To the University of Wyoming:

The members of the Committee approve the dissertation of Saeideh Esmaeili presented on 12/11/2020.

Jacob R. Goheen, Chairperson

Kenneth L. Driese, Outside Department Member

Mahmoud-Reza Hemami, External Department Member

Carlos Martinez Del Rio

Matthew J. Kauffman

APPROVED:

Dr. Melanie A. Murphy: Interdisciplinary Chair, Program in Ecology

Dr. James C. M. Ahern, Associate Vice Provost of Graduate Education

Esmaeili, Saeideh, Quantifying resource selection and community attitude to inform conservation of the globally-endangered onager, Ph.D., Ecology, December 2020.

Human-wildlife conflicts restrict conservation efforts, especially for wide-ranging animals whose home ranges overlap with human activities. In first chapter, I conducted a study to understand conflicts with and factors influencing the perceived value of an expanding population of onager (*Equus hemionus onager*) by local communities in southern Iran. I asked locals' agreement toward six potential management strategies intended to lessen human-onager conflict. I found that human-onager conflict was restricted to 45% of respondents within Bahram-e-Goor Protected Area, all of whom were involved in farming or herding activities. Locals within the protected area were more knowledgeable toward onagers and valued onagers more than locals living outside the protected area. Locals' level of education, total annual income, and perceptions of onager population trends (both decreasing and increasing) affected perceived value of onagers positively; conflict with onager negatively influenced their perceived value. Locals were most supportive of monetary compensation to tolerate onager conflicts, and changing from a traditional lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government; locals were least supportive of selling land to the government. The Forage Maturation Hypothesis states that energy intake for ungulates is maximized when forage biomass is at intermediate levels. Nevertheless, metabolic allometry and the disparate digestive systems possessed by ungulates suggest that resource selection should vary among species. Further, human activities may alter the availability of resources and thereby influence forage selection. In the second chapter, by combining relocation data from GPS telemetered individuals with remotely-sensed data on forage biomass, potential energy intake from forage, and surface water, I quantified the effect of body size, digestive system, and human activity in determining landscape-level movements of 26 populations of hindgut fermenters (equids) and ruminants inhabiting arid and semi-arid rangelands worldwide. Strength of selection for potential energy intake was negatively related to body size, regardless of digestive system. Selection for proximity to surface water was stronger for equids relative to ruminants, regardless of body size. Although human activity explained some variation in resource selection, body size and digestive system predicted resource selection better than human activity across all populations. Body size forces trade-offs in how ungulates prioritize forage characteristics, thereby driving the strength of selection for potential energy intake by free-ranging ungulates across the globe. In the third chapter, I quantified interactions between globally-endangered onagers and livestock in central Iran through a combination of remotely-sensed vegetation metrics, and GPS telemetry and diet quality of onagers. Resource selection and use by onagers provided varying support for exploitative competition, interference competition, and facilitation, depending on season and presence of livestock. Intensity of livestock grazing reduced forage biomass from pre- to post-grazing periods, demonstrating potential for competitive suppression of onagers by livestock during the dry season. Additionally, selection for high forage biomass was accentuated at night, when livestock were corralled, indicating avoidance by onagers. During the wet season, onagers exposed to livestock exhibited higher-quality diets than that did not co-occur with livestock, suggesting that livestock grazing may enhance forage quality for onagers. My work is the first investigation of one (of two) remaining populations of onagers, and highlights restoration potential for a large, endangered mammal alongside pastoralist livelihoods elsewhere in Iran.

QUANTIFYING RESOURCE SELECTION AND COMMUNITY ATTITUDES TO INFORM CONSERVATION OF THE GLOBALLY-ENDANGERED ONAGER

By
Saeideh Esmaeili

A dissertation submitted to the Department of Zoology and Physiology

and the University of Wyoming

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY
in
ECOLOGY

Laramie, Wyoming

December 2020

Copyright

To my family

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my advisor, Dr. Jake Goheen, for his support and patience and all efforts he invested in my education and academic development. I appreciate his contribution and the opportunity he provided for this study on onagers, which is the first telemetry study of any ungulate population in Iran. His contribution will be always admired and remembered. I am also very grateful to my committee members Dr. Kenneth Driese, Dr. Mahmoud-Reza Hemami, Dr. Matthew Kauffman, and Dr. Carlos Martinez Del Rio for their invaluable guidance and insightful feedback through this process. I especially thank Dr. Hemami for his efforts in coordinating field and lab work including capturing onagers. This work would not have been possible without his dedication and contribution.

Eva Mayr-Stihl Stiftung, the Cleveland Metroparks Zoo, the Chicago Zoological Society, the Mohamed Bin Zayed Species Conservation Fund, the American Society of Mammologists, the Biodiversity Institute and Berry Fellowship at the University of Wyoming generously supported this work. I would like to thank Department of Zoology and Physiology and Office of International Students and Scholars at the University of Wyoming for all office supports they provided for me. I would also like to thank Ms. Bahareh Shahriari and Mr. Mohammad Nosrati at Wildlife Management and Conservation Bureau at Iranian Department of Environment for their help and coordination during this project. Capture and collaring onagers could not have been completed without contribution of Dr. Chris Walzer, Dr. Behrang Ekrami, Mr. Davood Pakniat, Mr. Ahmad Rastegar, and all rangers at Bahram-e-Goor Protected Area. Also, supports from Dr. Petra Kaczensky, Dr. Dr Patricia Moehlman, and Dr. Stephan Hering-Hagenbeck was invaluable during this work. I thank my field assistants Mr. Ali Tabatabaee and Mr. Farzad Shanbadi for their efforts and help with collecting field data. My beloved brothers and nephew,

Majid, Esmaeil, and Rasoul supported me in the field, which I am more than grateful for their contribution.

The following colleagues generously shared their data and expertise for the second chapter of my work, I am grateful to all of them: Drs Brett R. Jesmer, Shannon E. Albeke, Briana Abrahms, Ellen O. Aikens, Bayarbaatar Buuveibaatar, Jeffrey L. Beck, Randall B. Boone, Simon Chamaillé-Jammes, Buyanaa Chimeddorj, Paul C. Cross, Nandintsetseg Dejid, Jagdag Enkhbyar, Ilya R. Fischhoff, Adam T. Ford, Kate Jenks, Mahmoud-Reza Hemami, Jacob D. Hennig, Takehiko Y. Ito, Petra Kaczensky, Matthew J. Kauffman, Sarah R. B. King, Badamjav Lkhagvasuren, John F. McEvoy, Joerg Melzheimer, Jerod A. Merkle, Thomas Mueller, Jeff Muntifering, Kirk Olson, John Payne, Daniel I. Rubenstein, Hall Sawyer, John. D. Scasta, Kathryn A. Schoenecker, Melissa Songer, Jared A. Stabach, Seth Stapleton, Theresa S. M. Stratmann, Siva R. Sundaresan, Dorj Usukhjargal, Ganbold Uuganbayar, and John M. Fryxell. Additionally, I should thank Dr. Kathryn Schoenecker and Dr. Sarah King for providing me with the opportunity of a summer internship at Colorado State University in 2018 and their support in the past several months.

In the last five years, I had the chance to get to know and work with young scientists at Dr. Goheen’s Lab. I would like to thank my labmates and other graduate students who provided friendship and support during lab meetings, as well as friendly gatherings. I established invaluable friends in Laramie, with whom I shared memorable events and enjoyed their companionship. I am thankful to all of them.

Lastly, but not at least, my heartfelt thanks to my beloved mom, siblings, and my husband Amir for their love, inspiration, and support. I am more than fortunate and thankful to have such an amazing family who always loves me and supports my decisions.

TABLE OF CONTENT

CHAPTER ONE

HUMAN DIMENSIONS OF WILDLIFE CONSERVATION: ASSESSMENT OF CONFLICTS IN RESTORING A WIDE-RANGING SPECIES IN A MULTI-USE LANDSCAPE

INTRODUCTION

Increasingly, wide-ranging animals share landscapes with humans and their livestock, triggering human-wildlife conflict which can impart harm on both sides (Woodroffe and Ginsberg 1998; Treves and Karanth 2003; Gordon 2009). Humans may directly kill wildlife in retaliation for livestock or crop depredation, thereby suppressing wildlife populations (Woodroffe, Thirgood, and Rabinowitz 2005; Redpath et al. 2013). Such retaliatory killings can lead to collapse of the species' geographic range, restricting small and isolated populations to formally-protected areas (Yackulic, Sanderson, and Uriarte 2011; Mace et al. 2008). Therefore, understanding and resolving human-wildlife conflict is a prerequisite for effective wildlife conservation in multi-use landscapes (Treves et al. 2006; Manfredo 2008; Dickman 2010).

Conservation efforts aimed at reducing human-wildlife conflict have been successful in bolstering population sizes and expanding geographic ranges for many species (Seddon et al. 2014). Nevertheless, expansion of wildlife populations into multi-use landscapes can reignite conflicts, thereby creating a negative feedback between recovery of wildlife populations and human-wildlife conflicts. Ultimately, such negative feedbacks can inhibit conservation success (Woodroffe, Thirgood, and Rabinowitz 2005; Hobbs et al. 2012)(Fig. 1). Because few protected areas are sufficiently large to conserve them (Pimm et al. 2014; Gaston et al. 2008; Woodroffe and Ginsberg 1998), such destructive loops are a major challenge for wide-ranging species that depend on access to multi-use landscapes (Chapron et al. 2014; Ripple et al. 2015; Watson et al.

2014). When stakeholders view human-wildlife conflict as a shared problem which all parties have a vested interest in solving, the destructive loops can be averted (Redpath et al. 2013; Ripple et al. 2015)(Fig. 1).

Positive attitudes toward wildlife are a powerful driver for wildlife recovery (Gusset et al. 2008). The most viable approaches toward mitigating human-wildlife conflict are those in which negative outcomes for both humans and wildlife are reduced, or where common benefits make coexistence desirable (i.e., a "win-win outcome", (Decker and Chase 1997; Redpath et al. 2013)). Anticipating conflicts can provide solutions before negative attitudes hinder dialogue. The first steps in managing conflict are to understand the nature of the conflict, local attitudes toward wildlife, and how wildlife impact the economic well-being of the local communities (Kansky and Knight 2014; Berkes 2004).

The Asiatic wild ass (*Equus hemionus*) is found throughout deserts and desert-steppes of Central Asia. With an estimated global population of 55,000, the species is still relatively abundant in some areas, but it occupies less than 3% of its historic range (Kaczensky et al. 2015). The Persian wild ass or onager (*E. h. onager*) is an endangered subspecies of Asiatic wild ass (Hemami et al. 2015; Kaczensky et al. 2015) that, over the last half century, declined precipitously because of poaching and reduced funds for conservation (Beck 1998). In 1997, a historically low population of 140 individuals was restricted to two protected area complexes: the Bahram-e-Goor Protected Area (BPA) and the Touran Biosphere Reserve in central Iran (Tatin et al. 2003)(Fig. 2). In 1997, Qatrouiyeh National Park (in which livestock grazing is prohibited; QNP) was established within the BPA, which houses a growing onager population (Hemami and Momeni 2013). Onagers remain rare across the wider BPA, where livestock grazing is permitted.

The mechanisms of onager population suppression within BPA are not well understood (Hemami and Momeni 2013), but poaching, agricultural expansion, and associated conflicts with pastoralists and their livestock are thought to have driven the decline (Hemami and Momeni 2013). Due to increasing human activity within BPA, onagers have become largely confined to QNP, where anti-poaching patrols are common. Further, QNP maintains artificial watering holes, and provides supplementary food in the dry season from May to October (Hemami and Momeni 2013). Consequently, onagers are now perceived as overabundant in QNP by wildlife managers (Pers. Comm. Iranian Department of Environment). Increasingly, however, farmers and nomadic herders (hereafter “herders”) in and around BPA are concerned about crop losses and competition between onagers and livestock, respectively (Esmaeili, personal observation). Thus, mitigating human-wildlife conflict should facilitate onager recovery within BPA as a first step to recovery in its historical range.

I sought to understand factors contributing to human-onager conflicts in rural communities in and around BPA. I used structured questionnaires to understand the nature and extent of the onager-human conflict, quantify local attitudes and knowledge, and assess support for potential management strategies. I hypothesized that (1) people residing within BPA would experience higher levels of conflict compared to those outside BPA; and (2) the occurrence and magnitude of conflicts would predict both people’s attitudes towards onagers, and their preferences for management strategies. My study provides the first quantitative data on human-onager interactions to guide future recovery strategies for this endangered subspecies.

METHODS AND MATERIALS

Study area

I conducted my study in the Fars, Kerman, and Yazd Provinces on the central plateau of Iran. I was especially interested in differences between locals from the 3,747 km^2 BPA and in a surrounding 50-kilometer buffer (26,938 km^2; Fig. 2). Bahram-e-Goor Protected Area has an arid climate (mean annual temperature 21 ± 1 °C, mean annual precipitation 186.11 ± 90.69 mm); September is the driest month and January is the wettest month (0.0 ± 0.0 mm and 38.13 ± 45.31 mm), respectively ("I.R. Iran Meteorological Organization" 2017). The area is characterized by desert steppe vegetation, dominated by *Artemisia sieberi*, *Zygophylllum eurypterum*, *Astragalus* spp., *Noaea mucronata*, and sparse perennial trees such as mountain almond (*Amygdalus horrida*) and Persian turpentine (*Pistacia atlantica*).

In 1972, BPA was established to protect onagers and other threatened species, including Indian gazelle (*Gazella bennettii*), wild sheep (*Ovis orientalis*), wild goat (*Capra aegagrus*), and Asian houbara bustard (*Chlamydotis maqueenii*). Additionally, BPA is home to wild boars (*Sus scrofa*) and gray wolves (*Canis lupus*), with the former regarded as a threat to crops (Ghoshtasb et al. 2012) and the latter regarded as a threat to livestock (Hosseini-Zavarei et al. 2013).

Approximately 14 head of livestock (mainly sheep *Ovis aries* and goat *Capra hircus*, occasionally camel *Camelus dromedarius*) per square kilometer are permitted to graze inside the BPA (Fars Province Department of Environment, unpublished report). Frequent droughts are the main impediment to farming in the area, which have led to a transition from water-intensive crops such as wheat to drought-resistant orchards and livestock (Iranian Department of Environment, unpublished report).

Approximately 2,600 semi-nomadic pastoralists and small-scale farmers reside within BPA (Statistical Center of Iran 2009). Outside BPA, about one-third of the total human population (ca. 470,000 individuals) lives in rural areas (centers of human activity with <15,000 inhabitants), whereas the other two-thirds live in urban centers with >15,000 inhabitants. Because the majority (60% of 190 individuals surveyed from urban centers) of urban residents had never heard of onagers, I focused on comparing responses from individuals residing within and along the boundary of BPA (hereafter "within BPA") to those living outside BPA in rural areas (hereafter "outside BPA").

Sampling design

From January 2014 to July 2016, I conducted 102 interviews within BPA and 153 outside BPA. Only 2 (2.0%) respondents within BPA and 11 (7.2%) outside BPA were unaware of onagers, resulting in a sample size of 100 interviews from within BPA and 142 from outside BPA (Table S1). I adopted a stratified random sampling design, in which the distribution of questionnaires was proportional to size of the rural population within the counties (which are nested within provinces) within my study area (Fig. 2 and Table S1). Outside BPA, and within each county, I randomly selected up to four villages in which to interview up to four people, each from a different household, without bias toward age or gender. I defined "households" as people from the same family and living within the same house. Within BPA, I randomly selected people across the entire area and along the boundary. Sampling intensity was 3.8% of the total population within BPA and 0.1% outside BPA (S1 Table).

Within BPA, I interviewed an additional 101 farmers and herders (16 farmers, 21 herders, and 64 individuals who were both farmers and herders) to quantify levels of agreement toward six strategies to reduce human-onager conflict.

Questionnaire design

To ensure that my questionnaires addressed the objectives of my study, I conducted 25 pilot interviews with locals where I explored their views about their livelihoods, BPA, onagers, and other wildlife. I subsequently used that information to modify a pre-existing questionnaire used to assess public attitudes toward Asiatic wild ass in Mongolia (Kaczensky et al. 2006). To initiate interviews, I first asked if locals were aware of the existence of onagers. If so, I proceeded with my questionnaire (Text S1); if not, I terminated the interview. Ninety-eight percent of individuals within BPA and 93.7% of individuals outside BPA were aware of the existence of onagers. The questionnaire consisted of four sections to quantify information on (1) locals' socio-economic background; (2) conflict with onagers; (3) knowledge about onagers; and (4) perceived value of onagers, plus an additional section (5) for the 101 additional respondents within BPA about acceptability toward the six potential strategies to reduce human-onager conflict (Text S1).

I used responses from sections #1-3 as predictors for answers to questions in section #4 (on the perceived value of onagers (for 100 respondents within BPA and 142 respondents outside BPA), and in section #5 (acceptability of potential management strategies to reduce human-onager conflict for 101 respondents within BPA).

Section 1: Locals' socio-economic background

I hypothesized that socio-economic background of locals would influence both the perceived value of onagers and acceptability of potential management strategies. I asked locals about their gender, age, and level of education (illiterate, primary and high school, university). I recorded livestock ownership (the number of livestock) for herders and farm size for farmers. I asked locals to categorize their total annual income in two categories of <$5000USD and >$5000 USD.

Section #2: Conflict with onagers

I hypothesized that conflict with onagers would influence both the perceived value of onagers and acceptability of potential management strategies. To assess the relative magnitude of human-onager conflict, I asked locals to rate the degree of conflict with onagers from no conflict to severe conflict, coded from one to five. I asked locals about the occurrence, type, and timing of conflicts with onagers.

Section #3: Knowledge about onagers

I hypothesized that knowledge of locals would influence the perceived value of onagers. To quantify local knowledge about onagers, I asked if four incorrect statements about onager biology were true or false. When respondents stated that incorrect statements were correct, I recorded answers as a “0”. When respondents stated that incorrect statements were incorrect, I recorded answers as a “1”. I averaged these four answers to generate a knowledge score about onagers ranging from zero to one, indicating low and high levels of knowledge, respectively. Additionally, I asked about perceived population trends of onagers (in four categories of decreasing, increasing, stable, and do not know); I predicted that those who thought onager population had been decreasing would value the species more.

Section #4: Perceived value of onagers

To quantify the perceived value of onagers, I asked locals to rank agreement with fifteen statements from “strongly disagree” (coded as 1) to “strongly agree” (coded as 5). I averaged answers to these fifteen statements to produce a semi-continuous “value score” ranging from one to five (Table S2). I measured the internal consistency of the fifteen statements comprising the value score using Cronbach’s alpha consistency analysis (Santos 1999; Gliem and Gliem 2003).

Section #5: Acceptability of potential management strategies

I inquired about the acceptability of six strategies aimed at reducing human-onager conflict, targeting only individuals within BPA (because individuals outside BPA did not experience conflict within onagers). I deliberately excluded fencing because I was most interested in management strategies that would not further fragment the distribution of onagers. The strategies were: (1) selling land to the government; (2) exchanging 50% farmland/pastureland within BPA for an equivalent amount of land outside BPA; (3) changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government; (4) accepting monetary compensation to tolerate onager conflict; (5) accepting a sedentary lifestyle instead of a nomadic one; and (6) supplementary feeding of livestock for a period in the year with the help of the government. The last two strategies were asked only from herders (who are nomadic within BPA) and not farmers (who are sedentary within BPA). I recorded responses in three categories: disagree, neutral, and agree. Unlike previous questions, I restricted responses to three categories because 5 categories were challenging for locals to understand.

Statistical analyses

I used R software (versions 3.2.2 and 3.4.1, R Development Core Team 2013) for statistical analysis. To compare responses within and outside BPA, I used Chi-square (χ^2) and Wilcoxon signed-ranks tests.

Using beta regression (Betareg package in R, Zeileis et al. 2016), I related region (whether respondents were within or outside of BPA), socio-economic predictors (gender, age, level of education, total annual income), level of conflict with onagers, knowledge score, and perceived population trends of onagers to the value score. In calculating the value score, 36% of respondents were neither farmers nor herders, so I did not include livestock ownership or farm size in this regression model to include all the respondents in a single model. I standardized the semi-continuous value score between zero and one as a response variable in the beta regression. Beta regression is suitable for modeling heteroskedastic and non-normal data restricted between zero and one (Cribari-Neto and Zeileis 2010). From generalized variance inflation factors, I detected no multicollinearity between predictors (Fox and Monette 1992).

To predict factors influencing acceptability of management strategies, I related socio-economic predictors (age, total annual income, livestock ownership, and farm size) and level of conflict with onagers to three response categories of disagree, neutral, and agree for each strategy (as an ordinal response variable) using ordinal logistic regression models (lrm function in package rms,(Harrell 2018)). Due to sample size constraints, I did not include level of education or gender in these regression models. I used likelihood ratio χ^2 tests to select models and used R^2 and a concordance-index (c-index) as a measure of predictive performance (Harrell 2018) .

RESULTS

Human-onager conflict was restricted to respondents involved in farming or herding within BPA (Table S3). No conflict with onagers was reported from outside BPA, whereas 44.4% of locals within BPA reported conflict with onagers (Text S2).

Knowledge about onagers was poor overall, but locals within BPA were more knowledgeable (who correctly answered two questions, on average) than those outside (who correctly answered one question, on average; Table 1, Wilcoxon signed-ranks test, $p < 0.001$; Text S3).

Fifteen statements produced a consistent value score (standardized alpha value = 0.79, n = 249, average inter-item correlation = 0.21; Table S2) ranging between 1.93 and 5.00. Value scores averaged 3.80 (SD = 0.45) and were slightly higher within BPA (mean ± SD: 3.86 ± 0.39;

n = 100), than outside BPA (mean ± SD: 3.76 ± 0.48; n = 142; Wilcoxon signed-ranks test w = 8747, $p = 0.05$). Locals' level of education, total annual income, and perceived onager population trends affected perceived value of onagers positively. Level of conflict with onagers negatively influenced the perceived value of onager, although explanatory power of the model was low (pseudo $R^2 = 0.21$, $z = 10.96$, $p < 0.001$; Table 2).

Presented with six potential management strategies, farmers and herders within BPA agreed most with accepting monetary compensation to tolerate onager conflicts and with changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government. Farmers and herders agreed least with selling land to the government. Farmers and herders were ambivalent towards exchanging 50% farmland/pastureland within BPA for land outside BPA and herders towards accepting a sedentary lifestyle instead of a nomadic one or supplementary feeding of livestock for a period in the year with the help of the government (Table 3).

Locals reporting high levels of conflict with onagers were less likely to agree with exchanging 50% of farmland/pastureland within BPA for land outside BPA, and were more likely to agree with monetary compensation to tolerate conflicts with onagers (Table 4). Age, livestock ownership, farm size, and total annual income were significant predictors of local agreement toward four of the six potential management strategies (Table 4). None of the selected predictors significantly affected locals' agreement toward changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government, which was the second most popular strategy (Table 4).

DISCUSSION

My study is among the first to assess attitudes of local people toward human-wildlife conflict (Farhadinia et al. 2017) and recovery of an endangered species in Iran. In Iran, wildlife conservation typically is conducted without involvement of local people (Kolahi et al. 2013). Only recently has public awareness been raised from efforts to protect and recover highly charismatic, rare predators, namely Asiatic cheetah (*Acinonyx jubatus venaticus*) and Persian leopard (*Panthera pardus saxicolor*) (Mohammadi and Kaboli 2016; Farhadinia et al. 2017). However, focus on non-predatory species has been unusual thus far, despite their prominence in history, culture, and traditions (Goldberg 2018). Although recent progress has been made toward recovery of onagers within QNP, expansion into their former geographic range within Iran has been slow. I believe that a better understanding of human-onager relationships within local communities in and around BPA represents a starting point from which to further conservation and recovery efforts (Teel and Manfredo 2010; Marshall, White, and Fischer 2007).

Although they were aware of onagers, knowledge scores of rural respondents both within and outside BPA were low; notably, onagers were viewed as widely distributed throughout Iran (Table 1). Although conflicts were restricted exclusively to rural respondents within BPA, these individuals did not value onagers less than respondents outside BPA. This lack of difference suggests that human-onager conflict is either low, or that even severe and reoccurring conflict with onagers has not yet lead to overly-negative attitudes (Yasmi, Schanz, and Salim 2006). Additionally, current levels of conflict with onagers did not drive agreement with potential management strategies. Not surprisingly, accepting monetary compensation to tolerate onager conflict was the most popular management strategy. Monetary compensation through direct payment is a common method to attenuate economic hardship caused by endangered wildlife

(Schwerdtner and Gruber 2007; Maclennan et al. 2009; Dickman, Macdonald, and Macdonald 2011). In Iran, there is currently no systematic compensation scheme for wildlife, and monetary compensation by the Department of Environment in BPA has been restricted to a few special cases. Systematic compensation schemes require significant budgets, provide little incentive to invest into mitigation measures (Nyhus et al. 2005; Bulte and Rondeau 2005), and hence are not a sustainable option when aiming for endangered species recovery by a budget-starved agency.

Farmers and herders seem willing to switch from a traditional farming/herding lifestyle to a more industrialized form of crop and livestock production. If managed well, this could reduce the need for land conversion and minimize competition for pasture between wild and domestic ungulates. However, the effects of such changes need to be carefully evaluated and local people and conservationists must come to a common understanding of the economic, cultural, and ecological consequences of such changes. Selling or exchanging land from inside BPA for land outside BPA, on the other hand, received little support. Although separating wildlife and people can be highly effective in reducing conflict, forcing people to leave can escalate human-wildlife conflict (Adams and Hutton 2007; Lele et al. 2010).

Given the localized nature of human-onager conflict, monetary compensation through insurance schemes may be the most cost-efficient means of conflict reduction. However, insurance schemes require that local farmers protect their farms to be eligible for coverage offered by local insurance services (Esmaeili, personal communication). Advice on fence design and initiating affordable technologies, like solar-powered electric fencing, could help to reduce conflicts by both onagers and wild boars (which are widespread and cause much damage to agriculture throughout Iran (Ghoshtasb et al. 2012) and the study area (Esmaeili, personal observation). However, fencing should be employed as a last resort, as it would result in the further fragmentation of the onager's distribution (Wingard et al. 2014).

My study highlighted that there is very little awareness for the precarious conservation status of onagers, as the majority of urban residents were unaware of the species' existence. Such low awareness likely reflects the restricted distribution of onagers (Tatin et al. 2003). The remoteness of BPA and the small numbers of onagers within it provided little opportunity for direct interaction, the key source of respondents' knowledge about onagers. Complicating matters further, the Farsi the word for onager and zebra is the same, creating confusion about the basic identity of the species. While Iranians distinguish between donkeys and domestic horses, there is a single word for all wild species of Family Equidae: "goor-e-khar". Given the low awareness about onagers among urban residents in the periphery of BPA, one can assume that there is almost no awareness about this species among the remaining, largely urban population in Iran (73%, Mohammadi and Kaboli 2016). Therefore, and currently, little public support can be expected from the civil society (Martín-López et al. 2009). The future of onager conservation may thus rely on the international conservation community, at least in the immediate future.

Currently, human-onager conflict is restricted within BPA; presently, there is little evidence for conflict escalation over onager conservation. As onager populations increase and expand outside QNP, however, these problems can be expected to intensify. To avoid entering a destructive loop (Fig. 1), national and local authorities need to develop and support mitigation strategies together with local communities. This should done while the conflict is still low and support for onager conservation is still relatively high.

Table 1: Four false statements comprising the “knowledge score” about onagers for respondents within and outside Bahram-e-Goor Protected Area (BPA) in southern Iran. N = 243 respondents. Chi-square tests compare results within and outside BPA.

Statement	**Within BPA**	**Outside BPA**	**n**	**X^2 (*p*)**
False statement	**% answers correctly identifying statement as false**			
Onagers can run more than 100 km/hour.	35.45	24.66	243	3.57 (0.06)
Onager mares often give birth to 2 foals.	52.72	25.33	243	20.45 (<0.001)
Onagers need to drink only once a week.	61.82	24.67	243	36.38 (<0.001)
Onagers live in many areas of Iran.	40.91	45.33	243	0.50 (0.47)

Table 2: Parameter estimates of factors influencing perceived value of onagers resulted from a beta regression model (Pseudo $R^2 = 0.21$, $z=10.96$, $p<0.001$) for locals within and outside the Bahram-e-Goor Protected Area, Iran. Positive estimates indicate positive association between a factor and perceived value of onagers.

Factor	**Estimate ± SE**	**Z**	**p**
intercept	-0.50±0.20	-2.53	0.01
outside BPA[1]	-0.08±0.14	-0.61	0.54
gender (male)[2]	0.04±0.12	0.35	0.72
age	0.04±0.06	0.66	0.51
education (primary and high school)[3]	0.22±0.15	1.30	0.19
education (university)[3]	0.65±0.22	3.00	**0.002**
total annual income (>$5000 USD)[4]	0.32±0.13	2.50	**0.01**
knowledge score	0.08±0.06	1.39	0.16
perceived onager population trend (decreasing)[5]	0.58±0.13	4.42	**<0.001**
perceived onager population trend (increasing)[5]	0.48±0.16	2.92	**0.003**
perceived onager population trend (stable)[5]	0.46±0.33	1.40	0.16
level of conflict with onagers	-0.17±0.06	-2.82	**0.004**

1 reference level: within BPA
2 reference level: female
3 reference level: illiterate
4 reference level: total annual income < $5000 USD
5 reference level: do not know

Table 3: Acceptability of potential management strategies aimed at reducing human-onager conflict according to 101 farmers and herders within Bahram-e-Goor Protected Area (BPA), Iran.

Conservation strategy	**Number of responses**		
	agree	**neutral**	**disagree**
selling land to the government	4	6	91
exchanging 50% farmland/pastureland within BPA ifor an equivalent amount of land outside BPA	23	6	72
changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government	67	10	24
accepting monetary compensation to tolerate onager conflict	76	9	16
accepting a sedentary lifestyle instead of a nomadic one *	41	13	31
supplementary feeding of livestock for a period in the year with the help of the government *	50	6	29

*Only asked from herders.

Table 4: Parameter estimates (β±SE) and p-values (p) results of ordinal regression models to predict effects of socio-economic variables and level of conflict with onagers on accepting potential management strategies aimed at reducing human-onager conflict within Bahram-e-Goor Protected Area (BPA), Iran. Strategies included: (1) selling land to the government; (2) exchanging 50% farmland/pastureland within BPA for an equivalent amount of land outside BPA; (3) changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government;(4) accepting monetary compensation to tolerate onager conflict; (5) accepting a sedentary lifestyle instead of a nomadic one; and (6) supplementary feeding of livestock for a period in the year with the help of the government.

	selling land	**exchanging 50% of lands**	**changing from traditional farming/herding**	**accepting monetary compensation**	**accepting sedentary lifestyle**	**supplementary feeding of livestock**
intercept 1	-7.65±2.91 (0.008)					
intercept 2	-9.21±3.09 (0.003)					-2.31±1.19 (0.05)
age						0.03±0.02 (0.05)
livestock ownership	0.02±0.01 (0.004)				0.01±0.01 (0.04)	
farm size		0.09±0.04 (0.03)			*	*
total annual income (>$5000USD)	2.47±1.18 (0.035)					
level of conflict with onagers		-0.57±0.28 (0.04)		0.74±0.29 (0.01)		
model Likelihood ratio test χ^2 (*p*)	20.67 (0.002)	14.48 (0.02)	2.95 (0.81)	14.43(0.02)	11.66(0.04)	9.71(0.08)
R^2	0.41	0.21	0.041	0.19	0.16	0.14
c-index	0.88	0.71	0.58	0.73	0.70	0.67

** Predictors were not included in the analyses as the questions were asked from herders.*

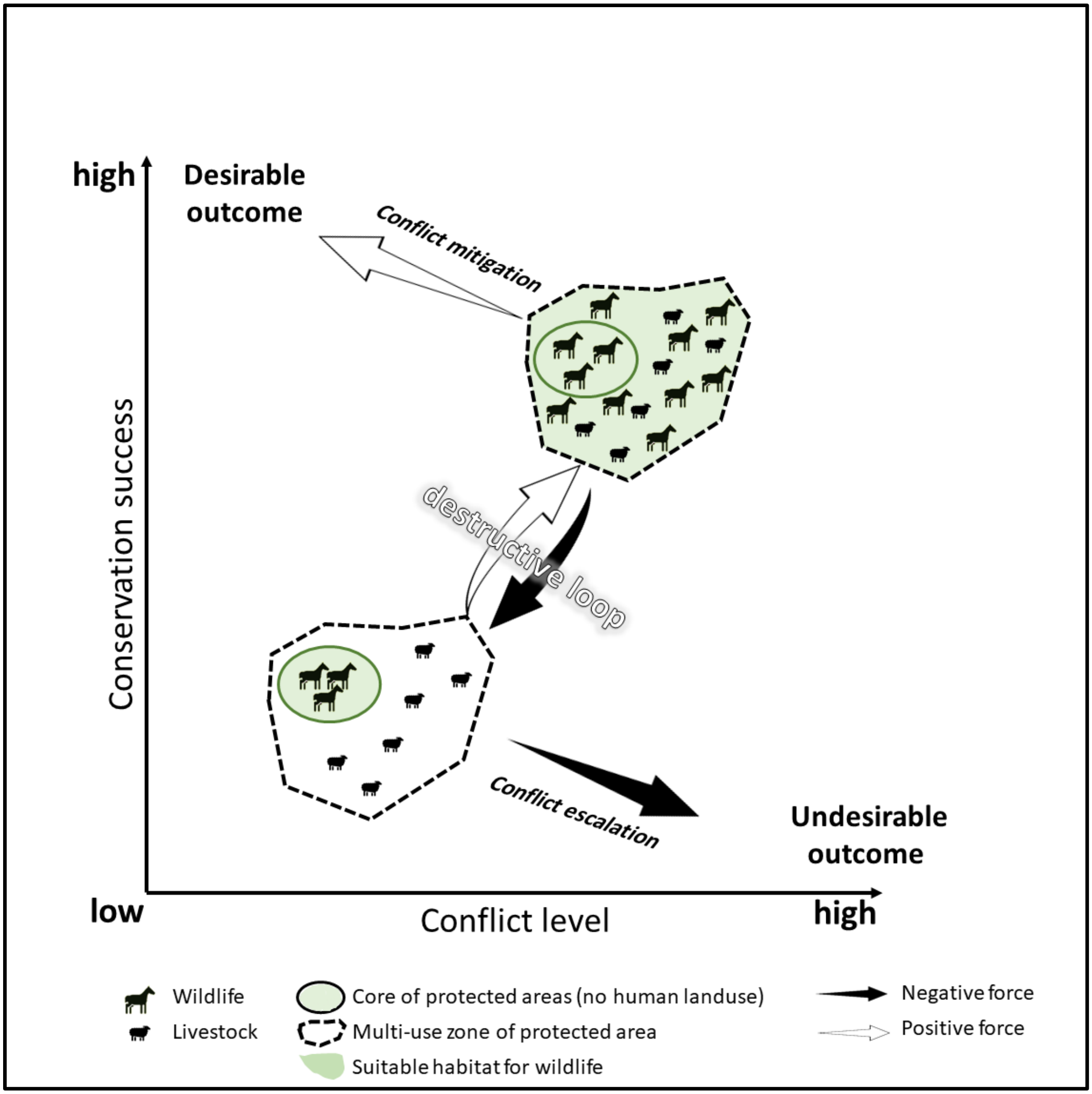

Fig 1: Possible outcomes of conservation activities for endangered species in multi-use landscapes. The black arrow shows a negative effect of conservation on human livelihoods, which can reduce or negate conservation efforts. A destructive loop is created when conservation success results in increased conflict levels, which results in a feedback of retaliatory killings and renewed conservation efforts. Although conflict escalation leads to conservation failure, conflict mitigation breaks the feedback loop and leads to conservation success.

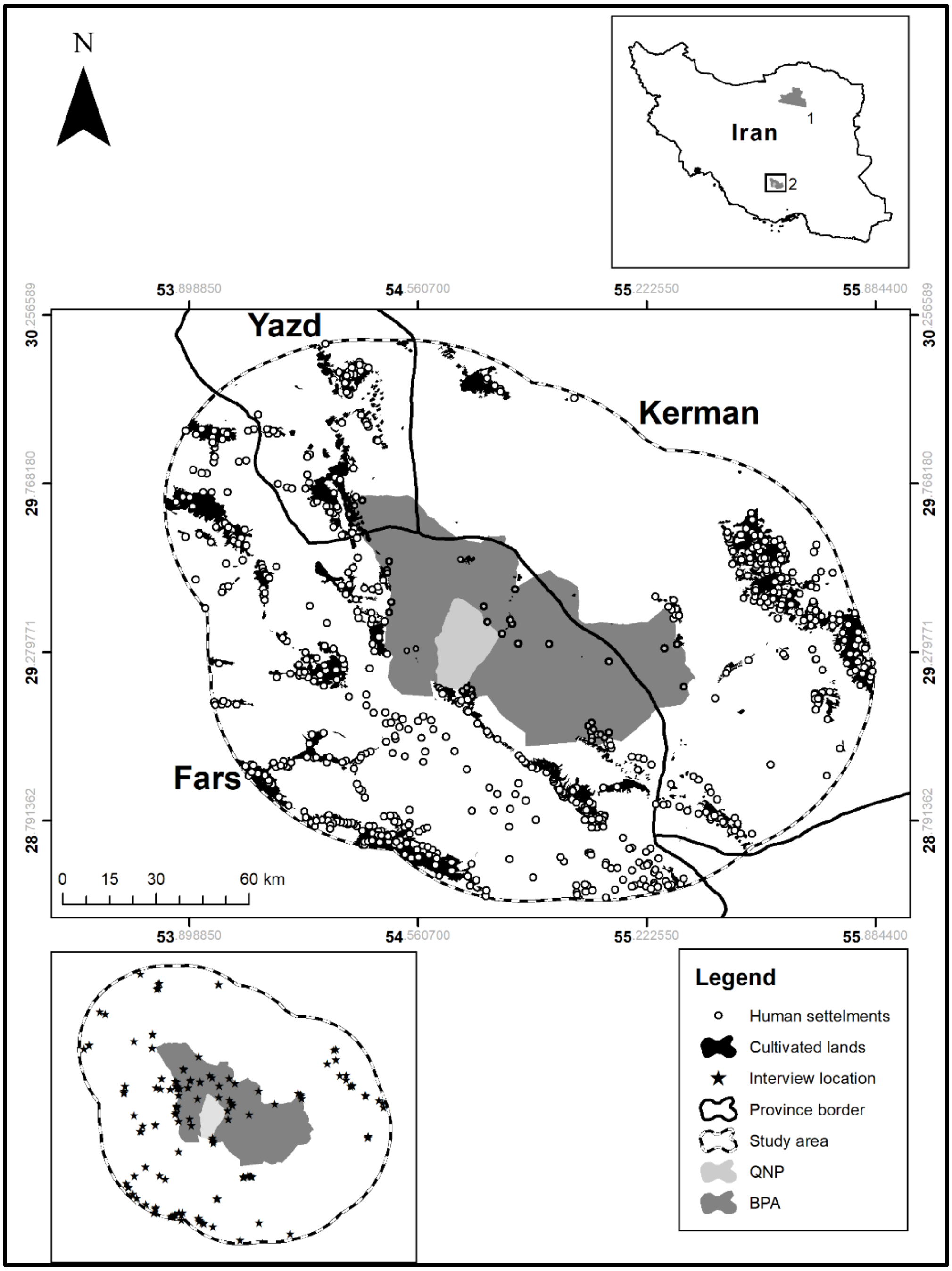

Fig 2. Current wild distribution of onager in Iran: (1) Touran Biosphere Reserve and (2) Bahram-e-Goor Protected Area (BPA) surrounding Qatrouiyeh National Park (QNP). Study area and location of interviews with local communities in BPA and a 50-kilometer surrounding buffer.

APPENDIX S1

Table S1. The total rural population of the study area residing within and along the boundary of Bahram-e-Goor Protected Area (within BPA) and outside BPA. A Stratified random sampling approach based on population size of counties was used to select the number of interviewees at each category. N questionnaires represent the total number of interviews (regardless of respondents' familiarity with onagers).

County (Dehestan)	District (Sharestan)	Province	Inhabitants in 2006	N Questionnaires	% of total population interviewed
Within BPA					
Villages	NA	NA	2,671	102	**3.8**
Outside BPA					
Tojerdi	Bavanat	Fars	6,347	4	0.06
Bakhtajerd	Darab	Fars	8,145	5	0.06
Balesh	Darab	Fars	8,016	4	0.05
Fasaroud	Darab	Fars	2,379	2	0.08
Hoshivar	Darab	Fars	9,119	6	0.07
Kouhestan	Darab	Fars	1,563	1	0.06
Paskhan	Darab	Fars	10,386	7	0.07
Qalebiaban	Darab	Fars	3,168	2	0.06
Qariekheir	Darab	Fars	6,586	4	0.06
Ij	Estahban	Fars	3,661	8	0.22
Kheir	Estahban	Fars	1,268	0	0.00
Roniz	Estahban	Fars	13	0	0.00
Qarebolaq	Fasa	Fars	17,396	13	0.07
Sheshdeh	Fasa	Fars	208	0	0.00
Abadetashk	Neiriz	Fars	4	0	0.00
Bakhtegan	Neiriz	Fars	7,082	6	0.08
Dehchah	Neiriz	Fars	2,748	2	0.07
Hannad	Neiriz	Fars	9,594	7	0.07
Horagan	Neiriz	Fars	1,110	1	0.09
Moshgan	Neiriz	Fars	167	4	2.40
Qatrouyeh	Neiriz	Fars	3,685	3	0.08
Rostaq	Darab	Fars	2,506	3	0.12
Rostaq	Neiriz	Fars	5,511	6	0.12
Rizab	Neiriz	Fars	10,832	7	0.06
Estabraq	Shahr-e-Babak	Kerman	9	0	0.00
Khorsand	Shahr-e-Babak	Kerman	931	4	0.43
Golestan	Sirjan	Kerman	2,638	3	0.11
Mahmoudabad	Sirjan	Kerman	7,982	4	0.05
Malekabad	Sirjan	Kerman	7,656	5	0.06
Najafabad	Sirjan	Kerman	4,980	11	0.22
Sharifabad	Sirjan	Kerman	8,758	6	0.07
Zeidabad	Sirjan	Kerman	3,021	7	0.23
Chahak	Khatam	Yazd	5,225	5	0.10
Fathabad	Khatam	Yazd	3,035	10	0.33

Harabarjan	Khatam	Yazd	0	0	0.00
Isar	Khatam	Yazd	0	0	0.00
Total			**165,729**	**153**	**0.10**

Text S1. Questionnaire for proposed human-onager survey in Bahram-e-Goor Protected Area.

(Farsi version of the questionnaire was used in interviews)
Village / GPS point: _______
Municipality: _____________
Date: _______

Section #1: Locals' socio-economic background

Age: _____
Sex: ☐ male ☐ female
Education: _________
Main occupation:____

If farmer,

What does he / she cultivate: ____
Size of land:____________
How much is his /her annual harvest (tons/ hectare):____________________________________
Location of the farmland: ____________

If herder;

how many livestock: ____
what type: ____

Answering the following question is optional:

- How much is your family income in a month/a year (I asked them in IRI Rials)
  - A- Less than $5000 in year
  - B- More than $5000 in year

Section #2: Conflict with onagers

1. Do you experience any conflicts with wildlife in last 10 years? ☐ yes ☐ no
2. How do you rank your level of conflicts with onagers?

no conflict	little conflict	some conflict	high conflict	sever conflict
1	2	3	4	5

3. How many years have you been experiencing onager damage?
4. What percent of your overall wildlife damage is due to onager? __________
5. What is the main damage by onagers?
   ☐ barley & wheat ☐ alfalfa ☐ corn ☐ vegetables ☐ fruit trees ☐ nut trees ☐ pastureland (competition with livestock) ☐ potatoes ☐ other:__________
6. What season do most onagers damages happen:
   ☐ spring ☐ summer ☐ fall ☐ winter ☐ all year round
7. Are there more damages now than in the past?
   ☐ Yes ☐ No
   Why?____
   ____
   ____

10. What do you do to avoid damages by onagers?

    ____
    ____
    ____

12. What would you like DoE or the National park to do to reduce wildlife / onagers damages?

    ____
    ____

13. Have you heard about any dead onagers during the last 5 years?

    ☐ Yes ☐ No
    Where?____
    ____

Section #3: Knowledge about onagers

1. Which of the following statements do you consider correct?

Knowledge score	Not correct	correct	do not know
1- Onager can run more than100 km/hour.	1	0	0
2- Onager mares often give birth to 2 foals.	1	0	0
3- Onagers need to drink only once a week.	1	0	0
4- Onagers live in many areas of Iran.	1	0	0

2. Do you think onager numbers are?

☐ increasing ☐ remain the same ☐ decreasing ☐ do not know

3. What do you think has the strongest influence on onager numbers in Bahram-o-Goor?

4. From where did you get your knowledge about onager?

☐ own observation ☐ family ☐ school ☐ books ☐ newspaper ☐ radio ☐ TV ☐ DoE / rangers ☐ other:

Section #4: Perceived value of onagers

How do you feel about the following statements?

	strongly disagree	disagree	neutral	agree	strongly agree
1- Onagers presence is important for Iran's nature.	1	2	3	4	5
2- It is important to maintain onager for our children.	1	2	3	4	5
3- It is not necessary to protect onagers in Iran, because large populations are elsewhere.	1	2	3	4	5
4- Onagers are beautiful animals.	1	2	3	4	5
5- I am proud that Iran has onagers.	1	2	3	4	5
6- Onagers only cause problems for us.	1	2	3	4	5
7- I like onagers, but not near my home.	1	2	3	4	5
8- Onager should be fully protected in Bahram-e-Goor.	1	2	3	4	5
9- It should not be that many onagers are in Bahram-e-Goor.	1	2	3	4	5
10- Local people should be allowed to hunt onagers	1	2	3	4	5
11- More money should be spent on onagers conservation/protection.	1	2	3	4	5
12- Local people would be willing to help protect onagers.	1	2	3	4	5
13- Onagers should be restricted to inside the Qatrouyeh National Park.	1	2	3	4	5
14- Poaching of onagers needs to be counteracted by better control.	1	2	3	4	5
15- It is important to protect some areas like Qatrouiyeh National Park primarily for onagers.	1	2	3	4	5

Section #5: Acceptability of potential management strategies

How are you willing to take the following decisions if government supports you?

	disagree	neutral	agree
1- selling land to the government	0	1	2
2- exchanging 50% farmland/pastureland within BPA for an equivalent amount of land outside BPA	0	1	2
3- changing from a traditional farming/herding lifestyle to industrialized farming (for farmers) or livestock production (for herders) with the help of government	0	1	2
4- accepting monetary compensation to tolerate onager damage	0	1	2
5- accepting a sedentary lifestyle instead of a nomadic one	0	1	2
6- supplementary feeding of livestock for a period in the year with the help of the government	0	1	2

Table S2. Internal consistency of the fifteen statements comprising value score, reflecting perceived value of onagers in and around Bahram-e-Goor Protected Area, Iran. Cronbach's alpha consistency analysis is used to generate Cronbach's alpha score, which indicates high consistency between components of the value score.

Score / statements	**Cronbach's Alpha if statement deleted**
value score (standardized Cronbach's alpha = 0.80, n=249)	
Onagers presence is important for Iran's nature.	0.77
It is important to maintain onager for our children.	0.76
It is not necessary to protect onagers in Iran, because large populations are elsewhere.*	0.78
Onagers are beautiful animals.	0.77
I am proud that Iran has onagers.	0.76
Onagers only cause problems for us.*	0.78
I like onagers, but not near my home.*	0.79
Onager should be fully protected in Bahram-e-Goor.	0.79
It should not be that many onagers are in Bahram-e-Goor.*	0.80
Local people should be allowed to hunt onagers.*	0.79
More money should be spent on onagers conservation/protection.	0.79
Local people would be willing to help protect onagers.	0.79
Onagers should be restricted to inside the Qatrouyeh National Park.*	0.80
Poaching of onagers needs to be counteracted by better control.	0.79
It is important to protect some areas like Qatrouyeh National Park primarily for onagers.	0.79

*Coding reversed

Table S3. Locals' socio-economic background of respondents to the questionnaires in and around Bahram-e-Goor Protected Area, Iran. N questionnaires represent the total number of interviews (regardless of respondents' familiarity with onagers).

Variables	**Within BPA**	**Outside BPA**	**Total**
N interviews	102	153	255
Gender composition (%)			
Males	77.45	71.89	74.12
Females	22.55	28.10	25.88
Age			
Mean	44	39.48	41.28
SD	14.97	14.75	14.97
Min	16	20	16
Max	88	85	88
Education (%)			
Illiterate	15.69	15.03	15.29
School	72.55	69.28	70.59
University	11.76	15.69	14.12
Occupation (%)			
Farmer	10.78	31.37	22.35
Herder	16.66	3.92	9.02
Farmer and Herder	94.11	8.50	32.16
Government	0	5.23	3.14
Housewife	0.98	20.26	12.55
Other	3.92	32.03	20.78
Farm size[1]			
Mean	6.68	4.10	5.74
SD	12.44	5.08	10.17
Min	0.50	1	0.50
Max	80	35	80
N	70	48	118
Livestock ownership[2]			
Mean	101.4	54.23	86.2
SD	99.87	82.40	86.93
Min	3	1	1
Max	700	500	700
N	88	39	128

Text S2. Human-onager conflict patterns in Bahram-e-Goor Protected Area, Iran.

Of the 44 farmers and herders within Bahram-e-Goor Protected Area, which experienced onagers conflicts, this was largely a reoccurring issue over multiple years (median = 7 years, range 1 to 30 years, n = 40). The proportion of the total conflict cause by wildlife attributed to onagers ranged between 1% and 100% (median = 30%). Conflicts by onagers primarily concerned local crops and were reported to occur most in summer (58.0%), least in winter (20.0%), and at intermediate frequency in fall (40.0%) and spring (30.0%); with 4.0% of respondents claiming that conflicts to happen year-round. The cultivations receiving most damage by onager were alfalfa (85.7%), wheat and barley (46.4%), corn (10.7%), orchard and vegetables (8.9%). Only four respondents (7.4%) reported conflicts over livestock and rangelands.

Methods used by local farmers and herders to avert or reduce onager conflicts were (n = 40): filling complaints to the Iranian Department of Environment (27.0%), fencing the property (17.5%), digging deep trench around their farms (12.5%), making fire or noise, using scarecrow and standing watch (12.5%). However, a majority of 45.0% stated they did nothing to address the problem.

Expected solutions from the Iranian Department of Environment by the affected farmers were: keeping onagers away from people's property by providing supplementary food and water (37.7%), fencing Qatrouiyeh National Park to avoid onagers conflicts (28.3%), monetary compensation of the conflict (26.4%), helping people fence or dig trench around their properties (26.4%), recruiting more rangers to protect people's property (11.3%), and purchasing people's property (3.8%).

Within the Bahram-e-Goor Protected Area 51.8% of respondents had known about onager kills in the past 5 years. The reasons of the death, as reported by 42 of the locals, were roadkill (42.8%), poaching (28.6%), both roadkill and poaching (16.7%), and other natural causes (11.9%). Outside the Bahram-e-Goor Protected Area, only 25% of locals heard about onager kills, of which 20 respondents knew about the reason of the death: roadkill (50%), poaching (35%), and other (15%).

Text S3. Locals' knowledge about onagers in and around Bahram-e-Goor Protected Area, Iran.
The main source of knowledge about onager for locals within BPA was own observations (91.8%), followed by family and friends (35.4%), DoE staff /rangers (27.3%), and TV (22.7%). Locals outside BPA knew about onager from TV (72.7%), direct observation (42.7%), family and friends (35.3%), DoE staff/rangers (10.7%), and books (10.6%). Other sources of knowledge were reported by less than 5% of respondents.

Onager population estimates of locals within BPA averaged 317.80 ± 203.24 (n = 86), and 54.0% reported (n = 100) an increasing population trends in recent years (decreasing: 30.0%, stable: 7.0%, do not know: 9.0%). Few people outside BPA gave any population estimate (267.50 ± 422.32, n = 25) and 89.5% of respondents (n = 142) were not aware of the increasing trend of the onager population (decreasing: 28.0%, stable: 0.7%, do not know: 60.8%).
Sixty four percent of respondents gave an answer to the open-ended question asking them about the strongest influence on onager numbers in BPA. I pooled all answers, resulting in the following list of positive and negative influences: protection (27.3%), change in people's attitude (3.8%), poaching (21.9%), habitat lost due to anthropogenic factors (1.9%), droughts (18.1%), and natural effects (1.5%). However, 47.8% of respondents did not have any idea about this question.

CHAPTER TWO

DIGESTIVE SYSTEM AND BODY SIZE SHAPE RESOURCE SELECTION BY UNGULATES: A GLOBAL TEST OF THE FORAGE MATURATION HYPOTHESIS

INTRODUCTION

Patterns of animal movement should be influenced by the need to maintain a positive balance between energetic gains and losses (Senft et al. 1987; Nathan et al. 2008; Owen-Smith et al. 2010; Middleton et al. 2013). The foraging behaviors employed by ungulates vary according to both body size and digestive system (ruminant versus hindgut fermenters; Bell 1971; Demment & Van Soest 1985; Hofmann 1989; Olff et al. 2002; Hopcraft et al. 2012; Kartzinel et al. 2015). Smaller-bodied ungulates (i.e., ruminants, primarily) should forage in patches with highly digestible forage (high energy and nutrient concentrations) because they possess high mass-specific metabolic rates. In contrast, larger-bodied ungulates (i.e., both larger-bodied ruminants and hindgut fermenters) should forage in high biomass patches because their large digestive volume fuels higher absolute energy demands (Bell 1971; Jarman 1974; McNab 1974; Schmidt-Nielsen & Knut 1984; Illius & Gordon 1992; Barboza & Bowyer 2000). Consequently, body size creates trade-offs in how ungulates should prioritize forage biomass and forage digestibility (Bailey et al. 1996; Wilmshurst et al. 2000; Olff et al. 2002; Hopcraft et al. 2012).

For nearly 30 years, the Forage Maturation Hypothesis (hereafter "FMH"; Fryxell 1991) has provided a lens for understanding resource selection and movements of free-ranging ungulates (Fryxell 1991; Hebblewhite et al. 2008; Merkle et al. 2016). Digestibility of forage is highest at the beginning of the growing season because plants lack the large amounts of structural fiber needed to support high biomass (Van Soest 1996). At this earliest phenological stage, however, plants are small and biomass is limiting, so energy intake of ungulates may be limited by bite size (Spalinger and Hobbs 1992; Hebblewhite et al. 2008). Digestibility then declines as plants mature, gain biomass, and become more fibrous (Van Soest 1996). Because of this phenological trade-off between biomass and digestibility of plants, and according to the FMH, energy intake is maximized for ungulates at intermediate phenological stages (i.e., when rates of both forage intake and digestibility are at intermediate levels; Fig 1A). Although the FMH was originally developed to explain resource selection in tropical, bulk-grazing ruminants, its predictions are relevant for temperate ruminants that display a diversity of feeding strategies (e.g., Albon & Langvatn 1992; Langvatn & Hanley 1993; Hebblewhite et al. 2008; Mueller et al. 2008; Merkle et al. 2016; Aikens et al. 2017; Middleton et al. 2018). As a result, the FMH frequently forms the basis for conceptualizing resource selection and movements of ungulates—including large- and small-bodied species, and hindgut and ruminant fermenters—throughout the globe (e.g., Drescher et al. 2006; Edouard et al. 2010; Fleurance et al. 2010; Treydte et al. 2011; St-Louis and Cote 2014; Muntifering et al. 2019).

The central prediction of the FMH—that ungulates should select forage of intermediate biomass and intermediate digestibility to maximize energy intake—should hinge largely on body size. Specifically, resource selection should occur along a gradient from high digestibility/low biomass to low digestibility/high biomass, dependent on body size. Explicitly considering this contingency would refine the predictive capacity of the FMH and thereby advance understanding of how it applies to ungulates more generally (Fig. 1A, Fig. 1B).

In addition to forage biomass and energy content, reliance on surface water restricts the movement and distribution of ungulates across some landscapes (Rozen-Rechels et al. 2019; Veldhuis et al. 2019). Ruminants efficiently extract protein and water from fresh plant tissue since the fermentation site (rumen) occurs anterior to the absorption site (small intestine).

Ruminants therefore employ a “complete” urea cycle in which available nitrogen is recycled throughout the digestive tract, thereby conserving water (Janis 1976; Owens & Basalan 2016). In contrast, hindgut fermenters have reduced retention time (which enhances throughput), but lower rates of protein and water extraction (Janis 1976; Duncan et al. 1990; Van Soest 1996). Consequently, hindgut fermenters excrete more urea, which must be accompanied by water. Larger-bodied ungulates—and larger-bodied hindgut fermenters in particular—consume large amounts of biomass and should therefore be further tied to surface water (i.e., water available for drinking, as opposed to contained within plants) because high-biomass forage tends to be drier (Bell 1971; Redfern et al. 2003; Schoenecker et al. 2016). In sum, natural selection should favor ungulate movement strategies that optimize net energy gain despite constraints imposed by forage biomass, the energy contained within forage, and surface water, with the relative importance of each arising as a function of body size and digestive system (Redfern et al. 2003; Fig. 1B, 1C).

Increasingly, human activities have restricted the movements and space use of free-ranging ungulates and other wildlife, with potential to alter their foraging behavior (Baillie et al. 2004; Berger 2007; Tucker et al. 2018). Through resource competition and direct interference, humans reduce resource availability, and thereby suppress the potential for free-ranging (i.e., wild and feral) ungulates to exploit spatiotemporal variability in forage biomass, potential energy intake, and access to surface water (e.g., Sanderson et al. 2002; Mishra et al. 2004; Kinnaird & O’Brien 2012; Ogutu et al. 2014; but see Young et al. 2018; Graham et al. 2019; Fig. 1D). Additionally, human activity tends to compress free-ranging ungulates into ever-shrinking areas, increasing the potential for interspecific competition and eventual extirpation of populations (Owen-Smith & Mills 2006; Ogutu et al. 2010; Van Beest et al. 2014; Corlatti et al. 2019). By constraining movements of free-ranging ungulates, human activity could therefore dampen any effects of digestive system and body size on resource selection.

I tested the central prediction of the FMH by linking high-resolution movement trajectories (unavailable when the FMH was conceptualized) with selection of forage biomass, potential energy intake, and surface water by free-ranging ungulates. I evaluated the relative influence of body size and digestive system on selection for these resources by ruminants and equids (Family Equidae, representing hindgut fermenters) using GPS telemetry data from 26 populations of 17 species distributed across the globe. I predicted that (1) smaller-bodied ungulates (all of which exhibit ruminant fermentation in our study) would select for resource patches that maximize energy intake, thereby conforming to the central prediction of the FMH (Fig. 1A); whereas (2) by virtue of their larger body sizes, resource selection patterns of both larger-bodied ruminants and equids would deviate from this prediction (Fig. 1B). Specifically, I expected that larger-bodied ruminants would select most strongly for patches of high forage biomass, whereas equids (by virtue of their hindgut fermentation) would select most strongly for patches close to water. Further, I hypothesized that support for these predictions would be most pronounced in landscapes with low amounts of human activity, where free-ranging ungulates are able to move freely and select resources without impediment (Fig. 1C, Fig. 1D).

METHODS AND MATERIALS

Data Collection

I compiled a global data set of GPS locations for 11 populations of equids and 15 populations of ruminants totaling 453 individuals; data for all study populations were collected between 2005 and 2018 (Figure 2A; Table S1). The equid data set comprised GPS relocations for seven (out of nine) extant species of wild and feral equids: Asiatic wild ass (khulan, *Equus hemionus hemionus* and onager, *E. h. onager*), feral burro (*E. asinus*), feral horse (*E. caballus*), Grevy's zebra (*E. grevyi*), mountain zebra (*E. zebra*), plains zebra (*E. quagga*), and Przewalski's horse (*E. ferus*). The ruminant data set included GPS relocations for 10 species: African buffalo (*Syncerus caffer*), elk (*Cervus canadensis*), goitered gazelle (*Gazella subgutturosa*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), Mongolian gazelle (*Procapra gutturosa*), mule deer (*Odocoileus hemionus*), saiga antelope (*Saiga tatarica*), springbok (*Antidorcas marsupialis*), and white-bearded wildebeest (*Connochaetes taurinus*). Equid species ranged in body size from 180 kg (feral burro, Schoenecker, personal communication) to 430 kg (feral horse, Godfrey & Berger 1987); ruminant species ranged in body size from 25 kg (goitered gazelle) to 592 kg (African buffalo; Wilson & Mittermeier 2011). Hereafter, I distinguish between "study areas" (the geographic locales in which resource selection were quantified) and "study populations" (the individuals fit with GPS collars within a study area; Table S1). Five of my study areas contained multiple study populations: (1) khulan, Przewalski's horse, and saiga antelope in western Mongolia; (2) khulan, goitered gazelle, and Mongolian gazelle in southern Mongolia; (3) feral horse, mule deer, and elk in the western United States; (4) Grevy's zebra and impala in central Kenya; and (5) plains zebra and springbok in Namibia. Additionally, khulan, plains zebra, Przewalski's horse, Mongolian gazelle, mule deer, and elk were represented by 2 study populations, each in a different study area. White-bearded wildebeest were represented by 3 study populations, each in a different study area.

Forage Biomass and Potential Energy Intake

To delineate study areas, I computed the minimum convex polygon (MCP) around each population's GPS locations and buffered the MCP by 5 km to ensure that I captured adjacent habitats that were available to telemetered individuals. Within each study area, I extracted

Modified Soil-Adjusted Vegetation Index (MSAVI; MODIS terra satellite imagery Version 6.0 MOD09Q1; spatial resolution 250 x 250 m, temporal resolution eight days) using the MSAVI2 method and equations described in Qi et al. (1994) as a proxy of forage biomass (Pettorelli et al. 2005). In arid environments, MSAVI and other soil-adjusted indices of vegetation are more appropriate than the more commonly used Normalized Difference Vegetation Index (NDVI) because they minimize the influence of bare ground on estimates of vegetation (Qi et al. 1994). I removed pixels categorized as snow, cloud, or shadow using quality assessment bands, then smoothed each time-series of MSAVI using a moving three-scene median filter and applied a linear interpolation (Branco et al. 2019).

To estimate the instantaneous rate of green-up (IRG), I calculated the rate of change in MSAVI for every three consecutive dates by using a three-scene moving window (Avgar et al. 2013; Branco et al. 2019). The IRG is a metric that combines both forage biomass and forage digestibility, which collectively equate to potential energy intake (Bischof et al. 2012; Avgar et al. 2013). The IRG is positively correlated with the peak in fecal crude protein in ungulates (Hamel et al. 2009) and has been used widely as an index of the energy contained in forage across space and time (Merkle et al. 2016; Rivrud et al. 2016; Aikens et al. 2017; Branco et al. 2019); days from peak IRG is strongly correlated with N:C ratios in grasses (Geremia et al. 2019). Hereafter, I refer to selection for IRG as selection for “potential energy intake”. Similarly, and hereafter, I refer to selection for peak biomass of forage as simply selection for “forage biomass”. Although IRG combines both forage biomass and forage digestibility, it is not redundant with metrics that solely represent forage biomass; while high IRG values represent intermediate plant biomass, low values of IRG may represent either low or high biomass (see Fig. 1A). I therefore used both IRG and MSAVI to disentangle selection for potential energy intake and forage biomass. I normalized both MSAVI and IRG values between 0 and 1 based on the lowest and highest value of each pixel in a year, respectively. Thus, for each pixel, an MSAVI value of 1 represented the highest biomass and a value of 0 represented the lowest biomass in a given year, for a given study population. Similarly, an IRG value of 1 represents forage at a state of intermediate biomass (and the peak rate of green-up), whereas an IRG value of 0 represents forage at a low rate of change (at peak biomass). Collectively, these two layers therefore represent metrics of plant phenology across space and time (see also Bischof et al. 2012; Merkle et al. 2016; Branco et al. 2019).

To evaluate how body size and digestive system influenced selection for forage biomass, potential energy intake, and surface water, I temporally constrained my analysis times when plants were actively growing (to ensure positive IRG was available to the animals). I determined the duration of growing seasons in each study population by randomly generating 10,000 points within each study area, extracting MSAVI and IRG values associated with each of the random points, and plotting annual MSAVI and IRG profiles (Fig. S1). For study areas with a single "growing season" (21 out of 26 study populations), I defined the beginning of the "growing season" as the Julian day when IRG became positive for three consecutive scenes, and the end of the "growing season" as the Julian day when IRG reached the minimum negative point, followed by IRG values less than or equal to zero (Fig. S1A; sensu Jesmer et al. 2018). For study areas with multiple growing seasons, I attempted to define each "growing season" consistent with the method described above (Fig. S2B). I then filtered the data set to only those relocations that occurred during growing seasons (Table S1).

Distance to Surface Water

Unlike estimates of forage biomass and availability, fine-scale data on surface water is challenging to acquire via remote sensing due to computational restrictions, and usually requires intensive field surveys (Redfern et al. 2003; Pekel et al. 2016; Huang et al. 2018). Further, globally-collected precipitation data may underestimate water available to wildlife, in light of the occurrence of artificial water sources (Ogutu et al. 2010). I treated the distribution of surface water as fixed throughout each growing season. I used the following data to identify the occurrence of surface water:

1-Remotely-sensed data on surface water: I used monthly data from the Global Surface Water Explorer (Pekel et al. 2016) to estimate occurrence of surface water during the growing season for each study area. With a spatial resolution of 30 x 30 m and temporal resolution of one month, Global Surface Water Explorer constitutes the most precise data on the distribution of surface water (Pekel et al. 2016). For each study area and growing season, I extracted monthly time series of pixels, where each pixel was assigned a 1 or 0, indicating presence versus absence of surface water. I then merged monthly layers into a single layer of surface water.

2-Locally-collected data on surface water: to increase accuracy of my estimates of surface water for each study population, I compiled data on springs, streams, small ponds, and man-made water sources (i.e., surface water sources <30 x 30 m that were undetectable using the Global Water Surface Explorer). These data were recorded by the data contributors and their research teams for study areas in which they worked. I merged the locations of locally-collected surface water with the layer on remotely-sensed data on surface water (Text S1 and Table S2). From the data on surface water, I generated a distance to surface water layer by calculating linear distances between centroids of pixels classified as “surface water” and centroids of non-surface water pixels. To ensure that the distance to surface water layer occurred at a comparable scale with

MSAVI and IRG, I normalized values for distance to surface water between 0 and 1 for each study area based on the lowest and highest value of pixels in each growing season, respectively.

Human Activity

To estimate human activity, I calculated the most common (i.e., modal) value of the global terrestrial human footprint at a resolution of 1 x 1 km (Venter et al. 2016) within the MCP of each study population during each growing season. The global terrestrial human footprint combines a diversity of anthropogenic features (i.e., built environments, crop land, pasture land, human population density, nighttime lights, railways, roads, and navigable waterways) to map the presence and degree of human activity in 2009 (Venter et al. 2016), and it has been widely used as a proxy of human disturbance (Venter et al. 2016; Johnson et al. 2017; Jones et al. 2018; Tucker et al. 2018).

Statistical Analyses

I built step-selection functions (Thurfjell et al. 2014; Avgar et al. 2016) to quantify how spatiotemporal patterns of forage biomass, potential energy intake, and surface water influenced movements by ungulates in each study population during growing seasons. To meet the assumption of uncorrelated successive steps (since the step-selection method assumes Brownian motion), I used a semi-variance approach to estimate the average time at which 99% of the correlation between successive steps had decayed (Fleming et al. 2014). I then rarified (i.e. temporally subsampled) the GPS locations of each population, which resulted in uncorrelated, successive steps (Table S1; Fleming et al. 2014; Dupke et al. 2017). For each observed (used) step, I generated 100 potential (unused) steps using the empirical distribution of observed step lengths and turning angles, then compared observed and potential steps using conditional logistic regression (Fortin et al. 2005; Avgar et al. 2016). In addition to step length, logarithm of step length, and cosine of turning angles, I extracted values of forage biomass, potential energy intake, and distance to surface water at the end points of each observed and potential step. I used conditional logistic regression to estimate selection coefficients, with each stratum consisting of an observed step and its associated 100 potential steps, and each individual as an independent cluster in fitting a separate model for each study population (Roever et al. 2010; Merkle et al. 2016; Prima et al. 2017). Correlation among the independent variables was minimal (mean r between MSAVI and IRG = -0.08, range = -0.35 to 0.20; mean r between MSAVI and distance to surface water = 0.04, range = -0.17 to 0.55; mean r between IRG and distance to water = 0.003, range = -0.31 to 0.16; Table S3). Sample sizes (numbers of individuals telemetered, and the range in numbers of individuals telemetered for a given year) are presented for each study population in Table S1.

I interpreted that significant, positive selection for IRG (i.e., representing forage with intermediate biomass and digestibility) was indicative of movements consistent with the FMH (Merkle et al. 2016; Aikens et al. 2017). I used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the best models for each study population (Roever et al. 2010; Ali et al. 2017; Attias et al. 2018). I averaged the parameter estimates of competing models when the difference between AICc was <2 (Burnham et al. 2011). I considered variables significant in the averaged models when 85% confidence intervals around parameter estimates did not encompass zero (Arnold 2010). I performed these analyses using packages "amt", "survival", and "MuMIn" in Program R (Therneau & Lumley 2015; Bartoń 2019; R Core Team 2019; Signer et al. 2019).

I next tested the effect of body size, digestive system, and human activity on resource selection across populations using weighted least square regressions and analysis of covariance

(ANCOVA). Because resource selection could intensify if a particular resource was scarce, variable, or both (for example, selection for surface water might be stronger in drier environments, or where surface water is highly variable through space and time), I performed pairwise correlation tests between selection coefficients for each resource and the (1) mean value of MSAVI, IRG, and distance to surface water; and (2) the coefficient of variation (CV) of MSAVI, IRG, and distance to surface water, for each study population in each study area. I found little support for the effect of resource availability and variability on resource selection (Fig. S2), so I attributed variation in selection coefficients to some combination of body size, digestive system, and human activity. For each test, I used the log-transformed parameter estimates (to meet assumptions of linear regression) derived from the step-selection functions as response variables, and the number of telemetered individuals in each population as a weighting factor. First, I controlled the effect of body size (i.e., mean species-specific, sex-unspecific body weight of an adult individual; Wilson & Mittermeier 2011) in resource selection across populations using weighted ANCOVA. When I did not find a statistically significant effect of digestive system on resource selection after controlling for body size, I pooled equids and ruminants into single weighted regression models to test how resource selection was influenced by body size. When the effect of digestive system on resource selection was statistically significant after controlling for body size, I used weighted regression models with body size as a predictor for equids and for ruminants separately. Next, to test whether selection for resources was influenced by human activity, I used weighted regression models with human activity as a predictor for equids and ruminants pooled in one model (as I did not expect human activity to influence equids and ruminants differently). For ease of interpretation, I switched the direction of parameter estimates for distance to surface water in all analyses and graphs. Therefore, positive and negative values show selection and avoidance for forage biomass, potential energy intake, and surface water, respectively.

RESULTS

Forage biomass, potential energy intake, distance to surface water, or some combination thereof explained resource selection in 24 out of 26 equid and ruminant populations (with plains zebra and springbok populations as the two exceptions; Fig. 2B, 2C; Fig. S4; Table S5). Selection for forage biomass was exhibited by four equids (36%) and five ruminants (33%); avoidance of forage biomass was exhibited by two equids (18%) and three ruminants (20%). Six ruminants (40%) and one equid (9%) selected for potential energy intake (i.e., had movement consistent with the FMH), and two ruminants (13%) avoided potential energy intake. Eight out of 11 equid populations (72%) selected for surface water (Fig. 2B). Ruminant populations displayed a diversity of selection behaviors toward surface water. Overall, equids consistently selected for surface water, while resource selection of ruminants was variable (Fig. 2B, 2C).

After controlling for the effect of body size, I did not detect any difference in selection for forage biomass ($P = 0.38$; Fig. 3A) or potential energy intake ($P = 0.13$; Fig. 3C) between equids and ruminants. Across all study populations, body size did not explain variation in selection for forage biomass (Fig. 3B). Body size explained 40% of the variation in selection for potential energy intake across all study populations (Fig. 3D). Equids, however, selected more strongly for surface water than ruminants after controlling for the effect of body size ($F_{(1, 23)} = 6.13$, $P = 0.02$; Fig. 3E). Body size marginally explained selection for surface water in ruminants ($F_{(1, 13)} = 3.60$, adj. $R^2 = 0.16$, $P = 0.08$; Fig. 3F) but not in equids ($P = 0.22$; Fig. 3G). Human activity explained 26% and 15% of variation in the strength of selection for potential energy intake ($F_{(1, 24)} = 9.69$, $P = 0.004$, parameter estimate ± SE of human activity = -0.02 ± 0.01) and surface water ($F_{(1, 24)} = 5.28$, $P = 0.03$, parameter estimate ± SE of human activity = 0.06 ± 0.03), respectively, for all free-ranging ungulates (Table S6). Selection for forage biomass was not explained by human activity (Table S6).

DISCUSSION

I quantified how forage biomass, potential energy intake, and surface water shaped the resource selection of free-ranging ungulates across the globe. In support of the FMH, selection for potential energy intake (i.e., intermediate forage biomass and intermediate forage digestibility) was most frequent among smaller-bodied ungulates (all of which exhibited ruminant fermentation in this study). Selecting forage at early to intermediate states of phenology stemming reflects the higher mass-specific energetic requirements of smaller-bodied herbivores (Illius & Gordon 1987; Hopcraft et al. 2012). In contrast, larger-bodied ungulates (comprising both equids and larger-bodied ruminants) foraged in a manner distinct from the central prediction of the FMH. In accord with my expectations based on hindgut fermentation, equids selected consistently for proximity to surface water. In contrast to my expectations based on ruminant digestion coupled with higher absolute energetic requirements, larger-bodied ruminants did not consistently select for forage biomass. I offer two (non-exclusive) explanations for lack of support for the hypothesis that larger-bodied ruminants should prioritize high forage biomass: (1) methodological limitations; and (2) taxonomic and functional diversity.

Methodological limitations are inherent to remotely-sensed vegetation indices. At the resolution of MODIS, such indices cannot distinguish between sources of “greenness” resulting from different vegetation types, such as woody plants and grasses (Archibald & Scholes 2007; Gaughan et al. 2013). So, pixel values could be associated with vegetation that did not necessarily represent forage from an ungulate’s perspective. I attempted to minimize the effect of this potential limitation by restricting my analysis to defined growing seasons. Since the green-up profile in leaves of woody plants is usually constant, the dramatic change in MSAVI (which I used to define the growing seasons) is mostly associated with the green-up of grasses rather than green-up of woody plants (Archibald & Scholes 2007; Higgins et al. 2011). Therefore, the potential for such phenological confounding should be restricted to ecosystems in which woody plants and grasses co-occur in similar proportions yet exhibit different seasonality (e.g., white-bearded wildebeest and plains zebra in savannas of eastern and southern Africa). Nevertheless, remotely-sensed vegetation indices have been employed successfully to predict movements of wildebeest elsewhere (e.g., Boone et al. 2006; Hopcraft et al. 2014; Stabach et al. 2016), and movements of the majority (six of seven) of wildebeest and zebra populations were driven at least partly by forage biomass or potential energy intake.

Second, differences in the strength and consistency of resource selection were likely due in part to the relatively high diversity of ruminants in this study, which incorporated 10 genera exhibiting a >20-fold difference in body size (from 25 kg goitered gazelle to 590 kg African buffalo) with additional variation in feeding strategies (e.g., unselective grazing, selective browsing, mixed feeding). However, except for greater kudu, all species of ruminants in my study foraged largely or wholly in the understory layer or in open rangelands, for which phenological dynamics were captured by the selected forage biomass metrics. My results also are consistent with site-specific studies on ungulate assemblages, where multiple ruminants coexist by specialization on different resources, and therefore exhibit a diverse array of resource selection (Wilmshurst et al. 2000; Stewart et al. 2003; Cromsigt & Olff 2006; Cromsigt et al. 2009).

Hindgut fermenters were represented exclusively by equids in this study which, in contrast to ruminants, are restricted to a single genus (Equus), and exhibit limited (~2.5-fold) variation in body size (from 180 kg feral burros to 430 kg feral horses). Consequently, resource selection was relatively consistent across equid populations, with eight of 11 populations selecting areas in close proximity to surface water. Equids do not conserve water in the body as efficiently as ruminants, and they excrete proportionately more water (Janis 1976; Ogutu et al. 2014); such differences in digestion likely explain the strong selection for surface water by equids across the globe. Conversely, ruminants that selected for surface water weighed >180 kg, and use water for thermoregulation (Veldhuis et al. 2019), whereas ruminants <70 kg avoided surface water altogether. During growing seasons, smaller-bodied ruminants can meet their water requirements by selecting plants at an intermediate phenological state, and via behavioral thermoregulation, which are largely independent from surface water (Veldhuis et al. 2019; Kihwele et al. 2020).

Consistent selection for surface water across equid populations likely is rooted in their evolutionary history and low species diversity in this family (Janis 1976; Forsten 1989). During the Oligocene, climatic conditions in the grasslands of North America—the center of equid evolution—supported relatively larger-bodied genera capable of exploiting high-fiber plants (Macfadden 1992; Mihlbachler et al. 2011). Additionally, the spread of open, dry, and seasonal grasslands during the Miocene favored the dental adaptations that facilitate feeding on more fibrous grasses (Forsten 1989; MacFadden 2005). These adaptations allowed equids to persist by consuming a variety of high and low abrasion diets (Mihlbachler et al. 2011). Following the contraction of grasslands and mass-killing of equids by humans in late Pleistocene (Janis 2008), several genera of equids went extinct, leaving only the genus *Equus* in the Afrotropical and

Palearctic zoogeographic regions. Following the diversification of ruminants, equids never regained their former taxonomic, functional, or trait (body size) diversity. Coupled with their evolutionary history, the similarity in resource use among equid populations highlights the fragility of this family, in which six out of seven wild species are currently threatened with extinction (IUCN 2020).

My remotely-sensed imagery of surface water existed at a coarser temporal resolution compared to our remotely-sensed imagery of vegetation indices, and did not comprise exhaustive data on all sources of water available to study populations. For example, ephemeral ponds and streams are not captured by the Global Surface Water Explorer. However, and with a resolution of 30 x 30 m, the Global Surface Water Explorer constitutes (by far) the most precise data on the global distribution of surface water (Pekel et al. 2016), and I was able to supplement this remotely-sensed imagery with locations of locally-collected surface water. The strength of selection for surface water did not depend on availability of surface water within study areas (Fig. S2) and, per my initial prediction based on digestive physiology, the strength of selection for surface water was significantly stronger for equids than for ruminants. In sum, I believe that such methodological limitations associated with remotely-sensed imagery of surface water were unlikely to have had undue influence on my results and associated inferences (but see Text S2). More generally, I believe that the Global Surface Water Explorer has strong potential as a tool for wildlife and movement ecologists, and its potential methodological limitations will be overridden by its value in many study systems.

Human activity dampened selection for potential energy intake and intensified selection for surface water, although both effects were relatively weak (Table S6). Shifts in land use and vegetation cover triggered by human activities can result in less diverse landscapes and fewer resources for wildlife (Sanderson et al. 2002; Hansen et al. 2005; Geri et al. 2010). Additionally, wildlife can shift their resource use through temporal partitioning, spatial separation, or both to minimize encounters with humans (Berger 2007; Gaynor et al. 2018). Because potential energy intake is highest only during narrow windows of time (i.e., growing seasons), opportunities for free-ranging ungulates to habituate to human activities are relatively limited, possibly explaining the reduced selection for potential energy intake as human activity increased (Table S6). Alternatively, the weak effect of human activity on resource selection might have arisen solely because of the locations of the study populations: human footprint values in my study areas were relatively low, ranging from 0 to 9 (out of a maximum of 50, indicative of urban areas). A recent meta-analysis—conducted over a wider range of human footprint values—concluded that human activity reduces movements of mammals across the globe (Tucker et al. 2018).

By necessity, my synthetic approach sacrifices some area- and population-specific precision in attempt to identify general trends (Levin 1992, Brown 1995). For example, all ruminant populations in this study were sympatric with other wild and domestic ruminants, which could influence resource selection of free-ranging ungulates (e.g., Mishra et al. 2004; Kinnaird and O’Brien 2012; Ng’weno et al. 2019). Future efforts to synthesize patterns of resource selection for free-ranging ungulates might incorporate the occurrence and abundance of livestock (through, e.g., the Gridded Livestock of the World mapping project by the Food and Agriculture Organization of the United Nations [http://www.fao.org/livestock-systems/en/]). Additionally, physical constraints inherent to different study areas (e.g., the spatial scale over which variation in forage biomass and potential energy intake arise) likely influence the movement and resource selection of free-ranging ungulates to some degree (Aikens 2019). Such area- and population-specific variability almost certainly contributes to differences in resource selection between populations of the same species (e.g., khulan populations in western versus southern Mongolia; Text S2; elk populations in xeric shrublands of Wyoming versus coniferous forests of Colorado), and could explain variation around the general trends depicted in Figures 2 and 3. Nevertheless, my analyses point to important generalities—stronger selection of surface water by equids relative to ruminants, and stronger selection for potential energy intake by smaller-bodied ruminants—which conform to expectations based on metabolic allometry and digestive physiology. In combination with intensive, longitudinal work within study populations, I believe that my comparative cross-taxa study has helped illuminate general ecological rules and their associated contingencies, thereby advancing conservation capacity.

My synthetic approach provides the first global test of the Forage Maturation Hypothesis. By using a combination of remotely-sensed data to quantify forage biomass, potential energy intake, and surface water, I assessed differential selection of resources by free-ranging ungulates across the terrestrial surface. In doing so, I have refined the Forage Maturation Hypothesis relative to its original formulation to explicitly consider variation in ungulate body size and digestive system, thus extending the applicability of this key concept in large herbivore ecology. Thus, the forage characteristics that influence population persistence of free-ranging ungulates should differ according to body size and digestive system, such that access to a combination of resource gradients is key to maintaining viable populations of diverse free-ranging ungulates across the globe.

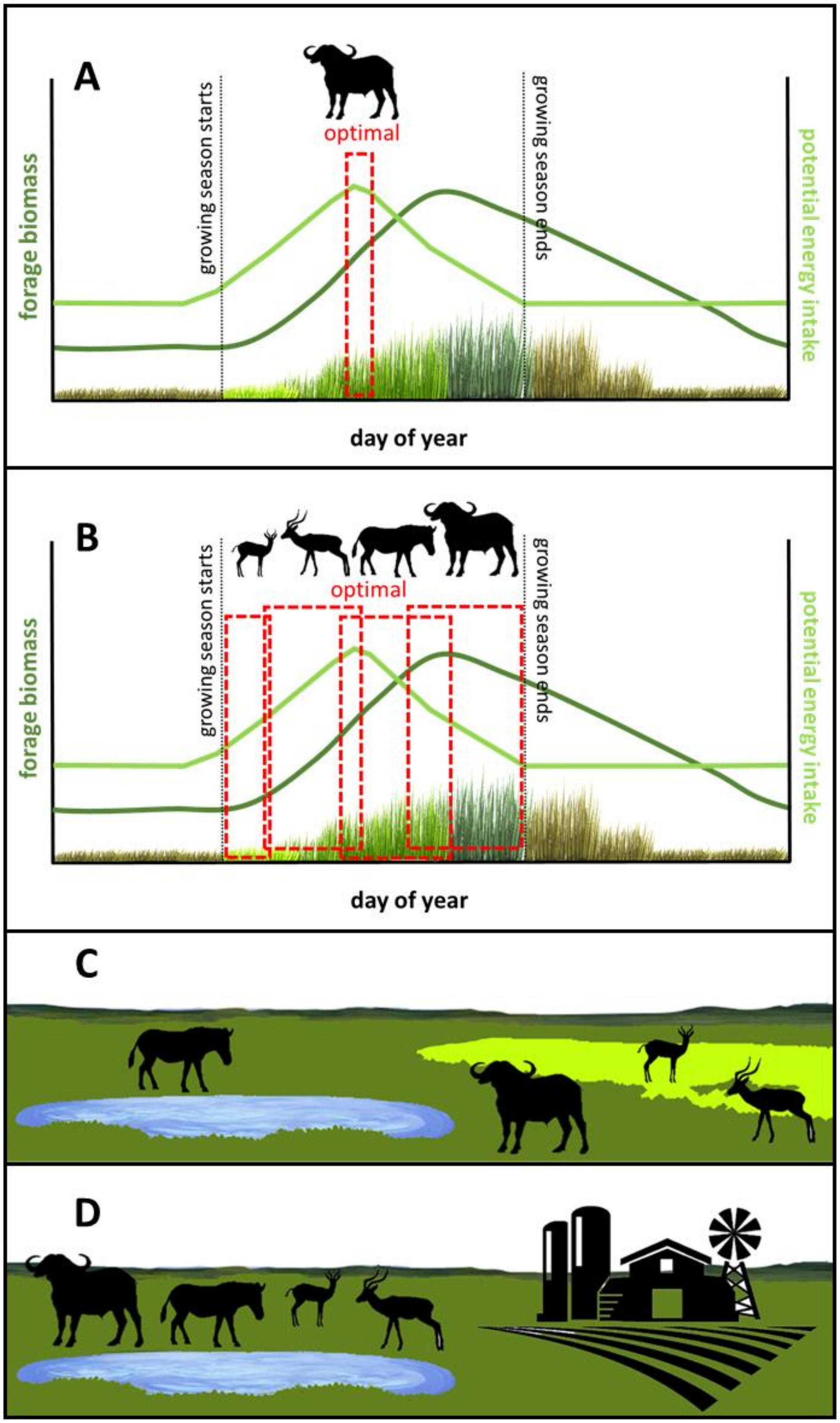
A
growing season starts
optimal
growing season ends
forage biomass
potential energy intake
day of year
B
growing season starts
optimal
growing season ends
forage biomass
potential energy intake
day of year
C
D

Figure 1. Illustrated predictions for resource selection by equids and different sizes of ruminants during a hypothetical growing season and in a hypothetical landscape. Forage biomass (dark green line) and potential energy intake (light green line; measured by rate of change in forage biomass) increase at beginning of the growing season. The potential for maximum energy intake occurs at the middle of the growing season, when forage biomass is at intermediate levels. Different sizes and shades of grass represent phenological stages of forage biomass and digestibility. At early phenological stages (i.e., the lightest shade of green grass), potential energy intake is low because forage biomass is low. At late phenological and senescent stages (i.e., the darkest shade of green grass and brown grass, respectively), potential energy is low because forage digestibility is low. (A) The Forage Maturation Hypothesis predicts that ungulates maximize their energy intake by selecting forage of intermediate biomass at intermediate phenological stages. (B) However, selection for forge characteristics should also depend on body size. (C) Smaller-bodied ungulates (which exhibit ruminant digestion) should select most strongly for maximal energy intake (light green), larger-bodied ruminants should select for forage biomass (dark green), and equids should select for surface water (blue) to meet their physiological needs. (D) Humans may constrain the potential for resource selection by reducing total area and by decreasing resource diversity that otherwise would be available for free-ranging ungulates.

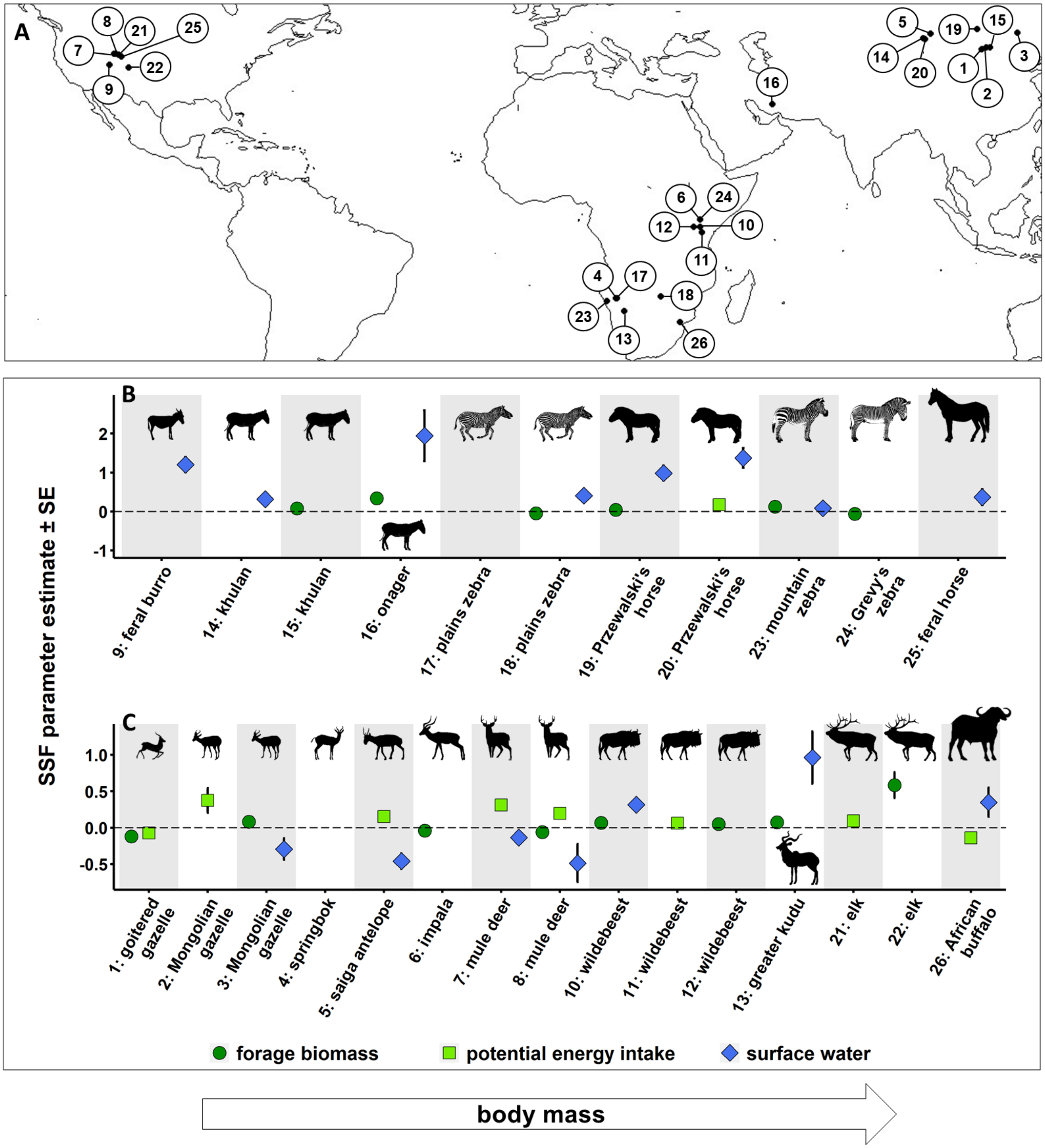

Figure 2. Locations of the study populations (A) and mean ± SE parameter estimates (for significant variables with 85% confidence intervals excluding zero) of step-selection functions (SSF) for 11 populations of equids (B) and 15 populations of ruminants (C) during growing seasons. Populations are numbered in increasing order of a focal species' body size.

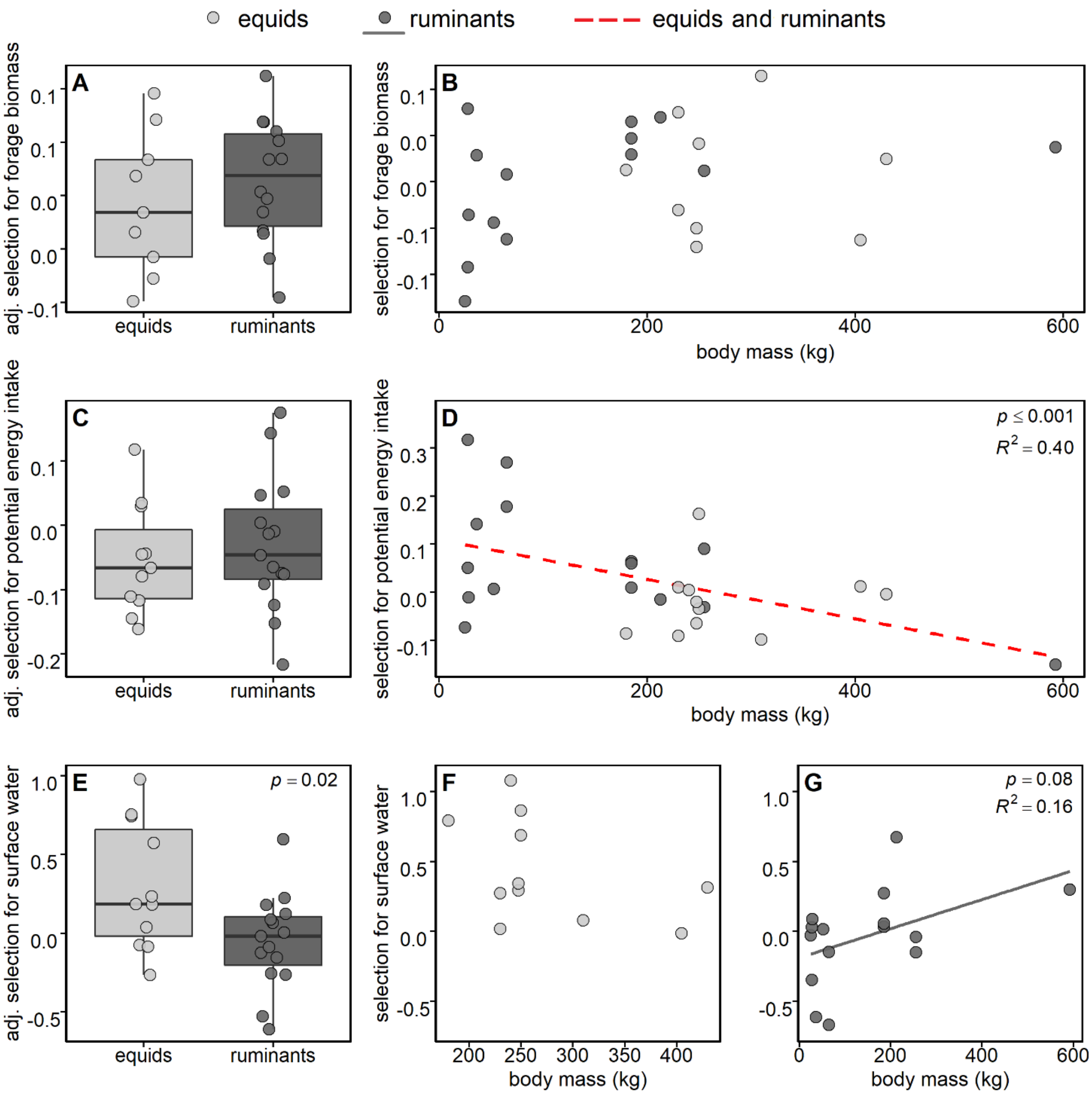

Figure 3. Relationship between population-level resource selection coefficients and digestive system (A, C, E; weighted analysis of covariance [ANCOVA]) and body size (B, D, F, G; weighted least squares regression). Equid populations more strongly selected surface water after controlling the effect of body size (E), but I detected no significant difference in selection for forage biomass (A) and potential energy intake (C) after controlling for the effect of body size differences between equids and ruminants. The effect of body size on selection for potential energy intake was statistically significant for all free-ranging ungulates (D; red dashed line). The effect of body size on selection for surface water was not statistically significant for equids (F), but was marginally significant for ruminants (G).

APPENDIX S2

Text S1. Locally-collected data on surface water.

To increase accuracy of estimates of surface water for each study population, I compiled data on springs, streams, small ponds, and man-made water sources (i.e., surface water sources <30 x 30 m, that are undetectable using the Global Surface Water Explorer). These data were recorded primarily by data contributors during previous research efforts (Table S1). For study populations at which principal investigators had not collected any local data on surface water (i.e. Grevy's zebra, impala, both elk populations, Mongolian gazelle in eastern Mongolia, white-bearded wildebeest in Kenya-Tanzania Amboseli, and white-bearded wildebeest in Kenya-Tanzania Mara), I used national water databases to extract permanent sources of water including springs and rivers, which were not detected in remotely-sensed surface water layers. Additionally, data contributors confirmed if there was any fencing around water sources that would prohibit access by free-ranging ungulates. If fencing existed, the location of fences was digitized and used to mask out locally-collected surface water data. For the white-bearded wildebeest population in Kenya-Tanzania Amboseli, I was not able to obtain information regarding fencing. For the mountain zebra population, where small ephemeral springs existed, locally-collected data on surface water was not available because these data were protected in an effort to protect black rhino (*Diceros bicornis bicornis*). However, movements of mountain zebra in this study area were likely less influenced by small water sources compared to larger, more permanent water, which could be detected in remotely sensed water data (pers. comm., Muntifering). To match the resolution of the remotely-sensed data on surface water, I rasterized a 30 x 30 m grid of locally-collected water data and I merged the layer of locally-collected surface water with the layer on remotely-sensed surface water for each study population. I was not able to detect surface water associated with small, ephemeral water sources created by rainfall, livestock troughs, nor any temporally variable man-made water sources. I was also unable to distinguish between salt and fresh water.

Text S2. Importance of ephemeral sources of water for khulan in southern Mongolia.

In the Dzungarian Gobi and South Gobi Region of Mongolia, khulan (*Equus hemionus hemionus*) typically access water on a daily basis (Kaczensky et al. 2010, Nandintsetseg et al. 2016, Payne et al. 2020). This pattern was undetected in the current study, likely because of the difficulty of detecting small, ephemeral water bodies through the Global Surface Water Explorer (see also Payne et al. 2020). Consequently, the data owners believe that the resulting distance to water layer underestimates the true distribution of surface water available to this study population in southern Mongolia (study population 15). Therefore, they urge readers to exercise caution in interpreting the apparent differences in resource selection between the two khulan populations (study populations 14 and 15).

Table S1. Properties of study populations and associated study areas. Number of telemetered individuals (n). Range in number of individuals telemetered in a given year (range of n) for those study populations generating data over multiple years. Years over which GPS relocations were collected and vegetation and surface water characteristics were quantified (study years). MSAVI (Modified Soil-Adjusted Vegetation Index; index of forage biomass) and IRG (Instantaneous Rate of Green-up; index of potential energy intake) were calculated using MODIS terra satellite imagery Version 6.0 (MOD09Q1) with spatial resolution of 250 x 250 meters and temporal resolution of 8 days. Start of growing season, end of growing season, day of maximum IRG, and day of maximum MSAVI are reported as Julian day and averaged across years for populations that included more than one year of tracking data. For populations with more than one growing season, I report the date the first growing season started and the date the last growing season ended. Mean Julian day of maximum IRG or MSAVI are not reported for populations with more than one growing season because those dates are not useful phenological metrics.

common name	scientific name	country/region	n	range of n	study years	annual MSAVI mean ± sd	one growing season?	start of growing season	end of growing season	day of maximum IRG	day of maximum MSAVI
Equids											
Asiatic wild ass (khulan)*	*Equus hemionus hemionus*	western Mongolia	7	7 – 7	2009-2010	0.04±0.01	yes	89	233	129	201
Asiatic wild ass (khulan)#	*E. h. hemionus*	southern Mongolia	9	9 – 9	2013-2015	0.07±0.01	yes	100	252	148	225
Asiatic wild ass (onager)	*E. h. onager*	Iran	9	9 – 9	2017-2018	0.06±0.01	yes	61	145	85	121
feral burro	*E. asinus*	USA	10	8 – 10	2016-2018	0.10±0.00	yes	75	257	91	190
feral horse^	*E. cabalus*	USA	22	22	2018	0.09±0.01	yes	81	177	97	137
Grevy's zebra**	*E. grevyi*	Kenya	7	1 – 7	2007-2008	0.19±0.04	no	92	334	-	-
mountain zebra	*E. zebra*	Namibia	5	4 – 5	2011-2013	0.09±0.03	yes	267	73	29	65
plains zebra+	*E. quagga*	Namibia	9	8 – 9	2009-2010	0.17±0.05	yes	277	65	33	57
plains zebra	*E. quagga*	Zimbabwe	31	7 – 18	2009-2015	0.27±0.07	yes	260	52	337	15
Przewalski's horse	*E. ferus*	central Mongolia	14	14	2018	0.15±0.06	yes	81	233	193	217
Przewalski's horse*	*E. ferus*	western Mongolia	5	4 – 5	2013-2014	0.05±0.01	yes	85	252	109	189
Ruminants											
African buffalo	*Syncerus caffer*	South Africa	4	3 – 4	2005-2006	0.21±0.09	yes	317	76	321	21
elk^	*Cervus canadensis*	USA Wyoming	22	6 – 17	2011-2014	0.08±0.01	yes	71	214	119	156
elk	*Cervus canadensis*	USA Colorado	7	4 – 7	2006-2007	0.14±0.04	yes	85	253	141	205

goitered gazelle#	*Gazella subgutturosa*	Mongolia	6	6	2014	0.07±0.01	yes	121	273	161	2
greater kudu	*Tragelaphus strepsiceros*	Namibia	6	1 – 5	2012-2016	0.15±0.04	yes	320	92	33	64
impala**	*Aepyceros melampus*	Kenya	21	10 – 20	2011-2012	0.20±0.05	no	96	250	-	-
Mongolian gazelle#	*Procapra gutturosa*	southern Mongolia	6	6	2014	0.07±0.01	yes	97	217	161	177
Mongolian gazelle	*Procapra gutturosa*	eastern Mongolia	5	1 – 5	2015-2018	0.12±0.04	yes	109	255	191	209
mule deer^	*Odocoileus hemionus*	USA Wyoming	100	5 – 70	2014-2018	0.12±0.02	yes	81	188	130	180
mule deer	*Odocoileus hemionus*	USA Colorado/Wyoming	78	34 – 46	2016-2018	0.14±0.03	yes	75	179	107	163
saiga*	*Saiga tatarica*	Mongolia	26	7 – 15	2016-2018	0.07±0.02	yes	110	233	174	203
springbok+	*Antidorcas marsupialis*	Namibia	10	10 – 10	2009-2010	0.17±0.05	yes	277	65	33	57
white-bearded wildebeest	*Connochaetes taurinus*	Kenya-Tanzania Amboseli	9	5 – 9	2010-2012	0.16±0.04	no	294	125	-	-
white-bearded wildebeest	*C. taurinus*	Kenya	12	6 – 12	2010-2012	0.20±0.05	no	302	147	-	-
white-bearded wildebeest	*C. taurinus*	Kenya-Tanzania Mara	13	6 – 13	2010-2012	0.22±0.05	no	262	125	-	-

*, #, **, +, ^ = symbols indicate sympatric populations

Table S1 (continued)

common name	fix rate of uncorrelated steps (hours)	length of uncorrelated steps mean (m) ± SD	number of used steps in analysis	body mass (kg)[1]	modal value of human footprint[4]	distance to water (km) mean ± SD in growing season	maximum distance to water (km) used to scale distance to water layer
Equids							
Asiatic wild ass (khulan)	4	2053.88±2616.98	5922	230	1	6.18±3.69	31.77
Asiatic wild ass (khulan)	8	2372.36±2551.07	15729	230	0	11.42±6.87	63.09
Asiatic wild ass (onager)	6	2283.50±2060.21	5873	240	7	4.74±3.06	29.88
feral burro	4	640.61±653.33	24094	180[2]	7	1.61±0.93	10.95
feral horse	4	819.69±855.85	12172	430[3]	3	4.80±3.48	23.08
Grevy's zebra	2	596.00±648.54	8612	405	9	3.15±1.71	15.04
mountain zebra	9	1464.3±1472.32	2849	310	3	19.16±8.02	42.78
plains zebra	7	2931.78±2973.92	4012	247.5	2	4.42±3.51	26.97
plains zebra	4	896.00±1073.83	47686	247.5	9	7.17±5.31	28.75
Przewalski's horse	3	717.3±712.58	15356	250	4	2.32±1.39	9.99
Przewalski's horse	4	2337.04±2370.76	5058	250	1	7.75±4.33	24.63
Ruminants							
African buffalo	4	772.9±759.126	2464	592.5	7	6.09±3.11	22.36
elk	6	1195.6±1322.23	32877	255	3	3.87±2.32	21.37
elk	10	1348.095±1274.29	2987	255	1	4.06±2.88	16.67
goitered gazelle	4	1201.4±1405.10	5047	25	0	8.34±4.89	50.00
greater kudu	2	380.65±482.59	7227	213	6	6.65±4.80	28.69
impala	2	154.54±162.75	36955	52.75	8	1.33±0.81	7.20
Mongolian gazelle	24	2599.7±4557.45	370	27.75	0	7.35±4.77	83.25
Mongolian gazelle	23	7342.27±6197.05	1718	27.75	5	8.09±6.69	46.61
mule deer	100	6452.63±12722.87	4239	65	1	2.65±2.34	20.24
mule deer	45	1681.27±3349.74	6370	65	3	2.25±1.50	20.50
saiga antelope	24	4318.00±4801.23	2286	38.62	0	6.71±5.66	32.60
springbok	6	1329.85±1576.81	5964	36.45	0	3.75±3.06	25.31
white-bearded wildebeest	5	1351.19±1835.02	8383	185	9	6.62±4.35	33.79
white-bearded wildebeest	3	393.69±588.20	17425	185	8	1.76±1.38	11.86
white-bearded wildebeest	7	1111.75±1352.60	3302	185	7	23.56±16.25	67.75

Table S1 (continued)

common name	biome[5]	population number on Figure 2	example references
Equids			
Asiatic wild ass (khulan)	Deserts and Xeric Shrublands	14	Kaczensky et al. 2008; Nandintsetseg et al. 2019
Asiatic wild ass (khulan)	Deserts and Xeric Shrublands	15	Payne et al. 2020; Nandintsetseg et al. 2019
Asiatic wild ass (onager)	Deserts and Xeric Shrublands	16	
feral burro	Deserts and Xeric Shrublands	9	
feral horse	Deserts and Xeric Shrublands	25	Henning et al. 2018
Grevy's zebra	Tropical and Subtropical Grasslands, Savannas and Shrublands	24	Sundaresan et al. 2007
mountain zebra	Deserts and Xeric Shrublands	23	Muntifering et al. 2019
plains zebra	Tropical and Subtropical Grasslands, Savannas and Shrublands	17	
plains zebra	Tropical and Subtropical Grasslands, Savannas and Shrublands	18	Chamaillé-Jammes et al. 2016; Courbin et al. 2019
Przewalski's horse	Temperate Grasslands, Savannas and Shrublands	19	
Przewalski's horse	Deserts and Xeric Shrublands	20	Kaczensky et al. 2008
Ruminants			
African buffalo	Temperate Grasslands, Savannas and Shrublands	26	Cross et al. 2004
elk	Deserts and Xeric Shrublands	21	Merkle et al. 2016; Cole et al. 2015
elk	Temperate Conifer Forests	22	Schoenecker 2012
goitered gazelle	Deserts and Xeric Shrublands	1	Nandintsetseg et al. 2019
greater kudu	Deserts and Xeric Shrublands	13	Skinner and Chimimba 2005
impala	Tropical and Subtropical Grasslands, Savannas and Shrublands	6	
Mongolian gazelle	Deserts and Xeric Shrublands	2	Ito et al. 2006, 2013, 2018; Imai et al. 2017, 2019, 2020
Mongolian gazelle	Temperate Grasslands, Savannas and Shrublands	3	Nandintsetseg et al. 2019
mule deer	Deserts and Xeric Shrublands / Temperate Conifer Forests	7	Sawyer et al. 2017
mule deer	Deserts and Xeric Shrublands / Temperate Conifer Forests	8	Monteith et al. 2018
saiga antelope	Deserts and Xeric Shrublands	5	Nandintsetseg et al. 2019
springbok	Tropical and Subtropical Grasslands, Savannas and Shrublands	4	
white-bearded wildebeest	Tropical and Subtropical Grasslands, Savannas and Shrublands	10	Stabach et al. 2016
white-bearded wildebeest	Tropical and Subtropical Grasslands, Savannas and Shrublands	11	Stabach et al. 2016
white-bearded wildebeest	Tropical and Subtropical Grasslands, Savannas and Shrublands	12	Stabach et al. 2016

1 Wilson and Mittermeier 2011
2 Schoenecker personnal communication.
3 Godfrey and Berger 1987
4 Venter et al. 2016
5 Olson et al. 2001

Table S2. Sources used to generate locally-collected data on surface water for 11 populations of equids and 15 populations of ruminants across the globe.

study population	study population	local water data exists	local water data incorporated?	reference for local water data	fenced water existed?	fenced water excluded?
Asiatic wild ass (khulan)	western Mongolia	yes	yes	Kaczensky unpublished report	no	
Asiatic wild ass (khulan)	southern Mongolia	yes	yes	Kaczensky unpublished report	no	
Asiatic wild ass (onager)	Iran	yes	yes	Esmaeili unpublished report	no	
feral burro	USA	yes	yes	Schoenecker unpublished report	no	
feral horse	USA	yes	yes	Henning unpublished report; USGS (2018)	yes	yes
Grevy's zebra	Kenya	yes	yes	Fischhoff unpublished report; ICPAC 2017a; ICPAC 2017b	yes	yes
mountain zebra	Namibia	yes	No	Muntifering unpublished report	no	
plains zebra	Namibia	yes	yes	Etosha Ecological Institute, pers. comm. with Abrahams	no	
plains zebra	Zimbabwe	yes	yes	Chamaillé-Jammes et al. 2016	no	
Przewalski's horse	central Mongolia	yes	yes	Dejid unpublished report	no	
Przewalski's horse*	western Mongolia	yes	yes	Kaczensky unpublished report	no	
African buffalo	South Africa	yes	yes	Skukuza GIS Lab, Kruger National Park, pers. comm. with Esmaeili	no	
elk	USA Wyoming	yes	yes	USGS (2018)	yes	yes
elk	USA Colorado	yes	yes	Schoenecker unpublished report	no	
goitered gazelle	Mongolia	yes	yes	Kaczensky unpublished report; Buuveibaatar unpublished report	no	
greater kudu	Namibia	yes	yes	Melzheimer unpublished report	no	
impala	Kenya	yes	yes	ICPAC 2017a; ICPAC 2017b	yes	yes
Mongolian gazelle	southern Mongolia	yes	yes	Kaczensky unpublished report; Buuveibaatar unpublished report	no	
Mongolian gazelle	eastern Mongolia	yes	yes	International Steering Committee for Global Mapping (2010)	no	
mule deer	USA Wyoming	yes	yes	USGS (2018)	yes	yes
mule deer	USA Colorado/Wyoming	yes	yes	USGS (2018)	yes	yes
saiga antelope	Mongolia	yes	yes	Buuveibaatar unpublished report	no	
springbok	Namibia	yes	yes	Etosha Ecological Institute, pers. comm. with Abrahams	no	
white-bearded wildebeest	Kenya-Tanzania Amboseli	yes	yes	ICPAC 2017a; ICPAC 2017b	unknown	
white-bearded wildebeest	Kenya	yes	yes	Reid et al. (2008)	yes	yes
white-bearded wildebeest	Kenya-Tanzania Mara	yes	yes	ICPAC 2017a; ICPAC 2017b; ICPAC 2017c	no	

Table S3. Pearson's correlation coefficients between MSAVI, IRG, and surface water used in step-selection models for 11 populations of equids and 15 populations of ruminants across the globe.

Asiatic wild ass (khulan), western Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.345	1.00	
water	0.048	0.063	1.00
Asiatic wild ass (khulan), southern Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.10	1.00	
water	0.063	-0.036	1.00
Asiatic wild ass (onager), Iran	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.152	1.00	
water	-0.003	-0.046	1.00
feral burro, USA	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.108	1.00	
water	-0.144	0.047	1.00
feral horse, USA	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.281	1.00	
water	-0.099	0.159	1.000
Grevy's zebra, Kenya	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.107	1.00	
water	-0.174	-0.179	1.00
mountain zebra, Namibia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.042	1.000	
water	0.243	0.152	1.000
plains zebra, Namibia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.201	1.00	
water	0.127	0.147	1.00
plains zebra, Zimbabwe	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.127	1.00	
water	-0.079	-0.006	1.00
Przewalski's horse, central Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.043	1.00	
water	0.025	-0.002	1.00
Przewalski's horse, western Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.134	1.00	
water	0.012	-0.006	1.00
African buffalo, South Africa	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.321	1.00	
water	0.371	-0.308	1.00

elk, USA Wyoming	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.166	1.00	
water	-0.002	0.036	1.00
elk, USA Colorado	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.187	1.00	
water	-0.086	0.022	1.00
goitered gazelle, Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.068	1.00	
water	-0.053	-0.255	1.00
greater kudu, Namibia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.085	1.00	
water	0.248	0.090	1.00
impala, Kenya	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.016	1.00	
water	0.073	-0.08	1.00
Mongolian gazelle, southern Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.075	1.00	
water	0.552	0.159	1.00
Mongolian gazelle, eastern Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.263	1.00	
water	0.032	0.013	1.00
mule deer, USA Wyoming	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.179	1.00	
water	0.014	0.001	1.00
mule deer, USA Colorado/Wyoming	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.33	1.00	
water	0.000	0.023	1.00
saiga antelope, Mongolia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.045	1.00	
Water	0.036	0.046	1.00
springbok, Namibia	MSAVI	IRG	Water
MSAVI	1.00		
IRG	0.143	1.00	
Water	-0.079	-0.045	1.00
white-bearded wildebeest, Kenya-Tanzania Amboseli	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.04	1.00	
Water	-0.006	0.068	1.00
white-bearded wildebeest, Kenya	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.029	1.00	

Water	0.044	-0.073	1.00
white-bearded wildebeest, Kenya-Tanzania Mara	MSAVI	IRG	Water
MSAVI	1.00		
IRG	-0.011	1.00	
Water	-0.059	0.086	1.00

Table S4. Relative empirical support for step-selection models for 11 populations of equids and 15 populations of ruminants across the globe. Models represent combinations of step length, logarithm of step length, and cosine of turning angles (the null model) in addition to MSAVI, IRG, and distance to surface water. Support was assessed using Akaike's Information Criterion corrected for small sample sizes (AICc). I averaged the parameter estimates of competing models when the difference between AICc (ΔAICc) was < 2. AICc wt and Cum.wt show the weight and the cumulative weight of each model, respectively. The letter k represents the number of parameters in each model.

Model	**k**	**AICc**	**Δ AICc**	**AICc wt**	**Cum.wt**
Asiatic wild ass (khulan), western Mongolia					
IRG + water	5	76953.52	0.00	0.41	0.41
water	4	76954.70	1.17	0.23	0.64
MSAVI + IRG + water	7	76955.12	1.60	0.19	0.83
MSAVI + water	5	76956.70	3.17	0.08	0.91
IRG	4	76957.98	4.45	0.04	0.96
MSAVI + IRG	5	76959.68	6.16	0.02	0.98
null	3	76959.78	6.26	0.02	0.99
MSAVI	4	76961.76	8.24	0.01	1.00
Asiatic wild ass (khulan), southern Mongolia					
MSAVI	4	212851.6	0.00	0.44	0.44
MSAVI + water	5	212853.5	1.88	0.17	0.62
MSAVI + IRG	5	212853.5	1.91	0.17	0.79
null	3	212855.0	3.44	0.08	0.86
MSAVI + IRG + water	6	212855.4	3.81	0.07	0.93
water	4	212857.0	5.41	0.03	0.96
IRG	2	212857.0	5.44	0.03	0.99
IRG + water	5	212859.0	7.41	0.01	1.00
Asiatic wild ass (onager), Iran					
MSAVI + water	5	79625.80	0.00	0.73	0.73
MSAVI + IRG + water	6	79627.80	1.99	0.27	1.00
water	4	79669.14	43.34	0.00	1.00
IRG + water	5	79670.15	44.35	0.00	1.00
MSAVI	4	79688.15	62.34	0.00	1.00
MSAVI + IRG	5	79689.97	64.17	0.00	1.00
null	3	79731.30	105.49	0.00	1.00
IRG	4	79732.88	107.07	0.00	1.00
feral burro, USA					
IRG + water	5	321624.0	0.00	0.70	0.70
MSAVI + IRG + water	6	321626.0	1.97	0.26	0.97
water	4	321630.8	6.78	0.02	0.99
MSAVI + water	5	321632.6	8.56	0.01	1.00
MSAVI + IRG	5	321755.9	131.91	0.00	1.00
IRG	4	321756.5	132.49	0.00	1.00
MSAVI	4	321764.6	140.57	0.00	1.00
null	3	321766.4	142.41	0.00	1.00

feral horse, USA					
water	4	186289.2	0.00	0.48	0.48
MSAVI + water	5	186290.7	1.52	0.22	0.71
IRG + water	5	186291.2	1.99	0.18	0.88
MSAVI + IRG + water	6	186292.7	3.52	0.08	0.97
null	3	186296.1	6.93	0.02	0.98
MSAVI	4	186297.2	7.97	0.01	0.99
IRG	4	186297.8	8.59	0.01	1.00
MSAVI + IRG	5	186299.1	9.87	0.00	1.00
Grevy’s zebra, Kenya					
null	3	102923.9	0.00	0.30	0.30
MSAVI	4	102924.4	0.49	0.22	0.53
IRG	4	102925.9	1.94	0.11	0.64
water	4	102925.9	1.98	0.11	0.75
MSAVI + IRG	5	102926.4	2.47	0.09	0.84
MSAVI + water	5	102926.4	2.49	0.09	0.93
IRG + water	5	102927.8	3.91	0.04	0.97
MSAVI + IRG + water	6	102928.4	4.47	0.03	1.00
mountain zebra, Namibia					
MSAVI	4	34004.07	0.00	0.27	0.27
MSAVI + IRG	5	34004.89	0.81	0.18	0.45
null	3	34005.08	1.01	0.16	0.61
MSAVI + water	5	34005.76	1.68	0.12	0.73
IRG	4	34006.07	1.99	0.10	0.83
MSAVI + IRG + water	6	34006.70	2.63	0.07	0.90
water	4	34007.07	3.00	0.06	0.96
IRG + water	5	34008.07	3.99	0.04	1.00
plains zebra, Namibia					
water	4	53098.74	0.00	0.31	0.31
MSAVI + water	5	53099.04	0.30	0.27	0.58
IRG + water	5	53099.84	1.10	0.18	0.76
MSAVI + IRG + water	6	53100.50	1.76	0.13	0.88
MSAVI	4	53102.97	4.22	0.04	0.92
null	3	53103.40	4.66	0.03	0.95
IRG	4	53103.78	5.04	0.02	0.98
MSAVI + IRG	5	53103.96	5.22	0.02	1.00
plains zebra, Zimbabwe					
MSAVI + water	5	726358.4	0.00	0.60	0.60
MSAVI + IRG + water	6	726359.3	0.86	0.39	1.00
water	4	726369.0	10.57	0.00	1.00
IRG + water	5	726370.7	12.27	0.00	1.00
MSAVI	4	726447.3	88.86	0.00	1.00
MSAVI + IRG	5	726448.7	90.27	0.00	1.00
null	3	726452.6	94.17	0.00	1.00
IRG	4	726454.4	96.03	0.00	1.00
Przewalski’s horse, central Mongolia					

MSAVI + IRG + water	6	60333.84	0.00	0.97	0.97
MSAVI + water	5	60340.79	6.95	0.03	1.00
IRG + water	5	60357.61	23.77	0.00	1.00
water	4	60369.40	35.55	0.00	1.00
MSAVI + IRG	5	60447.96	114.11	0.00	1.00
MSAVI	4	60454.89	121.04	0.00	1.00
IRG	4	60470.67	136.83	0.00	1.00
null	3	60482.38	148.54	0.00	1.00
Przewalski’s horse, western Mongolia					
MSAVI + water	5	221904.9	0.00	0.38	0.38
water	4	221905.5	0.63	0.28	0.67
MSAVI + IRG + water	6	221906.2	1.35	0.20	0.86
IRG + water	5	221906.9	2.06	0.14	1.00
null	3	222013.2	108.34	0.00	1.00
MSAVI	4	222013.6	108.70	0.00	1.00
IRG	4	222014.7	109.78	0.00	1.00
MSAVI + IRG	5	222015.0	110.07	0.00	1.00
African buffalo, South Africa					
IRG + water	5	27259.59	0.00	0.034	0.34
IRG	4	27260.36	0.77	0.57	0.57
MSAVI + IRG + water	6	27261.44	1.85	0.71	0.71
MSAVI + water	5	27261.84	2.25	0.82	0.82
MSAVI	4	27262.11	2.52	0.91	0.91
MSAVI + IRG	5	27262.34	2.75	1.00	1.00
null	3	27274.52	14.93	1.00	1.00
water	4	27274.63	15.04	1.00	1.00
Elk, USA Wyoming					
IRG	4	473256.7	0.00	0.47	0.47
IRG + water	5	473258.1	1.45	0.23	0.69
MSAVI + IRG	5	473258.3	1.61	0.21	0.90
MSAVI + IRG + water	6	473259.7	3.06	0.10	1.00
null	3	473274.1	17.39	0.00	1.00
water	4	473275.2	18.54	0.00	1.00
MSAVI	4	473276.1	19.38	0.00	1.00
MSAVI + water	5	473277.2	20.53	0.00	1.00
Elk, USA Colorado					
MSAVI	4	35564.88	0.00	0.47	0.47
MSAVI + water	5	35566.21	1.33	0.24	0.72
MSAVI + IRG	5	35566.74	1.86	0.19	0.90
MSAVI + IRG + water	6	35568.07	3.19	0.10	1.00
IRG	4	35632.13	67.25	0.00	1.00
IRG + water	5	35634.04	69.16	0.00	1.00
null	3	35635.14	70.26	0.00	1.00
water	4	35636.99	72.11	0.00	1.00
goitered gazelle, Mongolia					
MSAVI	4	63931.83	0.00	0.33	0.33
MSAVI + IRG	5	63932.57	0.74	0.23	0.55

MSAVI + water	5	63933.72	1.90	0.13	0.68
null	3	63934.09	2.27	0.11	0.79
MSAVI + IRG + water	6	63934.57	2.74	0.08	0.87
IRG	4	63935.14	3.31	0.06	0.93
water	4	63935.87	4.05	0.04	0.98
IRG + water	5	63937.08	5.25	0.02	1.00
greater kudu, Namibia					
MSAVI + water	5	85531.31	0.00	0.44	0.44
water	4	85532.50	1.19	0.24	0.68
MSAVI + IRG + water	6	85533.22	1.91	0.17	0.85
IRG + water	5	85534.35	3.04	0.10	0.95
null	3	85537.35	6.03	0.02	0.97
MSAVI	4	85537.99	6.68	0.02	0.99
IRG	4	85539.27	7.95	0.01	0.99
MSAVI + IRG	5	85539.95	8.63	0.01	1.00
Impala, Kenya					
MSAVI	4	554574.1	0.00	0.39	0.39
MSAVI + water	5	554576.0	1.88	0.55	0.55
MSAVI + IRG	5	554576.0	1.90	0.70	0.70
null	3	554576.4	2.29	0.82	0.82
MSAVI + IRG + water	6	554577.9	3.79	0.88	0.88
water	4	554578.2	4.02	0.93	0.93
IRG	4	554578.3	4.21	0.98	0.98
IRG + water	5	554580.1	5.97	1.00	1.00
Mongolian gazelle, southern Mongolia					
IRG	4	4321.04	0.00	0.30	0.30
null	3	4321.64	0.59	0.22	0.52
MSAVI + IRG	5	4322.87	1.82	0.12	0.64
IRG + water	5	4323.04	2.00	0.11	0.75
water	4	4323.54	2.50	0.09	0.83
MSAVI	4	4323.56	2.52	0.08	0.92
MSAVI + IRG + water	6	4324.82	3.77	0.05	0.96
MSAVI + water	5	4325.27	4.22	0.04	1.00
Mongolian gazelle, eastern Mongolia					
null	3	19853.59	0.00	0.23	0.23
water	4	19853.69	0.09	0.22	0.44
MSAVI	4	19854.71	1.12	0.13	0.57
MSAVI + water	5	19854.87	1.28	0.12	0.69
IRG	4	19855.32	1.73	0.10	0.79
IRG + water	5	19855.43	1.83	0.09	0.88
MSAVI + IRG	5	19856.09	2.50	0.06	0.94
MSAVI + IRG + water	6	19856.29	2.69	0.06	1.00
mule deer, USA Wyoming					
IRG	4	74541.10	0.00	0.39	0.39
IRG + water	5	74541.41	0.31	0.34	0.73
MSAVI + IRG	5	74543.07	1.97	0.15	0.87
MSAVI + IRG + water	6	74543.39	2.29	0.13	1.00

null	3	74567.16	26.06	0.00	1.00
water	4	74567.46	26.36	0.00	1.00
MSAVI	4	74568.63	27.53	0.00	1.00
MSAVI + water	5	74568.89	27.79	0.00	1.00
mule deer, USA Colorado/Wyoming					
IRG + water	5	106019.3	0.00	0.43	0.43
MSAVI + IRG + water	6	106019.8	0.41	0.35	0.79
IRG	4	106022.0	2.63	0.12	0.91
MSAVI + IRG	5	106022.4	3.09	0.09	1.00
MSAVI + water	5	106032.1	12.81	0.00	1.00
MSAVI	4	106035.2	15.83	0.00	1.00
water	4	106037.2	17.87	0.00	1.00
null	3	106040.2	20.86	0.00	1.00
saiga antelope, Mongolia					
IRG + water	5	33157.85	0.00	0.43	0.43
water	4	33158.76	0.91	0.27	0.71
MSAVI + IRG + water	6	33159.69	1.84	0.17	0.88
MSAVI + water	5	33160.52	2.67	0.11	0.99
IRG	4	33167.66	9.81	0.00	1.00
null	3	33169.15	11.30	0.00	1.00
MSAVI + IRG	5	33169.49	11.64	0.00	1.00
MSAVI	4	33170.91	13.05	0.00	1.00
springbok, Namibia					
null	3	80566.36	0.00	0.33	0.33
MSAVI	4	80567.65	1.29	0.17	0.51
water	4	80568.05	1.69	0.14	0.65
IRG	4	80568.33	1.97	0.12	0.77
MSAVI + water	5	80569.25	2.89	0.08	0.85
MSAVI + IRG	5	80569.65	3.29	0.06	0.92
IRG + water	5	80570.01	3.65	0.05	0.97
MSAVI + IRG + water	6	80571.24	4.89	0.03	1.00
white-bearded wildebeest, Kenya-Tanzania Amboseli					
MSAVI + IRG + water	6	108451.7	0.00	0.27	0.27
MSAVI + water	5	108451.8	0.07	0.26	0.52
water	4	108452.6	0.95	0.17	0.69
IRG + water	5	108452.7	1.03	0.16	0.85
MSAVI	4	108455.2	3.52	0.05	0.89
MSAVI + IRG	5	108455.4	3.66	0.04	0.94
null	3	108455.8	4.12	0.03	0.97
IRG	4	108456.1	4.39	0.03	1.00
white-bearded wildebeest, Kenya					
IRG	4	237362.4	0.00	0.32	0.32
MSAVI + IRG	5	237363.2	0.80	0.21	0.53
IRG + water	5	237364.2	1.84	0.13	0.65
null	3	237364.5	2.13	0.11	0.76
MSAVI + IRG + water	6	237365.0	2.60	0.09	0.85
MSAVI	4	237365.3	2.94	0.07	0.92

water	4	237366.2	3.84	0.05	0.97
MSAVI + water	5	237367.0	4.60	0.03	1.00
white-bearded wildebeest, Kenya-Tanzania Mara					
null	3	44786.89	0.00	0.36	0.36
MSAVI	4	44788.38	1.49	0.17	0.52
water	4	44788.77	1.88	0.14	0.66
IRG	4	44788.88	1.98	0.13	0.80
MSAVI + water	5	44790.27	3.38	0.07	0.86
MSAVI + IRG	5	44790.36	3.46	0.06	0.92
IRG + water	5	44790.74	3.85	0.05	0.98
MSAVI + IRG + water	6	44792.23	5.34	0.02	1.00

Table S5. Parameter estimates for the best supported step-selection models. Model support was assessed using Akaike’s Information Criterion corrected for small sample sizes (AICc; see Table S3). I averaged parameter estimates of competing models when the difference between AICc (ΔAICc) was smaller than 2. Variables for which 85% confidence intervals did not encompass zero are denoted by asterisks. For ease of interpretation, I switched the direction of parameter estimates for surface water in all of the analyses and presentations. Therefore, positive and negative values show selection and avoidance, respectively, for all three variables.

parameter	**estimate**	**SE**	**z value**	***p***
Asiatic wild ass (khulan), western Mongolia				
MSAVI	-0.030	0.071	0.424	0.671
IRG	-0.087	0.066	1.308	0.191
water	0.315	0.130	2.421	0.015*
Asiatic wild ass (khulan), southern Mongolia				
MSAVI	0.078	0.053	1.470	0.141*
IRG	0.010	0.032	0.310	0.756
water	0.018	0.043	0.420	0.674
Asiatic wild ass (onager), Iran				
MSAVI	0.336	0.089	3.773	<0.001*
IRG	0.004	0.076	0.052	0.959
water	1.943	0.652	2.979	0.002*
feral burro, USA				
MSAVI	0.013	0.105	0.120	0.904
IRG	-0.082	0.091	0.896	0.370
water	1.204	0.190	6.330	<0.001*
feral horse, USA				
MSAVI	0.025	0.030	0.843	0.399
IRG	-0.004	0.033	0.108	0.914
water	0.367	0.197	1.861	0.062*
Grevy’s zebra, Kenya				
MSAVI	-0.061	0.032	1.906	0.056*
IRG	0.012	0.049	0.245	0.807
water	-0.014	0.074	0.193	0.847
mountain zebra, Namibia				
MSAVI	0.121	0.039	3.106	0.001*
IRG	-0.094	0.073	1.289	0.1976
water	0.083	0.039	2.140	0.032*
plains zebra, Namibia				
MSAVI	-0.068	0.085	0.803	0.422
IRG	-0.063	0.074	0.851	0.395
water	0.341	0.263	1.299	0.194
plains zebra, Zimbabwe				
MSAVI	-0.049	0.022	2.208	0.027*
IRG	-0.020	0.040	0.501	0.616
water	0.407	0.098	4.143	<0.001*

Przewalski's horse, central Mongolia				
MSAVI	0.042	0.023	1.801	0.072*
IRG	-0.034	0.043	0.800	0.423
water	0.985	0.191	5.164	<0.001*
Przewalski's horse, western Mongolia				
MSAVI	-0.290	0.249	-1.163	0.245
IRG	0.177	0.119	1.489	0.136*
water	1.375	0.253	-7.387	<0.001*
African buffalo, South Africa				
MSAVI	0.038	0.053	0.719	0.472
IRG	-0.140	0.038	1.751	0.079*
water	0.348	0.199	3.647	<0.001*
elk, USA Wyoming				
MSAVI	0.012	0.055	0.220	0.825
IRG	0.094	0.045	2.083	0.037*
water	-0.039	0.074	0.528	0.597
elk, USA Colorado				
MSAVI	0.584	0.178	3.285	0.001*
IRG	-0.031	0.152	0.202	0.839
water	-0.138	0.164	0.839	0.401
goitered gazelle, Mongolia				
MSAVI	-0.121	0.056	2.171	0.030*
IRG	-0.071	0.045	1.568	0.117*
water	-0.029	0.050	0.570	0.568
greater kudu, Namibia				
MSAVI	0.072	0.020	3.646	<0.001*
IRG	-0.015	0.052	0.297	0.767
water	0.962	0.358	2.691	0.007*
Impala, Kenya				
MSAVI	-0.043	0.014	2.940	0.003*
IRG	0.007	0.016	0.442	0.658
water	0.016	0.035	0.467	0.641
Mongolian gazelle, southern Mongolia				
MSAVI	-0.088	0.100	0.879	0.380
IRG	0.373	0.169	2.205	0.027*
water	0.029	0.303	0.095	0.924
Mongolian gazelle, eastern Mongolia				
MSAVI	0.082	0.025	3.341	<0.001*
IRG	0.052	0.072	0.722	0.470
water	-0.294	0.147	2.000	0.045*
mule deer, USA Wyoming				
MSAVI	0.008	0.053	0.159	0.874
IRG	0.309	0.070	4.415	<0.001*
water	-0.136	0.081	1.671	0.095*
mule deer, USA Colorado/Wyoming				

MSAVI	-0.060	0.037	1.626	0.104*
IRG	0.195	0.036	5.364	<0.001*
water	-0.488	0.259	1.884	0.060*
saiga antelope, Mongolia				
MSAVI	0.029	0.051	0.573	0.566
IRG	0.152	0.062	2.448	0.014*
water	-0.459	0.107	4.285	<0.001*
springbok, Namibia				
MSAVI	-0.035	0.026	1.347	0.178
IRG	-0.011	0.067	0.165	0.869
water	0.092	0.128	0.715	0.475
white-bearded wildebeest, Kenya-Tanzania Amboseli				
MSAVI	0.067	0.027	2.474	0.013*
IRG	0.066	0.051	1.291	0.197
water	0.314	0.101	3.100	0.001*
white-bearded wildebeest, Kenya				
MSAVI	0.030	0.034	0.888	0.375
IRG	0.062	0.025	2.509	0.012*
water	0.034	0.085	0.395	0.693
white-bearded wildebeest, Kenya-Tanzania Mara				
MSAVI	0.048	0.022	2.139	0.032*
IRG	0.009	0.028	0.333	0.739
water	0.057	0.046	1.246	0.213

Table S6. Parameter estimates of weighted least squares regression models describing the effect of human activity on resource selection of 26 populations of globally distributed equids and ruminants. Human activity was indexed by the modal value of the global terrestrial human footprint (Venter et al. 2016) within the minimum convex polygon of each study population during each growing season.

	Selection for forage biomass			***Selection for potential energy intake***			***Selection for surface water***		
	estimate	**SE**	***p***	**estimate**	**SE**	***p***	**estimate**	**SE**	***p***
intercept	-0.005	0.016	0.748	0.179	0.032	<0.001	-0.263	0.122	0.042
human footprint	-0.0008	0.003	0.808	-0.022	0.007	0.004	0.061	0.026	0.031
F-statistic (df)	$F_{(1,21)} = 0.060$			$F_{(1,24)} = 9.690$			$F_{(1,24)} = 5.275$		
p	0.808			0.004			0.031		
Adjusted R^2	-0.044			0.264			0.146		

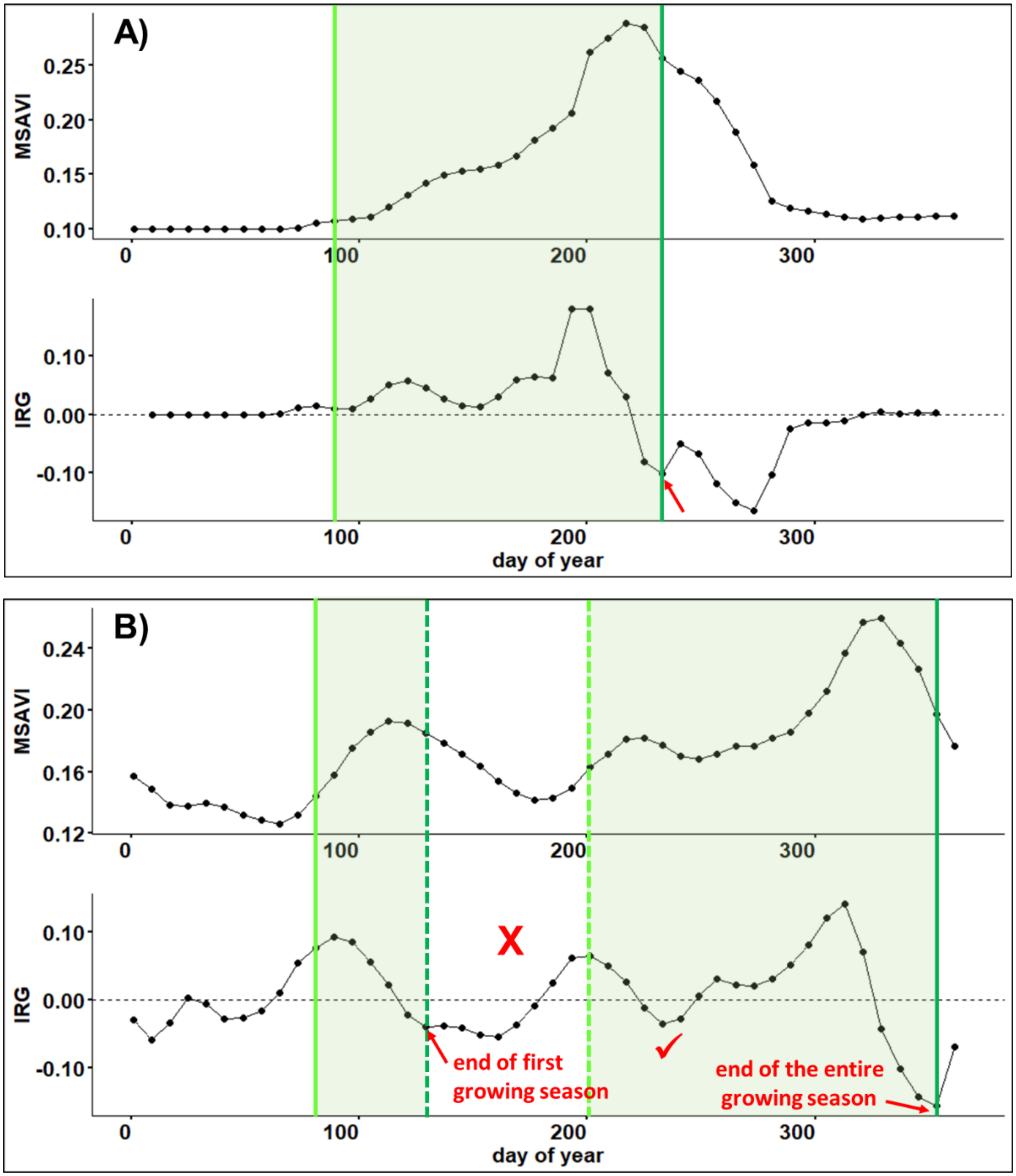

Figure S1. Illustrations of phenology profiles for study areas with a (A) single growing season (e.g., Przewalski's horse habitat in Hustai National Park, Mongolia) and (B) multiple growing seasons (e.g., Grevy's zebra in Laikipia, Kenya). To ensure that positive values of IRG were available to all individuals, I restricted the data set to only those relocations that occurred during growing seasons. For study areas with a single growing season (21 out of 26 study populations), I plotted annual MSAVI and IRG profiles and operationally defined the beginning of the "growing season" as the Julian day when IRG became positive for three consecutive scenes (solid, light green line), and the end of the growing season as the Julian day when IRG reached the minimum negative point (red arrow and solid, dark green line) followed by IRG values less than or equal to zero (sensu Jesmer et al. 2018). For study areas with multiple growing seasons (B), I excluded non-growing season periods following the end of the first growing season (dashed, dark green line), which I identified as the period between when IRG minimized and remained negative for more than 3 to 4 scenes (e.g. red X). The start of subsequent growing seasons (dashed, light green line) was identified as the Julian day when IRG became positive for three consecutive dates (consistent with panel A). Dashed lines indicate the start and end of each single growing season, whereas the solid lines indicate the entire growing season (Julian day reported in Table S1). I did not exclude periods possessing negative IRG values if positive IRG was observed within any three scenes preceding or proceeding the negative IRG value (e.g., red check mark).

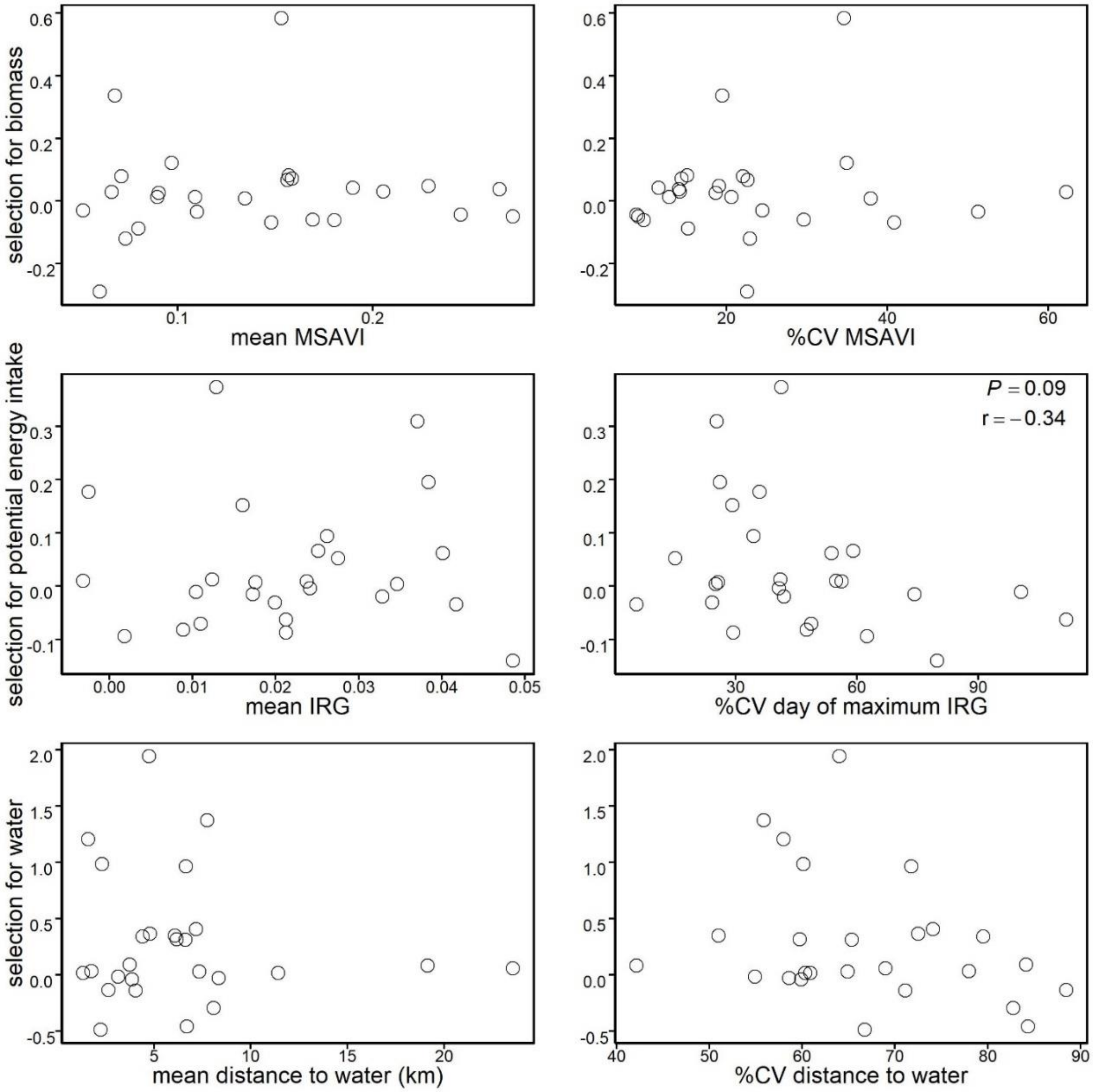

Figure S2. Pearson’s correlations between mean and percent of coefficient of variation (% CV) and selection for forage biomass (MSAVI), selection for potential energy intake (i.e., instantaneous rate of green-up: IRG), and selection for surface water within the minimum convex polygon of each study population during growing seasons. I calculated the CV in day of maximum IRG across each study area to represent spatial variability in IRG. Pearson’s correlation between selection for potential energy intake and % CV of day of maximum IRG was marginally significant (r = -0.34, p = 0.09). All other correlations were not statistically significant (p > 0.10).

CHAPTER THREE

DO LIVESTOCK LEAVE ROOM FOR WILDLIFE? COMPETITION AND FACILITATION BETWEEN LIVESTOCK AND A GLOBALLY-ENDANGERED EQUID IN A MULTI-USE LANDSCAPE

INTRODUCTION

Wide-ranging animals require resources outside the boundaries of formally protected areas, such that their persistence hinges on an ability to share landscapes with humans and their livestock (Woodroffe and Ginsberg 1998; Gaston et al. 2008; Harris et al. 2009; Ripple et al. 2015; Kullberg et al. 2019). Additionally, increasing populations of humans and their livestock reduce the space exclusively available for wildlife conservation (i.e., ‘protected areas’; Distefano et al. 2005; Venter et al. 2016; Schulze et al. 2017; Allan et al. 2018; Bowyer et al. 2019). Consequently, population persistence of large-bodied, wide-ranging species of wildlife hinges on whether and under what conditions such species are compatible with livestock production (Herrero et al. 2009, Berger et al. 2013; Ripple et al. 2015; Keesing et al. 2018). These questions are particularly pressing in arid and semi-arid rangelands, which comprise >40% of the terrestrial surface (Safriel et al. 2005; Middleton and Sternberg 2013), which increasingly are changing due to climate warming and drying (Batsaikhan et al. 2014; Pravalie et al. 2019), and in which livestock and wildlife share space and resources (Fynn et al. 2016).

Two perspectives have characterized attempts to quantify how and why interactions among wild and domestic ungulates are often negative, and occasionally positive. Historically, such interactions have been viewed through a lens of competition: some combination of resource and interference competition forces trade-offs between the abundance and individual performance of livestock on the one hand, and those of wild ungulates on the other (Namgail et al. 2007; Mysterud and Austrheim 2008; Kittur et al. 2010; Schroeder et al. 2013; Fynn et al. 2016). Along with shared parasites and pathogens (Holdo et al. 2009, Ali et al. 2018, Cotteril et al. 2020), competitive interactions have the potential to trigger population declines, resulting in the eventual replacement of wild ungulates by livestock (Gordon 2009; Schieltz and Rubenstein 2016; du Toit et al. 2017). Alternatively, interactions between wild and domestic ungulates can be neutral, or even positive. Grazing and browsing by livestock can enhance habitat for wild ungulates, and vice versa, through facilitation of plant growth (Augustine et al. 2011, Odadi et al. 2017a). However, such facilitation depends on environmental context, and is governed by the joint effects of precipitation (with greater potential for facilitation during wetter times [Kimuyu et al. 2017] and in wetter places [Fynn et al. 2015; Fynn et al. 2016]) and livestock density (with greater potential for facilitation at lower densities of livestock [Mysterud and Austrheim 2008; Bhola et al. 2012, Keesing et al 2018, Stears and Shrader 2020]). If wild ungulates are attracted to areas recently grazed by livestock, such facilitation could offset (or altogether override) any negative effects of competition, thereby promoting coexistence in multi-use rangelands.

Across arid and semi-arid rangelands of central Asia, most populations of the Asiatic wild ass (*Equus hemionus*) co-occur with humans and domestic ungulates (Singh 2000; Kaczensky et al. 2008; Hemami and Momeni 2013; Nandintsetseg et al. 2016; Esmaeili et al. 2019). The Persian wild ass or onager (*E. h. onager*) is an endangered subspecies of the Asiatic wild ass restricted to two protected area complexes – the Bahram-e-Goor Protected Area (BPA, including Qatrouiyeh National Park, QNP) and the Touran Biosphere Reserve –

in central Iran. Onagers are imperiled from a combination of poaching, conflict with pastoralists, and agricultural expansion (Tatin et al. 2003; Hemami and Momeni 2013). Covering a total area of 3,747 km^2, the BPA was established in 1972, of which 310 km^2 was dedicated to QNP in 2008 to protect what is now the globe’s largest population of onagers (Figure 1). Qatrouiyeh’s designation as a national park is comparable to an IUCN Ib Wilderness Area category, such that livestock grazing and other human activities are prohibited. Additionally, QNP maintains anti-poaching patrols, and supplemental forage is provided to onagers outside the growing season. In response, the onager population of QNP (and thus BPA) increased from ca. 90 individuals in 2000 to ca. 900 individuals in 2019 (Iranian Department of Environment, unpublished report).

In contrast to QNP, BPA (comparable to IUCN V Protected Landscape/Seascape category) hosts ca. 4000 semi-nomadic pastoralists and small-scale farmers who herd primarily sheep (*Ovis aries*) and goat (*Capra hircus*), with approximately 14 head of livestock per km^2 (Iranian Department of Environment, unpublished report). Livestock grazing is regulated through a lease schedule, in which pastures within BPA are leased to pastoralists for either seasonal or annual (i.e., year-round) use. During the daytime, livestock are accompanied by at least one herder, and are kept in corrals overnight to minimize depredation by gray wolves (*Canis lupus*) and striped hyenas (*Hyaena hyaena*).

Combining data on plant productivity, movements of onagers, and assays of onager diet quality, I quantified the relative influence of competition and facilitation between onagers and livestock. In so doing, I sought to inform efforts to better conserve onagers in central Iran. I tested three main hypotheses (and combinations thereof) to explain how variation in the intensity and timing of livestock grazing affected resource selection and diet quality of onagers:

(1) *Interference Competition*: any selection for forage and water by onagers is more pronounced during the night (when livestock are corralled) because onagers avoid coming into contact with livestock.

(2) *Exploitative Competition*: livestock remove forage and water that otherwise would be available to onagers, causing onagers to select areas in which livestock grazing is minimal. Diet quality of onagers is depressed in the presence of livestock (i.e., within BPA relative to QNP). Both effects are more pronounced during the dry season, when high-quality forage (and forage in general) is relatively scarce.

(3) *Facilitation*: livestock stimulate forage regrowth, causing onagers to select areas in which livestock grazing has occurred recently. Diet quality of onagers is enhanced by the presence of livestock. Both effects are more pronounced during the wet season, when forage is both relatively abundant, and of relatively high quality.

(4) *Interference Competition x Exploitative Competition*: any selection for forage and water by onagers is more pronounced during the night, and in areas in which livestock grazing is minimal. Diet quality of onagers is depressed in the presence of livestock. Both effects are more pronounced during the dry season, when high-quality forage (and forage in general) is relatively scarce.

(5) *Interference Competition x Facilitation*: any selection for forage and water by onagers is more pronounced during the night, and in areas recently grazed by livestock. Diet quality of onagers is enhanced in the presence of livestock. Both effects are more

pronounced during the wet season, when forage is both relatively abundant, and of relatively high quality.

(6) *Exploitative Competition x Facilitation*: during the dry season, onagers select areas in which livestock grazing is minimal; however, during the wet season, onagers select areas recently grazed by livestock. Similarly, diet quality of onagers is depressed in the presence of livestock during the dry season, and is enhanced in the presence of livestock during the wet season.

(7) *Interference Competition x Exploitative Competition x Facilitation*: during the dry season, onagers select areas in which livestock grazing is minimal; however, during the wet season, onagers select areas recently grazed by livestock. Both effects are more pronounced during night. Diet quality of onagers is depressed in the presence of livestock during the dry season, and is enhanced in the presence of livestock during the wet season.

METHODS AND MATERIALS

Study area and species

Qatrouiyeh National Park (QNP) and Bahram-e-Goor Protected Area (BPA) have an arid, seasonal climate (mean annual temperature 21.00 ˚C ± 1.00 SD, mean annual precipitation 186.11 mm ± 90.69 SD), with September the driest and January the wettest months (0.00 mm ± 0.00 SD and 38.10 mm ± 45.30 SD), respectively. The growing season starts in early March, peaks in late March, and ends in late May/early June, sometimes with additional growth of annual plants in response to occasional rain in November. Vegetation cover is sparse (mean cover 32.40% ± 4.80% SD), and is dominated by *Artemisia sieberi*, *Zygophylllum eurypterum*, *Astragalus* spp., and *Noaea mucronata.* In addition to onagers, other large mammals in BPA include Indian gazelle (*Gazella bennettii*), mouflon (*Ovis orientalis*), wild goat (*Capra aegagrus*), and wild boar (*Sus scrofa*). Large carnivores include gray wolf and striped hyena; however, no predation by these species has been documented on adult onagers.

Onagers exhibit a diverse diet, consuming 63 plant species from 21 families; seedling germination from onager dung includes forbs (84%), grasses (11%), and shrubs (5%; Ghasemi 2012; Mahmoudi 2014). Onagers mate between May and July; parturition peaks in May, following a gestation period of about 11 months. Anecdotally, foals are weaned after ca. 8 months, and stay with mothers for a year (Iranian Department of Environment, unpublished report). In QNP, group size of onagers ranges between 2 to 63 individuals, with a mean group size (including solitary stallions) of 8.00 ± 11.80 SD (Hemami and Momeni 2013). Similar to the Asiatic wild ass (*E. hemionus hemionus*), and with the exception of mothers and foals, herd composition of onagers is fluid and changes regularly in a fission-fusion manner (Kaczensky et al. 2008).

Effects of livestock on forage biomass

The design and schedule of leases within BPA permitted me to employ a quasi-experimental design to quantify the impact of livestock grazing on forage biomass, and thus evaluate the potential for exploitative competition and facilitation between livestock and onagers. Enforcement of the lease schedule is inconsistent, however, and livestock numbers within leases occasionally exceed those permitted, particularly during drought years or times of economic hardship. In sum, data on entry and exit dates of livestock and livestock density were available for 26 seasonal leases covering ca. 30% of the BPA (Figure 1, Table S1).

Eleven of these 26 leases were grazed by livestock in the dry season (May – October) and 15 were grazed by livestock in the wet season (November – April). Average grazing duration in dry season leases was 160 ± 5 SE days, and livestock density was 46.00 ± 12.60 SE sheep and goat/km^2. In wet-grazed leases, mean of grazing duration was 153 ± 3 SE days and livestock density was 40.00 ± 8.91 SE sheep and goat/km^2.

I combined data on the intensity and timing of livestock grazing (regulated through the BPA lease schedule) with remotely-sensed data on forage biomass. I used MODIS Modified Soil-Adjusted Vegetation Index (MSAVI; MODIS terra satellite imagery Version 6.0 MOD09Q1; spatial resolution 250 × 250 m, temporal resolution eight days) as a measure of forage biomass within each of the 26 leases in 2017 and 2018 (Qi et al. 1994; Boschetti et al. 2007; Ren and Zhou 2019). Before calculating MSAVI within each lease, I masked out farmlands and pixels with topographic slope >20 degrees (representing rocks and non-vegetated areas). For each lease, I used the most recent MSAVI layer ≥15 days before livestock entry (range = 15-22 days, depending on the availability of MODIS images) to estimate forage biomass prior to livestock entrance (hereafter 'pre-grazing'). Similarly, and for each individual lease, I selected the most recent MSAVI layer ≥15 days after livestock exit (range = 16-21 days) to measure forage biomass following livestock exit (hereafter 'post-grazing'). I calculated the average MSAVI value across each lease as "mean forage biomass" in pre-grazing and post-grazing periods. For each lease, I subtracted the post-grazing forage biomass from the pre-grazing forage biomass to estimate change in forage biomass caused by livestock grazing.

I tested for effects of grazing intensity and season on changes in forage biomass using a Generalized Linear Mixed Model (GLMM). I calculated grazing intensity by multiplying the density of livestock (number of livestock divided by lease area) by the duration of grazing (# of days) within each of the 26 leases. Grazing intensity was standardized to a mean of 0.00 and standard deviation of 1.00 in the GLMM analysis, and was used as a continuous predictor. Additionally, I included season (dry versus wet) in the analysis, and an interaction between grazing intensity and season. Since I did not detect differences in change in forage biomass between years 2017 and 2018 for each lease (paired *t*-test, t = 1.01, df = 25, *P* = 0.32), I did not include year as a predictor in the GLMM. To incorporate spatial variation among the 26 leases, I included lease identity as a random intercept in the GLMM (Zuur et al. 2009) using "nlme" package (Pinheiro et al. 2017). Marginal and conditional R^2 for the GLMM was estimated following Nakagawa and Schielzeth (2013) using "MuMIn" package (Barton, 2018).

Onager capture and GPS telemetry

In QNP, and from December 2016 through January 2017, nine mare onagers were captured and fitted with GPS telemetry collars (Vertex Lite 2 Iridium, Vectronic Aerospace GmbH, Berlin, Germany). Onagers were captured at night in corral traps, which were located ca. 15 km apart. Trapping was conducted in collaboration with the Iranian Department of Environment and Isfahan University of Technology. A single concrete trap and a single fenced corral trap were used (Levanov et al. 2013). The dimension of the concrete trap was rectangular (ca. 10×15 m); the fenced trap was round (ca. 10 m radius). The walls of the fenced trap were covered with carpet to obscure vision for trapped animals (Levanov et al. 2013). Both traps had remotely-controlled doors and were monitored using close-circuit cameras for at least three nights before captures. Traps were pre-baited with hay and water for a month such that herds would enter and acclimatize to traps. Frequently, onagers entered traps at night, and capture crew recorded up to 15 individuals within each trap. To ensure the safety of animals, the capture crew waited until fewer than 10 individuals occurred inside each trap, then closed the trap doors (remotely) at night.

During each capture, 3 mares were immobilized (selected randomly), releasing other individuals before handling and deployment of GPS collars in the morning following the capture night. Since onagers exhibit fission-fusion herds (Kaczensky et al. 2008), no attempt was made to ensure that individuals selected for collaring belonged to a single herd (Sundaresan et al. 2007; Rubenstein et al. 2016). Onagers were darted inside traps using a CO_2 rifle (Daninject JM™, Wildlife Pharmaceuticals, Fort Collins, CO 80524, USA) by a licensed veterinary team, then immobilized with 4.40 mg Ethorphine (M99, C-Vet Veterinary Products, Lancs, UK), 10 mg Detomidine–HCl (Domosedan, Orion Corp. Farmos Finland) and 10 mg Buthorphanol (Torbugesic, Fort Dodge Animal Health, Iowa, USA) in 15 ml syringes with a 16 gauge 1.50 mm × 30.00 mm needle. After fitting GPS collars, anesthesia was reversed with an intravenous combination of 200 mg Naltrexone (Trexonil Wildlife Laboratories Inc., Fort Collins, Colorado, USA) and the alpha2-antagonist 20 mg Atipamezole (Antisedan, Orion Corp. Farmos Finland) using 15ml syringes with a 16 gauge 1.50 mm x 30.00 mm needle. To facilitate a smooth reversal, 12 mg of the opioid antagonist-agonist diprenorphine (Revivon, C-Vet Veterinary Products, Lancs, UK) was used (Walzer et al. 2006).

I programmed GPS collars to collect a location every-other hour and to self-release two years after deployment. I did not include first two weeks of GPS locations after deployment of collars in the analysis to reduce the effect of capture and handling process on movement of animals (Dechen Quinn et al. 2012). I screened GPS locations with a dilution of precision (DOP) > 10 to enhance the accuracy of the results, and ultimately used 71,658 locations from January 2017 to December 2018 in my analyses. The capture and telemetry methods followed protocols approved by the Iranian Department of Environment (# 95/12631) and the University of Wyoming Institutional Animal Care and Use Committee (#20160225SE00212-01), and adhered to guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Diel and seasonal resource selection by onager

To test whether onagers' resource selection was altered simply by the presence of livestock (per the '*Interference Competition*' hypothesis), I evaluated responses of onagers to forage biomass and water using diel and seasonal resource selection functions (RSFs) based on a use-availability design (Boyce et al. 2002, Manly et al. 2007). I assumed that any differences in resource selection by onagers between diel periods should at least partly reflect attempts to minimize interference with livestock. Because livestock were active during daytime and were corralled during nighttime, I expected that livestock suppressed resource selection by onagers during daytime with minimal influence during nighttime. I classified GPS locations of onagers into dry (May - October) and wet (November - April) seasons. Within each season, I divided GPS locations of onagers into day and at night times using the function "time_of_day" in package amt (Signer et al 2019). For each location of a telemetered onager (i.e., for each 'used' point), I generated 10 random (unused) points within each individual's MCP to quantify third-order resource selection (Johnson 1980).

I extracted forage biomass (average MODIS MSAVI in each season, for years 2017 and 2018) and linear distance to nearest water sources for all used and available points. I did not detect strong correlation among these predictors (Pearson's pairwise correlation | r | <

0.20), so I built RSFs using forage biomass and distance to nearest water sources (hereafter 'habitat variables'). Habitat variables were standardized to a mean of 0.00 and a standard deviation of 1.00. I fitted weighted logistic regression models with each individual as random intercept and slope, and fixed the variance of individual-specific intercepts to 1000 following the procedure outlined in Muff et al. (2020). I assigned a weight of 1000 to available points to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (Muff et al. 2020). I switched the direction of parameter estimate for distance to nearest water sources; therefore, positive and negative values of RSF parameter estimate show selection and avoidance for the two habitat variables.

Diet quality of onagers

Crude fecal protein is a reliable indicator of diet quality in ungulates and crude fecal fiber is inversely correlated with digestibility (i.e., nitrogen accessibility) of forage (Leslie & Starkey 1985, Osborn & Jenks 1998, Hamel et al 2009, Jesmer et al. 2020). Taken together, crude fecal protein and crude fecal fiber provide a proxy of diet quality for ungulates (Villamuelas et al. 2016; Ramanzin et al. 2017). To test whether livestock grazing shifted diet quality of onagers, I measured percent crude fecal protein and fiber in 252 fecal samples of onagers collected approximately every-other month between December 2017 and November 2018. Fresh fecal samples were targeted based on physical properties of softness and dark color. Samples were air-dried and were extracted percent crude fecal protein and percent crude fecal fiber following the methods of macro Kjedahl acid digestion procedure and Weende method, respectively (AOAC 1984) at the Department of Agriculture, Isfahan University of Technology, Isfahan, Iran. Average retention time in equids is ~30 hours (Steuer et al. 2011; Van Soest 2018); although telemetered individuals typically did not move from BPA to QNP (and vice versa) over the course of 30 hours, such movements did occur (dry season mean: 0.58 ± 0.12 SE times per 30 hours per individual; wet season mean: 0.82 ± 0.09 SE times per 30 hours per individual). In other words, and while it was possible for individuals to have fed in one property and defecated in another within the span of 30 hours, any differences that I detected between BPA and QNP should be conservative. To test whether diet quality of onagers was different between BPA and QNP in each season, I compared percent crude fecal protein and percent crude fecal fiber between BPA and QNP using *t*-tests in dry and wet seasons, separately.

RESULTS

Leases that were more intensely grazed by livestock exhibited reduced forage biomass from pre- to post-grazing periods, but only during the dry season (parameter estimate: -0.006 ± 0.001 SE, $P < 0.001$; Table 1, Figure 2). Forage biomass neither increased nor decreased with grazing intensity during the wet season (Table 1; Figure 2). The marginal and conditional R^2 of the GLMM were identical ($R^2 = 0.80$), reflecting a lack of statistical significance for lease identity as a random effect (Table 1).

I recorded 7962 ± 412 SE (range = 5806-8756) points per individuals over 664.22 ± 34.39 SE days (range = 484-729 days). Home range size (100% MCP) was 359.70 ± 83.60 SE km^2 during dry seasons and 507.38 ± 106.00 SE km^2 during wet seasons. Between successive relocations, onagers moved 0.91 ± 0.03 SE km in the dry season and 0.83 ± 0.03 SE km in the wet season. During both seasons, onagers selected for forage biomass at nighttime (parameter estimate, dry season: 0.30 ± 0.05 SE, $P < 0.001$; wet season: 0.27 ± 0.12 SE, $P = 0.02$) but not daytime ($P \geq 0.34$ for both seasons; Figure 3). During the dry season, onagers selected for water during daytime (parameter estimate: 0.42 ± 0.15 SE, $P < 0.01$) and nighttime (parameter estimate: 0.19 ± 0.10 SE, $P = 0.05$). During the wet season, onagers neither selected nor avoided water during the daytime ($P = 0.07$) or nighttime ($P = 0.40$; Figure 3).

During the wet season, onagers in BPA (i.e., those exposed to livestock) exhibited higher-quality diets than those in QNP, where livestock grazing did not occur (Figure 4). During the wet season, fecal samples collected in BPA (n = 84, mean crude protein 4.81% ± 0.14% SE) had significantly higher crude protein compared to those collected in QNP (n = 75, mean crude protein 4.39% ± 0.12% SE; *t*-test: t = 2.32, df = 156.77, $P = 0.02$). Additionally, fecal samples collected in BPA during the wet season had lower crude fiber (mean crude fiber 39.65% ± 0.52% SE) compared to those collected in QNP (mean crude fiber: 43.40% ± 0.55% SE; *t*-test: t = -5.00, df = 155.44, $P \leq 0.001$). During the dry season, I did not detect differences in percent crude protein or percent crude fiber between fecal samples collected in BPA (n = 49) and QNP (n = 44).

DISCUSSION

My results highlight the potential for livestock grazing to directly shape the activity and resource selection of onagers. In support of the hypothesis of interference competition, selection for high forage biomass was accentuated at night, when livestock were corralled, and regardless of season. Elsewhere, activity of livestock and humans shape the distribution and resource selection of wild ungulates across space (e.g., Ogutu et al. 2010; Olson et al. 2011; Ford et al. 2014) and over both diel and annual cycles (e.g., Namgail et al. 2007; Suryawanshi et al. 2010; Gaynor et al 2018).

In addition to direct interference, the intensity of grazing by livestock further affected resource selection by onagers. Onagers selected for forage biomass across seasons, and livestock grazing reduced the forage biomass available to onagers from pre- to post-grazing periods in the dry season. Critically, and over the stocking densities in BPA, livestock neither reduced nor stimulated forage biomass in the wet season, regardless of grazing intensity. Relative to the wet season, the stronger impact of livestock grazing on forage biomass during the dry season is congruent with other human-occupied rangelands, in which the forage available for wild ungulates is reduced by livestock during dry times (Kimuyu et al. 2017) or in dry places (Fynn et al. 2016), particularly when livestock densities are high (Bhola et al. 2012, Stears and Shrader 2020).

In arid and semi-arid rangelands, precipitation boosts vegetation quality (i.e., nitrogen content and digestibility), which can be further enhanced by grazing (Anderson et al. 2007; Odadi et al. 2011b; Riginos et al. 2012; Fynn et al. 2015; Fynn et al. 2016). Such dynamics underlie grazing successions or hotspots, in which grazing by one species of ungulate results in the attraction of others (Bell 1971; Kuijper et al. 2009; Anderson et al. 2010; Ng'weno et al. 2019). Given that diet quality of onagers was highest in the wet season in the presence of livestock (i.e., within BPA), some potential exists for facilitation of onagers via livestock grazing. Equids and other hindgut fermenters are more tolerant of low protein/high fiber vegetation than ruminants, and therefore can persist in areas where forage quality is low (Odadi et al. 2011a; Odadi et al. 2011b; Kimuyu et al 2017). Along these lines, onagers in BPA and QNP exhibited comparable, low-quality diets during the dry season, probably as a result of plant senescence and a lack of compensatory regrowth following grazing by livestock (Briske et al. 2008; Fynn 2012; Hempson et al. 2015; Fynn et al. 2016). Only during the wet season and in the presence of livestock did we detect an increase in the diet quality of onagers.

My results lend support to a shifting dynamic of competition and facilitation between livestock and onagers: onagers avoid encounters with livestock, and livestock reduce the biomass of forage available for onagers during the dry season, but livestock enhance diet quality of onagers during the wet season. Whether my findings extend from functional (i.e., behavioral) to population-level responses hinges on the degree to which forage biomass, forage quality, or both limit onager populations. Future efforts might employ replicated exclusion (i.e., fenced) plots within a series of dry and wet season leases, in both QNP and BPA, to quantify productivity and offtake by onagers and livestock separately and in tandem. Although livestock grazing is prohibited in QNP, a large population of onagers occurs throughout the year, exerting patterns of grazing pressure that differ from those in dry and wet season leases.

Although protected areas can enhance prospects for endangered species conservation (Georgiadis et al. 2007; Suryawanshi et al. 2010; Nandintsetseg et al. 2016; Pringle 2017), major restrictions on pastoralism and other forms of livestock production are unfeasible (and often unethical) in many rangelands across the globe. If behavioral responses are a precursor for numerical changes, my results point to the potential for which livestock grazing might be used as a tool for onager conservation. To boost the production of forage biomass throughout BPA, the number of pastures leased for wet-season grazing might be increased along with a reduction in the number of dry-season leases. Such decisions on the timing of pasture leases require close collaboration with pastoralists, as well as alternative dry season leases outside the BPA (where onagers do not occur). As an intermediate step, rotation of the current leases (i.e., switching the timing of grazing in dry and wet season leases every few years) could potentially dampen the effect of livestock grazing across BPA. Further experimental work could be used to identify optimal (seasonal) stocking densities for livestock to enhance forage quality for onagers.

Interactions between wild and domestic ungulates have been the subject of study in well-known, often long-term manipulations (e.g., Knapp et al. 1999; Stewart et al. 2002; Young et al. 2005; Keesing et al. 2018). To the best of my knowledge, mine is the first investigation in a poorly-known ecosystem hosting one of the last viable populations of a large, endangered mammal, thereby providing a baseline for future studies and conservation efforts. Sharing landscapes with rare and declining wildlife ultimately requires policies, programs, and compromises that are agreeable—and even beneficial to—local communities.

Table 1- Results of a Generalized Linear Mixed Model for effects of season (dry vs. wet) and grazing intensity (number of livestock divided by lease area multiplied by the duration of grazing (# of days)) on differences between post-grazing and pre-grazing forage biomass in dry season (n=11) and wet season (n=15) leases in Bahram-e-Goor Protected Area. Identical values for marginal and conditional R^2 reflect a lack of statistical significance for lease identity as a random effect.

	estimate	SE	t	*P*
variable				
grazing intensity	-0.006	0.001	-4.16	<0.001
season*	0.026	0.002	13.47	<0.001
grazing intensity × season*	0.006	0.002	3.15	0.005
Marginal R^2 = 0.80; Conditional R^2 = 0.80				
* dry season lease is the reference category				

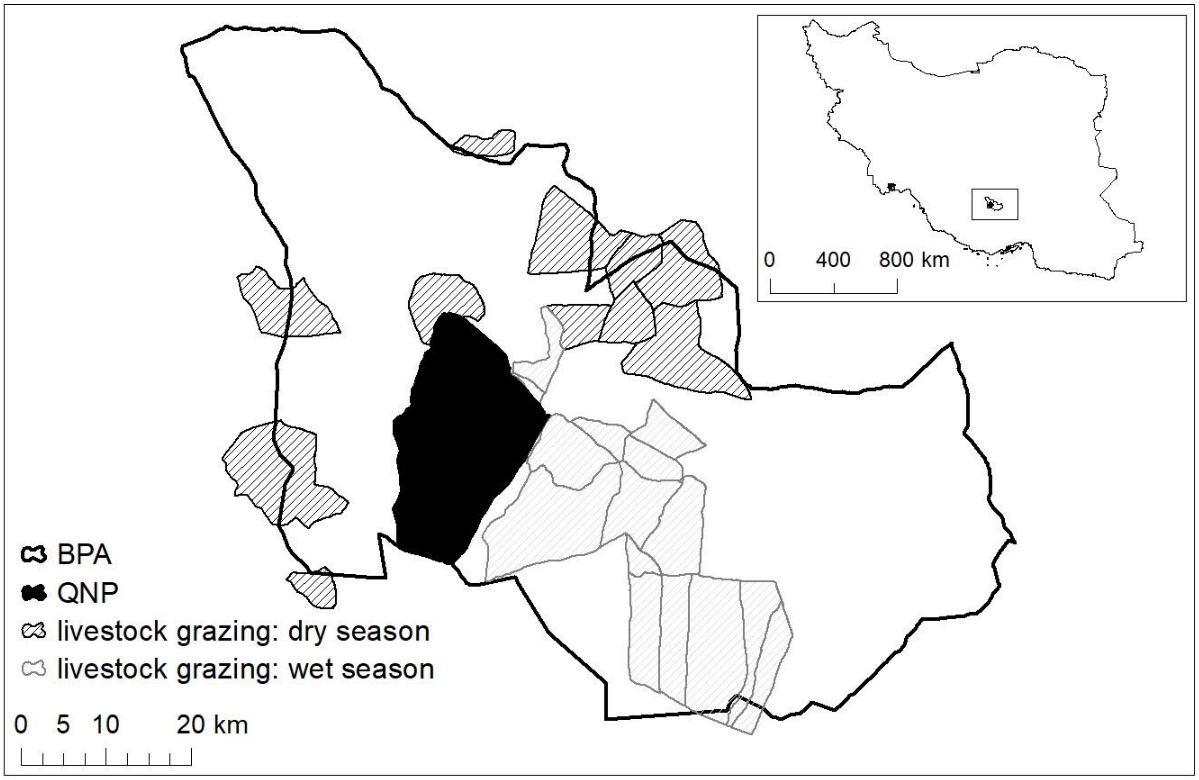

Figure 1- Bahram-e-Goor Protected Area (BPA) and Qatrouiyeh National Park (QNP) in south-central Iran (inset). Location of 26 dry-season and wet-season leases in BPA, Eleven of these leases (dark gray polygons) were grazed by livestock in the dry season (May – October) and 15 leases (light gray polygons) were grazed by livestock in the wet season (November – April).

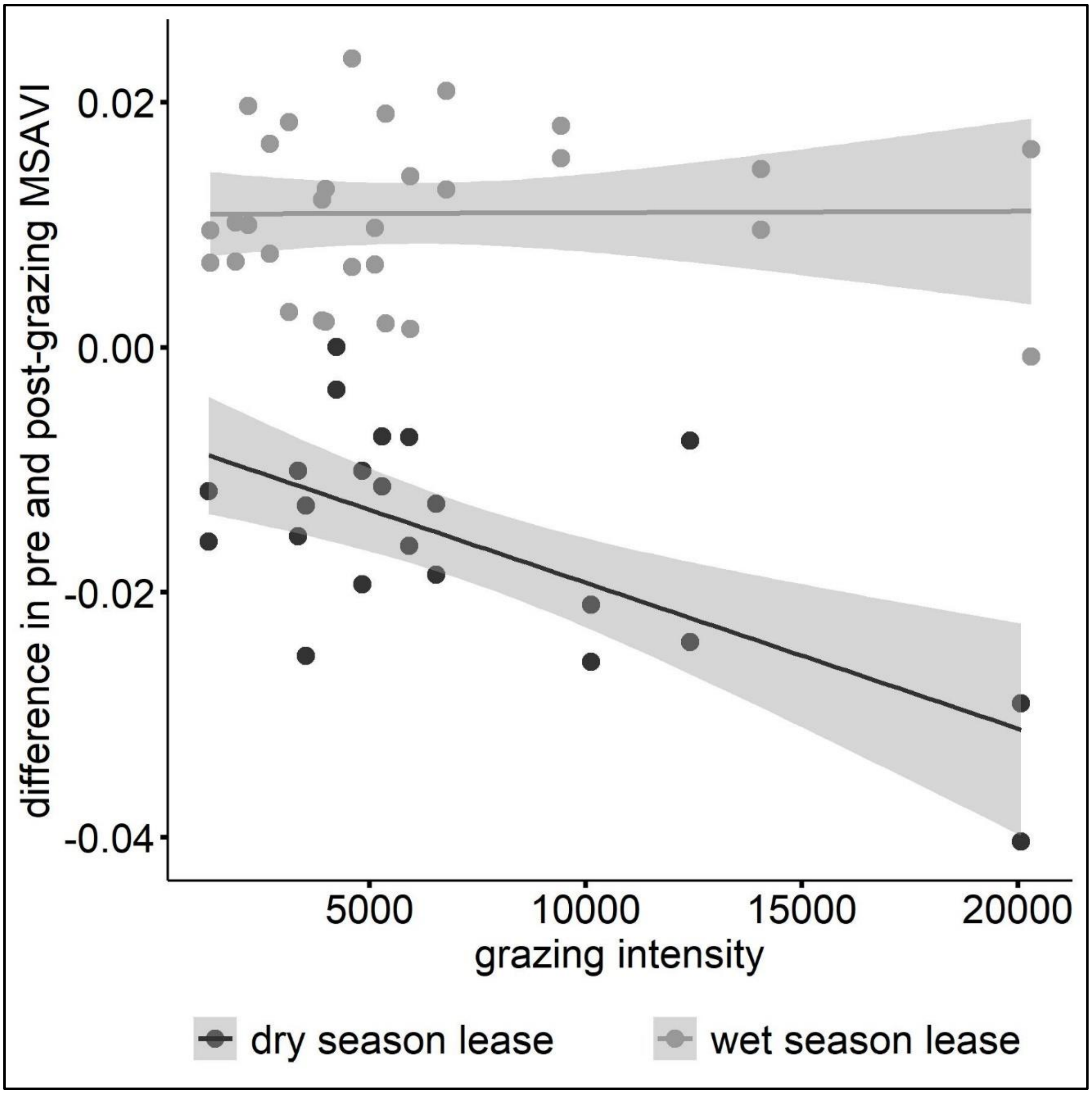

Figure 2- Effect of grazing intensity (number of livestock divided by lease area multiplied by the duration of grazing (# of days)) on differences between post-grazing and pre-grazing forage biomass (measured by Modified Soil-Adjusted Vegetation Index MSAVI) in the dry season (black points and line, n = 11) and wet season (gray points and line, n = 15) leases in Bahram-e-Goor Protected Area. Gray shading represent 95% confidence intervals around each relationship.

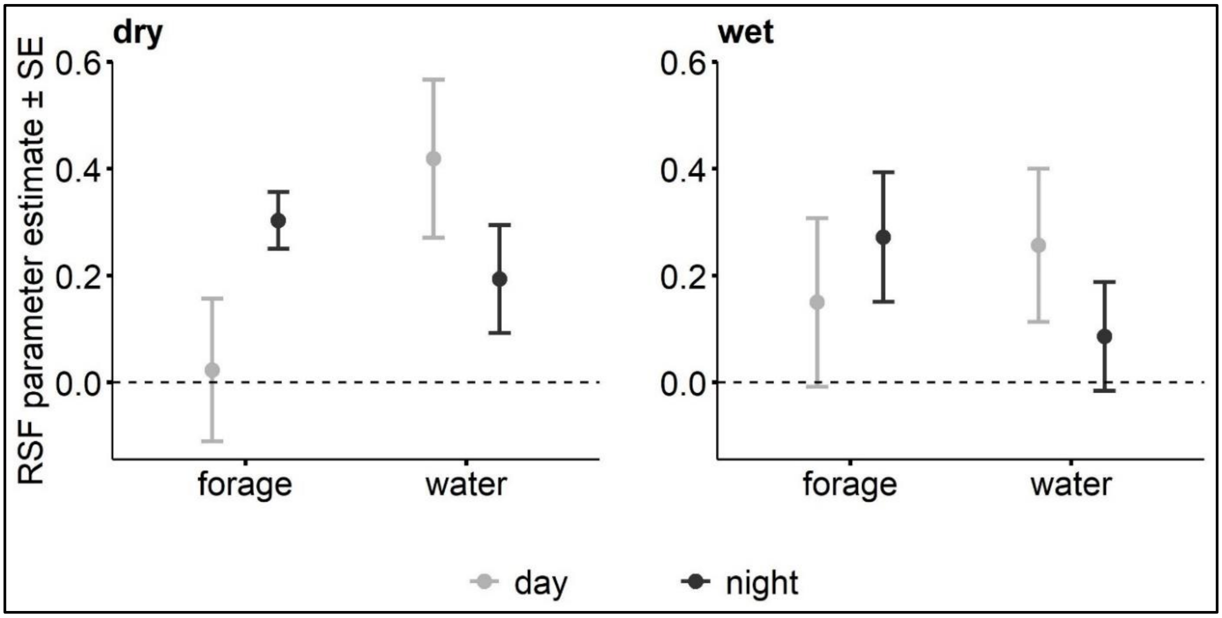

Figure 3- Parameter estimates ± standard error (SE) for seasonal and diel resource selection functions (RSF) for onagers in BPA and QNP in response to forage biomass (forage) and distance to nearest water source (water). The direction of parameter estimates for distance to nearest water source is switched; therefore, positive and negative values show selection and avoidance for forage biomass and water.

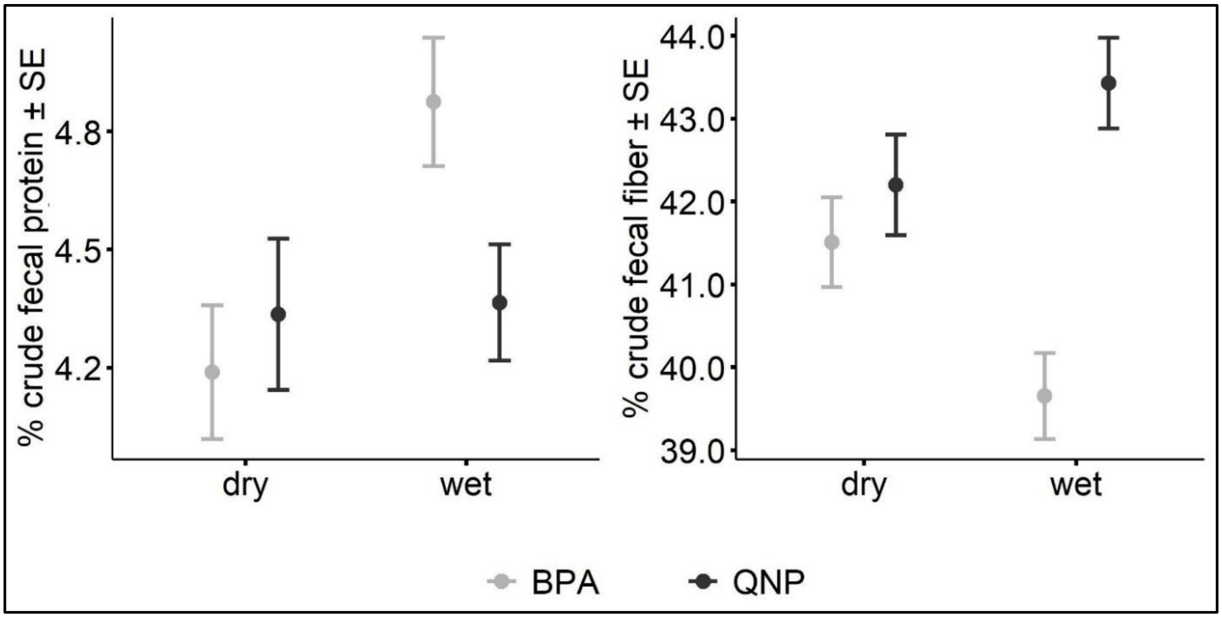

Figure 4- Percent crude fecal protein and percent crude fecal fiber in 252 fecal samples of onagers collected in dry and wet seasons in Bahram-e-Goor Protected area (BPA) and Qatrouiyeh National Park (QNP). Points represent mean values and bars are standard errors.

APPENDIX S3

Table S1. Information on 26 leases grazed in dry and wet seasons in Bahram-e-Goor Protected Area, Iran.

Lease #	**Date of livestock entry**	**Date of livestock exit**	**Grazing duration (days)**	**Livestock density (individuals/km^2)**	**Grazing intensity (grazing duration x livestock density)**	**Grazing season**
1	May-5	Oct-7	155	21.60	3348.29	dry
2	May-5	Oct-7	155	34.14	5292.59	dry
3	May-5	Nov-6	185	19.08	3529.54	dry
4	May-5	Oct-7	155	38.19	5919.34	dry
5	May-5	Oct-7	155	31.20	4836.71	dry
6	May-5	Oct-7	155	42.21	6543.17	dry
7	May-5	Oct-7	155	8.29	1285.01	dry
8	Apr-20	Sep-22	155	27.34	4237.17	dry
9	May-5	Nov-6	185	54.73	10125.21	dry
10	Jun-5	Oct-7	124	161.82	20065.19	dry
11	May-5	Nov-6	185	67.12	12416.55	dry
12	Nov-22	Apr-20	149	45.50	6779.53	wet
13	Nov-22	Apr-20	149	94.27	14046.02	wet
14	Oct-23	Apr-20	179	12.28	2198.02	wet
15	Nov-22	Apr-20	149	21.12	3146.78	wet
16	Dec-6	May-5	150	62.83	9423.97	wet
17	Nov-22	Apr-20	149	30.86	4598.44	wet
18	Nov-22	Apr-20	149	18.13	2701.52	wet
19	Nov-22	Apr-20	149	12.77	1902.91	wet
20	Dec-6	May-5	150	8.85	1328.03	wet
21	Nov-6	Apr-4	149	136.25	20301.21	wet
22	Nov-6	Apr-4	149	26.77	3988.90	wet
23	Nov-6	Apr-4	149	26.18	3900.98	wet
24	Nov-6	May 5	180	28.48	5126.78	wet
25	Nov-6	Apr-4	149	36.10	5379.79	wet
26	Nov-6	Apr-4	149	39.88	5943.08	wet

LITERATURE CITED

Adams, William M, & Hutton, J. 2007. “People, Parks and Poverty: Political Ecology and Biodiversity Conservation.” Conservation and Society, 5 (2): 147–83.

Aikens, E.O. 2019. Surfing green waves of forage: evaluating the causes and consequences of ungulate migration. PhD. Dissertation. University of Wyoming.

Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinnell, S.P.H., Fralick, G.L. & Monteith, K.L. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters, 20, 741–750.

Albon, S.D. & Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos, 65, 502-513.

Ali, A. H., Ford, A. T., Evans, J. S., Mallon, D. P., Hayes, M. M., et al. 2017. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology, 54, 1720-1729.

Ali, A. H., Kauffman, M. J., Amin, R., Kibara, A., King, J., Mallon, D., ... & Goheen, J. R. 2018. Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroductions of hirola. Ecological Applications, 28(2), 275-283.

Allan, J. R., Kormos, C., Jaeger, T., Venter, O., Bertzky, B., Shi, Y., ... & Watson, J. E. 2018. Gaps and opportunities for the World Heritage Convention to contribute to global wilderness conservation. Conservation Biology, 32(1), 116-126.

Anderson, T. M., Ritchie, M. E., & McNaughton, S. J. 2007. Rainfall and soils modify plant community response to grazing in Serengeti National Park. Ecology, 88(5), 1191-1201.

Anderson, T. M., Hopcraft, J. G. C., Eby, S., Ritchie, M., Grace, J. B., & Olff, H. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. Ecology, 91(5), 1519-1529.

AOAC. 1984. Official methods of analysis, 14th ed. Washington, DC: Association of Official Analytical Chemists.

Archibald, S. & Scholes, R.J. 2007. Leaf green-up in a semi-arid African savanna –separating tree and grass responses to environmental cues. Journal of Vegetation Science, 18, 583-594.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike’s Information Criterion. The Journal of Wildlife Management, 74, 1175–1178.

Attias, N., Oliveira-Santos, L. G. R., Fagan, W. F., & Mourão, G. 2018. Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms. Animal behaviour, 140, 129-140.

Avgar, T., Mosser, A., Brown, G.S. & Fryxell, J.M. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. Journal of Animal Ecology, 82, 96–106.

Avgar, T., Potts, J.R., Lewis, M.A. & Boyce, M.S. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution, 7, 619–630.

Augustine, D. J., Veblen, K. E., Goheen, J. R., Riginos, C., & Young, T. P. 2011. Pathways for Positive Cattle Wildlife Interactions in Semiarid Rangelands. Smithsonian Contributions to Zoology, 632, 55-71.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., et al. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Rangeland Ecology & Management/Journal of Range Management Archives, 49, 386–400.

Baillie, J., Hilton-Taylor, C. & Stuart, S.N. 2004. A Global Species Assessment. A Glob. Species Assess. IUCN, Gland, Switzerland and Cambridge, UK, IUCN Publications Services Unit, 219c Huntingdon Road, Cambridge CB3 0DL, UK.

Barboza, P.S. & Bowyer, R.T. 2000. Sexual segregation in demorthic deer: a new gastrocentric hypothesis. Journal of Mammalogy, 81, 473–489.

Barton, K. 2019. MuMIn: Multi-Model Inference. R Package.

Batsaikhan, N., Buuveibaatar, B., Chimed, B., Enkhtuya, O., Galbrakh, D., Ganbaatar, O., ... & Edwards, A. E. 2014. Conserving the world's finest grassland amidst ambitious national development. Conservation Biology, 28(6), 1736-1739.

Beck, L. 1998. Use of land by nomadic pastoralists in Iran: 1970-1998. Bull. Ser. Yale School of Forestry and Environmental Studies Bulletin Series, 103, 58–80.

Bell, R.H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American, 225, 86–93.

Berkes, F. 2004. Rethinking community-based conservation. Conservation biology, 18, 621-630.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology letters, 3, 620–623.

Berger, J., Buuveibaatar, B., & Mishra, C. 2013. Globalization of the cashmere market and the decline of large mammals in Central Asia. Conservation Biology, 27(4), 679-689.

Bhola, N., Ogutu, J. O., Piepho, H. P., Said, M. Y., Reid, R. S., Hobbs, N. T., & Olff, H. 2012. Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. Biodiversity and Conservation, 21(6), 1509-1530.

Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., van Moorter, B. & Mysterud, A. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? The American Naturalist, 180, 407–424.

Boone, R.B., Thirgood, S.J., & Hopcraft, J.G.C. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology, 87:1987-1994.

Boschetti, M., Bocchi, S., & Brivio, P. A. 2007. Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information. Agriculture, ecosystems & environment, 118(1-4), 267-272.

Bowyer, R. T., Boyce, M. S., Goheen, J. R., & Rachlow, J. L. 2019. Conservation of the world's mammals: status, protected areas, community efforts, and hunting. Journal of mammalogy, 100(3), 923-941.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. 2002. Evaluating resource selection functions. Ecological modelling, 157(2-3), 281-300.

Branco, P.S., Merkle, J.A., Pringle, R.M., Pansu, J., Potter, A.B., Reynolds, A., et al. 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: Is brown the new green? Journal of Animal Ecology, 88, 780–792.

Briske, D. D., Derner, J. D., Brown, J. R., Fuhlendorf, S. D., Teague, W. R., Havstad, K. M., ... & Willms, W. D. 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. Rangeland Ecology & Management, 61(1), 3-17.

Brown, J.H. 1995. Macroecology. University of Chicago Press, Chicago, IL.

Bulte, E.H. & Rondeau, D. 2005. Research and management viewpoint: why compensating wildlife damages may be bad for conservation. The Journal of Wildlife Management, 69, 14–19.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral ecology and sociobiology, 65, 23-35.

Chamaillé-Jammes, S., Charbonnel, A., Dray, S., Madzikanda, H., & Fritz, H. 2016. Spatial distribution of a large herbivore community at waterholes: an assessment of its stability over years in Hwange National Park, Zimbabwe. PloS one, 11(4).

Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346, 1517–1519.

Cole, E. K., Foley, A. M., Warren, J. M., Smith, B. L., Dewey, S. R., Brimeyer, D. G., ... & Cross, P. C. 2015. Changing migratory patterns in the Jackson elk herd. Journal of Wildlife Management, 79, 877-886.

Corlatti, L., Bonardi, A., Bragalanti, N. & Pedrotti, L. 2019. Long-term dynamics of Alpine ungulates suggest interspecific competition. Journal of Zoology, 309, 241–249.

Cotterill, G. G., Cross, P. C., Merkle, J. A., Rogerson, J. D., Scurlock, B. M., & Du Toit, J. T. 2020. Parsing the effects of demography, climate and management on recurrent brucellosis outbreaks in elk. Journal of Applied Ecology, 57(2), 379-389.

Courbin, N., Loveridge, A. J., Fritz, H., Macdonald, D. W., Patin, R., Valeix, M., & Chamaillé-Jammes, S. 2019. Zebra diel migrations reduce encounter risk with lions at night. Journal of Animal Ecology, 88, 92-101.

Cribari-Neto, F. & Zeileis, A. 2010. Beta regression in R. Journal of statistical software, 34, 1-24.

Cromsigt, J.P.G.M. & Olff, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. Ecology, 87, 1532–1541.

Cromsigt, J.P.G.M., Prins, H.H.T. & Olff, H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Diversity and Distributions, 15, 513–522.

Cross, P. C., Owen-Smith, N., & Macandza, V. A. 2004. Forage selection by African buffalo in the late dry season in two landscapes. South African Journal of Wildlife Research, 34, 113-121.

Dechen Quinn, A. C., Williams, D. M., & Porter, W. F. 2012. Postcapture movement rates can inform data-censoring protocols for GPS-collared animals. Journal of Mammalogy, 93(2), 456-463.

Decker, D.J. & Chase, L.C. 1997. Human Dimensions of Living with Wildlife: A Management Challenge for the 21st Century. Wildlife Society Bulletin, 25, 788–795.

Demment, M.W. & Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist, 125, 641–672.

Dickman, A.J. 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. Animal conservation, 13, 458–466.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. 2011. A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. Proceedings of the National Academy of Sciences, 108, 13937–13944.

Distefano, E. 2005. Human-Wildlife Conflict worldwide: collection of case studies, analysis of management strategies and good practices. Food and Agricultural Organization of the United Nations (FAO), Sustainable Agriculture and Rural Development Initiative (SARDI), Rome, Italy. Available from: FAO Corporate Document repository http://www. fao.org/documents.

Drescher, M., Heitkönig, I. M., Van Den Brink, P. J., & Prins, H. H. 2006. Effects of sward structure on herbivore foraging behaviour in a South African savanna: an investigation of the forage maturation hypothesis. Austral Ecology, 31, 76-87.

Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G. & Lloyd, M. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia, 84, 411–418.

Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M., et al. 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. Ecography, 40, 1014–1027.

du Toit, J. T., Cross, P. C., & Valeix, M. 2017. Managing the livestock–wildlife interface on rangelands. In Rangeland systems (pp. 395-425). Springer, Cham, Switzerland.

Edouard, N., Duncan, P., Dumont, B., Baumont, R., & Fleurance, G. 2010. Foraging in a heterogeneous environment—An experimental study of the trade-off between intake rate and diet quality. Applied Animal Behaviour Science, 126, 27-36.

Esmaeili, S., Hemami, M. R., & Goheen, J. R. 2019. Human dimensions of wildlife conservation in Iran: Assessment of human-wildlife conflict in restoring a wide-ranging endangered species. PloS one, 14(8), e0220702.

Farhadinia, M.S., Johnson, P.J., Hunter, L.T.B. & Macdonald, D.W. 2017. Wolves can suppress goodwill for leopards: Patterns of human-predator coexistence in northeastern Iran. Biological Conservation, 213, 210–217.

Fleming, C.H., Calabrese, J.M., Mueller, T., Olson, K.A., Leimgruber, P. & Fagan, W.F. 2014. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. The American Naturalist, 183, E154–E167.

Fleurance, G., Duncan, P., Fritz, H., Gordon, I. J., & Grenier-Loustalot, M. F. 2010. Influence of sward structure on daily intake and foraging behaviour by horses. Animal, 4, 480-485.

Ford, A. T., Goheen, J. R., Otieno, T. O., Bidner, L., Isbell, L. A., Palmer, T. M., ... & Pringle, R. M. 2014. Large carnivores make savanna tree communities less thorny. Science, 346(6207), 346-349.

Forsten, A. 1989. Horse diversity through the ages. Biol. Rev. Cambridge Philos. Soc., 64, 279–304.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology, 86, 1320–1330.

Fox, J. & Monette, G. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association, 87, 178–183.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist, 138, 478–498.

Fynn, R. W. 2012. Functional resource heterogeneity increases livestock and rangeland productivity. Rangeland Ecology & Management, 65(4), 319-329.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. 2015. African wetlands and their seasonal use by wild and domestic herbivores. Wetlands Ecology and Management, 23(4), 559-581.

Fynn, R. W., Augustine, D. J., Peel, M. J., & de Garine-Wichatitsky, M. 2016. Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence. Journal of Applied Ecology, 53(2), 388-397.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. 2008. The Ecological Performance of Protected Areas. Annual review of ecology, evolution, and systematics, 39, 93–113.

Gaughan, A.E., Holdo, R.M. & Anderson, T.M. 2013. Using short-term MODIS time-series to quantify tree cover in a highly heterogeneous African savanna. International Journal of Remote Sensing, 34, 6865–6882.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. 2018. The influence of human disturbance on wildlife nocturnality. Science, 360, 1232–1235.

Georgiadis, N. J., Olwero, J. N., & Romañach, S. S. 2007. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. Biological conservation, 137(3), 461-472.

Geremia, C., Merkle, J.A., Eacker, D.R., Wallen, R.L., White, P.J., Hebblewhite, M., & Kauffman, M.J. 2019. Migrating bison engineer the green wave. Proceedings of the National Academy of Sciences, 116, 25707-25713.

Geri, F., Amici, V. & Rocchini, D. 2010. Human activity impact on the heterogeneity of a Mediterranean landscape. Applied geography, 30, 370–379.

Ghasemi, A. 2012. Food habits and seed dispersal by Persain wild ass (*Equus hemionus onager*) in Qatruiyeh National Park. Unpublished M.Sc. dissertation, Isfahan University of Technology, Iran.

Ghoshtasb, H., Shams, B.E., Ataii, F. & Mozafari, A. 2012. Habitat Suitability Modeling for Wild Boar (Sus scrofa) in Eastern Alamut, Qazvin Province. Journal of Natural Environments (Iraninan J. Nat. Resources), 65, 247-258. in Farsi (English abstract).

Gliem, J. A., & Gliem, R.R. 2003. Calculating, interpreting, and reporting Cronbach's alpha reliability coefficient for Likert-type scales. Midwest Research-to-Practice Conference in Adult, Continuing, and Community Education.

Godfrey, E.B. & Berger, J. 1987. Wild Horses of the Great Basin: Social Competition and Population Size. West. Hist. Q. University of Chicago Press.

Goldberg, E.J. 2018. The Emperor's Ass - Hunting for the Asiatic Onager (Equus hemionus) in the ʿAbbasid, Byzantine, and Carolingian Worlds. In: The ʿAbbasid and Carolingian Empires - Comparative Studies in Civilizational Formation (ed. Tor, D.J.). Koninklijke Brill NV, Leiden, The Netherlands and Boston, USA.

Gordon, I.J. 2009. What is the Future for Wild, Large Herbivores in Human-Modified Agricultural Landscapes? Wildlife Biology, 15, 1–9.

Graham, S.I., Kinnaird, M.F., O'Brien, T.G., Vågen, T., Winowiecki, L.A., Young, T.P., et al. 2019. Effects of land-use change on community diversity and composition are highly variable among functional groups. Ecological Applications, 29, e01973.

Gusset, M., Maddock, A.H., Gunther, G.J., Szykman, M., Slotow, R., Walters, M., et al. 2008. Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. Biodiversity and Conservation,17, 83–101.

Harrell, F.E. 2018. Package 'rms'. R package.

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J.-M. & Côté, S.D. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology, 46, 582–589.

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P., & Berger, J. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research, 7, 55-76.

Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., et al. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications, 15, 1893–1905.

Hebblewhite, M., Merrill, E. & McDermid, G. 2008. A multi-scale test of the Forage Maturation Hypothesis in a partially migratory ungulate population. Ecological monographs, 78, 141–166.

Hemami, M.R., Kaczensky, P., Lkhagvasuren, B., Pereladova, O. & Bouskila, A. 2015. Equus hemionus ssp. onager. IUCN Red List Threat. Species.

Hemami, M.R. & Momeni, M. 2013. Estimating abundance of the Endangered onager Equus hemionus onager in Qatruiyeh National Park, Iran. Oryx, 47, 266–272.

Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., ... & Smit, I. P. 2015. Ecology of grazing lawns in Africa. Biological Reviews, 90(3), 979-994.

Hennig, J. D., Beck, J. L., & Scasta, J. D. 2018. Spatial ecology observations from feral horses equipped with global positioning system transmitters. Human–Wildlife Interactions, 12, 9.

Herrero, M., Thornton, P. K., Gerber, P., & Reid, R. S. 2009. Livestock, livelihoods and the environment: understanding the trade-offs. Current Opinion in Environmental Sustainability, 1(2), 111-120.

Higgins, S.I., Delgado-Cartay, M.D., February, E.C. & Combrink, H.J. 2011. Is there a temporal niche separation in the leaf phenology of savanna trees and grasses? Journal of Biogeography, 38, 2165–2175.

Hobbs, N.T., Andrén, H., Persson, J., Aronsson, M. & Chapron, G. 2012. Native predators reduce harvest of reindeer by Sámi pastoralists. Ecological Applications, 22, 1640–1654.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia, 78, 443–457.

Holdo, R. M., Sinclair, A. R., Dobson, A. P., Metzger, K. L., Bolker, B. M., Ritchie, M. E., & Holt, R. D. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. PLoS Biology, 7(9), e1000210.

Hopcraft, J.G.C., Anderson, T.M., Pérez-Vila, S., Mayemba, E. & Olff, H. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. Journal of Animal Ecology, 81, 201–213.

Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Mwangomo, E., Sinclair, A.R.E., et al. 2014. Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs, 84, 355–372.

Hosseini-Zavarei, F., Farhadinia, M.S., Beheshti-Zavareh, M. & Abdoli, A. 2013. Predation by grey wolf on wild ungulates and livestock in central Iran. Journal of Zoology, 290, 127–134.

Huang, C., Chen, Y., Zhang, S. & Wu, J. 2018. Detecting, extracting, and monitoring surface water from space using optical sensors: a review. Reviews of Geophysics, 56, 333–360.

ICPAC. 2017a. Kenya – Rivers. Available at: http://geoportal.icpac.net/

ICPAC. 2017b. Kenya - Water points. available at: http://geoportal.icpac.net/

ICPAC. 2017c. Tanzania - Rivers. available at: http://geoportal.icpac.net/

Illius, A.W. & Gordon, I.J. 1987. The allometry of food intake in grazing ruminants. The Journal of Animal Ecology, 56, 989.

Illius, A.W. & Gordon, I.J. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia, 89, 428–434.

Imai, S., Ito, T.Y., Kinugasa, T., Shinoda, M., Tsunekawa, A. & Lhagvasuren, B. 2017. Effects of spatiotemporal heterogeneity of forage availability on annual range size of Mongolian gazelles. Jounral of Zoology, 301, 133-140.

Imail, S., Ito, T.Y., Kinugasa, T., Shinoda, M., Tsunekawa, A. & Lhagvasuren, B. 2019. Nomadic movement of Mongolian gazelles identified through the net squared displacement approach. Mammal study, 44, 111-119.

Imai, S., Ito, T.Y., Shinoda, M., Tsunekawa, A. & Lhagvasuren, B. The benefit and strategy of spring movements in Mongolian gazelles. Journal of Mammalogy, 2020. Published online: DOI: 10.1093/jmammal/gyz209

International Steering Committee for Global Mapping. 2010. Inland waters, Mongolia. available at: https://earthworks.stanford.edu/

I.R. Iran Meteorological Organization. In: Specialized products and services weather. 2017. Available: http://www.irimo.ir/eng/wd/720-Products-Services.html

Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A. et al. 2006. Satellite tracking of Mongolian gazelles (Procapra gutturosa) and habitat shifts in their seasonal ranges. Journal of Zoology, 269, 291-298.

Ito, T. Y., Tsuge, M., Lhagvasuren, B., Buuveibaatar, B., Chimeddorj, B., Takatsuki., et al. 2013. Effects of interannual variations in environmental conditions on seasonal range selection by Mongolian gazelles. Journal of Arid Environments, 91, 61-68.

Ito, T.Y., Sakamoto, Y., Lhagvasuren, B., Kinugasa, T. & Shinoda, M. 2018. Winter habitat of Mongolian gazelles in areas of southern Mongolia under new railroad construction: An estimation of interannual changes in suitable habitats. Mammalian Biology, 93, 13-20.

Janis, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution, 30, 757-774.

Janis, C. 2008. An Evolutionary History of Browsing and Grazing Ungulates. In: The Ecology of Browsing and Grazing. Springer, Berlin, Heidelberg, pp. 21–45.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behaviour, 48, 215-267.

Jesmer, B. R., Kauffman, M. J., Murphy, M. A., & Goheen, J. R. 2020. A test of the Niche Variation Hypothesis in a ruminant herbivore. Journal of Animal Ecology, 00:1-15.

Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., et al. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science, 361, 1023–1025.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., et al. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science, 356, 270-275.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 61(1), 65-71.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., et al. 2018. One-third of global protected land is under intense human pressure. Science, 360, 788–791.

Kaczensky, P., Ganbaatar, O., Von Wehrden, H., & Walzer, C. 2008. Resource selection by sympatric wild equids in the Mongolian Gobi. Journal of Applied Ecology, 45, 1762-1769.

Kaczensky, P., Lkhagvasuren, B., Pereladova, O., Hemami, M.R. & Bouskila, A. 2015. Equus hemionus. IUCN Red List Threat. Species. Available at: http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T7951A45171204.

Kaczensky, P., Sheehy, D.P., Walzer, C., Johnson, D.E.J., Lkhagvasuren, D. & Sheehy, C. 2006. Room to Roam? The threat to Khulan (Wild Ass) from human Intrusion. East Asia and Pacific Environment and Social Development Department Washington, DC World Bank.

Kansky, R. & Knight, A.T. 2014. Key factors driving attitudes towards large mammals in conflict with humans. Biological Conservation, 179, 93–105.

Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., et al. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Sciences, 112, 8019–8024.

Keesing, F., Ostfeld, R. S., Okanga, S., Huckett, S., Bayles, B. R., Chaplin-Kramer, R., ... & Warui, C. M. 2018. Consequences of integrating livestock and wildlife in an African savanna. Nature Sustainability, 1(10), 566-573.

Kihwele, E.S., Mchomvu, V., Owen-Smith, N., Hetem, R., Potter, A., Hutchinson, M., et al. 2020. Quantifying water requirements of African ungulates using combined functional traits. Ecological Monographs, accepted manuscript.

Kimuyu, D. M., Veblen, K. E., Riginos, C., Chira, R. M., Githaiga, J. M., & Young, T. P. 2017. Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores. Ecological Applications, 27(3), 786-798.

Kinnaird, M.F. & O’Brien, T.G. 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. Conservation Biology, 26, 1026–1039.

Kittur, S., Sathyakumar, S., & Rawat, G. S. 2010. Assessment of spatial and habitat use overlap between Himalayan tahr and livestock in Kedarnath Wildlife Sanctuary, India. European Journal of Wildlife Research, 56(2), 195-204.

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience, 49(1), 39-50.

Kolahi, M., Sakai, T., Moriya, K., Makhdoum, M.F. & Koyama, L. 2013. Assessment of the effectiveness of protected areas management in Iran: Case study in Khojir National Park. Environmental management, 52, 514–530.

Kuijper, D. P., Cromsigt, J. P., Churski, M., Adam, B., Jedrzejewska, B., & Jedrzejewski, W. 2009. Do ungulates preferentially feed in forest gaps in European temperate forest?. Forest Ecology and Management, 258(7), 1528-1535.

Kullberg, P., Di Minin, E., & Moilanen, A. 2019. Using key biodiversity areas to guide effective expansion of the global protected area network. Global Ecology and Conservation, 20, e00768.

Langvatn, R. & Hanley, T.A. 1993. Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. Oecologia, 95, 164-170.

Lele, S., Wilshusen, P., Brockington, D., Seidler, R. & Bawa, K. 2010. Beyond exclusion: Alternative approaches to biodiversity conservation in the developing tropics. Current Opinion in Environmental Sustainability, 2, 94–100.

Leslie, D. M., & Starkey, E. E. 1985. Fecal indices to dietary quality of cervids in old-growth forests. The Journal of Wildlife Management, 49(1), 142-146.

Levanov, V. F., Sokolov, S. V., & Kaczensky, P. 2013. Corral mass capture device for Asiatic wild asses *Equus hemionus*. Wildlife Biology, 19(3), 325-334.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, 73, 1943-1967.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., et al. 2008. Quantification of extinction risk: IUCN’s system for classifying threatened species. Conservation biology, 22, 1424-1442.

MacFadden, B.J. 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge University Press, Cambridge, UK.

MacFadden, B.J. 2005. Fossil horses: evidence for evolution. Science, 307, 1728-1730.

Maclennan, S.D., Groom, R.J., Macdonald, D.W. & Frank, L.G. 2009. Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biological Conservation, 142, 2419–2427.

Mahmoudi, H. 2014. Seed dispersal by a guild of mammalian herbivores in Qatrouiyeh National Park. Unpublished M.Sc. dissertation, Isfahan University of Technology, Iran.

Manfredo, M.J. 2008. Who cares about wildlife? Springer, New York, NY.

Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

Marshall, K., White, R. & Fischer, A. 2007. Conflicts between humans over wildlife management: On the diversity of stakeholder attitudes and implications for conflict management. Biodiversity and Conservation, 16, 3129–3146.

Martin-Lopez, B., Montes, C., Ramírez, L. & Benayas, J. 2009. What drives policy decision-making related to species conservation? Biological Conservation, 142, 1370–1380.

McNab, B.K. 1974. The energetics of endotherms. The Ohio Journal of Science, 74, 370–380.

Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., et al. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B: Biological Sciences, 283, 20160456.

Middleton, A.D., Kauffman, M.J., Mcwhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A., et al. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology, 94, 1245–1256.

Middleton, A.D., Merkle, J.A., McWhirter, D.E., Cook, J.G., Cook, R.C., White, P.J., et al. 2018. Green-wave surfing increases fat gain in a migratory ungulate. Oikos, 127, 1060–1068.

Middleton, N. J., & Sternberg, T. 2013. Climate hazards in drylands: A review. Earth-Science Reviews, 126, 48-57.

Mihlbachler, M.C., Rivals, F., Solounias, N. & Semprebon, G.M. 2011. Dietary change and evolution of horses in North America. Science, 331, 1178–1181.

Mishra, C., Van Wieren, S.E., Ketner, P., Heitkönig, I.M.A. & Prins, H.H.T. 2004. Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. Journal of Applied Ecology, 41, 344–354.

Mohammadi, A. & Kaboli, M. 2016. Evaluating wildlife-vehicle collision hotspots using kernel-based estimation: A focus on the endangered Asiatic cheetah in central Iran. Human–Wildlife Interactions, 10, 103–109.

Monteith, K. L., Hayes, M. M., Kauffman, M. J., Copeland, H. E., & Sawyer, H. 2018. Functional attributes of ungulate migration: landscape features facilitate movement and access to forage. Ecological applications, 28, 2153-2164.

Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G. & Leimgruber, P. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. Journal of Applied Ecology, 45, 649-658.

Muff, S., Signer, J., & Fieberg, J. 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology, 89(1), 80-92.

Muntifering, J.R., Ditmer, M.A., Stapleton, S., Naidoo, R. & Harris, T.H. 2019. Hartmann's mountain zebra resource selection and movement behavior within a large unprotected landscape in northwest Namibia. Endangered Species Research, 38, 159-170.

Mysterud, A., & Austrheim, G. 2008. The effect of domestic sheep on forage plants of wild reindeer; a landscape scale experiment. European Journal of Wildlife Research, 54(3), 461-468.

Nakagawa, S., & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in ecology and evolution, 4(2), 133-142.

Namgail, T., Fox, J. L., & Bhatnagar, Y. V. 2007. Habitat shift and time budget of the Tibetan argali: the influence of livestock grazing. Ecological Research, 22(1), 25.

Nandintsetseg, D., Bracis, C., Leimgruber, P., Kaczensky, P., Buuveibaatar, B., Lkhagvasuren, B., et al. 2019. Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates. Ecosphere, 10, e02924.

Nandintsetseg, D., Kaczensky, P., Ganbaatar, O., Leimgruber, P., & Mueller, T. 2016. Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study. Biological Conservation, 204, 313-321.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008). A movement paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences, 105, 19052-19059.

Newmark, W. D. 2008. Isolation of African protected areas. Frontiers in Ecology and the Environment, 6(6), 321-328.

Ng'weno, C.C., Buskirk, S.W., Georgiadis, N.J., Gituku, B.C., Kibungei, A.K., Porensky, L.M., Rubenstein, D.I. & Goheen, J.R. 2019. Apparent competition, predation, and livestock production: can conservation value be enhances? Frontiers in Ecology and Evolution, 7, 123.

Nyhus, P., Osofsky, S., Ferraro, P., Fischer, H. & Madden, F. 2005. Bearing the costs of human-wildlife conflict : The challenges of compensation schemes. In: People and wildlife: Conflict or coexistence? Cambridge University Press.

Odadi, W. O., Young, T. P., & Okeyo-Owuor, J. B. 2007. Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. Rangeland Ecology & Management, 60(2), 179-185.

Odadi, W. O., Jain, M., Van Wieren, S. E., Prins, H. H., & Rubenstein, D. I. 2011a. Facilitation between bovids and equids on an African savanna. Evolutionary Ecology Research, 13(3), 237-252.

Odadi, W. O., Karachi, M. K., Abdulrazak, S. A., & Young, T. P. 2011b. African wild ungulates compete with or facilitate cattle depending on season. Science, 333(6050), 1753-1755.

Odadi, W. O., Fargione, J., & Rubenstein, D. I. 2017a. Vegetation, wildlife, and livestock responses to planned grazing management in an African pastoral landscape. Land Degradation & Development, 28(7), 2030-2038.

Odadi, W. O., Kimuyu, D. M., Sensenig, R. L., Veblen, K. E., Riginos, C., & Young, T. P.

2017b. Fire-induced negative nutritional outcomes for cattle when sharing habitat with native ungulates in an African savanna. Journal of Applied Ecology, 54(3), 935-944.

Ogutu, J.O., Piepho, H.P., Reid, R.S., Rainy, M.E., Kruska, R.L., Worden, J.S., et al. 2010. Large herbivore responses to water and settlements in savannas. Ecological Monographs, 80, 241–266.

Ogutu, J.O., Reid, R.S., Piepho, H.P., Hobbs, N.T., Rainy, M.E., Kruska, R.L., et al. 2014. Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. Biodiversity and conservation, 23, 573–596.

Olff, H., Ritchie, M.E. & Prins, H.H. 2002. Global environmental controls of diversity in large herbivores. Nature, 415, 901-904.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E. C., et al. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience, 51, 933-938.

Olson, K. A., Mueller, T., Kerby, J. T., Bolortsetseg, S., Leimgruber, P., Nicolson, C. R., & Fuller, T. K. 2011. Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles. Conservation Letters, 4(4), 304-312.

Osborn, R. G., & Jenks, J. A. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. Journal of Mammalogy, 79(2), 437-447.

Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B: Biological Sciences, 365, 2267-2278.

Owen-Smith, N. & Mills, M.G.L. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecological Monographs, 76, 73–92.

Owens, F.N. & Basalan, M. 2016. Ruminal fermentation. In: Rumenology. pp. 63–102. Springer, Cham.

Pekel, J.F., Cottam, A., Gorelick, N. & Belward, A.S. 2016. High-resolution mapping of global surface water and its long-term changes. Nature, 540, 418–422.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in ecology & evolution, 20, 503-510.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science, 344, 1246752–1246752.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. 2017. Package ‘nlme’. Linear and nonlinear mixed effects models, version, 3(1).

Pravalie, R., Bandoc, G., Patriche, C., & Sternberg, T. 2019. Recent changes in global drylands: Evidences from two major aridity databases. Catena, 178, 209-231.

Prima, M.-C., Duchesne, T. & Fortin, D. 2017. Robust inference from conditional logistic regression applied to movement and habitat selection analysis. PLoS One, 12, e0169779.

Pringle, R. M. 2017. Upgrading protected areas to conserve wild biodiversity. Nature, 546(7656), 91-99.

Payne, J. C., Buuveibaatar, B., Bowler, D. E., Olson, K. A., Walzer, C., & Kaczensky, P. 2020. Hidden treasure of the Gobi: understanding how water limits range use of khulan in the Mongolian Gobi. Scientific reports, 10 (1), 1-13.

Qi, J., Chehbouni, A., Huete, A.R., Kerr, Y.H. & Sorooshian, S. 1994. A modified soil adjusted vegetation index. Remote Sensing of Environment, 48, 119–126.

R Core Team. 2019. R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria. URL http//www.R-project.org/.

Ramanzin, M., Aguado, M. A. P., Ferragina, A., Sturaro, E., Semenzato, P., Serrano, E., ... & Bittante, G. 2017. Methodological considerations for the use of faecal nitrogen to assess diet quality in ungulates: The Alpine ibex as a case study. Ecological Indicators, 82, 399-408.

Redfern, J. V., Grant, R., Biggs, H. & Getz, W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology, 84, 2092–2107.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., et al. 2013. Understanding and managing conservation conflicts. Trends in ecology & evolution, 28, 100–109.

Reid, R., H. Gichohi, and M. Said. 2008. Fragmentation of a peri-urban savanna, Athi-Kaputiei Plains, Kenya. Pages 195–224 in K. A. Galvin, R. S. Reid, R. H. Behnke Jr., and N. T.Hobbs, editors. Fragmentation in semi-arid arid landscapes: consequences for human and natural systems. Springer, New York, USA.

Ren, H., & Zhou, G. 2019. Estimating green biomass ratio with remote sensing in arid grasslands. Ecological Indicators, 98, 568-574.

Riginos, C., Porensky, L. M., Veblen, K. E., Odadi, W. O., Sensenig, R. L., Kimuyu, D., ... & Young, T. P. 2012. Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). Pastoralism: Research, Policy and Practice, 2(1), 10.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., et al. 2015. Collapse of the world’s largest herbivores. Science advances, 1, e1400103–e1400103.

Rivrud, I.M., Heurich, M., Krupczynski, P., Müller, J. & Mysterud, A. 2016. Green wave tracking by large herbivores: an experimental approach. Ecology, 97, 3547-3553.

Roever, C.L., Boyce, M.S. & Stenhouse, G.B. 2010. Grizzly bear movements relative to roads: Application of step selection functions. Ecography, 33, 1113–1122.

Rozen-Rechels, D., Dupoué, A., Lourdais, O., Chamaillé-Jammes, S., Meylan, S., Clobert, J., et al. 2019. When water interacts with temperature: Ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. Ecology and evolution, 9, 10029–10043.

Rubenstein, D. I., Cao, Q. I. N. G., & Chiu, J. 2016. Equids and ecological niches: behavioral and life history variations on a common theme. Wild equids: ecology, management and conservation, 58-68.

Safriel, U., Adeel, Z., Neimeijer, D., Puigdefabregas, J., White, R., Lal, M., ... & King, C. 2005. Dryland Systems (Chapter 22). Millennium Ecosystem Assessment. Island Press, New York, 625-662.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A. V. & Woolmer, G. 2002. The human footprint and the last of the wild. Bioscience, 52, 891-904.

Santos, J.R.A. 1999. Cronbach's alpha: A tool for assessing the reliability of scales. Journal of extension, 37, 1–5.

Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L., & Strickland, D. 2017. Mule deer and energy development—Long-term trends of habituation and abundance. Global Change Biology, 23, 4521-4529.

Schmidt-Nielsen, K., & Knut, S. N. 1984. Scaling: why is animal size so important?. Cambridge university press.

Schieltz, J. M., & Rubenstein, D. I. 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know?. Environmental Research Letters, 11(11), 113003.

Schoenecker, K. A. 2012. Ecology of bison, elk, and vegetation in an arid ecosystem. Doctoral dissertation, Colorado State University.

Schoenecker, K.A., King, S.R.B., Nordquist, M.K., Nandintsetseg, D. & Cao, Q. 2016. Habitat and diet of equids. In: Wild Equids: Ecology, Management, and Conservation. Johns Hopkins University Press, pp. 41–57.

Schroeder, N. M., Ovejero, R., Moreno, P. G., Gregorio, P., Taraborelli, P., Matteucci, S. D., & Carmanchahi, P. D. 2013. Including species interactions in resource selection of guanacos and livestock in N orthern P atagonia. Journal of Zoology, 291(3), 213-225.

Schulze, K., Knights, K., Coad, L., Geldmann, J., Leverington, F., Eassom, A., ... & Burgess, N. D. 2018. An assessment of threats to terrestrial protected areas. Conservation

Letters, 11(3), e12435.

Schwerdtner, K. & Gruber, B. 2007. A conceptual framework for damage compensation schemes. Biol. Conserv., 134, 354–360.

Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. 2014. Reversing defaunation: Restoring species in a changing world. Science, 345, 406–412.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. Bioscience, 37, 789–799.

Signer, J., Fieberg, J. & Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and evolution, 9, 880–890.

Sikes, R. S., & Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of mammalogy, 97(3), 663-688.

Singh, H. S. 2000. Status of Indian wild ass (*Equus hemionus Khur*) in the Little Rann of Kutch. Zoos Print Journal, 5, 253-256.

Skinner, J. D., & Chimimba, C. T. (2005). The mammals of the southern African sub-region. Cambridge University Press.

Spalinger, D.E., & N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. The American Naturalist, 140, 325-348.

Stabach, J. A., Wittemyer, G., Boone, R. B., Reid, R. S., & Worden, J. S. 2016. Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. Ecosphere, 7, e01428.

Statistical center of Iran, 2009, Iran census 2009: Fars Province. Statistical Centre of Office of the Head, Public Relations and International Cooperation, Tehran, Iran.

Stears, K., & Shrader, A. M. 2020. Coexistence between wildlife and livestock is contingent on cattle density and season but not differences in body size. Plos one, 15(7), e0236895.

Steuer, P., Südekum, K. H., Müller, D. W., Franz, R., Kaandorp, J., Clauss, M., & Hummel, J. 2011. Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 160(3), 355-364.

Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., & Johnson, B. K. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of mammalogy, 83(1), 229-244.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L. & Ben-David, M. 2003. Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? Ecoscience, 10, 297-302.

St-Louis, A., & Côté, S. D. 2014. Resource selection in a high-altitude rangeland equid, the kiang (Equus kiang): influence of forage abundance and quality at multiple spatial scales. Canadian journal of zoology, 92, 239-249.

Sundaresan, S. R., Fischhoff, I. R., Dushoff, J., & Rubenstein, D. I. 2007. Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. Oecologia, 151(1), 140-149.

Sundaresan, S. R., Fischhoff, I. R., & Rubenstein, D. I. (2007). Male harassment influences female movements and associations in Grevy's zebra (Equus grevyi). Behavioral Ecology, 18, 860-865.

Suryawanshi, K. R., Bhatnagar, Y. V., & Mishra, C. 2010. Why should a grazer browse? Livestock impact on winter resource use by bharal Pseudois nayaur. Oecologia, 162(2), 453-462.

Tatin, L., Darreh-Shoori, B.F., Tourenq, C., Tatin, D. & Azmayesh, B. 2003. The last populations of the Critically Endangered onager Equus hemionus onager in Iran: urgent requirements for protection and study. Oryx, 37, 488-491.

Teel, T.L. & Manfredo, M.J. 2010. Understanding the diversity of public interests in wildlife conservation. Conservation Biology, 24, 128–139.

Therneau, T.M. & T. Lumley. 2015. Package ‘ survival . R Package.

Treves, A. & Karanth, K.U. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conservation Biology, 17, 1491–1499.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. 2006. Co-managing human–wildlife conflicts: A review. Human Dimensions of Wildlife, 11, 383–396.

Treydte, A.C., van der Beek, J., Perdok, A.A. & van Wieren, S.E. 2011. Grazing ungulates select for grasses growing beneath trees in African savannas. Mammalian Biology, 76, 345-350.

Thurfjell, H., Ciuti, S. & Boyce, M.S. 2014. Applications of step-selection functions in ecology and conservation. Movement ecology, 2/1/4.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science., 359, 466–469.

USGS. 2018. National Hydrography Dataset (NHD) Best Resolution 20180226 for Wyoming state or Territory Shapefile Model Version 2.2.1. available at: https://catalog.data.gov/organization/usgs-gov.

Van Beest, F.M., Uzal, A., Vander Wal, E., Laforge, M.P., Contasti, A.L., Colville, D., et al.

2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. Journal of Animal Ecology, 83, 147–156.

Van Soest, P.J. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association, 5, 455-479.

Van Soest, P. J. 2018. Nutritional ecology of the ruminant. Cornell university press.

Veldhuis, M.P., Kihwele, E.S., Cromsigt, J.P.G.M., Ogutu, J.O., Hopcraft, J.G.C., Owen-Smith, N., et al. 2019. Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. Ecolology Letters, 22, 1536–1546.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature communications, 7, 12558.

Villamuelas, M., Fernández, N., Albanell, E., Gálvez-Cerón, A., Bartolomé, J., Mentaberre, G., ... & Pérez-Barbería, J. 2016. The Enhanced Vegetation Index (EVI) as a proxy for diet quality and composition in a mountain ungulate. Ecological Indicators, 61, 658-666.

Walzer, C., Kaczensky, P., Ganbaatar, O., Lengger, J., Enkhsaikhan, N., & Lkhagvasuren, D. 2006. Capture and anaesthesia of wild Mongolian equids–the Przewalski's horse (*Equus ferus przewalskii*) and khulan (*E. hemionus*). Mongolian Journal of Biological Sciences, 4(1), 19-28.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. 2014. The performance and potential of protected areas. Nature, 515, 67-73.

Wilmshurst, J.F., Fryxell, J.M. & Bergman, C.M. 2000. The allometry of patch selection in ruminants. Proceedings of the Royal Society of London. Series B: Biological Sciences, 267, 345-349.

Wilson, D.E. & Mittermeier, R.A. 2011. Handbook of the mammals of the world: v.2: Hoofed mammals. Barcelona, Spain: Lynx Edicions.

Wingard, J., Zahler, P., Victurine, R., Bayasgalan, O. & Bayarbaatar, B. 2014. Guidelines for Addressing the Impact of Linear Infrastructure on Large Migratory Mammals in Central Asia. In Convention on the Conservation of Migratory Species of Wild Animals (CMS) Technical Report.

Woodroffe, R. & Ginsberg, J.R. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science, 280, 2126–2128.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. 2005. The impact of human-wildlife conflict on natural systems. In: People and Wildlife, Conflict or Coexistence? Cambridge University Press.

Yackulic, C.B., Sanderson, E.W. & Uriarte, M. 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. Proceedings of the National Academy of Sciences, 108, 4024–4029.

Yasmi, Y., Schanz, H. & Salim, A. 2006. Manifestation of conflict escalation in natural resource management. Environmental science & policy, 9, 538–546.

Young, T. P., Palmer, T. M., & Gadd, M. E. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biological conservation, 122(2), 351-359.

Young, T.P., Porensky, L.M., Riginos, C., Veblen, K.E., Odadi, W.O., Kimuyu, D.M., et al. 2018. Relationships between cattle and biodiversity in a multiuse landscape revealed by the Kenya Long-Term Exclosure Experiment. Rangeland Ecology & Management, 71, 281–291.

Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B. & Rocha, A. V. 2016. Package 'betareg.' R package.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.