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Rainfall reduces the potential for competitive suppression of a globally endangered ungulate by livestock

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ABSTRACT

Protected areas often are too small to house populations of wide-ranging species. Viability of wildlife populations therefore depends on whether interactions with humans and their land uses are negative, neutral, or positive. In central Iran, we measured interactions between globally endangered onagers (*Equus hemionus onager*) and livestock by analyzing remotely-sensed vegetation metrics within livestock grazing areas, tracking 9 animals with GPS telemetry, and assessing onagers' diet quality through analysis of fecal samples. Resource selection by onagers depended both on season and the presence of livestock. During the dry season, livestock reduced forage (some combination of forage biomass and forage quality) compared to pre-grazing periods, demonstrating potential for competitive suppression of onagers by livestock when resources are scarce. Additionally, and during both seasons, selection for forage by onagers was accentuated at night when livestock were absent, indicating onager avoidance of livestock. During the wet season, onagers exposed to livestock exhibited higher-quality diets than those that did not co-occur with livestock, suggesting that livestock grazing may potentially enhance forage quality for onagers. Consequently, collaboration with pastoralists to regularly rotate the locations of dry and wet season leases could alleviate negative effects of livestock grazing on onagers. Similar to other cases in multi-use landscapes, temporal shifts in the strength of competition—driven by diel cycles and seasonal rainfall—may characterize wildlife-livestock interactions in Iran and elsewhere in Asian rangelands. Our study is the first in-depth investigation of one of the world's remaining populations of onager, and highlights the possibility that conservation of an endangered mammal could be compatible with livestock production, at least during wet seasons.

1. Introduction

Increasing populations of humans and their land uses reduce the space that can mainly be dedicated to wildlife conservation (i.e., 'protected areas'; Venter et al., 2016; Bowyer et al., 2019). Therefore, 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 (e.g., Ripple et al., 2015; Kullberg et al., 2019). Consequently, population persistence of large bodied, wide-ranging species of wildlife depends on whether and under what conditions such species are compatible with livestock production (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 (Middleton and Sternberg, 2013), which are rapidly changing due to climate warming and drying (Pravalie et al., 2019), and in which livestock and wildlife share space and resources

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Table 1
Predictions and methods associated with 2- and 3-way interactions between the three main hypotheses of (1) interference competition, (2) exploitative competition, and (3) facilitation for how livestock grazing could affect resource selection and diet quality of onagers.

Interactive hypotheses	Predictions
Interference competition × Exploitative competition	• selection for forage and water by onagers will be more pronounced at night • selection for forage and water by onagers will be more pronounced where livestock grazing is minimal • diet quality of onagers is depressed in the presence of livestock • each of the above predictions is more pronounced in the dry season
Interference competition × Facilitation	• selection for forage and water by onagers will be more pronounced at night • selection for forage and water by onagers will be more pronounced where livestock grazing has occurred • diet quality of onagers is enhanced in the presence of livestock • each of the above predictions is more pronounced in the wet season
Exploitative competition × Facilitation	• during the dry season, selection for forage and water by onagers will be more pronounced where livestock grazing is minimal • during the wet season, selection for forage and water by onagers will be more pronounced where livestock grazing has occurred • during the dry season, diet quality of onagers is depressed in the presence of livestock • during the wet season, diet quality of onagers is enhanced in the presence of livestock
Interference competition × Exploitative competition × Facilitation	• during the dry season, selection for forage and water by onagers will be more pronounced where livestock grazing is minimal • during the wet season, selection for forage and water by onagers will be more pronounced where livestock grazing has occurred • each of the above predictions is more pronounced at night • during the dry season, diet quality of onagers is depressed in the presence of livestock • during the wet season, diet quality of onagers is enhanced in the presence of livestock

(Fynn et al., 2016).

Two perspectives have characterized attempts to quantify how and why interactions among wild and domestic ungulates often are negative, and occasionally are positive (reviewed by Schieltz and Rubenstein, 2016; Pozo et al., 2021). Such interactions typically are negative: 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 (Mysterud and Austrheim, 2008; Schroeder et al., 2013; Fynn et al., 2016). Competitive interactions can trigger population declines of wild ungulates, resulting in their eventual replacement by livestock (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., 2017). 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., 2016]) and livestock density (with greater potential for facilitation at lower densities of livestock [Mysterud and Austrheim, 2008; Keesing et al., 2018; Stears and Shrader, 2020]). If wild ungulates are attracted to and benefit from 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 Near Threatened Asiatic wild ass (*Equus hemionus*) co-occur with humans and domestic ungulates (Kaczensky et al., 2008; 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 in central Iran: the Bahram-e-Goor Protected Area (BPA, which includes Qatrouiyeh National Park, QNP) and the Touran Biosphere Reserve. Onagers are imperiled from a combination of poaching, conflict with pastoralists, and agricultural expansion (Hemami and Momeni, 2013) and are categorized as "Endangered" under the IUCN Red List of Threatened Species (Hemami et al., 2015).

Combining data on remotely sensed vegetation indices, movements of onagers, and assays of onager diet quality, we quantified whether and how rainfall might reduce competitive interactions between onagers and livestock. We tested three main hypotheses (and combinations thereof; Table 1) to explain how variation in the intensity and timing of livestock grazing affected resource selection and diet quality of onagers:

(1) *Interference Competition*: humans and their livestock prevent onagers from accessing forage and water. Here, we follow Holdridge et al. (2016) in defining interference competition as inhibition of "the ability of others to access a shared resource, either aggressively or passively". We acknowledge that this definition encompasses illegal killing (i.e., poaching) by humans, such that any shift toward nighttime activity would reflect some combination of the avoidance of livestock (to maximize access to forage and water) and the avoidance of humans (to maximize access to forage and water, to minimize the threat of being poached, or both). The Interference Competition hypothesis predicts that any selection for forage and water by onagers will be more pronounced at night (when livestock are corralled [see "*Study area and species*" below], and when humans are less active) because onagers avoid coming into contact with livestock and humans. However, depression of vegetation from livestock grazing has negligible effects on resource selection and diet quality of onagers.
(2) *Exploitative Competition*: livestock remove forage and water that otherwise would be available to onagers. The Exploitative Competition hypothesis predicts that onagers should avoid areas recently grazed by livestock, regardless of the physical presence of livestock (i.e., during both day and night). Additionally, diet quality of onagers should be depressed in the presence of livestock (i.e., within BPA relative to QNP). Both effects should be more pronounced during the dry season, when high-quality forage (and forage in general) is relatively scarce.
(3) *Facilitation*: herbivory by livestock stimulates forage regrowth. The Facilitation hypothesis predicts that onagers should select areas in which livestock grazing has occurred recently. Additionally, diet quality of onagers should be enhanced by the presence of livestock (i.e., within BPA relative to QNP). Both effects should be more pronounced during the wet season, when forage is both relatively abundant and of relatively high quality.

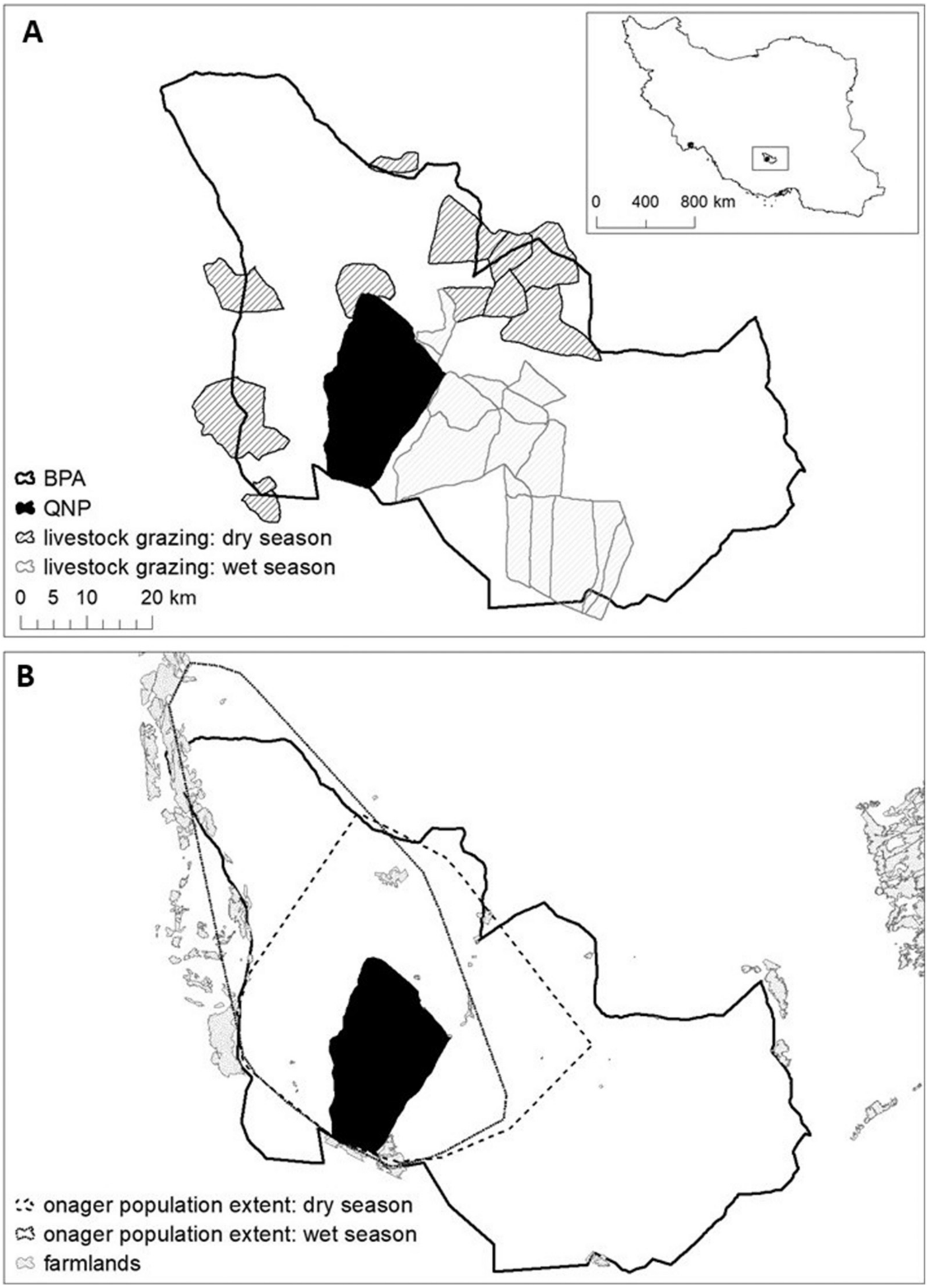

Fig. 1. (A) Bahram-e-Goor Protected Area (BPA) and Qatrouiyeh National Park (QNP) in south-central Iran (inset), with locations of 27 dry-season and wet-season leases in BPA. Twelve of these leases (dark gray polygons) were grazed by livestock in the dry season (May – October) and 15 leases (light gray polygons) were grazed by livestock in the wet season (November – April). (B) The extent of movements for nine GPS telemetered onagers (100 % minimum convex polygon), in dry and wet seasons, and locations of farmlands within and around BPA.

2. Methods

2.1. Study area and species

Covering a total area of 3747 km^2, the Bahram-e-Goor Protected Area (BPA) was established in 1972; 310 km^2 was dedicated to Qatrouiyeh National Park (QNP) in 2008 to protect what is now the world's largest population of onagers (Fig. 1). Although it technically is considered Category II by IUCN, Qatrouiyeh's designation as a national park is comparable to an IUCN Ib Wilderness Area, because developed tourism and other human activities such as livestock grazing are prohibited. Historically, QNP served as the core zone of the BPA, hosting concentrated wildlife populations and conservation enforcement. The national park was specifically established to safeguard its onager population and, since 2008, it has maintained anti-poaching patrols and provided water (and occasionally supplementary forage) to onagers outside the growing season. In response, the onager population of QNP (and thus BPA) increased from ca. 90 individuals in 1997 to ca. 900

individuals in 2019 (Iranian Department of Environment, unpublished report).

Unlike QNP, the BPA (comparable to an IUCN V Protected Landscape/Seascape) permits human activities such as livestock grazing and small-scale farming. It accommodates approximately 4000 semi-nomadic pastoralists and small-scale farmers residing in small residential areas within or on the boundary of the BPA.

Qatrouiyeh National Park (QNP) and Bahram-e-Goor Protected Area (BPA) have an arid, seasonal climate (mean annual temperature 21.27 °C ± 0.29 SE, mean annual precipitation 185.00 mm ± 107.00 SE), with May to September the driest and February the wettest months (0.00 mm ± 0.00 SE and 93.50 mm ± 76.00 SE), respectively (from 2017 and 2018 climate data, Table A1). 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 sagebrush (*Artemisia sieberi*). In addition to onagers, other large, wild mammals in BPA include chinkara (*Gazella bennettii*), mouflon (*Ovis gmelini*), wild goat (*Capra aegagrus*), and wild boar (*Sus scrofa*). Of these wild ungulates, chinkara are most common (though still rare, with a population size of ca. 200) in the sagebrush habitats in which onagers and livestock co-occur. Large carnivores include gray wolf (*Canis lupus*) and striped hyena (*Hyaena hyaena*); however, no predation by these species has been documented on adult onagers.

Onagers exhibit a diverse diet, consuming 69 species representing forbs, grasses, and shrubs from 23 families (Mahmoudi, 2014; Ghasemi, unpublished data). In QNP, group size of onagers ranges between 1 and 63 individuals, with a mean group size (including solitary males) of 8.00 ± 11.80 SD (Hemami and Momeni, 2013). Similar to the Gobi khulan (*E. h. hemionus*), and with the exception of mothers and their foals, herd composition of onagers is fluid and changes regularly in a fission-fusion manner (Kaczensky et al., 2008). In 2017 and 2018, The Iranian Department of Environment counted 793 ± 62 SE onagers in QNP and BPA (0.19 ± 0.01 SE/km^2, approximating 1.33 ± 0.05 sheep and goats units/km^2; Butler et al., 2003), with the majority of the population concentrated in QNP. Onagers are commonly considered crepuscular; however, *E. hemionus* as a whole is predominantly diurnal, though certain populations may feed at night (Nowak, 1999).

2.2. Onager capture and GPS telemetry

In QNP, and from December 2016 through January 2017, we captured nine female onagers in corral traps (Section A1) and fitted them with GPS telemetry collars (Vertex Lite 2 Iridium, Vectronic Aerospace GmbH, Berlin, Germany). We programmed GPS collars to collect a location every-other hour and to self-release two years after deployment. We did not include the first two weeks of GPS locations after deployment of collars in our analysis to reduce the effect of capture and the handling process on movement of animals (Dechen Quinn et al., 2012). We acknowledge that capturing animals exclusively within QNP could affect our conclusions about individual space use due to site fidelity by individuals; however, based on over 20 years of ranger reports in both QNP and BPA, it is doubtful that resident individuals occur exclusively within BPA (personal comm. With park rangers). Instead, and as we demonstrate further (see Results: *GPS telemetry*), individuals tend to either reside wholly within QNP or move between QNP and BPA. We screened GPS locations with a dilution of precision (DOP) > 10 to enhance the accuracy of our results; ultimately, we used 72,168 locations from January 2017 to December 2018 in our analyses. Our 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).

Given the potential for fission-fusion dynamics coupled with our small sample size, we calculated coefficients of association among all pairwise combinations of collared individuals. Coefficients of association quantify the proportion of simultaneous relocations below a specified distance threshold (Cole, 1949). We categorized as 'simultaneous' locations within 2 h (our sampling rate) of each other, and we selected a distance threshold of 200 m. A cut-off value of 0.5 is suggested to determine attraction (>0.5) and avoidance (<0.5). We used the wildlifeDI package in Program R to estimate coefficients of association (Long and Long, 2021; Long et al., 2022). Coefficients of association indicated avoidance among all pairs of collared individuals (mean ± SD = 0.04 ± 0.05; range = 0.0–0.19). Therefore, we considered individuals in our study to be independent.

2.3. Livestock grazing in Bahram-e-Goor protected area

In contrast to QNP, livestock grazing is the main activity of the 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, sometimes with herding dogs, and are kept in corrals overnight to minimize predation by gray wolves and striped hyenas.

The lease system was established and has been overseen by the Iranian Department of Watershed and Rangeland Management since 1990s, based on the count of livestock and herders in each human settlement, along with the approximate availability of forage and water within each lease (pers. comm. the Iranian Department of Environment). The purpose behind establishing these leases was to manage livestock in attempt to prevent overgrazing of the protected area. On rare occasion, and owing to inconsistent enforcement of the lease schedule, livestock sometimes exceed the permitted levels during wet years.

In sum, data on entry and exit dates of livestock and livestock density were available for 27 seasonal leases covering ca. 30 % of the BPA (Fig. 1, Table A2, Iranian Department of Watershed and Rangeland Management, unpublished data). Twelve of these 27 leases were grazed by livestock in the dry season (May – October), and 15 leases were grazed by livestock in the wet season (November – April). Vegetation cover and composition within seasonal leases in BPA are comparable to those in QNP; however, surface water in QNP is more available to onagers through water troughs by park managers (Table A2). In BPA, permanent water sources occur mostly as springs, although pastoralists collect water from wells and provide it to their livestock in troughs.

2.4. Testing the interference competition hypothesis: diel resource selection by onagers

To test whether onagers' resource selection was altered by the presence of livestock, humans, or both (per the Interference Competition hypothesis), we evaluated responses of onagers to vegetation and water using diel and seasonal resource selection functions (RSFs) based on a use-availability design (Manly et al., 2007). In addition to locations of springs in both QNP and BPA, locations of supplemental water (i.e., troughs) in QNP were known, and were incorporated into RSFs. Supplemental feeding occurred sporadically within QNP between 25 May 2018 and 31 December 2018. Because we did not record the locations of supplemental feed, we constructed two RSFs for QNP: one using all GPS relocation data (1 January 2017 through 31 December 2018), and one from which the period of supplemental feeding had been removed.

Because livestock were active during the day and corralled overnight, we expected that livestock would constrain resource selection by onagers during daytime with minimal influence during nighttime. We classified GPS locations of onagers into dry (May–October) and wet (November–April) seasons. Within each season, we divided GPS

Table 2

Parameter estimates (β) standard errors (SE) of diel and seasonal second-order resource selection for onagers' GPS locations in the presence of livestock (BPA) and in the absence of livestock (QNP) in response to forage (measured by Modified Soil-Adjusted Vegetation Index) 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 and water. Parameters and *P*-values for parameters <0.01 in each model are italicized in bold. Parameters and *P*-values for parameters between 0.01 and 0.10 are italicized. Variances (σ^2) and standard deviations (SD) of individual-level (random) effects are provided for each habitat variable.

		Livestock (BPA)						No livestock (QNP)					
		Day			Night			Day			Night		
		β (SE)	*P*	σ^2 (SD)	β (SE)	*P*	σ^2 (SD)	β (SE)	*P*	σ^2 (SD)	β (SE)	*P*	σ^2 (SD)
Dry seasons	Water	*−0.24 (0.14)*	*0.07*	0.15 (0.39)	−0.04 (0.09)	0.67	0.07 (0.26)	***1.47 (0.15)***	***<0.001***	0.22 (0.46)	***1.15 (0.09)***	***<0.001***	0.07 (0.27)
	Forage	*0.40 (0.23)*	*0.08*	0.47 (0.68)	***0.37 (0.14)***	***0.003***	0.16 (0.41)	*−0.22 (0.11)*	*0.04*	0.11 (0.33)	−0.03 (0.06)	0.65	0.03 (0.18)
Wet seasons	Water	−0.11 (0.15)	0.47	0.18 (0.43)	***−0.19 (0.06)***	***0.002***	0.03 (0.18)	***1.00 (0.09)***	***<0.001***	0.07 (0.26)	***0.88 (0.05)***	***<0.001***	0.01 (0.10)
	Forage	0.17 (0.15)	0.24	0.18 (0.42)	***0.55 (0.12)***	***<0.001***	0.13 (0.36)	−0.09 (0.15)	0.54	0.20 (0.44)	−0.05 (0.13)	0.71	0.25 (0.50)

locations of onagers into day and night times using the function "time_of_day" in the R package amt (Signer et al., 2019). We separated GPS locations in BPA from those in QNP, then built diel and seasonal RSF models for each of the two areas independently. Since GPS locations in BPA and QNP belonged to the same onagers moving between the two areas (rather than different individuals residing in each area), we selected random locations within the entire population's minimum convex polygon (MCP) for each season and diel period (representing second-order resource selection, Johnson, 1980).

2.5. Testing the exploitative competition and facilitation hypotheses: seasonal resource selection by onagers

To test whether onagers' resource selection was altered by the presence of livestock, humans, or both (per the Exploitative Competition hypothesis), we extracted vegetation primary productivity (average Modified Soil-Adjusted Vegetation Index, MSAVI, in each season for years 2017 and 2018) and linear distances to nearest water sources for all used and available points. We used the MSAVI derived from surface reflectance measured by the Moderate Resolution Imaging Spectroradiometer (MODIS) terra satellite (Version 6.0 MOD09Q1; spatial resolution 250 × 250 m, temporal resolution eight days) to measure vegetation greenness. MSAVI is highly correlated with green vegetation cover in dryland ecosystems because it includes a correction for variation in the effect of bare soil color and reflectance (Qi et al., 1994). We did not detect strong correlation among these predictors within just BPA, within just QNP, and within both together (Pearson's pairwise correlation $|r| < 0.20$), so we built RSFs using MSAVI 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. We fit 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). We assigned a weight of 1000 to available points to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (Muff et al., 2020).

Additionally, resource selection may not be constant when resource availability changes (i.e., animals may exhibit functional responses in resource selection). We evaluated whether resource selection by onagers was influenced by the availability of forage (MSAVI) and water (Section A2). We 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.

2.6. Testing the exploitative competition and facilitation hypotheses: effects of livestock on vegetation characteristics

The lease schedule within BPA permitted us to employ a quasi-experimental design to quantify the impact of livestock grazing on vegetation, and thus evaluate the potential for exploitative competition and facilitation between livestock and onagers. We combined data on the intensity and timing of livestock grazing (regulated through the BPA lease schedule, Iranian Department of Watershed and Rangeland Management, unpublished data) with remotely-sensed data on vegetation greenness. We used MSAVI to measure the change in vegetation greenness pre- versus post-grazing (ΔMSAVI) by livestock in each of two seasons for each of the 27 leases in 2017 and 2018 (Qi et al., 1994; Jin et al., 2014). Before calculating MSAVI within each lease, we masked out farmlands and pixels with topographic slope > 20 degrees (which represent rocks and non-vegetated areas, Esmaeili, personal observations). For each lease, we calculated pre-grazing MSAVI using the MODIS layer available immediately prior to livestock entry, subject to the constraint that the layer was from at least 15 days before livestock entry (range = 15–22 days, depending on the availability of MODIS images; hereafter 'pre-grazing'). Similarly, we calculated post-grazing MSAVI using the first MODIS layer available from at least 15 days after livestock exit (range = 16–21 days;hereafter 'post-grazing'). We verified that MSAVI did change appreciably or consistently over the periods of interest (Fig. A1).

For each lease, we calculated seasonal change in MSAVI (ΔMSAVI) as the difference in post-grazing versus pre-grazing MSAVI. Within QNP, we calculated the mean MSAVI value for pre- and post-grazing periods in BPA to estimate ΔMSAVI associated with onager grazing in the absence of livestock. Additionally, and to test for any baseline differences in vegetation greenness between BPA and QNP, we calculated mean monthly absolute values of MSAVI across the two areas in 2017 and 2018 (Table A1).

We used Student's *t*-tests to compare monthly absolute values of MSAVI in BPA and QNP. We tested for effects of livestock grazing intensity and season on ΔMSAVI using a Generalized Linear Mixed Model (GLMM). We calculated livestock grazing intensity by multiplying the density of livestock (number of livestock divided by lease area in km^2) by the duration of grazing (# of days) within each of the 27 leases. Livestock grazing intensity was standardized to a mean of 0.00 and a standard deviation of 1.00 in our GLMM analysis, and was used as a continuous predictor. Additionally, we included season (dry versus wet) in the analysis, and an interaction between grazing intensity and season. Since we did not detect differences in ΔMSAVI between years 2017 and 2018 for each lease (paired *t*-test, $t = 1.01$, df = 25, $P = 0.32$), we did not

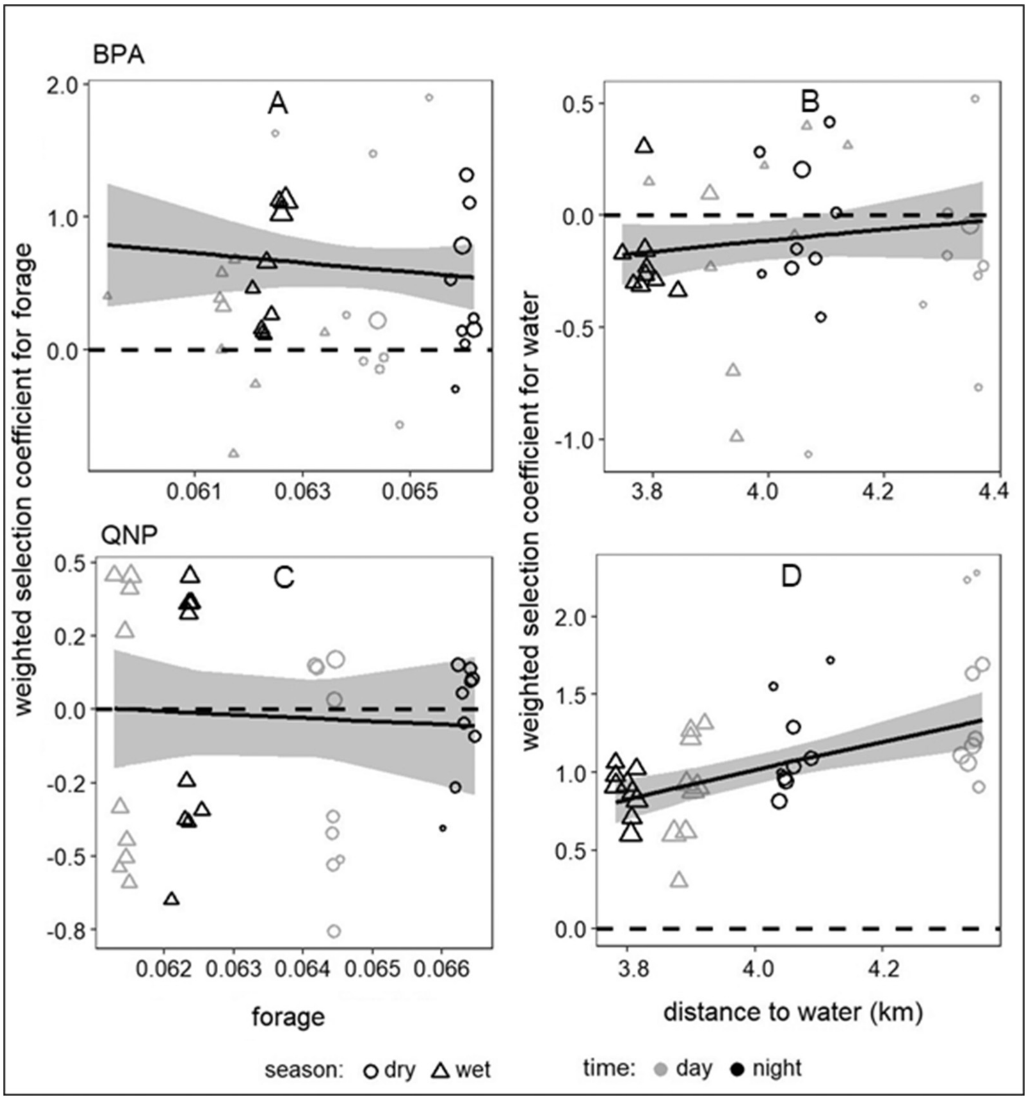

Fig. 2. Functional responses in resource selection by onagers in Bahram-e-Goor Protected Area (BPA) and Qatrouiyeh National Park (QNP) in response to variation in availability of forage (MSAVI, Modified Soil-Adjusted Vegetation Index) and distance to water. In all panels, the dashed lines show the pattern expected under proportional resource selection (i.e., no functional response). Each point (circle or triangle) represents a single parameter estimate (β) of the diel and seasonal resource selection function for each of the nine onagers telemetered in our study, weighted by standard error of the parameter estimate, such that there are 9 points for each season (dry v wet) x time-of-day (day v night) combination. Point size represents the relative precision of a parameter estimate (larger circles = higher precision). Solid black lines are linear regression models with 95 % confidence intervals in gray shadows. Selection for forage was strong overall in BPA (A), while selection for water was strong overall in QNP (D). Except for selection for water in QNP (D), none of the regression lines had slopes significantly different from zero (A, B, C), indicating no functional response in resource selection of onagers in the presence (BPA) or absence (QNP) of livestock. In QNP, selection for water increased as distance to water increased (lower-right panel, θ_1 (SE) = 3.71 (0.89), $R^2 = 0.32$, $P \leq 0.001$). The direction of parameter estimates for distance to nearest water source is switched; therefore, positive and negative values show selection and avoidance for forage and water.

include year as a predictor in our GLMM. We identified statistical outliers as those in the 2.5 and 97.5 percentiles of the observed data. This identified two dry season leases (or 17 % of the dry season leases), with grazing intensity values of 1285 and 48,191, as outliers. The most extreme (99.7 percentile) outlier was a single dry season lease (or 8 % of the dry season leases) with a grazing intensity value of 48,191 (Fig. A2). Below, we report on analyses based on a total of 10 dry season leases.

To incorporate spatial variation among the leases, we included lease identity as a random intercept in our GLMM (Zuur et al., 2009) using the nlme package in Program R (Pinheiro et al., 2017). Marginal and conditional R^2 for our GLMM were estimated following Nakagawa and Schielzeth (2013) using the MuMIn package in Program R (Barton, 2018).

2.7. Testing the exploitative competition and facilitation hypotheses: 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 of forage (Osborn and Jenks, 1998; 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). To test whether livestock grazing affected the diet quality of onagers, we measured percent crude fecal protein and fiber in 252 fecal samples of onagers collected approximately every-other month between December 2017 and November 2018 in QNP and its 1 km buffer and in BPA (Table A3). We targeted fresh fecal samples based on physical properties of softness and dark color.

Because (domestic) donkeys (*Equus asinus*) in BPA are always accompanied by pastoralists and their livestock, we used the following criteria to distinguish between the dung of onagers versus that of donkeys. Equid dung was classified as donkey dung when it (1) occurred among that of livestock (sheep and goat); and (2) was the same age (color) as that of livestock. Equid dung was classified as onager dung when it was not associated with livestock, or it clearly was more recent (and hence darker) than the livestock dung with which it occurred. In QNP, which was characterized by a high concentration of onager dung, we collected fresh samples across the park and in predetermined, random locations from a random number generator. In BPA, we relied on local knowledge and information from residents to locate fresh fecal samples. We air-dried samples and extracted percent crude fecal protein and percent crude fecal fiber following the 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 h (Steuer et al., 2011; Van Soest, 1994). Although telemetered individuals typically did not move from BPA to QNP (and vice versa) over the course of 30 h, such movements did occur (dry season mean = 0.58 ± 0.12 SE times per 30 h per individual; wet season mean = 0.82 ± 0.09 SE times per 30 h per individual). While it therefore was possible for individuals to have fed in one property and defecated in another within the span of 30 h, this occurred less frequently than the alternative (individuals feeding and defecating in the same property within the span of 30 h). Consequently, we believe that any differences that we detected between BPA and QNP should be considered conservative. To test whether diet quality of onagers was different between BPA and QNP in each season, we compared percent crude fecal protein and percent crude fecal fiber between BPA and QNP using Student's *t*-tests in dry and wet seasons, separately.

3. Results

3.1. GPS telemetry

We recorded 8018 ± 375 SE (range = 5897–8756) points per individual over 669 ± 31 SE days (range = 491–729 days). All collared individuals moved between QNP and BPA; however, collared individuals spent most of their time in QNP, with 17 % of total GPS locations occurring outside QNP. This finding aligns with our observations and ranger reports indicating that this onager population is primarily concentrated in QNP. Onagers' visits to BPA occurred mostly during nighttime in both dry (24 % at night vs. 13 % during the day) and wet seasons (25 % at night vs. 7 % during the day). Range size (100 % MCP) was 359.7 km^2 ± 83.6 SE during dry seasons and 507.5 km^2 ± 106.0 SE during wet seasons, with 29 % ± 5 % SE and 30 % ± 6 % SE of individuals' ranges occurring outside QNP in dry and wet seasons, respectively. Finally, and using the "amt" package in R (Signer et al., 2019), the mean and standard errors of annual home range and core areas (from 95 % and 50 % contours of autocorrelated kernel densities, Fleming et al., 2015) were 372.14 ± 87.34 km^2 and 62.81 ± 15.71 km^2, respectively.

Table 3
Results of a Generalized Linear Mixed Model for effects of season (dry vs. wet) and grazing intensity (number of livestock divided by lease area in km^2 multiplied by the duration of grazing (# of days)) on ΔMSAVI (change in Modified Soil-Adjusted Vegetation Index from pre-grazing to post-grazing periods) in dry season ($n = 10$) 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	−0.007	0.001	−4.279	<0.001
Season*	0.026	0.002	12.734	<0.001
Grazing intensity × season*	0.007	0.002	3.332	0.003

Marginal R^2 = 0.80; Conditional R^2 = 0.80.
Random effects intercept <0.001; residual = 0.007.
* Dry season lease is the reference category.

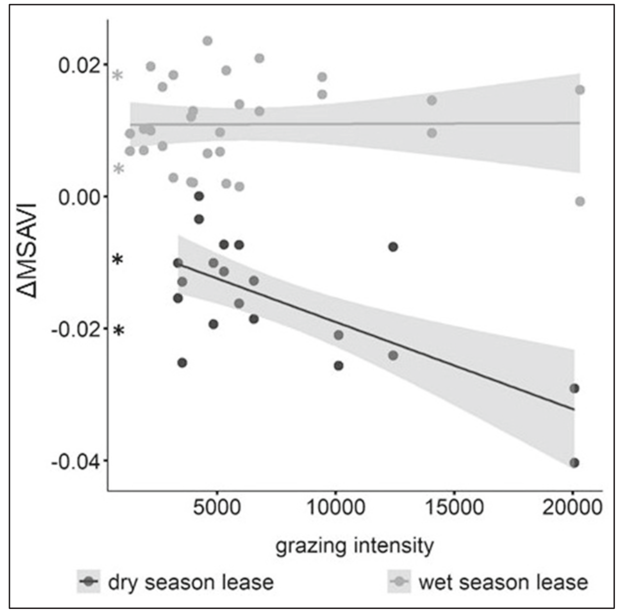

Fig. 3. Effect of grazing intensity (number of livestock divided by lease area in km^2 multiplied by the duration of grazing (# of days)) on the ΔMSAVI between pre-grazing and post-grazing periods (change in Modified Soil-Adjusted Vegetation Index MSAVI) in dry season (black points and line, n = 10) and wet season (gray points and line, n = 15) leases in Bahram-e-Goor Protected Area (BPA). Negative values represent a depletion of MSAVI between pre-grazing and post-grazing periods; positive values represent an accumulation of MSAVI between pre-grazing and post-grazing periods. A pair of data points is plotted for each lease, one for 2017 and one for 2018. Gray shading represents 95 % confidence intervals around each relationship. To illustrate the ΔMSAVI expected in the absence of livestock grazing (in Qatrouiyeh National Park, QNP), asterisks are plotted for dry and wet seasons, one for 2017 and one for 2018.

3.2. Diel and seasonal resource selection by onagers

In the presence of livestock (i.e., within BPA), and during both seasons, onagers selected for MSAVI significantly only at nighttime ($P \leq 0.01$; Table 2), although we did detect a positive but not statistically significant trend for selection of MSAVI during the day ($\beta = 0.40 \pm 0.23$ SE, $P = 0.08$; Table 2). During daytime and in dry seasons, onagers avoided areas with high MSAVI in the absence of livestock (i.e., within QNP; $\beta = -0.22 \pm 0.11$ SE, $P = 0.04$; Table 2). Additionally, onagers consistently selected for proximity to water in the absence of livestock, regardless of season and time of day ($P \leq 0.001$). In contrast, there was a marginal trend toward avoidance of water during the day in the dry season in the presence of livestock ($\beta = -0.24 \pm 0.14$ SE, $P = 0.07$; Table 2), which strengthened during nighttime in wet seasons ($\beta = -0.19 \pm 0.06$ SE, $P = 0.02$). We did not detect any functional responses in selection for MSAVI in the presence or absence of livestock (Fig. 2 A and Fig. 2 C; Section A2, Table A4). Therefore, selection for MSAVI was robust to any differences in the abundance or quality of vegetation between BPA and QNP. Selection for forage was strong overall in BPA (Fig. 2 A), while selection for water was strong overall in QNP (Fig. 2 D). Additionally, selection for MSAVI was robust to supplemental feeding within QNP. Supplemental feeding occurred periodically between 25 May 2018 and 31 December 2018; when GPS relocations from this time were removed from RSF analyses, our results were virtually unchanged (Table A5).

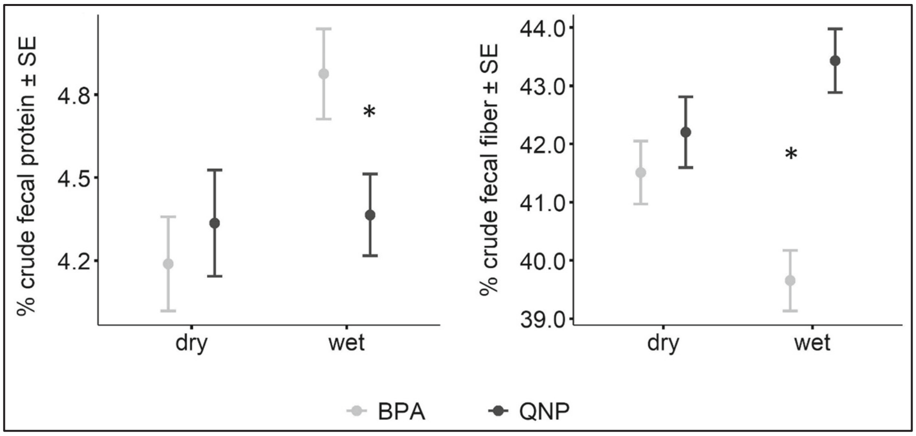

Fig. 4. Percent crude fecal protein and percent crude fecal fiber in 252 fecal samples of onagers collected in dry and wet seasons in Bahram-e-Goor Protected Area (BPA) and Qatrouiyeh National Park (QNP). Points represent mean values and bars are standard errors. Asterisks represent significant difference between the two bars.

3.3. *Effects of livestock on vegetation characteristics*

Leases that were more intensely grazed by livestock exhibited larger declines in MSAVI from pre- to post-grazing periods, but only during dry seasons (parameter estimate: -0.006 ± 0.001 SE, $P < 0.001$; Table 3, Fig. 3). MSAVI neither increased nor decreased with grazing intensity during wet seasons (Table 2; Fig. 3). The marginal and conditional R^2 of our GLMM were identical ($R^2 = 0.80$), reflecting a lack of statistical significance for lease identity as a random effect (Table 3). Within QNP, ΔMSAVI values were similar to those in BPA (Fig. 3). Further, we did not find significant differences in monthly absolute value of MSAVI between BPA and QNP (mean ± SE in BPA = 0.064 ± 0.002 and in QNP = 0.059 ± 0.002; $t = 1.43$, df = 44.3, $P = 0.16$). Taken together, these results indicate that baseline MSAVI (i.e., MSAVI in the absence of livestock grazing) was comparable between BPA and QNP (Table A2).

3.4. *Diet quality of onagers*

During wet seasons, onagers grazing in areas with livestock acquired higher-quality diets than those where livestock grazing did not occur (Fig. 4; in BPA, $n = 84$, mean crude protein = 4.81 % ± 0.14 % SE; 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 wet seasons 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, $P \leq 0.001$). In contrast, during dry seasons, we did not detect differences in percent crude protein or percent crude fiber between fecal samples collected in BPA ($n = 49$) and QNP ($n = 44$). Our results remained robust upon removing samples collected within a 1 km ($n = 18$) and 2 km ($n = 30$) buffer surrounding QNP.

4. Discussion

Across the world, livestock and wild ungulates co-occur in human occupied rangelands. Effects of livestock on wild ungulates often are negative (in the case of displacement or competitive suppression of wild ungulates by livestock), but they are occasionally positive. Much of this evidence has accrued from North America (Clark et al., 2000; Du Toit et al., 2017; Hughey et al., 2021), South America (Schroeder et al., 2013; Di Bitetti et al., 2020), and sub-Saharan Africa (Augustine et al., 2011; Odadi et al., 2011b; Fynn et al., 2016; Keesing et al., 2018). Our results highlight the potential for livestock grazing to directly shape the activity and resource selection of a globally endangered equid in southwestern Asia. In support of the Interference Competition hypothesis, selection for MSAVI was accentuated at night in BPA (when livestock were corralled) regardless of season. Our results contribute to a growing body of literature demonstrating that the 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), and over both diel and annual cycles (e.g., Gaynor et al., 2018). In addition to direct interference (through inhibiting access to resources, poaching, or both), our results suggest that the intensity of grazing by livestock further affected resource selection by onagers. In the presence of livestock, onagers preferentially used areas of high MSAVI in all seasons, and the intensity of livestock grazing was inversely associated with the amount of forage available to onagers in dry seasons. Critically, and across the stocking densities observed in BPA, livestock neither reduced nor stimulated forage availability in wet seasons, regardless of grazing intensity. Relative to wet seasons, the stronger impact of livestock grazing on vegetation during dry seasons 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 often boosts vegetation quality (i.e., nitrogen content and digestibility) early in the growing season, which can be further enhanced by grazing (Anderson et al., 2007; Odadi et al., 2011b; Riginos et al., 2012; 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 (Kuijper et al., 2009; Ng'weno et al., 2019). Given that diet quality of onagers was highest in wet seasons 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 consumed low-quality diets in both BPA and QNP during dry seasons, probably as a result of plant senescence and a lack of compensatory regrowth following grazing by livestock (Briske et al., 2008; Hempson et al., 2015; Fynn et al., 2016).

While our results are consistent with those expected under a hypothesis of facilitation by livestock, we cannot rule out two factors that may have influenced the elevated diet quality of onagers within BPA. First, and in human-occupied landscapes, agriculture and other human activities provide food that can subsidize wildlife (Oro et al., 2013; Manlick and Pauli, 2020). The enhanced diet quality of onagers during wet seasons could be attributed to their feeding on farmlands within and around BPA. Ninety-seven percent and 61 % of onagers' visits to farmlands occurred during wet seasons in 2017 and 2018, respectively. However, the majority of such events occurred in farmlands close to QNP, where onagers could move back to the park after feeding on nearby crops. Additionally, we found that selection for vegetation productivity in BPA was not affected by onagers' visiting farmlands (Table A6). Given the timing of crop phenology (coupled with the fact that onagers could move readily between BPA and QNP), we believe that the enhanced diet quality of onagers in wet seasons is reflective of higher-quality forage in at least some parts of BPA, relative to QNP.

Second, vegetative differences between QNP and BPA might have contributed to (or altogether driven) increases in protein (and concomitant decreases in fiber) in onager diets. Although QNP exhibited vegetation greenness comparable to lightly-grazed areas of BPA (as assayed by MSAVI; Fig. 3), forage plants with higher nitrogen content, lower fiber content, or both may have been partly or wholly responsible for the increases in diet quality we observed (e.g., Leslie Jr et al., 2008; Stapelberg et al., 2008). Additionally, background variation in soil nutrient content may have further exacerbated differences in diet quality between QNP and BPA. A major goal for future research entails quantifying background variation (in vegetation and soil properties) between these sites, then disentangling any such variation from facilitation per se in driving the observed patterns of diet quality.

Remotely-sensed vegetation indices (e.g., MSAVI, NDVI) are metrics of "greenness", which often is interpreted as some combination of forage biomass and forage quality. The use of such metrics is potentially problematic, in the event that changes in one of these factors (forage biomass or forage quality) are erroneously attributed to the other. For example, and in our study during the dry season, MSAVI—which we believe primarily reflects forage biomass—declined as livestock grazing intensity increased. If this pattern were due primarily to declining forage quality (rather than declining forage biomass), forage quality would have been reduced by livestock over relatively short (5–6 month) windows of time. We believe this scenario is unlikely for three reasons. First, and in other rangeland ecosystems, livestock grazing tends either to enhance or not affect forage quality at the same time it reduces forage biomass (e.g., Milchunas et al., 1995; Clark et al., 2000; Eldridge et al., 2016; Ng'weno et al., 2019). Second, field validations of NDVI have demonstrated that it is consistently and positively associated with forage biomass (Kawamura et al., 2005; Borowik et al., 2013; Garroutte et al., 2016), but its relationship with forage quality is site- and system-specific (e.g., Ryan et al., 2012; Garroutte et al., 2016; Kearney et al., 2022a). Third, and within our study system in particular, livestock grazing appears to have increased diet quality of onagers, at least with respect to fecal protein and fiber metrics (Fig. 4). Still, a challenge for future work in our study system is to validate remotely-sensed vegetation indices against field-derived metrics of forage biomass and quality (Garroutte et al., 2016; Kearney et al., 2022a; Kearney et al., 2022b).

Only during wet seasons and in the presence of livestock did we detect an increase in the diet quality of onagers, which may indicates facilitation by livestock. Because onagers typically moved between QNP and BPA every 37 h, and because passage time in equids is ca. 30 h, we are reasonably confident that the higher protein and lower fiber content in samples from BPA reflect higher quality diets in wet seasons. However, we are less confident in the apparent lack of distinction in diet quality during dry seasons. That stated, our results are aligned with a priori expectations, in which any facilitation by livestock should be more likely to manifest in relatively wet places, during relatively wet times.

We used a combination of remotely sensed vegetation indices, movements of onagers, and assays of onager diet quality to quantify the relative influence of competition and facilitation between onagers and livestock. In so doing, we sought to inform efforts to better conserve onagers in Iran. In sum, our results demonstrate that potential for exploitative competition is reduced during the wet season. Additionally, our results hint at the potential for a shifting dynamic of competition and facilitation between livestock and onagers: onagers avoid encounters with livestock, and livestock reduce the forage available for onagers during dry seasons, but livestock enhance diet quality of onagers during wet seasons. Our results should be interpreted with caution, because of the global rarity of onagers, because behavioral responses of onagers to livestock grazing may not translate to increased vital rates, and because documentation of facilitation by bovids on equids is both rare and geographically restricted. Although facilitative effects of equid grazing on the occurrence (Herrik et al., 2023), bite rates (Odadi et al., 2011a), diet quality (Bell, 1971), and weight gain (Odadi et al., 2011a, 2011b) of bovids have been shown repeatedly (and principally in sub-Saharan Africa), the reverse—facilitative effects of bovid grazing on equids—has been shown less frequently (see also Potter and Pringle, 2023). In East Africa, Odadi et al. (2011a) demonstrated that cattle grazing increased weight gain, bite rates, and protein intake by surrogate zebra (i.e., donkeys); each species facilitated the other when herded together, relative to where each species occurred in isolation. Odadi et al. (2011a) postulated that these patterns were driven by positive feedbacks via grass stem removal by donkeys, which promoted grazing by cattle, which then stimulated vegetative regrowth to the benefit of both. Whether a similar dynamic might exist between livestock and onagers and BPA remains unknown. It is noteworthy that Odadi et al.'s study system occurred in an area receiving 2-3× the precipitation of BPA, and their results hinged on stocking density: when densities of either cattle or donkeys were high, facilitative effects on each were muted (see also Wells et al., 2022). Any potential benefit to onagers that might arise through livestock grazing would need to be weighed carefully against the unambiguous evidence for interference competition, and then only after it was documented more clearly.

Whether our findings extend from behavioral to population-level responses hinges on the degree to which forage biomass, forage quality, or both limit onager populations. Further, the degree to which livestock limit preferred food plants of onagers remains an open question. Sheep and (especially) goats are generalist herbivores (e.g., Coblentz, 1978; Heriot et al., 2019; Bowden et al., 2022) whose diets likely have high overlap with onagers. Although livestock grazing is prohibited in QNP, a large population of onagers occurs there throughout the year, exerting patterns of grazing pressure that differ from those in BPA. In particular, future efforts might employ replicated exclusion (i.e., fenced) plots within a series of dry and wet seasons leases in both QNP and BPA to quantify compositional shifts, productivity, and offtake by onagers and livestock separately and in tandem.

Although protected areas can enhance prospects for endangered species conservation, major restrictions on pastoralism and other forms of livestock production are often infeasible and unethical in many rangelands across the world. Results from our study are congruent with others demonstrating that competitive suppression of wild ungulates by livestock is likely to be most pronounced during dry conditions (e.g., Odadi et al., 2011b; Fynn et al., 2016; Kimuyu et al., 2017; Stears and Shrader, 2020). At the same time, and if behavioral responses are a precursor for numerical changes, our results also point to the potential for livestock grazing to be used as a tool for onager conservation. To the extent that low to moderate stocking rates enhance forage quality during the wet season without a concomitant reduction in forage greenness (Figs. 3), livestock grazing could be used to bolster nutritional condition of onagers or, minimally, be conducted without competitively suppressing onagers (see also Wells et al., 2022; Young et al., 2018). Future efforts to experimentally quantify offtake by onagers and livestock (using movable productivity cages, e.g., Charles et al., 2017; Schoenecker et al., 2022) could be used to inform decisions regarding the timing of livestock grazing, and the number and size of pastures leased in wet versus dry season. 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 potentially 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., Young et al., 2005; Keesing et al., 2018). To the best of our knowledge, ours is the first in-depth investigation in a poorly-known ecosystem hosting one of the last viable populations of a large, endangered herbivore, 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.

Statement

During the preparation of this work the author(s) did not use any generative AI and AI-assisted technologies.

CRediT authorship contribution statement

Saeideh Esmaeili: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Mahmoud-Reza Hemami:** Conceptualization, Data curation, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Petra Kaczensky:** Conceptualization, Funding acquisition, Writing – review & editing. **Kathryn A. Schoenecker:** Funding acquisition, Resources, Writing – review & editing. **Sarah R.B. King:** Resources, Writing – review & editing. **Bahareh Shahriari:** Funding acquisition, Project administration, Resources, Writing – review & editing. **Chris Walzer:** Funding acquisition, Resources, Writing – review & editing. **Jacob R. Goheen:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare to have no conflict of interests. This work is all original research carried out by the authors. All authors agreed with the contents of the manuscript and its submission to the journal. No part of the research has been published in any form elsewhere. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. All sources of funding are acknowledged in the manuscript, and authors have declared no direct financial benefits that could result from publication. Onager 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.

Data availability

Data associated with resource selection analyses are available via Dryad repository at: https://datadryad.org/stash/dataset/doi:10.5061/dryad.dr7sqvb5q.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110476.

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