i>Callipepla gambelii</i>	Drank	0.00	0.00	2.00	1.13
Harris's antelope ground squirrel	<i>Ammospermophilus harrisi</i>	Drank	0.00	0.00	1.00	0.56



Mourning Dove	<i>Zenaida macroura</i>	Drank	0.00	0.00	1.00	0.56
Cottontail Rabbit	<i>Sylvilagus audubonii</i>	Detecte d	0.00	0.00	1.00	0.56
Mountain lion	<i>Puma concolor</i>	Detecte d	0.00	0.00	1.00	0.56
<i>Water type: Dry</i> <i>Site: Greenwood Spring; 5190 hours sampling effort, 54.8 hours in use, 1041 distinct visits</i>						
Horse	<i>Equus ferus</i>	Detecte d	17.57	32.01	378.00	36.31
Burro	<i>Equus asinus</i>	Drank	17.60	32.06	245.00	23.54
Mule deer	<i>Odocoileus hemionus</i>	Detecte d	10.29	18.74	190.00	18.25
Cattle	<i>Bos taurus</i>	Detecte d	8.70	15.85	99.00	9.51
Gambel's Quail	<i>Callipepla gambelii</i>	Detecte d	0.26	0.48	45.00	4.32
Coyote	<i>Canis latrans</i>	Detecte d	0.09	0.16	16.00	1.54
Mountain lion	<i>Puma concolor</i>	Detecte d	0.01	0.01	16.00	1.54
Cottontail Rabbit	<i>Sylvilagus audubonii</i>	Detecte d	0.02	0.04	13.00	1.25
Gray fox	<i>Urocyon cinereoargenteus</i>	Detecte d	0.03	0.06	11.00	1.06
Javelina	<i>Pecari tajacu</i>	Detecte d	0.11	0.20	7.00	0.67
White-winged Dove	<i>Zenaida asiatica</i>	Detecte d	0.00	0.00	7.00	0.67
Bobcat	<i>Lynx rufus</i>	Detecte d	0.00	0.01	5.00	0.48
Common Raven	<i>Corvus corax</i>	Detecte d	0.00	0.00	2.00	0.19
Rock squirrel	<i>Otospermophilus variegatus</i>	Detecte d	0.21	0.37	1.00	0.10
Hooded Oriole	<i>Icterus cucullatus</i>	Detecte d	0.00	0.00	1.00	0.10
Myiarchus flycatcher	<i>Myiarchus spp.</i>	Detecte d	0.00	0.00	1.00	0.10
unk bird	Unknown	Detecte d	0.00	0.00	1.00	0.10
Harris's antelope ground squirrel	<i>Ammospermophilus harrisi</i>	Detecte d	0.00	0.00	1.00	0.10
Unknown	Unknown	Detecte d	0.00	0.00	1.00	0.10
Ringtail cat	<i>Bassariscus astutus</i>	Detecte d	0.00	0.00	1.00	0.10
<i>Water type: Natural spring</i> <i>Site: Greenwood Spring; 3270 hours sampling effort, 257 hours in use, 1568 distinct visits</i>						
Horse	<i>Equus ferus</i>	Drank	103.4 8	40.27	315.00	20.09

Gambel's Quail	<i>Callipepla gambelii</i>	Drank	23.78	9.25	220.00	14.03
Cattle	<i>Bos taurus</i>	Drank	35.16	13.69	211.00	13.46
Burro	<i>Equus asinus</i>	Drank	43.56	16.95	206.00	13.14
Common Raven	<i>Corvus corax</i>	Drank	32.65	12.71	192.00	12.24
Mule deer	<i>Odocoileus hemionus</i>	Drank	10.24	3.99	164.00	10.46
White-winged Dove	<i>Zenaida asiatica</i>	Drank	1.78	0.69	75.00	4.78
Mountain lion	<i>Puma concolor</i>	Drank	1.22	0.48	30.00	1.91
Rock squirrel	<i>Otospermophilus variegatus</i>	Drank	0.23	0.09	25.00	1.59
Gila Woodpecker	<i>Melanerpes uropygialis</i>	Drank	0.25	0.10	13.00	0.83
Myiarchus flycatcher	<i>Myiarchus spp.</i>	Drank	0.21	0.08	12.00	0.77
Western Screech-owl	<i>Megascops kennicottii</i>	Drank	0.10	0.04	11.00	0.70
Coyote	<i>Canis latrans</i>	Drank	0.42	0.16	10.00	0.64
Javelina	<i>Pecari tajacu</i>	Drank	0.25	0.10	10.00	0.64
Hooded Oriole	<i>Icterus cucullatus</i>	Drank	0.12	0.05	10.00	0.64
Gray fox	<i>Urocyon cinereoargenteus</i>	Drank	0.06	0.02	9.00	0.57
Western Scrub-jay	<i>Apelocoma californica</i>	Drank	0.11	0.04	8.00	0.51
House Finch	<i>Haemorhous mexicanus</i>	Drank	0.18	0.07	6.00	0.38
Greater Roadrunner	<i>Geococcyx californianus</i>	Drank	0.11	0.04	5.00	0.32
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Drank	0.01	0.00	5.00	0.32
Scott's Oriole	<i>Icterus parisorum</i>	Drank	0.15	0.06	4.00	0.26
Turkey Vulture	<i>Cathartes aura</i>	Drank	2.62	1.02	3.00	0.19
Gilded Flicker	<i>Colaptes chrysoides</i>	Drank	0.05	0.02	3.00	0.19
Curve-billed Thrasher	<i>Toxostoma curvirostre</i>	Drank	0.00	0.00	3.00	0.19
Northern Mockingbird	<i>Mimus polyglottos</i>	Drank	0.00	0.00	3.00	0.19
Spiny lizard	<i>Sceloporus spp.</i>	Detected	0.13	0.05	2.00	0.13
Cottontail Rabbit	<i>Sylvilagus audubonii</i>	Drank	0.01	0.01	2.00	0.13
Rattlesnake	<i>Crotalus spp.</i>	Detected	0.06	0.02	1.00	0.06
Ringtail cat	<i>Bassariscus astutus</i>	Detected	0.00	0.00	1.00	0.06
Lesser Nighthawk	<i>Chordeiles acutipennis</i>	Detected	0.00	0.00	1.00	0.06
Western Tanager	<i>Piranga ludoviciana</i>	Detected	0.00	0.00	1.00	0.06
Ladder-backed Woodpecker	<i>Dryobates scalaris</i>	Drank	0.00	0.00	1.00	0.06
Great-horned Owl	<i>Bubo virginianus</i>	Detected	0.00	0.00	1.00	0.06
Cooper's Hawk	<i>Accipiter cooperii</i>	Detected	0.00	0.00	1.00	0.06
Gopher snake	<i>Pituophis catenifer affinis</i>	Detected	0.00	0.00	1.00	0.06
Canyon Towhee	<i>Melospiza fusca</i>	Drank	0.00	0.00	1.00	0.06

Loggerhead Shrike	<i>Lanius ludovicianus</i>	Detected	0.00	0.00	1.00	0.06
Spotted skunk	<i>Spilogale gracilis</i>	Drank	0.00	0.00	1.00	0.06
<i>Water type: Burro wells</i>						
<i>Site: Hackberry Wash; 2100 hours sampling effort, 57 hours in use, 514 distinct visits</i>						
Cattle	<i>Bos taurus</i>	Drank	20.45	35.65	270.00	52.53
Burro	<i>Equus asinus</i>	Drank	22.57	39.36	131.00	25.49
Javelina	<i>Pecari tajacu</i>	Drank	12.83	22.37	59.00	11.48
Mule deer	<i>Odocoileus hemionus</i>	Drank	0.84	1.47	14.00	2.72
Coyote	<i>Canis latrans</i>	Drank	0.40	0.70	13.00	2.53
Black-tailed jackrabbit	<i>Lepus californicus</i>	Drank	0.01	0.02	9.00	1.75
Gray fox	<i>Urocyon cinereoargenteus</i>	Drank	0.04	0.06	4.00	0.78
Striped skunk	<i>Mephitis mephitis</i>	Drank	0.00	0.00	3.00	0.58
Bighorn Sheep	<i>Ovis canadensis</i>	Drank	0.01	0.02	2.00	0.39
White-winged Dove	<i>Zenaida asiatica</i>	Drank	0.00	0.00	2.00	0.39
Gambel's Quail	<i>Callipepla gambelii</i>	Detected	0.16	0.28	1.00	0.19
Raccoon	<i>Procyon lotor</i>	Drank	0.02	0.04	1.00	0.19
unk bird	Unknown	Detected	0.01	0.01	1.00	0.19
Black Bear	<i>Ursus americanus</i>	Drank	0.00	0.00	1.00	0.19
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Drank	0.00	0.00	1.00	0.19
Unknown	Unknown	Detected	0.00	0.00	1.00	0.19
Killdeer	<i>Charadrius vociferus</i>	Detected	0.00	0.00	1.00	0.19
<i>Water type: Dry</i>						
<i>Site: Hackberry Wash; 8911 hours sampling effort, 33 hours in use, 940 distinct visits</i>						
Cattle	<i>Bos taurus</i>	Drank	26.48	79.22	646.00	68.72
Burro	<i>Equus asinus</i>	Drank	2.83	8.45	71.00	7.55
Black-tailed jackrabbit	<i>Lepus californicus</i>	Detected	0.92	2.75	55.00	5.85
Javelina	<i>Pecari tajacu</i>	Drank	1.46	4.38	40.00	4.26
Mule deer	<i>Odocoileus hemionus</i>	Drank	0.28	0.85	26.00	2.77
Coyote	<i>Canis latrans</i>	Drank	0.26	0.77	26.00	2.77
Striped skunk	<i>Mephitis mephitis</i>	Detected	0.01	0.02	17.00	1.81
Gambel's Quail	<i>Callipepla gambelii</i>	Detected	0.08	0.24	12.00	1.28
Unknown	Unknown	Detected	0.23	0.69	6.00	0.64
Gray fox	<i>Urocyon cinereoargenteus</i>	Detected	0.04	0.11	5.00	0.53
Raccoon	<i>Procyon lotor</i>	Detected	0.01	0.02	2.00	0.21

Say's Phoebe	<i>Sayornis saya</i>	Detecte d	0.00	0.00	2.00	0.21
unk bird	Unknown	Detecte d	0.00	0.00	2.00	0.21
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Detecte d	0.00	0.00	1.00	0.11
American Badger	<i>Taxidea taxus</i>	Detecte d	0.00	0.00	1.00	0.11
Spotted skunk	<i>Spilogale gracilis</i>	Detecte d	0.00	0.00	1.00	0.11
Common Raven	<i>Corvus corax</i>	Detecte d	0.00	0.00	1.00	0.11
Bobcat	<i>Lynx rufus</i>	Detecte d	0.00	0.00	1.00	0.11
<i>Water type: Natural surface water</i>						
<i>Site: Hackberry wash; 149 hours sampling effort, 27 hours in use, 83 distinct visits</i>						
Cattle	<i>Bos taurus</i>	Drank	25.18	92.14	39.00	46.99
Burro	<i>Equus asinus</i>	Drank	0.58	2.13	10.00	12.05
Mule deer	<i>Odocoileus hemionus</i>	Drank	0.63	2.29	5.00	6.02
Curve-billed Thrasher	<i>Toxostoma curvirostre</i>	Detecte d	0.04	0.15	4.00	4.82
Mourning Dove	<i>Zenaida macroura</i>	Detecte d	0.01	0.04	4.00	4.82
Black-tailed jackrabbit	<i>Lepus californicus</i>	Detecte d	0.23	0.85	3.00	3.61
White-winged Dove	<i>Zenaida asiatica</i>	Drank	0.06	0.23	3.00	3.61
Coyote	<i>Canis latrans</i>	Drank	0.15	0.55	2.00	2.41
Rock Wren	<i>Salpinctes obsoletus</i>	Drank	0.02	0.07	2.00	2.41
Gilded Flicker	<i>Colaptes chrysoides</i>	Detecte d	0.00	0.01	2.00	2.41
Common Raven	<i>Corvus corax</i>	Detecte d	0.16	0.59	1.00	1.20
Javelina	<i>Pecari tajacu</i>	Drank	0.16	0.57	1.00	1.20
Bighorn Sheep	<i>Ovis canadensis</i>	Drank	0.05	0.19	1.00	1.20
Gambel's Quail	<i>Callipepla gambelii</i>	Detecte d	0.05	0.17	1.00	1.20
Empidomax spp.	<i>Empidomax spp.</i>	Detecte d	0.00	0.00	1.00	1.20
Turkey Vulture	<i>Cathartes aura</i>	Detecte d	0.00	0.00	1.00	1.20
unk bird	Unknown	Detecte d	0.00	0.00	1.00	1.20
Myiarchus flycatcher	<i>Myiarchus spp.</i>	Detecte d	0.00	0.00	1.00	1.20
Spiny lizard	<i>Sceloporus spp.</i>	Detecte d	0.00	0.00	1.00	1.20
<i>Water type: Other species' wells</i>						
<i>Site: Hackberry Wash; 542 hours sampling effort, 25 hours in use, 276 distinct visits</i>						
Gambel's Quail	<i>Callipepla gambelii</i>	Drank	13.09	37.72	79.00	28.62

Javelina	<i>Pecari tajacu</i>	Drank	16.48	47.51	53.00	19.20
Gray fox	<i>Urocyon cinereoargenteus</i>	Drank	0.47	1.35	28.00	10.14
Black-tailed jackrabbit	<i>Lepus californicus</i>	Drank	2.40	6.91	25.00	9.06
Mourning Dove	<i>Zenaida macroura</i>	Drank	0.15	0.43	25.00	9.06
Rock squirrel	<i>Otospermophilus variegatus</i>	Drank	0.53	1.53	21.00	7.61
Cattle	<i>Bos taurus</i>	Drank	0.45	1.31	7.00	2.54
Common Raven	<i>Corvus corax</i>	Drank	0.29	0.82	7.00	2.54
White-winged Dove	<i>Zenaida asiatica</i>	Drank	0.10	0.30	5.00	1.81
Northern Cardinal	<i>Cardinalis cardinalis</i>	Drank	0.00	0.01	5.00	1.81
Coyote	<i>Canis latrans</i>	Drank	0.34	0.98	4.00	1.45
Burro	<i>Equus asinus</i>	Detected	0.01	0.03	4.00	1.45
Striped skunk	<i>Mephitis mephitis</i>	Drank	0.02	0.07	3.00	1.09
Myiarchus flycatcher	<i>Myiarchus spp.</i>	Drank	0.01	0.04	2.00	0.72
Greater Roadrunner	<i>Geococcyx californianus</i>	Drank	0.00	0.00	2.00	0.72
Bighorn Sheep	<i>Ovis canadensis</i>	Detected	0.20	0.59	1.00	0.36
Bobcat	<i>Lynx rufus</i>	Drank	0.14	0.41	1.00	0.36
Mule deer	<i>Odocoileus hemionus</i>	Detected	0.00	0.00	1.00	0.36
Unknown	Unknown	Detected	0.00	0.00	1.00	0.36
Gila Woodpecker	<i>Melanerpes uropygialis</i>	Detected	0.00	0.00	1.00	0.36
unk bird	Unknown	Drank	0.00	0.00	1.00	0.36

APPENDIX E

USE OF BURRO WELLS BY LEPIDOPTERANS

[Consult Attached Files]