

RESEARCH ARTICLE

Coexistence between Przewalski's horse and Asiatic wild ass in the desert: The importance of people

Qing L. Cao^{1,2}  | Yongjun Zhang³ | Melissa Songer² | Peter Leimgruber² | Defu Hu⁴ | Jicai Li⁵ | Chen Wang⁵ | Daniel I. Rubenstein¹

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

²Conservation Ecology Center, Smithsonian National Zoo and Conservation Biology Institute, Front Royal, Virginia, USA

³School of Life Science, Xinjiang Normal University, Urumqi, China

⁴School of Ecology and Nature Conservation, Beijing Forestry University, Beijing, China

⁵Kalamaili Nature Reserve, Urumqi, China

Correspondence

Daniel I. Rubenstein
Email: dir@princeton.edu

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Abstract

1. Przewalski's horses and Asiatic wild asses were thought to have coexisted in the past. After reintroducing the extinct-in-the-wild Przewalski's horses within the range of Asiatic wild asses around 2000, it was hoped they would coexist through different resource utilization strategies. However, equid species worldwide rarely share landscapes. The Dzungarian Gobi, with limited water availability, also seems incapable of supporting two equids even though they exhibit differentiated niches.
2. We delimited their fundamental and realized niches in water use by captive experiments and camera traps at watering points at Kalamaili Nature Reserve, China. Using generalized linear models and circular statistics, we analysed how interspecific competition, human presence and environmental factors (temperature, precipitation, water salinity and water deficits) affected each species' daily water use patterns.
3. The two equids exhibited distinct water-use patterns. In captivity, Przewalski's horses showed higher water dependency than wild asses—drinking more frequently, consuming more water per unit body weight (0.095 vs. 0.032 L/kg) and displaying greater sensitivity to high temperatures. Field observations from 316,556 camera trap photos over 665 days revealed that horses relied on fixed watering points and avoided saline and near-depleted watering points, unlike asses. While both could drink freely day and night when separated, their interactions in shared territories showed a clear pattern: horses primarily drank during the daytime when heat loading peaked and used physical dominance to keep smaller-bodied asses away from low-salinity, long-lasting watering points until nightfall when they left to forage. This forced asses to either drink at low-salinity watering points at night or use high-salinity ones during the day.
4. The numerical advantage of wild asses—travelling in large herds—often results in their depleting watering points that were spring-fed. However, watering points near human settlement, though scarce, remain accessible to horses as asses avoid

Qing L. Cao and Yongjun Zhang co-first authors.

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them, thus providing reliable drinking spots for horses, particularly harems, after night-time foraging. They serve as crucial refuges, preventing competitive exclusion by the numerically—but not physically—dominant asses.

5. *Synthesis and applications*: Our findings highlight the importance of people in permitting sympatric coexistence during resource scarcity. However, human involvement requires careful management. Increased human presence may benefit horses but restrict wild asses' access to some quality water, potentially weakening their climate resilience.

KEYWORDS

camera trap, conservation reintroduction, Dzungarian Gobi, ecological niche, Kalamaili Nature Reserve, resource depletion, water dependence, water use experiment

1 | INTRODUCTION

Species coexistence in the same geographic area usually requires differences in morphology, physiology or behaviour to create diverse ecological niches (Bell, 1971; Hutchinson, 1957; MacArthur, 1958). Fossil records have suggested that caballoid horses ('true horses') and stenohipid horses (wild asses) cohabited across the Holarctic steppes from Alaska to Europe as early as the mid-Pleistocene, about 1 million years ago (MYA; Forsten, 1988; Ryder, 1990). Yet, their once-thriving populations nearly collapsed during the late Pleistocene (Feh et al., 2002; Orlando et al., 2013), likely as a result of climate change, overkill by early humans or both (Barnosky et al., 2004; Guthrie, 2003). Their modern descendants, the Przewalski's horse (*Equus ferus przewalskii*, IUCN status: Endangered) and the Asiatic wild ass (*E. hemionus*, Nearly Threatened), have formed a unique dual-equine assemblage in the Dzungarian Gobi (Kaczensky et al., 2008; Ransom & Kaczensky, 2016).

The two equids have distinct natural histories since their ancestors diverged around 4 MYA (Azzaroli, 1992; Orlando et al., 2013). The true horses emerged and thrived during the most recent Ice Age (Azzaroli, 1992; Guthrie, 2001). Larger and bulkier than wild asses, this group is characterized by its tolerance to extreme cold (Bennett & Hoffmann, 1999). Przewalski's horse, once believed to be widespread across cold and mesic steppes (Cao et al., 2023; Moehlman et al., 2016), was last found in the wild only in the Dzungarian Gobi—an arid desert at the periphery of its historical range—after its discovery in 1881 (Channell & Lomolino, 2000; Van Dierendonck & Wallis de Vries, 1996). It went extinct in the wild in the 1960s (Bouman & Bouman, 1994), likely due to severe weather, hunting and conflicts with pastoralist herders (Ryder, 1993; Wakefield et al., 2002). Breeding and reintroduction efforts have since helped restore wild populations in Mongolia and China (Kaczensky et al., 2016) and by 2023, over 600 Przewalski's horses roamed the Dzungarian Gobi. In contrast, the stenohipid horses evolved in the Old World long before the Pleistocene Ice Age (Janis & Bernor, 2019; Vilstrup et al., 2013). Once widespread across Eurasia and the Horn of Africa, wild ass populations declined in numbers in the northern and central parts of the Holarctic steppes after the rise and spread of true

horses in these regions (Azzaroli, 1983; Guthrie, 2001). However, they demonstrated adaptations to aridification and cooling (Janis & Bernor, 2019), which are abundant in semi-deserts and plateaus of tropical and temperate zones (Cao et al., 2023; Feh et al., 2002). Today, remnant populations are limited to a series of isolated desert and mountain areas in Asia and continue to face threats from habitat loss, poaching, and conflicts with livestock (Kaczensky et al., 2015). The Gobi deserts, including the Dzungarian Gobi, harbour the largest and the only increasing Asiatic wild ass population, numbering nearly 50,000 individuals (Moehlman et al., 2016).

Anthropogenic factors have been a major driver of equid population dynamics (Barnosky et al., 2004; Olsen, 2016), shaping how these species respond to human presence. Wild asses remain viewed as pastoral pests in some regions (Šturm et al., 2017), making them extremely sensitive to, and fearful of, humans. In contrast, Przewalski's horses—though shy and evasive in the past—have become less wary of human activities after years of captive breeding and post-release monitoring (Kaczensky et al., 2016). The ongoing conservation efforts and cultural significance have also fostered acceptance and tolerance from local communities (Zhang et al., 2015).

Moreover, horses have been reported to be more aggressive than other species when competing for water (Gooch et al., 2017; Hall et al., 2016). Zhang et al. (2015) reported that Przewalski's horse often drove wild asses away from water. Horses live in close-membership bands in which one stallion and 2–4 unrelated mares and their offspring establish long-term bonds (Boyd et al., 2016; Rubenstein et al., 2016). Strife among harem stallions is common since they drive away competitors, allowing their females to graze efficiently. Such frequent high-intensity aggression could enable horse stallions to defend localized limiting resources such as small watering points. In contrast, Asiatic wild asses live in a fission-fusion society, in which group membership is ephemeral with individuals coming and going depending upon individual needs. In the Dzungarian Gobi, they usually form small groups of 4–24 individuals, but these small groups can merge into herds of up to 1000 individuals (Boyd et al., 2016; Kaczensky et al., 2008).

Could these differences enable long-term survival and coexistence in the modern era? This is only possible if both species can

meet all their needs. Kaczensky et al. (2008) suggested coexistence was possible in the Dzungarian Gobi through habitat choice separation—Przewalski's horses primarily stayed in areas with abundant water, while Asiatic wild asses utilized both arid and mesic habitats. A camera trap study by Zhang et al. (2015) further concluded their segregated niches in sympatry through distinct water-use patterns: horses drank multiple times a day, mostly during daylight hours, and preferred low-salinity watering points, while asses tended to visit water at night, tolerated saline water and avoided settlements.

Conclusions drawn from these studies assumed water sources were consistently available. They failed to consider how environmental fluctuations and the impact of hundreds of thirsty animals could reduce water availability locally and make its regional distribution variable and unpredictable. Tolerance and coexistence between closely related species are more likely in highly productive and predictable systems, whereas competitive exclusion may be more pronounced in low productivity systems where resources are limited and fluctuate, preventing resource specialization (Chesson, 1986). In the African Savanna, one of the most speciose landscapes where bovids have diversified extensively through variations in body size, morphology and behaviour to adapt to subtle differences in resource structure, abundance and quality, the equids—three zebras and one ass—show limited diversification and mostly live in separate regions (Bauer et al., 1994; Nacarino-Meneses, 2023). The only exception occurs on the semi-arid grasslands of central and northern Kenya and southern Ethiopia, where both the mesic-adapted plains zebra (*E. quagga*) and the arid-adapted Grevy's zebra (*E. grevyi*) coexist through spatial segregation: the more numerous plains zebra outcompetes the larger Grevy's zebra for forage where their ranges overlap, but the latter moves into areas free of interspecific competition because of its water independence (Rubenstein, 2010). Most of the Dzungarian Gobi has a mean annual precipitation of lower than 200 mm, but interannual variability is high. Areas with favourable water and forage conditions are extremely rare and costly to maintain. Such low habitat productivity and predictability might limit niche differentiation among species phylogenetically closely related (Gersick & Rubenstein, 2017; Rubenstein et al., 2016). Moreover, the scarcity of water sources leaves the two equids vulnerable to drought and intensifies interspecies competition for water, especially the horses with greater water needs. Consequently, as the mesic-adapted horse was relegated to the Dzungarian Gobi, the two species experienced different fates: the Przewalski's horse once went extinct, while the Asiatic wild ass thrived (Kaczensky et al., 2015).

Since the Przewalski's horses were rewilded, coexistence with the Asiatic wild asses represents the ideal outcome of conservation efforts. However, we still do not fully understand the extent of niche differentiation between horses and asses, or its underlying drivers—whether physiological adaptations, morphological and behavioural traits, or human influence. To address this, we assessed which features define each species' fundamental niche and how various interactions shape their realized niches. This study focuses on water-use, a crucial factor for desert species (Cain

et al., 2006), to determine: (a) The degree to which the two equids' water use patterns differ? (b) If they do, how does this shape the fundamental water niche? And if (c) the relationship between the two fundamental niches should not allow coexistence, what additional factors enable the realized niches to diverge? To answer these questions, we first measured the water consumptions of captive individuals under a variety of ecological conditions. This enabled us to characterize the water fundamental niche. Then, by measuring visitation rates at different watering points of differing size and quality by camera traps, we were able to characterize the interactions that created the realized niches of the two species. Therefore, from a combination of the results of captive and field studies, we constructed both the fundamental and realized niches of these species along axes of climatic, environmental, and anthropogenic factors. In this way, we were able to identify how the interactions among key environmental factors and physiological needs, morphological features and behavioural abilities of these interacting species foster coexistence of sympatric horse and wild ass populations in deserts.

2 | MATERIALS AND METHODS

2.1 | Study area

The Kalamaili Nature Reserve (KNR) is one of China's largest protected areas, spanning approximately 14,000 km² (Figure 1). Located in the heart of the Dzungarian Gobi, it is characterized by a continental climate typical of cold deserts (Chu et al., 2009). The average annual temperature is about 2°C, with monthly averages reaching 20.5°C in the hottest month and dropping to −24.3°C in the coldest month. Water is scarce in the KNR, with annual precipitation averaging 159.1 mm and no permanent surface runoff. Natural springs, along with puddles formed by snowmelt or rain, are the primary water sources, but they can be temporarily or permanently depleted when consumption and evaporation exceed recharge (see Table S1 in Supporting Information). Evaporation before recharge tends to leach salts from the soil, thus increasing the salinity of these water sources. Rain-created puddles provide fresh water and are widely distributed, but are short-lived. In winter, springs and puddles are frozen, but water availability is no longer a problem because of frequent wide-spread snowfalls.

KNR was established in 1982 to conserve wild ungulates and their indigenous habitats. The Przewalski's horse was first discovered in KNR in 1881 (Rayfield, 2013). Hunting pressure and conflict with domestic horses and human activity greatly reduced the population's growth rate. Three surveys in the early 1980s found no sign of this species in Chinese Dzungaria (Gao & Gu, 1989). The Chinese government imported 24 Przewalski's horses from the western zoos in the 1980s and established the Xinjiang wild horse breeding center for ex-situ conservation. KNR initiated its Przewalski's horse reintroduction program in 2001 (Chen, 2008). By 2023, this population had grown to over 350 individuals. The

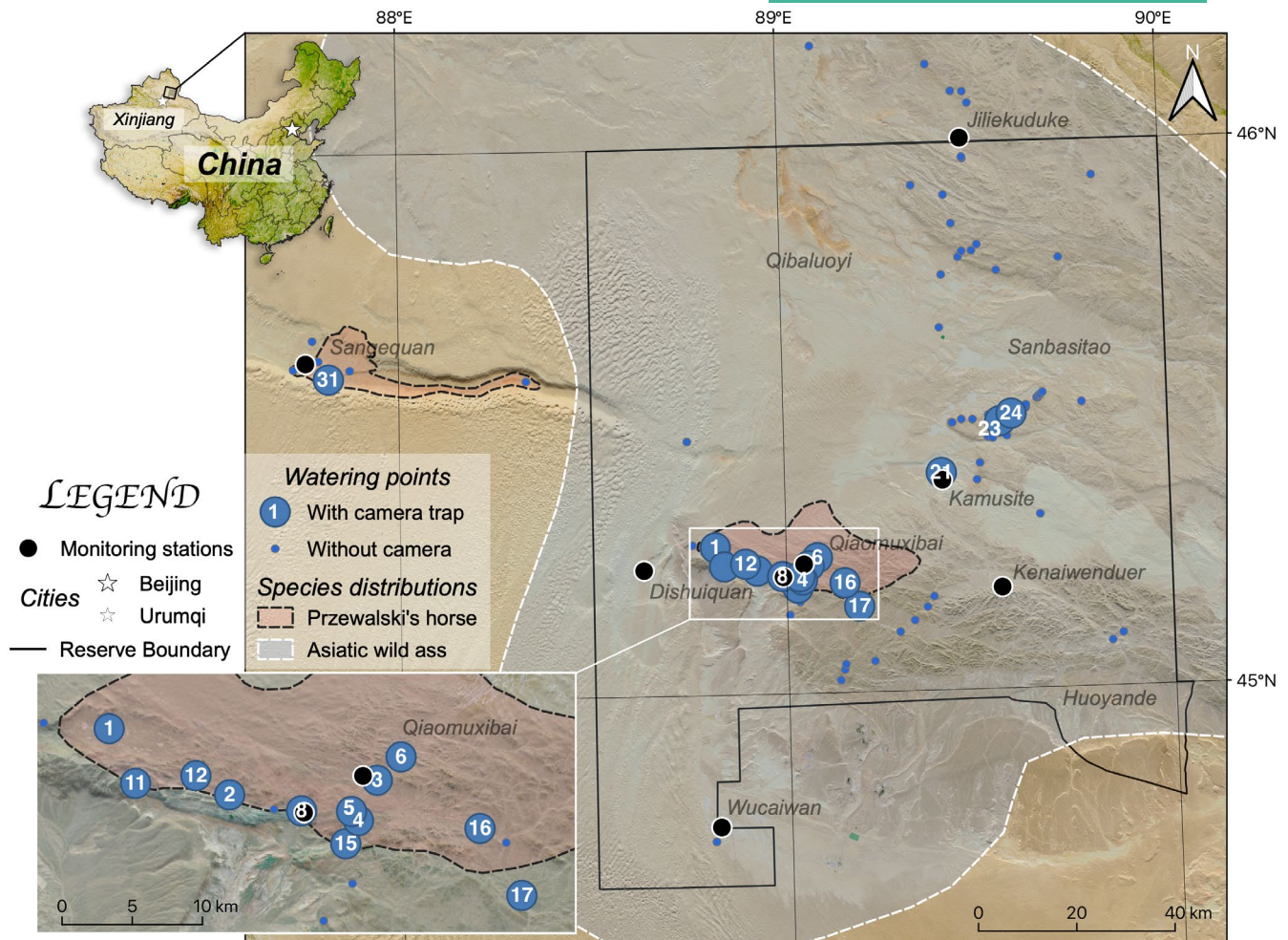


FIGURE 1 Distribution of watering points in Kalamaili Nature Reserve, Xinjiang, China, and locations of watering points used in this camera trap study. Small blue circles indicate the geographic locations of all known watering points in the area, with enlarged circles and numbers marking the watering points used in this study. Black circles represent monitoring station locations. The red and blue shaded areas show the main distribution of Przewalski's horse and Asiatic wild ass, respectively, based on both the IUCN Red List database and field observations.

Asiatic wild ass also suffered from habitat loss, poaching and conflicts with livestock in the Dzungarian Gobi (Feh et al., 2002), but it never went extinct. Since the founding of KNR, the number of Asiatic wild asses has increased from about 400 to over 4000 in 2008 (Chu, 2008; Zheng & Gao, 2000). Other indigenous ungulates, the goitered gazelle (*Gazella subgutturosa*) and the Gobi argali (*Ovis darwini*), rarely visit the watering points and, because of their small size, remain inferior competitors for water. The grey wolf (*Canis lupus*) is the primary predator, but their numbers are low in KNR, and they rarely pose a threat to adult equids.

2.2 | Water-use experiment

A water-use study of both Przewalski's horses and Asiatic wild asses was conducted at the National Zoo's Conservation Biology Institute (NZCBI) in Front Royal, Virginia, USA, from August 8 to September 2,

2012. It was designed to collect information on the drinking habits of the species under a variety of ecological conditions to help determine the fundamental niches of the two equids. Compared to KNR, NZCBI presents a more temperate habitat for the two equids. Temperatures averaged 25.5°C in July and 2.2°C in January, with annual precipitation averaging 1040mm (data acquired from NOAA). Four Przewalski's horses (three males and one female) and three Asiatic wild asses (three males) were chosen from the captive population based on their physical health and tolerant disposition towards the observer (see Table S2). Animals were kept in individual stalls where ad libitum amounts of prescribed foods and water were provided throughout the study period. The amount of food and water consumed were measured at the end of each day. Morning and afternoon temperatures are also recorded. We used Pearson's product-moment correlation coefficients to test our hypothesis that Przewalski's horses would consume more water than Asiatic wild asses on average and that their water consumption would increase with increasing temperature.

2.3 | Camera trapping

Since a species' realized niche is the result of interactions among key morphological features and behavioural abilities of these interacting species, we designed a camera trap study to determine if the two equids can share or divide up the water sources in ways that enable the survival of both species. From 2010 to 2013, during the 'ice-free' months between April and October, 16 watering points in KNR, varying in location, size, salinity, rate of recharge, and human presence (Figure 1), were outfitted with camera traps to record visits, drinking behaviour, and competitive interactions (see Table S1): 13 watering points originated as natural springs, eight of which were transformed into large waterholes 5–10m wide; two others were temporary puddles, typically forming after rain; and one was an artificial ditch shared with livestock. Six watering points that equids never visited were removed from the analysis. Salinity was recorded as a measure of water quality since it is highly correlated with other water quality measures (Wolanski & Gereta, 2001). We sampled the water salinity of all the watering points using a refractometer (Vital Sine SR6, Pentair Aquatic Eco-systems, Inc., Apopka, FL, USA) on a monthly basis and confirmed that their values remained largely constant. Consequently, we used the average salinity readings for each watering point.

Passive infrared triggered camera traps (ScoutGuard SG-550, Boly Media Communications Co. Ltd., Shenzhen, Guangdong, China) were positioned five meters from the edge of the watering point and situated at least 0.2m above-ground. We either attached the camera to natural stable objects along the bank, such as shrub branches or high rock piles, or to a 0.5m steel pole that blended in to the environment. Depending on the size of the watering point, full coverage of the site was ensured by deploying up to three camera traps. Cameras were set up according to Zhang et al. (2015). All cameras were visited twice per week to retrieve data and replace batteries. The longest monitoring period lasted for 383 days (see Table S1).

2.4 | Statistical analysis on camera trap data

Since individual identification of these non-distinctively marked equids was impossible, we used discrete time bins of 5minutes to quantify the circadian and seasonal water use of each species (see Appendix S1). A day is broken down into 288 five-minute bins. The proportion of these bins in which each species visited a watering point is used as the dependent variable and to evaluate water use preferences by each species. An independent generalized linear mixed model (GLMM) in the Poisson family was then drawn for each species, with the *lme4* package in R (Bates et al., 2014), in which a series of biotic and abiotic environmental factors (see Appendix S2; Table 1) were used to determine the water use pattern. To assess how strongly the two species shared watering points, we used each species' bin-based visiting frequency as covariates in the other species' model. The quadratic forms of all covariates were tested for high-order responses. We also included the interactions among abiotic covariates. Moreover, the watering points were used as the random effect in the

TABLE 1 Covariates used to model the daily water-use frequencies.

Covariate	Description
Fixed effects	
T	Daily maximum temperature (°C)
R	Daily rain precipitation (mm)
S	Average water salinity (‰)
H	Distance from water to nearest road or settlement (km)
W	Percent water depleted (%)
P or K	Daily visit rates by Przewalski's horse (P) or Asiatic wild ass (K)
Random effects	
L	Names of water springs

mixed models (see Table S3) after being validated in the analysis of variation (ANOVA). Candidate models were selected in a backward fashion (Bursac et al., 2008). The model performance and sensitivity of each covariate were evaluated based on the Akaike information criterion (AIC), unless there was a disagreement between AIC and the Bayesian information criterion (BIC; see Table S4). Given our large sample size (2023 camera days totally) and our goal of finding the 'correct' variables and relationships rather than letting the model grow in complexity (AIC), BIC was used in such scenarios to avoid overfitting (Aho et al., 2014; Burnham & Anderson, 2002). Finally, the results were cross-validated using the *K*-fold validation (see Appendix S3).

The interspecific effect of one species on the other's preferred water-use time is determined by fitting the probability distribution of the time of day of their visits with the circular kernel density, using the *R* package *activity*. We first identified watering points with low or high occupancy by each species. Since there are watering points visited only by wild ass, we categorized wild ass watering points as either jointly used or not. Almost all watering points used by Przewalski's horses were also used by wild asses. Only one watering point—a rain-fed puddle that lasted just 4 days—was not shared, and it was excluded from the analysis due to its small sample size. As a result, all Przewalski's horse drinking points were classified as shared between horses and asses, though the level of shared use varied among locations. We classified the wild ass visits into many visits (>10 average daily visits) and few visits (<10 average daily visits). We employed the Wald chi-squared test to compare the similarity of the two probability distributions of watering point use under different interspecific pressures.

We also examined whether the interspecific influence exerted uneven pressure on different reproductive states within the same species. These two equids maintain distinct societies and social relationships (Rubenstein, 1986). We categorized the visits of wild asses into those with foals or those without. Using Pearson's product moment correlation test, we analysed whether the proportions of breeding groups (harems for Przewalski's horse and groups with foals for wild ass) were subjected to the increase in interspecific pressure as measured by the visit rates of its congener counterpart.

All data handling and statistical testing were done in R. The mapping was done with QGIS 3.22.5.

2.5 | Niche illustrations

We identified five main niche dimensions influencing the water-use patterns of the two equids in our experiment and camera traps: physical strength, heat tolerance, water deficit tolerance, salinity tolerance, and sensitivity to humans. Using qualitative indices (detailed in Appendix S4), we assessed each equid's performance in these dimensions on a scale of 0 to 20. To visualize our findings, we created two spider plots using the R package *fmsb*. The first plot showcased four dimensions, omitting human stress, while the second incorporated all five axes. In each plot, the size of non-overlapping areas of the fundamental niches reveals the degree to which the realized niches differ.

2.6 | Ethics statement

This study was approved by the National Natural Science Foundation of China (grant no. 30970545) and passed its ethical evaluations. It was also reviewed by Princeton University IACUC (Protocol No. 1835). The fieldwork was carried out under the authority of a scientific permit issued by the Altai Forestry Bureau, Xinjiang, China.

3 | RESULTS

Controlled experiments highlighted the fundamental niche differences in the water needs of the two equids. Przewalski's horse drank water daily, while the Asiatic wild ass skipped drinking during 16 of 78 experiment days (chi-squared test, $\chi^2=20.301$, $p<0.001$). Moreover, at most temperatures, the Przewalski's horse consumed more water daily on a weight-specific basis than the Asiatic wild ass (Figure 2). With increasing temperature, the water consumption of the Przewalski's horse increased (Pearson's correlation test, $df=95$, $\rho=0.4741$, $t=5.249$, $p<0.001$), but that of the wild ass remained unchanged ($df=74$, $\rho=-0.0644$, $t=-0.555$, $p=0.5805$).

We collected a total of 316,556 valid photos of equids over 665 camera trapping days. Of the 16 watering points monitored with camera traps, only one was visited exclusively by Przewalski's horses and only six by Asiatic wild asses exclusively. The remaining nine, all natural springs, were shared by both equids (see Table S1). Furthermore, their visit rates at shared watering points during the same days were highly correlated (Pearson's correlation test, $df=1662$, $\rho=0.4485$, $t=20.46$, $p<0.001$).

The two independent GLMM models, based on recorded visitation rates of the two equids at shared watering points, revealed broad similarities in their realized water niches (Table 2), but some important differences emerged. First, as Figure 3a shows, there is a strong correlation in the frequency of visits to shared watering points. Yet, unlike in our captive study, the Asiatic wild ass

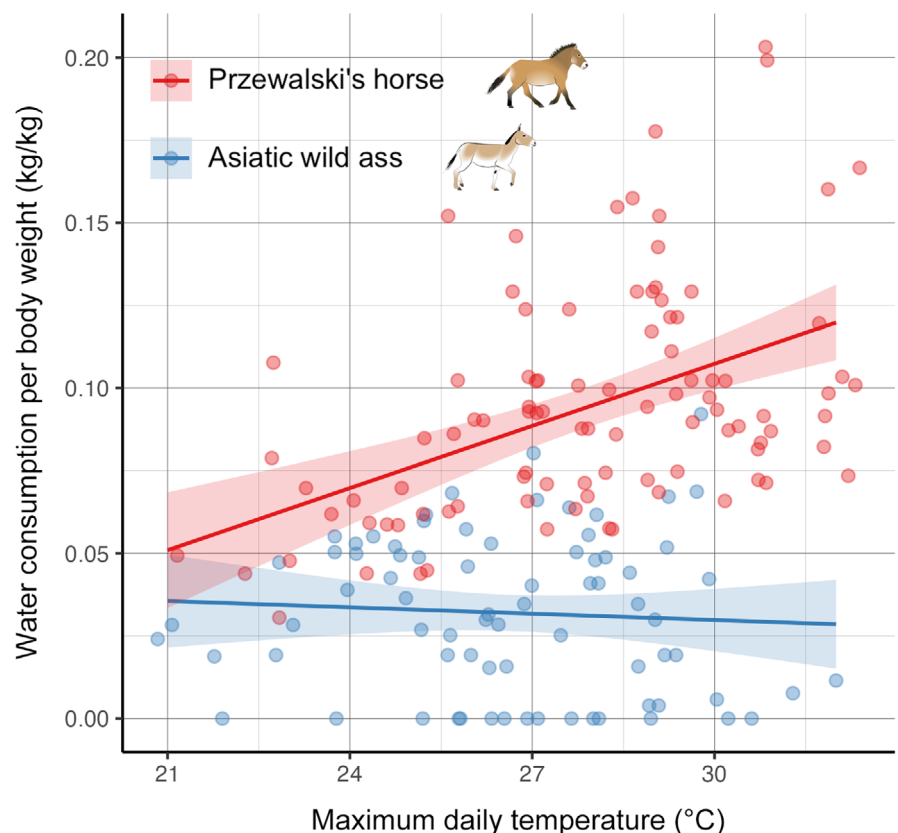


FIGURE 2 Daily water consumption per kg of body weight in relation to maximum daily temperature by the two equids in the water-use experiment under captivity. Water consumption of the two equids were fitted with the linear regressions. The ribbons in the plots represent the 95% confidence intervals.

Covariate ^a	Coefficient	SE	z value	p ^b	Random effect
Przewalski's horse					$\chi^2 = 694.5^c$, $p < 0.001^{***}$
Constant	0.899	0.113	7.952	<0.001***	
T	0.118	0.016	7.457	<0.001***	
(T ²)	0.158	0.014	11.635	<0.001***	
R	-0.067	0.016	-4.101	<0.001***	
S	-0.731	0.124	-5.886	<0.001***	
(S ²)	-0.256	0.095	-2.686	0.007**	
W	-0.223	0.054	-4.155	<0.001***	
K	0.469	0.016	29.690	<0.001***	
(K ²)	-0.123	0.009	-12.940	<0.001***	
(T×S)	-0.141	0.014	-10.181	<0.001***	
Asiatic wild ass					$\chi^2 = 8727.5$, $p < 0.001^{***}$
Constant	1.389	0.378	3.671	<0.001***	
T	0.187	0.010	18.034	<0.001***	
(T ²)	0.051	0.009	5.583	<0.001***	
R	-0.335	0.029	-11.591	<0.001***	
(R ²)	0.298	0.026	11.632	<0.001***	
H	1.305	0.603	2.166	0.030*	
(H ²)	-1.248	0.563	-2.214	0.027*	
W	0.340	0.044	7.667	<0.001***	
P	0.340	0.008	41.867	<0.001***	
(P ²)	-0.093	0.005	-17.411	<0.001***	
(T×H)	0.179	0.016	10.844	<0.001***	
(T×W)	0.221	0.036	6.099	<0.001***	
(H×W)	0.216	0.097	2.223	0.026*	
(T×H×W)	-1.508	0.095	-15.926	<0.001***	

TABLE 2 Top-ranked generalized linear mixed models (GLMM) for Przewalski's horse and Asiatic wild ass, respectively.

Note: The ranking is based on the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). In each model, the response variable is the proportion of the day the water was visited, and the fixed and random effects are listed in [Table 1](#).

^aThe covariates inside parentheses “()” are treated as a single covariate, to test the quadratic relationship (²) and interactions (x) of the covariates.

^bSignificance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^cAnalysis of variance (ANOVA) on random effect.

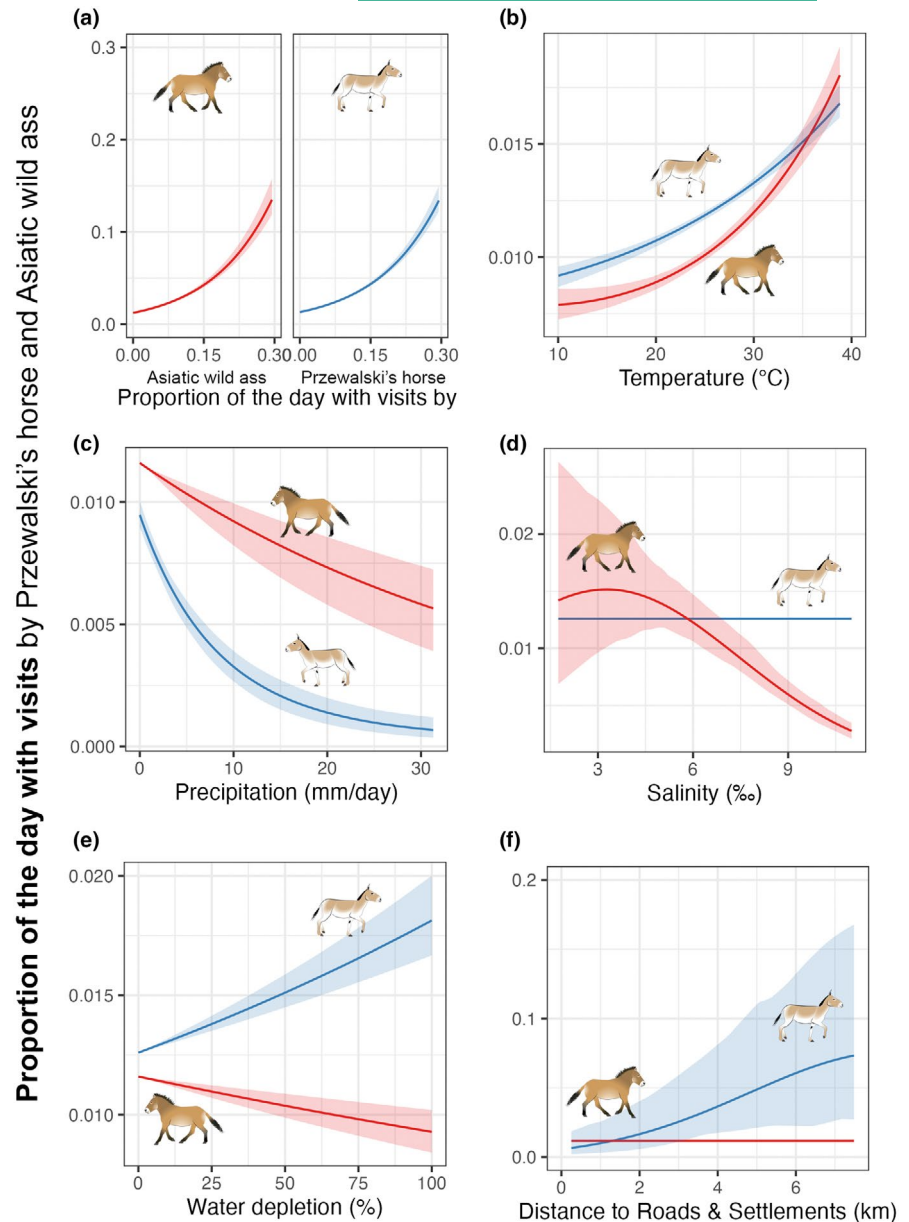
increased its water visitation rate in response to rising temperatures. The slope of the relationship, however, was not as steep as that of the Przewalski's horse ([Figure 3b](#)). And while hot and dry conditions, which were frequent during the summer, forced both species to visit shared watering points at similar rates ([Figure 3c](#)), high levels of precipitation created widespread puddles while also lowering ambient temperatures and heat loads. This enabled wild asses to reduce dependence on drinking from shared watering points. Horses, however, still made frequent visits to the fixed watering points.

In addition to these small seasonal differences in drinking from fixed permanent watering points, the two equids revealed differences in tolerance for water varying in quality and quantity. Horses preferred watering points with low salinity, while asses showed no particular preference for water varying in levels of salinity ([Figure 3d](#)). Horses also avoided fixed watering points

containing little standing water. The quantity of water typically declined after large groups of Asiatic wild asses visited a fixed watering site (see [Figure S1](#)). The model suggests that the asses can tolerate lower quality watering points that are of high salinity than horses, and because the asses regularly deplete them, horses are forced to avoid or abandon such sites, moving to those with more standing water of lower salinity ([Figure 3e](#)). This was especially the case for breeding harems, non-lactating females and lactating females with foals ([Figure 4a](#)). Only groups of Przewalski's horse comprised solely of bachelor males continued to use watering points frequently visited by wild asses. Overall, the composition of wild ass groups using shared watering points remained constant, even though demographic differences led to content differences in watering point use ([Figure 4b](#)).

The most sought-after long-lasting watering points that the horses used were near human infrastructures ([Figure 3f](#)). Given the

FIGURE 3 Generalized linear mixed model predictions on the proportion of the day that Przewalski's horse and Asiatic wild ass spent at permanent watering points, respectively. The covariates consisted of interspecific factor ([a] proportion of the day with visits by the sympatric competitor, Asiatic wild ass and Przewalski's horse, respectively), weather conditions ([b] daily maximum temperature, and [c] daily rain precipitation), as well as water characteristics ([d] water salinity, [e] water deficit, and [f] distance to nearest road or settlement). The ribbons in the figure represent the 95% confidence interval estimated from bootstrapping.



low visitation rates of wild asses to watering points associated with people, watering points associated with human activity became dominated by a large number of Przewalski's horse harems (see Figure S2). In essence, human associated watering points became a refuge for Przewalski's horses.

Although these two equids were active at watering points during different times of the day (Figure 5; Wald test, $\Delta = 0.0520 \pm 0.0138$, $W = 14.2822$, $p < 0.001$), watering points jointly shared with the larger and bulkier Przewalski's horses, were used by wild asses mostly during the night ($\Delta = 0.1208 \pm 0.0206$, $W = 34.5250$, $p < 0.001$). This is because Przewalski's horses need to drink many times during the day, and their larger body size enables them to repel approaches by smaller and lighter asses. Thus, Przewalski's horses monopolise fixed watering points near people, whether or not wild asses were in the vicinity ($\Delta = -0.0466 \pm 0.0245$, $W = 3.6136$, $p = 0.0573$).

4 | DISCUSSION

The distinct water-use patterns of the two equids stem from features that define their fundamental and realized niches. Our study confirms that Asiatic wild asses need less water and show greater tolerance to varying water types, quality, and quantity. When coupled with a physiology that frees them from drinking daily, wild asses are better adapted to arid conditions than Przewalski's horses which must drink daily from sites with abundant low-salinity water. Yet Przewalski's horses compensate for their strict water requirements through behavioural adaptations, including social dominance, aggressive behaviour, and tolerance of human presence (Zhang et al., 2015). By defending high-quality watering points during daylight hours—while wild asses, driven by fear, visit these sites at night when the horses leave to forage—the horses can meet their daily needs when they return the next day if water is still available. The continued

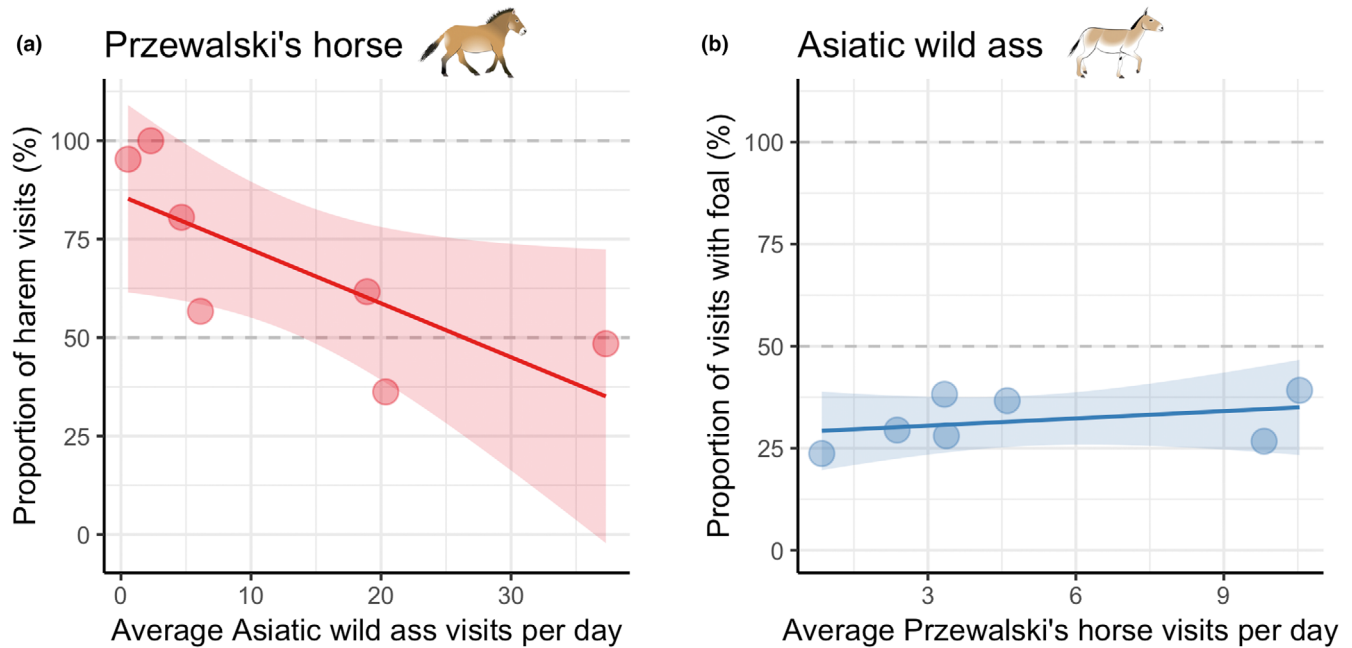


FIGURE 4 The two equids' responses in group composition to the average daily visit rates of the sympatric competitor at shared watering points. For each water point, we calculate the average visit rates of each equid, and the proportions of visits by different phenotypes. We identify the phenotypes of Przewalski's horse into harems (family groups consisting one male and several females and their offspring) and bachelor groups (all-male groups). Meanwhile, since Asiatic wild ass lack rigid groupings (fission-fusion sociality), we separate the visits into groups with and without foals. Linear regressions are used and the 95% confidence intervals are shown as grey ribbons.

availability of this water is partly ensured by an external factor—the presence of people on the landscape. Human intervention plays a crucial role, which is somewhat ironic since people who restricted the distribution and suppressed the numbers of both equids now provide a unique and critical refuge for Przewalski's horses, ensuring both species can meet their different water needs.

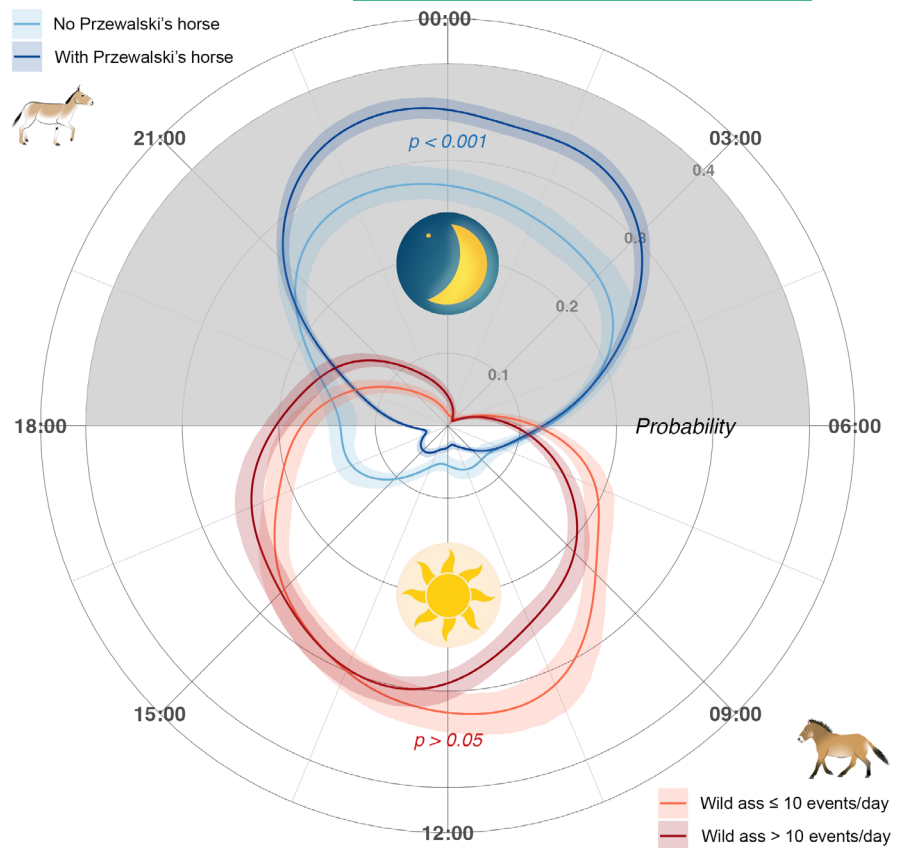
The different needs which lead to distinct fundamental niches are influenced by differences in physiology, body size, and behaviour. Physiologically, the Przewalski's horse requires both more water on a weight specific basis and higher intake rates than the Asiatic wild ass (Figure 2), supporting previous speculation about the Przewalski's horses' high water dependency and adaptation to mesic steppe (Kaczensky et al., 2008; Van Dierendonck & Wallis de Vries, 1996). As a result, free ranging Przewalski's horses are more sensitive to changes in temperature and precipitation, as well as to the quality and quantity of water at permanent watering points (Figure 3). Meanwhile, free-ranging Asiatic wild asses also increased visits to watering points as temperature in KNR rose, in part because summer is the breeding season for all equids and lactation requires a great amount of water (Cain et al., 2006; Rubenstein, 1993). Since low salinity watering points that Przewalski's horses prefer are also attractive to wild asses and other wildlife, it is not surprising that both equids tended to visit the same watering points on the same day (Figure 3a). The most notable difference between the species, however, lies in their contrasting circadian cycles, which reduces direct interspecies competition (Figure 5). Whilst many desert ungulates, including the wild ass, restrict most of their activities to the cooler nights in order to avoid heat and water loss during the day

(Alderman et al., 1989; Lewis, 1977), Przewalski's horses exhibit diurnal drinking behaviour not only in deserts where it is accentuated, but also in more mesic habitats (King, 2002), revealing an intrinsic species-specific high demand for water.

Could such niche partitioning in water-use patterns foster coexistence? It is feasible in regions where water is abundant since plentiful supplies will enable horses to leave watering points to feed during cool nights and return to full watering points the next morning. When water is more limited, no such assurances exist under conditions in the absence of people. Given that wild asses greatly outnumber Przewalski's horses in KNR, large herds of asses will deplete the watering points when the horses leave to graze at night. Thus without people populating the landscape, the asses would likely drive the horses to extinction (Figure 3e; Figure S1) as predicted from Tilman's (1982) proposition that when competing for a single limiting resource, the species that can survive at the lowest equilibrium level of that resource would outcompete all others sharing that resource.

Fortunately for the horses, watering points free of wild asses exist near human infrastructure (Figure 1; Table S1). In the KNR, only two monitoring stations serve as human infrastructure within the area where both wild equids coexist. Some of the highest quality, low salinity watering points in KNR are found near them. Given that wild asses shy away from people living and working near the stations (Figure 3f; Figure S2), the horses' size-enhanced aggressive dominance during the day (see Table S2), combined with the wild asses' fear of humans at night, creates essential water refuges for socially cohesive Przewalski's horses—especially for harems in which

FIGURE 5 Circadian probability of water-use by Asiatic wild ass and Przewalski's horse at watering points with low and high presences of sympatric competitor. We categorize watering points used by Asiatic wild ass into those shared with Przewalski's horse and those without the latter's visits. For Przewalski's horse, since all watering points it used are shared with Asiatic wild ass, we divide watering points according to visit frequencies of the wild ass, as rare (≤ 10 average daily visits) or frequent watering points (> 10 average daily visits). The ribbons of 95% confidence interval are calculated from bootstrapping.



breeding females reside (Rubenstein, 1986; Zhang et al., 2015), which allows the horses 24-h access to these watering points. As a result, desert-living Przewalski's horses avoid intense interspecies competition for water because water depletion by numerically abundant wild asses is essentially eliminated.

According to Hutchinson (1957), a species' fundamental niche can be visualized as an n-dimensional hypervolume. By projecting these differences onto a three-dimensional Hutchinsonian space, we can visualize the fundamental niches of two related equids in terms of factors that affect water use (Figure 6). The spider graph shows that before people (Figure 6a) shared the landscape with wild equids, the asses were more able to cope with arid conditions than the horses. On virtually each critical dimension—tolerance of salinity, low levels of replenishment, water deficit and high heat—of the polygon of the horses is completely embedded within that of the asses. Only with respect to physical strength, which enhances dominance and fighting ability, does the niche space of horses exceed that of asses. Only when people also share the landscape do the non-overlapping regions of the spider plot increase and become approximately equal (Figure 6b). People appear to create a “landscape of fear” for the wild asses, which enables the Przewalski's horse's niche to expand since wild and free-ranging horses are tolerated by people. Since each species dominates a unique niche space, sympatric coexistence becomes possible once the human factor is introduced.

Anthropogenic factors have increasingly become one of the main influencers of species' niche space (Boivin et al., 2016; Sévêque et al., 2020). In human-dominated landscapes, studies using camera

traps have found that many wildlife species adjust their habitat choices, times of activity, or behaviours to accommodate human presence (Carricondo-Sanchez et al., 2019; Gehr et al., 2017). Black bears (*Ursus americanus*) and red foxes (*Vulpes vulpes*) have been observed seeking shelter near human infrastructures to avoid dominant competitors (Apps et al., 2006; Mueller et al., 2018; Nickel et al., 2020). In KNR, the reintroduced Przewalski's horse avoids displacement by the Asiatic wild ass through human presence near their favoured watering points.

The in-situ conservation of reintroduced species must consider the wildlife community as a whole. Our results highlight what's critical for maintaining stable coexistence between reintroduced Przewalski's horses and indigenous Asiatic wild asses. Beyond KNR, Przewalski's horses roam several protected areas within their historical range (Kaczensky et al., 2016), sharing resources with wild asses, red deer (*Cervus canadensis*), humans, and livestock (King, 2002; Šturm et al., 2017). Many models predict a warmer, drier climate for the future Dzungarian Gobi (Luo et al., 2019), while overgrazing already plagues many parts of the steppe (Tuvshintogtokh & Ariungerel, 2013), intensifying resource competition. Although KNR may be drier than most sites due to its location and lack of surface runoff, such peripheral habitats actually became the resilient strongholds for conserving many endangered species worldwide (Channell & Lomolino, 2000). Moreover, its resource scarcity, mix of allopatric and sympatric populations, and manageable human presence help us disentangle key niche factors affecting both equids' behaviours and survival strategies—factors that might be obscured in more complex

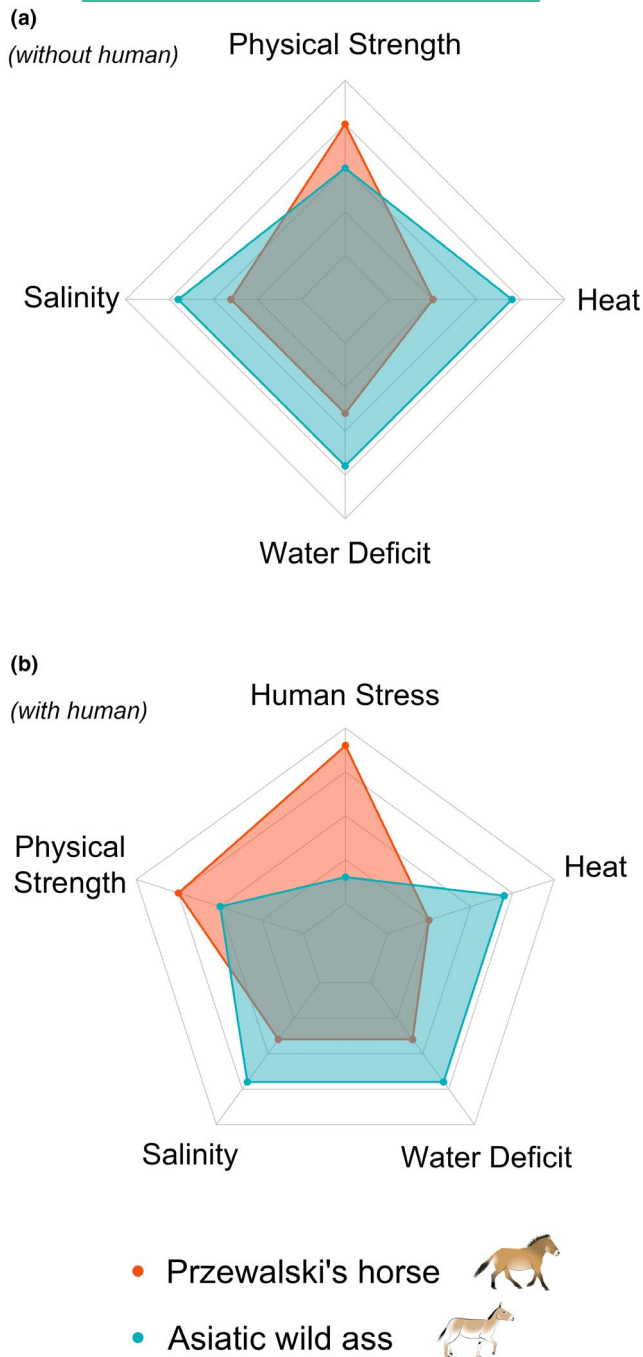


FIGURE 6 Fundamental niches of the two competing equids related to water-use, under the scenarios of without and without people. Subplot (a) illustrates the fundamental niches of Przewalski's horse and Asiatic wild ass in the Dzungarian Gobi without the presence of people. Subplot (b) shows their modern day differentiations in water-use niche with the presence of moderate people stress. The five niche dimensions related to water-use stem solely from our experiment and camera trap results and the values on each niche axis are based on qualitative indices, as detailed in the methods section.

systems. Our findings are thus broadly applicable and underscore the importance of human involvement in sustaining endangered species when critical resources are scarce and competition is high. However,

this doesn't mean human beneficial actions apply universally, partly due to the inherent unpredictability of human behaviour (Bland & Schaefer, 2012). Furthermore, managing human involvement must account for climate change impacts. As Przewalski's horses rely on human-sheltered water sources, increased human presence would expand their resources while potentially limiting those available to Asiatic wild asses, which depend on natural sources. This could compromise the wild asses' ability to withstand climatic fluctuations.

AUTHOR CONTRIBUTIONS

Defu Hu, Yongjun Zhang, Qing L. Cao and Daniel I. Rubenstein conceived the idea; Melissa Songer, Peter Leimgruber and Daniel I. Rubenstein provided the captive experiment data; Qing L. Cao and Yongjun Zhang collected the field data; Jicai Li and Chen Wang contributed to the acquisition and curation of data; Qing L. Cao and Daniel I. Rubenstein carried out the analysis and interpretation of data; Qing L. Cao and Daniel I. Rubenstein led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Figshare <https://doi.org/10.6084/m9.figshare.25972408.v2> (Cao et al., 2025).

ORCID

Qing L. Cao  <https://orcid.org/0000-0001-5544-2752>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Identifying water usage patterns of Przewalski's horses and Asiatic wild asses.

Appendix S2. Covariates used in the generalized linear mixed models.

Appendix S3. Validating the generalized linear mixed models.

Appendix S4. Qualitative evaluation of each equid's performance on niche axes.

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