Habitat use by the Persian onager, *Equus hemionus onager* (Perissodactyla: Equidae) in Qatrouyeh National Park, Fars, Iran

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Iran's Persian onager populations are critically endangered. This study of their natural history in Qatrouyeh National Park provides insights for enhancing their conservation. The population as a whole is greatly affected by weather. Wind, rain and cold drive populations from the plains to the valleys of hill-valley habitats. Vegetation features and water also influence habitat use, but differently for different sex and reproductive classes. Females with juveniles use plains with high-quality vegetation, whereas females without young and solitary territorial males choose those of intermediate quality. Females with young foals are also found closest to watering points. Future translocation of Persian onagers will only succeed if prospective habitats have sufficient hill-valley refuges and enough plains with winds to moderately hot conditions. Sufficient plains supporting high-quality vegetation near water for lactating females must co-exist with plains of moderate-quality vegetation that attract females without young, so reducing crowding and competition.

Keywords: habitat associations; equid; Normalized Difference Vegetation Index; environmental harshness; reproductive state

Introduction

Horses, zebras and asses, members of the family Equidae, flourished early in the Pleistocene and inhabited a range of habitats in North and South America as well as Europe, Africa and Asia. Today, five out of seven extant equids are now listed as threatened by the International Union for the Conservation of Nature (IUCN) including: *Equus africanus* as Critically endangered (CR), *Equus hemionus*, *Equus grevyi and Equus ferus* as Endangered (EN) and *Equus zebra* as Vulnerable (VU) species (IUCN 2008). Once distributed from Mongolia to Ukraine to Saudi Arabia and from India to Kazakhstan, the Asiatic wild ass, *E. hemionus*, now exists only in parts of China, India, Mongolia, Kazakhstan, Turkmenistan and Iran (Moehlman et al. 2008). The Persian onager *E. hemionus onager*, one of the five subspecies of *E. hemionus*, has been declining in numbers over recent decades and is restricted to two isolated populations in two semi-arid ecosystems of Iran. This taxon was categorized as critically endangered (CR) because of its small population size (IUCN 2002; Tatin et al. 2003).

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One of the central tenets of behavioural ecology is that features of the environment shape animal behaviour (Rubenstein 1986; Krebs and Davies 1997). Resource requirements affect habitat choice and resource use, which in turn affect competi- tion, grouping behaviour, mating activities and ultimately reproductive success and fitness (Lawes and Nanni 1993). Understanding the forces that shape habitat use (Henley et al. 2006; Nowzari et al. 2007) is essential for understanding how behaviour influences resource use and population dynamics (Sibly and Smith 1985). By deci- phering the rules determining how environmental features influence behaviour and population dynamics, conservation biologists should be able to assess the major threats facing species and intervene to manipulate this link by changing human behaviour to improve their survival prospects, enhance ecosystem function, and improve human livelihoods in environmentally sustainable ways (Rubenstein 2010). Overall, behavioural ecology has much to offer for solving conservation problems (Caro 1998).

Currently, Qatrouyeh National Park (QNP) and Touran National Park (TNP) are the last strongholds for the Persian onager in Iran (Ziaee 2008). Except for a few stud- ies (Groves 1974; Harrington 1977; Tatin et al. 2003), information about the ecology of populations in these protected areas is limited. There is a lack of information about population size, age structure and sex ratio and what factors influence habitat use (Duncan 1992; Moehlman 2002). The aim of this study is to identify patterns of habitat use, and how these patterns are shaped by environmental, social and reproductive factors and then determine how this information can help to guide conservation in QNP and management as has been demonstrated in other equids (Suring and Vohs 1979; Moehlman 2002; Hemami et al. 2004; Sundaresan et al. 2007; Kaczensky et al. 2008).

Material and methods

Study area

Bahramegoor Protected area was established in 1972. It is 408,000 ha in size and is located 55 km from Neyriz city and is near Qatrouyeh town in Fars province (Darvishsefat 2006). The Department of Environment identified QNP as the core zone of the Bahramegoor Protected area in 2007. It is located from 29°10′ to 29°26′ N, 54°36′ to 54°48′ E (Figure 1A, B), is 32,576 ha in size, and ranges in height from 2787 m to 1680 m above sea level. Its terrain consists of mountains and desert-like plains. Its average annual rainfall ranges from 150 to 250 mm, so it is considered a semi-arid ecosystem. Maximum temperatures reach 44°C and minimum temperatures drop to – 1°C during the hottest and the coldest months, respectively. The prevailing winds are east to west during the summer and switch to north to south during the winter. QNP includes part of the Zagros Mountains and consists of three main habitats: the Koohsorkh-e-bozorg Mountains, the Rigjamshid, Einaljalal and Dehvazir plains and many areas with hills and valleys. Water for wildlife is supplied by natural springs and human-made wells and associated drinking troughs. Three vegetation commu- nities predominate: *Artemisia–Zygophylum (Ar-Zy), Artemisia–Amygdalus (Ar-Am)* and Rock (Figure 1C) (Qatrouyeh National Park – Bahramegoor Protected Area comprehensive management plan 2010). Apart from the Persian onager, there are large herbivores such as wild sheep (*Ovis orientalis*), wild goat (*Capra aegagrus*) and Jebeer

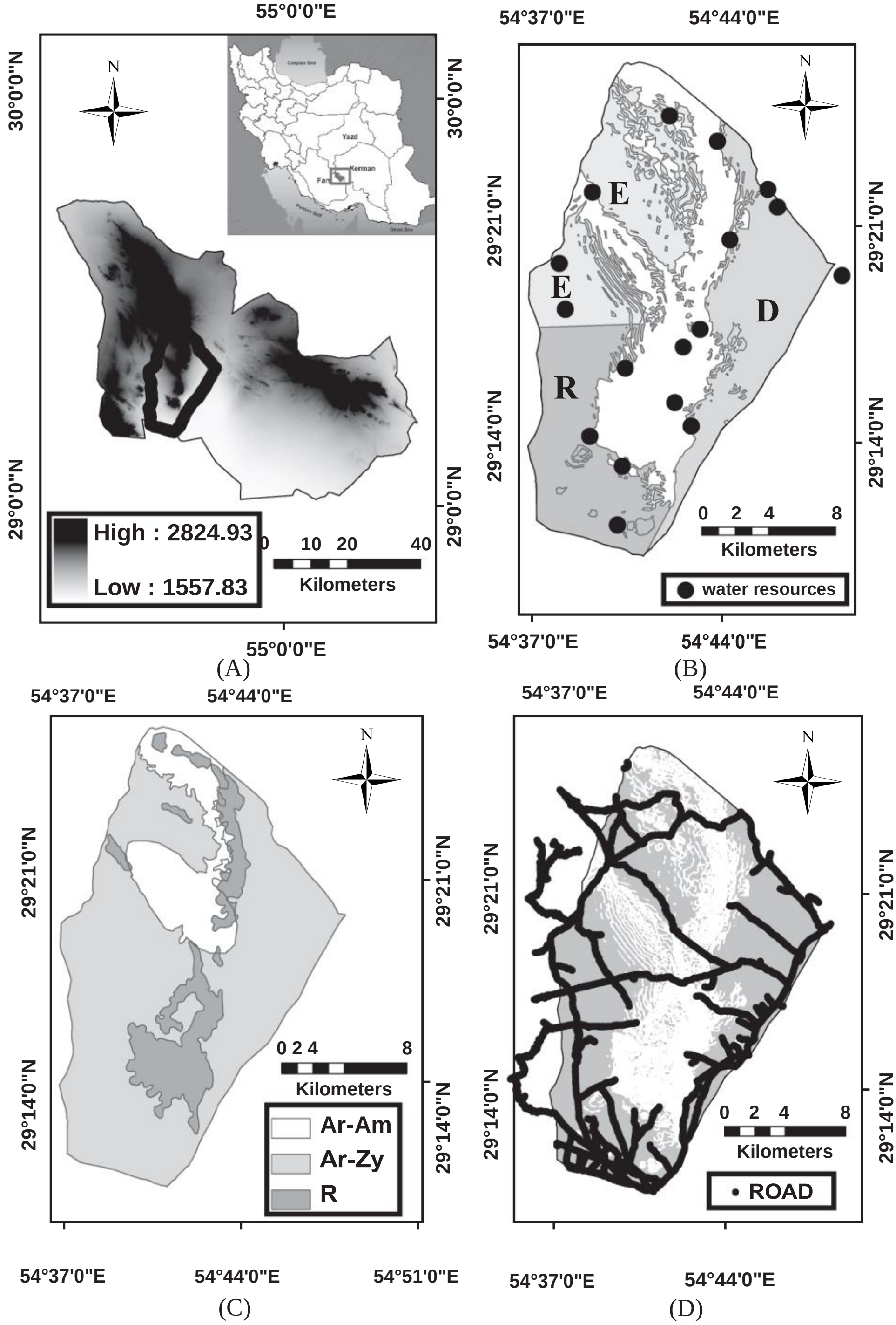

Figure 1. (A) DEM map of Bahramegoor Protected Area and its location in Iran; black lines show the boundaries of Qatrouyeh National Park. (B) There are 17 water resources in the park: four in Rigjamshid (R), four in Einaljalal (E) and nine in Dehvazir (D) plains. (C) The vegetation community map shows three vegetation communities predominate: *Artemisia–Zygophylum (Ar-Zy)*, *Artemisia–Amygdalus (Ar-Am)* and Rock. (D) The road map shows all available routes used through the park.

gazelle (*Gazella bennettii*), and carnivores such as grey wolf (*Canis lupus*), golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), striped hyaena (*Hyaena hyaena*), caracal (*Felis caracal*) and leopard (*Panthera pardus*) (Darvishsefat 2006). The number of onagers has been estimated to be 270 individuals in QNP (Hemami and Momeni 2013).

Field data collection

We recorded the latitude and longitude of all Persian onager sightings in QNP during four seasons (autumn 2009, winter, spring and summer 2010). We drove fixed loops from sunrise to sunset 3 days per week, 1 day for each area (Rigjamshid, Einaljalal and Dehvazir plains – often referred to as the R, E and D plains, respectively), during non-consecutive 2-week periods every month. Using mean track lengths of 13.0 km, 15.2 km and 16.7 km for Rigjamshid (65 km^2), Einaljalal (69 km^2) and Dehvazir (71 km^2) plains, respectively, and effective strip width (ESW) of 1.657 km, the proportions of each area surveyed are 0.66, 0.73 and 0.78, respectively. This resulted in two observations per area per month for a total of six observations every month, 18 per season and 60 per year. Since Department of Environment regulations prevented sampling during the mating and breeding season, no data were collected during February and June. We recorded the location of each group of onagers seen. A total of 682 sightings of herds were recorded throughout the 1-year period. The research team consisted of four observers, each a wildlife expert, and travelled along all available routes through QNP (Figure 1D), stopping wherever a herd was spotted using 8 × 30 binoculars. To record the location of each herd, one team member approached the herd, guided by walkie-talkie from team members left behind. When within 10 m of the herd, the GPS location was recorded along with herd size, habitat location and type, time (hour, day, month, year), recently left traces of the herd like faeces, urine and spoor tracks, and sky and weather conditions (cloudy, rainy, sunny/windy or not windy).

Furthermore, age and sex composition of individuals within herds were identified over non-consecutive 2-week periods immediately following two mating seasons (July 2009 and 2010) when natality was highest and during February 2010 when mortality was greatest. During these 3-month periods, 215 herds were aged and sexed using standard morphological and behavioural features by 20 × 60 spotting scope and 8 × 30 binoculars. Occasionally, determining the age and sex of all individuals was not possible and they were recorded as ‘unknown’.

Environmental harshness (EH)

QNP is divided into two different hydrological units, but three different ecological regions: Rigjamshid (R) and Einaljalal (E) plains, both located in hydrological unit five and Dehvazir (D) located in hydrological unit seven. Therefore, regions R and E are more similar climatically to each other than to region D (Qatrouyeh National Park – Bahramegoor Protected Area comprehensive management plan 2010). Because the impact of weather is affected by temperature, wind and rain (Gwazdauskas 1985), we combined these features to create an index of Environmental Harshness (EH). The index was computed for each habitat every month. Harshness was scaled for each variable in relation to its deviation from the yearly average. Values ranging from 25% above to 25% below the mean were considered "average" and assigned a score of A, whereas those falling in the lowest quartile were considered "low" and assigned a score of L while those falling in the highest quartile were consid- ered "high" and assigned a score of H. These relative values were then combined and used to estimate physiological impact on onagers depending on the time of year. Little impact was scored as neutral (N) whereas high impact could be deemed bad (B) or good (G). Hence values of low temperature (L) and/or high rainfall (H) during cold periods are likely to negatively impact onager physiology and are deemed "bad" (B) because low temperature and high rainfall levels intensify "coldness". Similarly, high temperature (H) and/or low rainfall (L) during hot periods are also consid- ered "bad" (B) because they intensify "warmness". Conversely average levels (A) of these two factors are likely to have little impact on onager physiology and are considered "neutral" (N). With respect to wind, low levels (L) will be considered "neutral" and receive a score (N) because windless conditions will leave baseline phys- iological states unchanged. However, high wind levels (H) during winter months can have debilitating physiological affects when the "wind chill" forces onagers to expend extra energy to maintain constant body temperatures. Hence high winter winds are scored as bad (B). Conversely, in the summer, strong winds are likely to provide cool- ing benefits and are therefore considered good (G). Average wind speeds (A) are assumed to be halfway between no wind and either high or low levels. Hence dur- ing hot periods the impact of average wind speeds are scored ($^1/_2$G), but during cold periods the impacts of average wind speeds are scored ($^1/_2$B). The expected monthly Total Environmental Harshness Score for each habitat was computed by summing the "goodness–badness" scores associated with temperature, wind and rain. The rel- ative scores used to compute the EH index were: B 1, N 0, and G – 1; $^1/_2$B 0.5 and $^1/_2$G – 0.5. EH scores ranged from Harsh (≥ 2) to Moderate (1–2) to Benign (< 1).

Habitat use

Locations of observed onager herds were recorded with GPS during 1 year (except February and June) in QNP. Sightings were assigned to plains or hill-valley habi- tats and proportionate use was computed by counting the total number of onagers observed in each area and dividing by the sum of all onagers seen in both areas.

Normalized Difference Vegetation Index

Normalized Difference Vegetation Index (NDVI) values were used to characterize veg- etation. Typically NDVI indicates the greenness of vegetation, or vegetation quality. We examined the NDVI values of the GPS locations of onagers to determine the features of the vegetation in areas used by onagers across seasons and by age and sex class. To determine selectivity or "electivity" of habitat use the values associated with points actually inhabited by onagers were compared with values associated with 200 random points chosen using ARCGIS 9.3 (Esri, Redlands, CA, USA) and the HAWTHS tools software (http://www.spatialecology.com/htools, accessed 31 October 2012). Ivlev's electivity index (Ivlev 1961) was used to measure habitat preferences based on season and phenotype.

Group structure

Groups consist of individuals with different sexes or ages. Most Asiatic wild asses exhibit a fission–fusion social system in which the only long-term bond is between mothers and infants (Rubenstein 1986, 1994; Klingel 1998; Kaczensky et al. 2008). Consequently, group structure and composition change over time. Typically, adult males are territorial, defending large portions of grasslands during the mating season. Sometimes they are alone and sometimes they are with females. Females are rarely alone, but the groups they form are often short-lived and the proportion of females of the same reproductive state – lactating or not – varies. Sub-adult males who are sexually mature but not strong enough to defend territories form all male groups known as bachelor groups. But these groups, like female associations, are also temporary. Therefore, groups that are sighted and recorded as groups may contain adult males (bachelors or territorial breeders), adult females (non-lactating or lactating) or both, foals and yearlings, which when combined, constitute a juvenile age class. Density of each onager demographic class is calculated by "total number seen of each class in each group/area of location". Groups were classified into relatively large or relatively small by first determining the distribution of onager group sizes. The size of multi-individual onager groups ranged from two individuals to a maximum of 47. Since the median of the distribution is five, relative group sizes greater than five were denoted as large groups while relative group sizes equal to or smaller than five were categorized as small groups. Then, we calculated 'number of each age or sex or reproductive state/total number in the group' to find the proportion of each age or sex or reproductive state (the proportions of adults is 0.86, the proportion of sub-adults is 0.14).

Analysis

Chi-squared contingency tests, *t*-tests, one-way and two-way analyses of variance (ANOVAs), and regression analyses were used to test specific hypotheses. Chi-squared contingency tests were used to determine the extent to which groups of differing sizes or compositions resulted from different weather conditions or differed in their use of habitats. Independent *t*-tests and one-way and two-way ANOVAs were used to assess how habitat and seasonal factors affected group sizes and group composition by age, sex and reproductive state class. Regression analyses were used to measure the strength relationships between environmental factors such as EH and NDVI and social factors such as group size and composition age and sex and reproductive state.

ARCMAP software and HAWTHS tools software were used to identify locations of onager herds on maps of QNP, measuring range overlap, finding distance between sightings and nearest water sources, extracting NDVI values of herd locations and for estimating group density by habitat area or location.

Results

Habitats and weather conditions

Associations among different weather features were strong. 85% of sunny days were without wind, whereas all cloudy and rainy days were windy ($\chi^2_1 = 15.38$, $p < 0.0001$, N = 159). Hence it is not surprising that the harshest conditions occurred during cold, wet and windy periods, which typically occur in the winter during December

Table 1. Classification of Environmental Harshness of each month for Rigjamshid, Einaljalal and Dehvazir plains (R, E and D) and prediction based only on environmental harshness.

Month	Location	EH Score	EH	Area preferred	Actual distribution
October	R,E	1	Moderate	=	D
	D	1	Moderate		
November	R,E	0	Beinign	=	ED*
	D	0	Benign		
December	R,E	2	Harsh	=	D
	D	2	Harsh		
January	R,E	2.5	Harsh	=	D
	D	2.5	Harsh		
February	R,E	2.5	Harsh	D	D*
	D	1.5	Moderate		
March	R,E	2.5	Harsh	D	D*
	D	1	Moderate		
April	R,E	0	Benign	=	E
	D	0	Benign		
May	R,E	0	Benign	=	ED*
	D	0.5	Benign		
June	R,E	0.5	Benign	=	
	D	0.5	Benign		
July	R,E	0	Benign	=	D
	D	0	Benign		
August	R,E	1	Moderate	=	E
	D	1	Moderate		
September	R,E	0.5	Benign	ER	R*
	D	1.5	Moderate		

Note: * Fit prediction based on harshness.

− Preferences when no preference indicated by harshness.

and January and at least in some habitats during early spring, February and March (Table 1). For much of the year the index of environmental harshness was similar in all three ecological regions. All habitats showed the highest harshness scores during December and January and the lowest scores between April and July. During February, March and September, however, differences among regions appear (Table 1). Area D exhibited more benign conditions than R and E in February and March and areas R and E showed more benign conditions than area D in September.

Weather and habitat use

Onager herds showed strong seasonal differences in habitat use (Figure 2), especially during the 3 months of the year when areas D, R and E showed marked differences in EH. During these periods, population sizes were largest in the areas where harshness scores were the lowest (Figure 2 and Table 1). During the other eight months of the year the habitats did not differ in their environmental harshness scores and in only two of these months did the onagers show differences in habitat use. Hence, overall, in

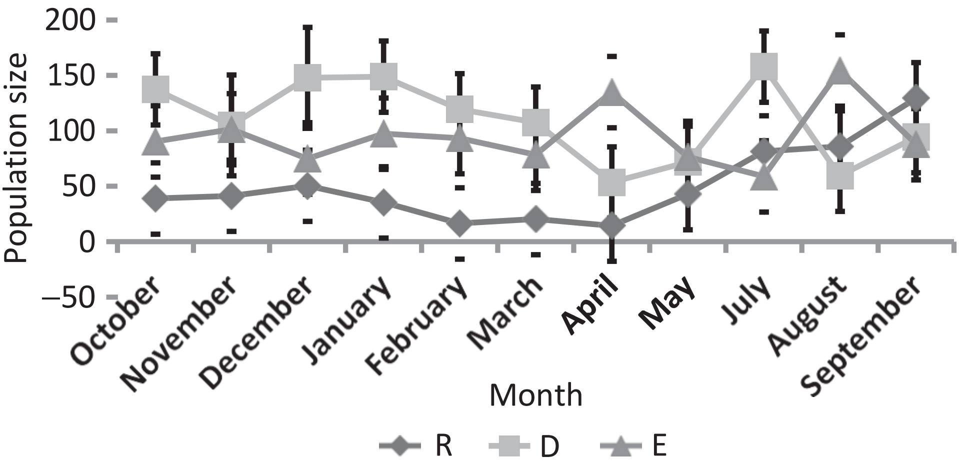

Figure 2. Mean SE± population size in different locations during whole year (2009–2010). Onager herds showed strong seasonal differences in habitat use. Overall, in 5 of 11 months (February, March, May, September and November) onagers distributed themselves in accor- dance with the harshness predictions ($p < 0.05$). R, Rigjamshid; E, Einaljalal; D, Dehvazir plains.

5 of 11 months of distributions the onagers distributed themselves in accordance with predictions based on minimizing harm from harsh environmental conditions.

Although QNP has three different habitats, plains, hill-valleys and mountains, onagers are only found in the first two and weather plays a role in determining when plains and hill-valley habitats are used. Contingency table analyses show that plain habitats are used most often during sunny periods (80%) whereas hill-valley habitats are used most during rainy conditions (78%) ($\chi^2 = 12.68$, $p < 0.0004$, $N = 134$). Similar contingency table analyses by season show that plain habitats are preferred during summer (77%), while hill-valley habitats are preferred during winter (65%) ($\chi^2 = 17.50$, $p < 0.0001$, $N = 159$).

Overall, weather has an impact on how onagers distribute themselves by habitat. When temperature, rain and wind are considered together (when EH scores are high), there is a strong tendency for onagers to seek refuge in the hills and valleys (Figure 3; $F_{2,57} = 3.65$, $p < 0.05$).

Figure 1B shows all water resources available for onagers in QNP. There are 17 water resources in the park: four in R, four in E and nine in D. The maximum distance onagers were ever found from water was 2000 m and that was during the hottest and driest months. For all onagers, the average distance from water sources did not show strong seasonal or habitat differences.

Vegetation cover

Figure 4 shows that average NDVI is higher in R than either D or E. Onager numbers do not appear to track vegetation quality. Analysis of NDVI values shows that for 7 of the 10 months of the year there are no significant differences between average NDVI

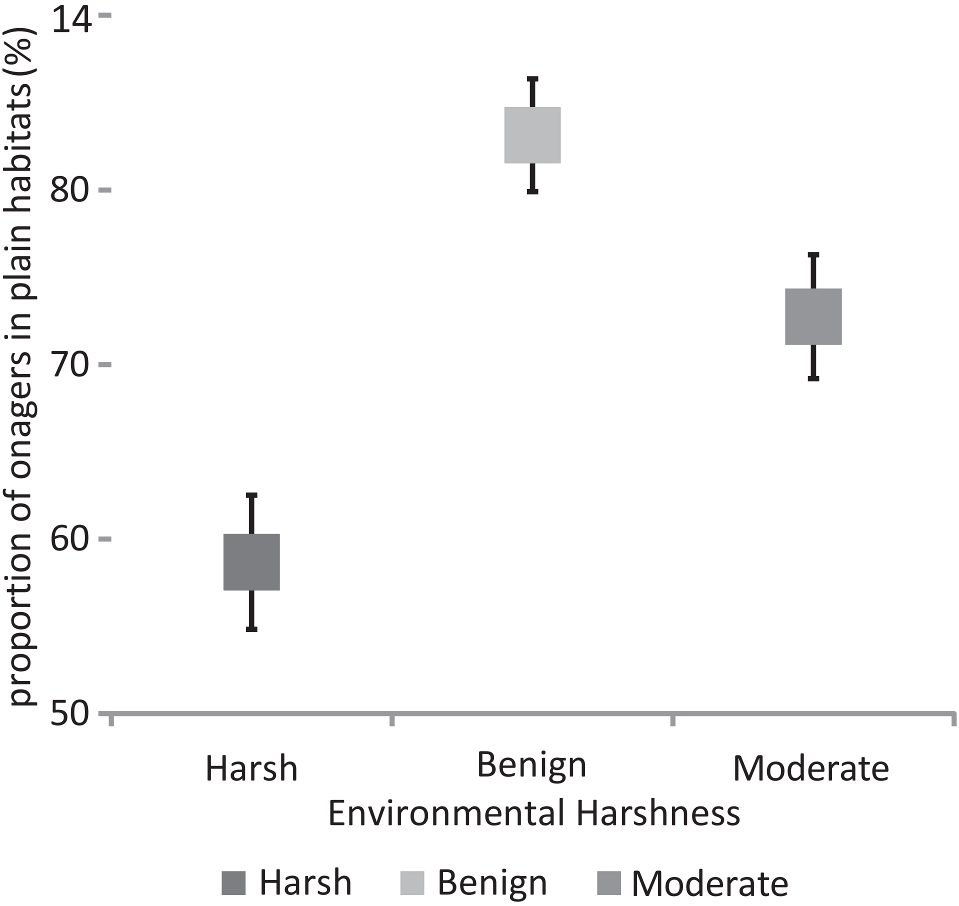

Figure 3. Environmental harshness (EH) and mean ± SE proportion of onagers in plain habitats (%). When EH scores are high, there is a strong tendency for onagers to seek refuge in the hills and valleys.

scores at locations where onagers are seen and average scores at randomly chosen locations (Table 2). In fact, during the most benign 3 months of the year – March, April and May – the locations used by onagers showed a significantly lower average NDVI value than the average value of random points (Table 2).

Group composition habitat use

In general, the number of juveniles, females and total number of onagers are greater in R than D or E and more are in D than E ($F_{2,195} = 12.96$, $p < 0.0001$; $F_{2,176} = 6.65$, $p < 0.002$ and $F_{2,214} = 7.67$, $p < 0.0006$, respectively). Figure 5 illustrates this pattern for average group size.

Although there was no overall relationship between habitat types and herd distance to water, age class and reproductive state affects the distribution of onagers with

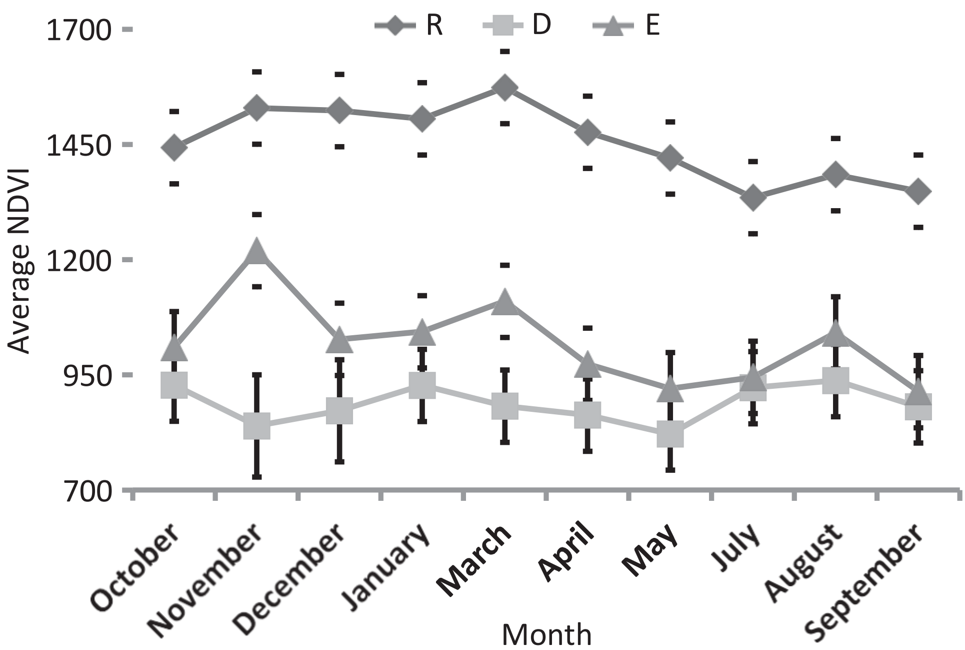

Figure 4. Mean ± SE average Normalized Difference Vegetation Index (NDVI) in different locations during whole year (2009–2010). Average NDVI is higher in Rigjamshid (R) than either Dehvazir (D) or Einaljalal (E) plains ($p < 0.05$).

Table 2. Normalized Difference Vegetation Index (NDVI) of actual points versus random points during whole year (2009–2010). During the most benign three months of the year— March, April and May—the locations used by onagers showed a significantly lower average NDVI value than the average value of random points.

Month	Actual NDVI	Random NDVI	F ratio, *p* value
October	1035 ± 43	1070 ± 27	$F_{1,277} = 0.46$, $p = 0.49$
November	1210 ± 63	1103 ± 32	$F_{1,249} = 2.27$, $p = 0.13$
December	1097 ± 58	1072 ± 26	$F_{1,239} = 0.16$, $p = 0.70$
January	1079 ± 48	1078 ± 26	$F_{1,258} = 0.0002$, $p = 0.98$
March	**1038 ± 69**	**1211 ± 37**	**$F_{1,256} = 4.91$, $p < 0.03$**
April	**979 ± 55**	**1100 ± 31**	**$F_{1,262} = 3.74$, $p < 0.05$**
May	**973 ± 44**	**1080 ± 28**	**$F_{1,281} = 4.17$, $p < 0.04$**
July	1001 ± 38	1046 ± 25	$F_{1,289} = 1.00$, $p = 0.31$
August	1073 ± 45	1078 ± 27	$F_{1,273} = 0.01$, $p = 0.92$
September	1042 ± 39	1039 ± 27	$F_{1,290} = 0.003$, $p = 0.95$

respect to water. More females with juveniles are seen near water than females without juveniles ($F_{1,158} = 1.60$, $p < 0.05$ and $F_{1,176} = 1.51$, $p < 0.05$). Figure 6 typifies the pattern for females with juveniles.

Weather not only affects the overall distribution of onagers, it determines habitat use by age and sex as well. Two-way ANOVAs of number of yearlings, size of female

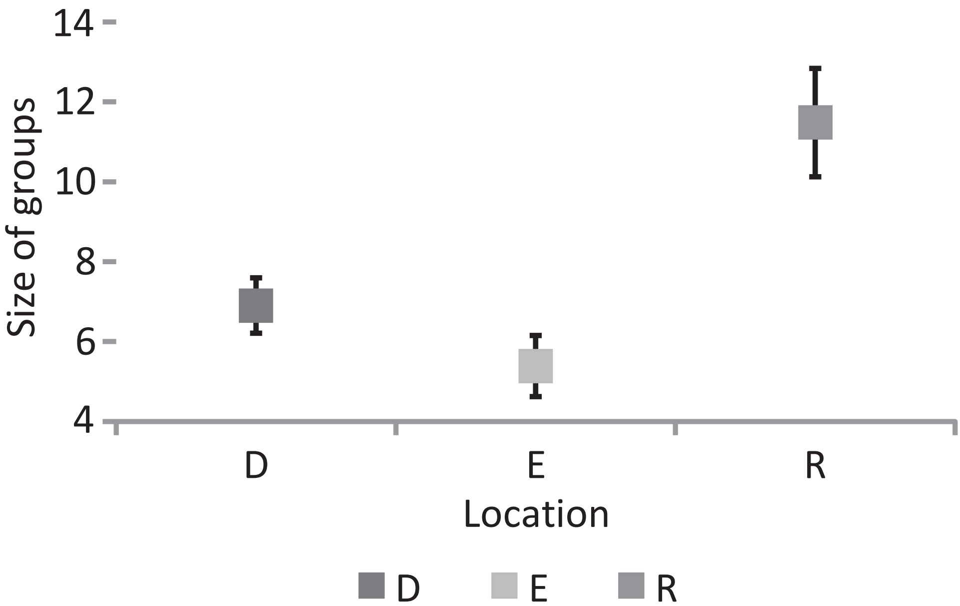

Figure 5. Mean $\pm$ SE group sizes in different locations. Average group sizes are greater in Rigjamshid (R) than in Dehvazir (D) and Einaljalal (E) plains.

groups (female with juveniles), number of mature onagers (females and males) and overall group size as a function of habitat and weather show strong statistical interactions. While the sizes of all the groups described above show no differences by habitat used under calm conditions, under windy conditions groups, irrespective of each type, in hill-valley habitats were larger than those found on the plains. Figure 7A illustrates this pattern for average group size. Two-way ANOVAs of number of juveniles and group size as a function of habitat and sky condition also show strong or nearly strong statistical interactions. While the sizes of all the groups described above are larger under cloudy–rainy conditions in the hill-valley habitats than on the plains, each group type shows no habitat-related size differences under sunny conditions. Figure 7B typifies the pattern for average group size. Similarly, average groups are significantly larger under cloudy–rainy conditions in the winter than during the summer while there is no difference in average herd size under different sky condition in the summer (Figure 7C).

Most territorial males are typically seen alone and without females or bachelor males outside the mating season. Our sightings, however, show that the abundance of lone males is lowest during the winter when conditions were harshest (Figure 8A, $F_{2,57} = 3.39$, $p < 0.05$) and highest in areas E and D before and during, the June–July breeding season (Figure 8B, $F_{2,57} = 4.66$, $p < 0.02$). Not surprisingly, males are rarely seen alone in area R where most females, especially those with juveniles, are likely to congregate (Figure 5), especially during the most benign parts of the year (Figure 8C). That the density of lone males is highest in habitats E and D during the most environmentally hospitable times of the year (Figure 8A, $F_{2,57} = 3.39$, $p < 0.05$ and Figure 8C), suggests that females are consistently associating with only a small subset of males, typically in area R.

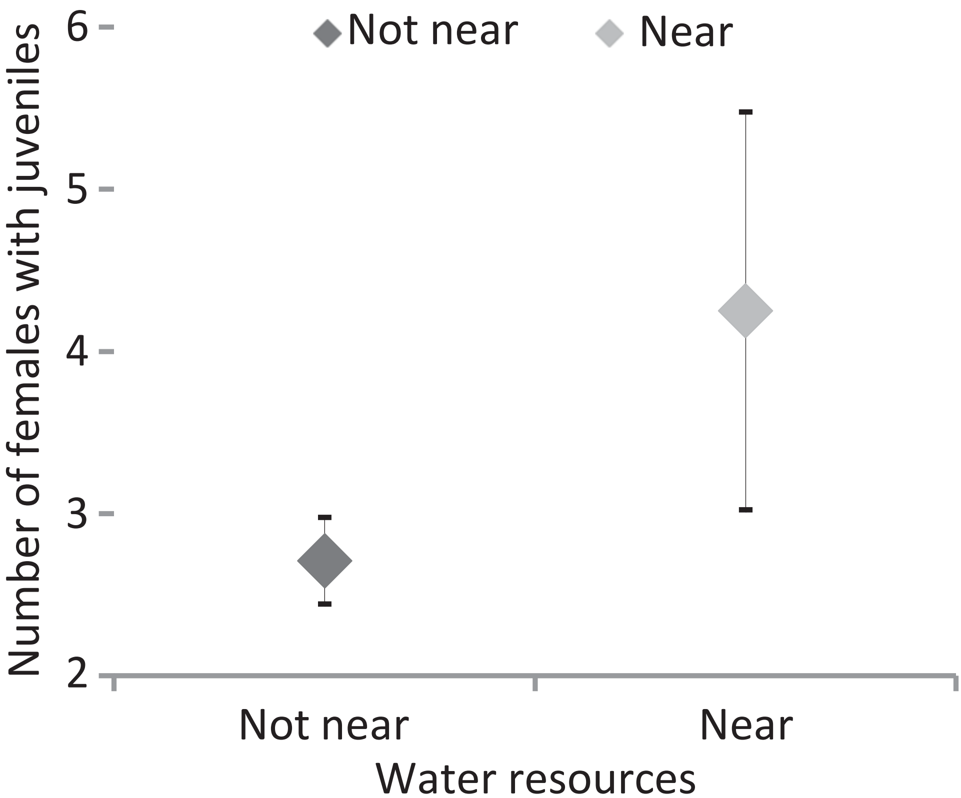

Figure 6. Mean ±SE number of females with juveniles and existence or lack of water resources near them (less than 200 m). Most females with juveniles are seen near water.

Determinants of herd density

Vegetation quality as measured by NDVI values, affects the density of onagers found in particular locations, but in different ways depending on sex and female reproductive state. The density of lone males and females without juveniles are highest at intermediate NDVI values (750–1500 for lone males and 750–1250 for females without juveniles) (Figure 9A, $F_{2,57}=15.88$, $p < 0.0001$ and Figure 9B, $F_{2,72}=3.94$, $P < 0.03$). Conversely, the abundance of females with juveniles increases as vegetation quality increases (Figure 9C, $F_{1,27} = 4.37$, $p < 0.05$), suggesting that this class of females is attracted to areas with the best vegetation. That lone males are not seen in these high-quality areas underscores the fact that territorial males in these areas are more successful in gaining mating opportunities than males in areas with lower vegetation quality.

Determinants of group size

Overall, both average and maximum herd size increases as onager density increases. Figure 10 illustrates this pattern for average group size. Relative group size is also influenced by habitat and weather. Larger than average groups are most often seen

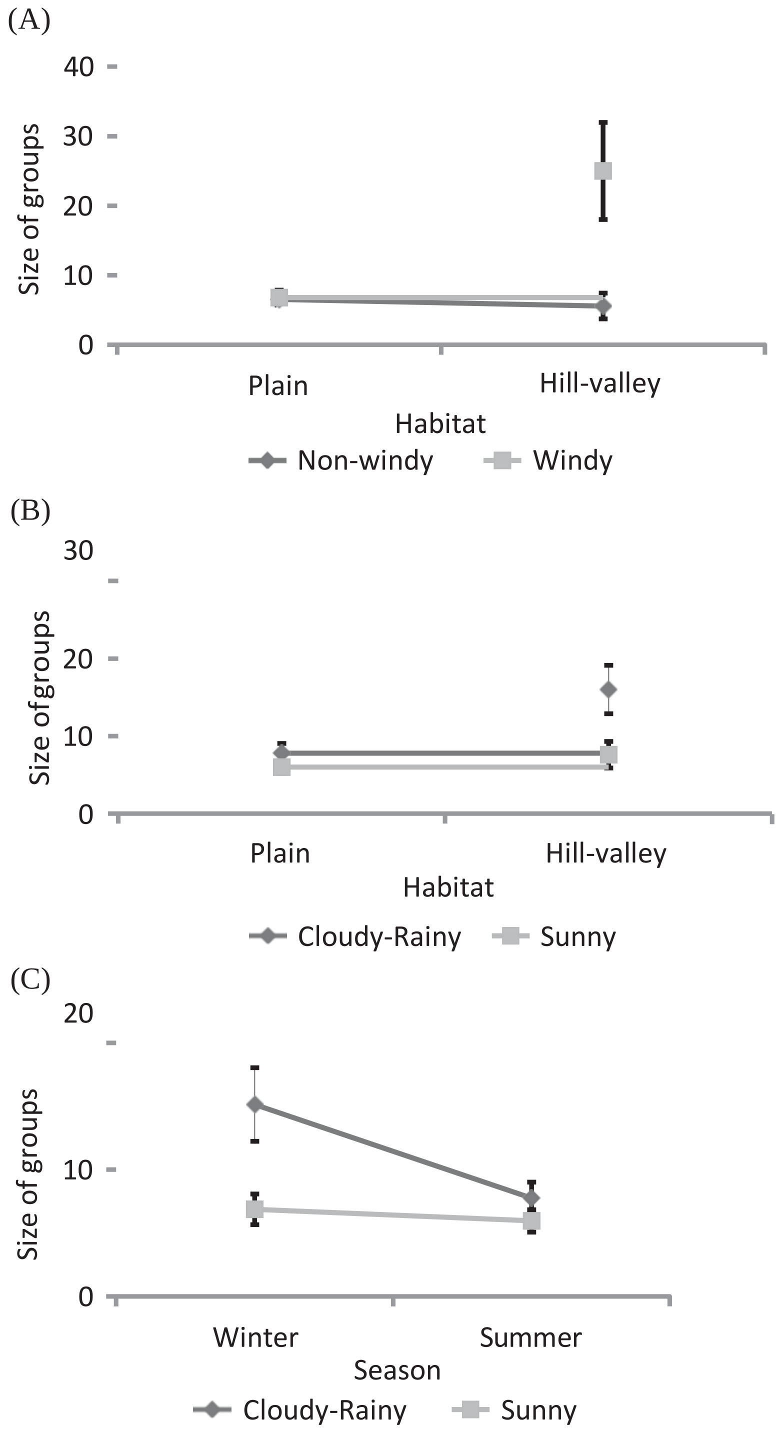

Figure 7. (A) Mean ±SE group sizes in different habitats in windy condition. Under windy condition average group sizes in hill-valley habitats were larger than those found on the plains ($p < 0.01$). (B) Mean ±SE group sizes in different habitats in sky condition. Average group sizes are larger under cloudy-rainy conditions in the hill-valley habitats than on the plains ($p < 0.08$). (C) Mean ±SE group sizes in different sky condition during summer and winter. Average groups are significantly larger under cloudy–rainy conditions in the winter than the summer ($p < 0.06$).

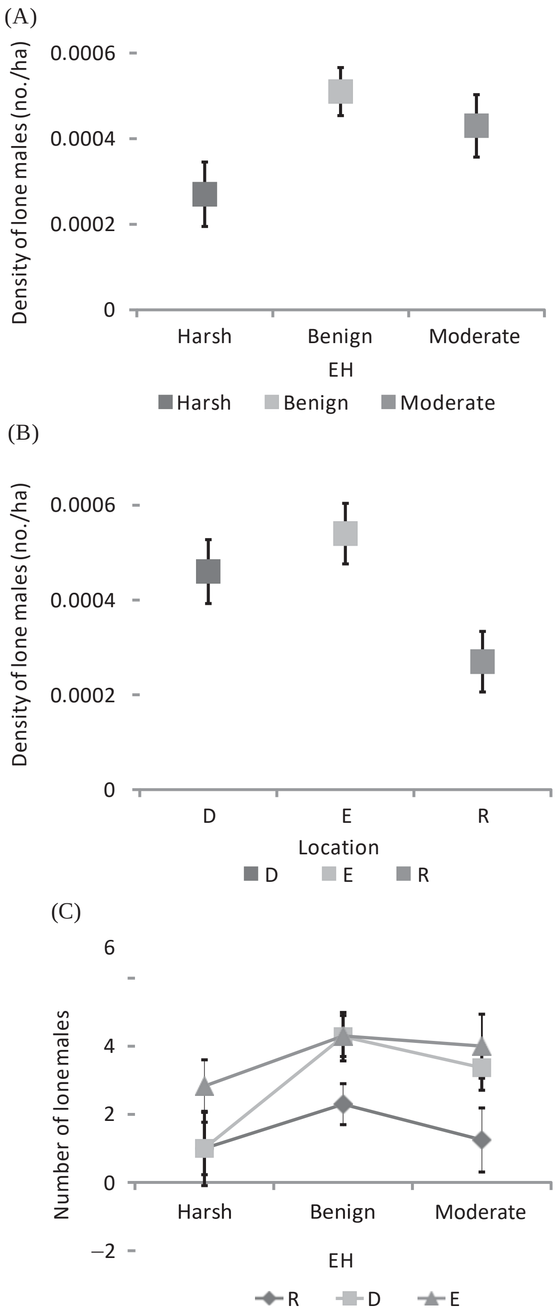

Figure 8. (A) Mean ± SE density of lone males in different seasons. Abundance of lone males is lowest when conditions were harshest. The density of lone males is highest during environmentally most hospitable times of the year. (B) Mean ± SE density of lone males in different locations. Abundance of lone males is highest in areas Einaljalal (E) and Dehvazir (D). (C) Mean ± SE number of lone males in different locations during three kinds of EH. While males are rarely seen alone in area Rigjamshid (R) especially during the most benign parts of the year, the number of lone males is highest in habitats E and D during environmentally most hospitable times of the year.

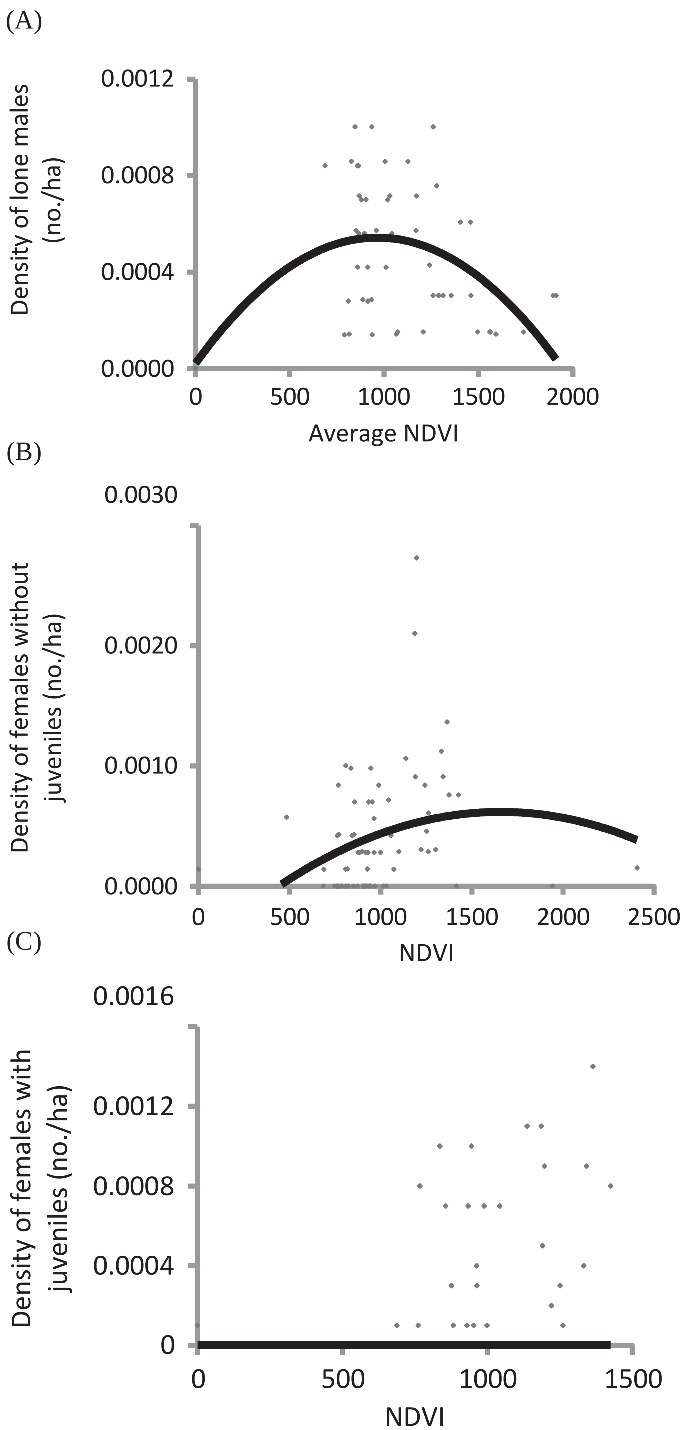

Figure 9. (A) Density of lone males and average Normalized Difference Vegetation Index (NDVI). The density of lone males is highest at intermediate (750–1500) NDVI values. (B) Density of females without juveniles and average NDVI. The density of females without juveniles is highest at intermediate (750–1250) NDVI values. (C) Density of females with juveniles and average NDVI. The density of females with juveniles increases as vegetation quality increases.

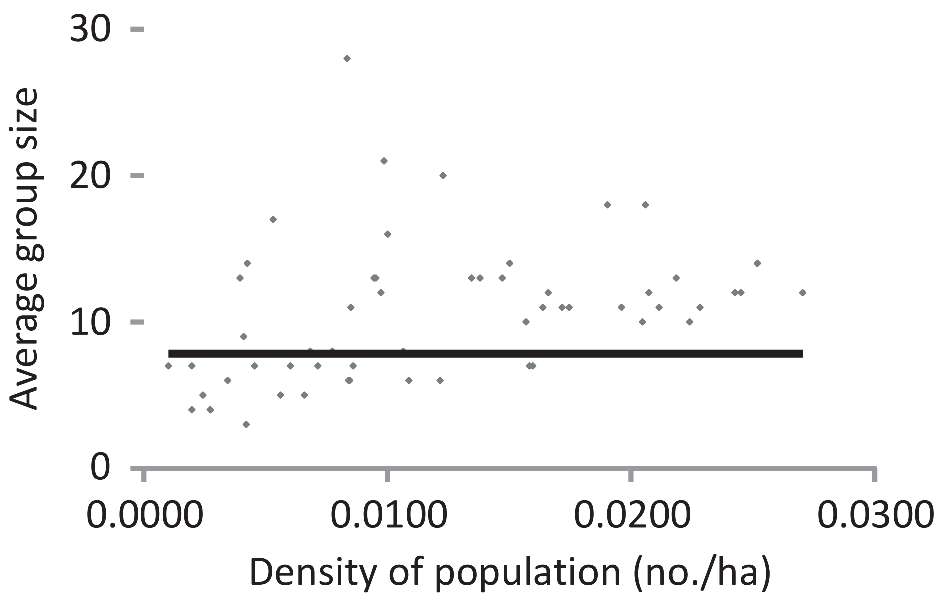

Figure 10. Density of population size versus average group size. Average herd size increases as onager density increases ($p < 0.004$).

in area R (Figure 11A) ($\chi^2 = 9.43$, $p < 0.01$, N = 159) or under rainy conditions (Figure 11B) ($\chi^2 = 6.99$, $p < 0.04$, N = 159).

Discussion

This is the first study in Iran to characterize patterns of seasonal habitat use of the Persian onager over two consecutive years. Spatial and temporal variability in vegetation and habitat use is common for many free-ranging herbivores across the world (Palmer et al. 2003) and our findings show that the Persian onager is no exception.

The co-occurrence of wind and rain, especially during cold periods, intensifies the harshness of environmental conditions in the QNP, and not surprisingly, the onagers through behaviour mitigate the impacts of these conditions. Our results show that all onagers irrespective of age, sex or reproductive state, disproportionately frequent hill-valley habitats on windy as well as cloudy–rainy days, especially during winter months. Access to valleys appears to reduce the impact of wind and rain during the coldest periods; groups also tend to be relatively larger under these conditions so that individuals can take advantage of others to block the wind or share their warmth. Conversely, onagers disproportionately aggregate on the plains during sunny days, typically during hot summer months.

Such weather-induced movements influence the use of the park's hydrological regions, but only to a limited extent. When regions differ in terms of our Environmental Harshness Index, onager abundance increases in regions with lower values. But because the distribution of onagers shows preferences for some regions over others when EH values are similar, factors other than weather must also play a role in shaping patterns of habitat use.

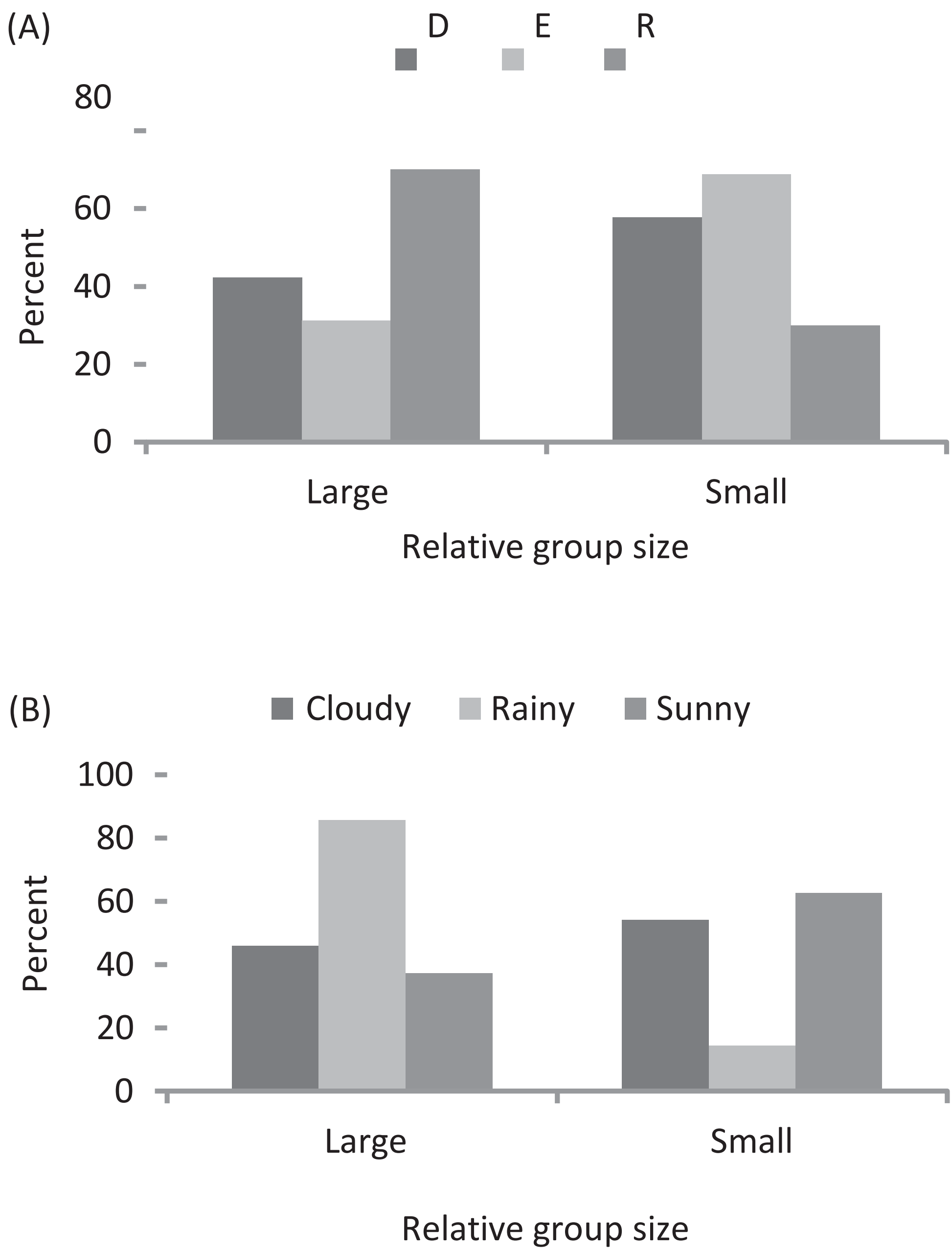

Figure 11. (A) Relative group size in different locations. Larger than average groups are most often seen in area Rigjamshid (R). (B) Relative group size and sky. Larger than average groups are most often seen under rainy conditions. E, Einaljalal; D, Dehvazir plains.

NDVI values derived from satellite images reveal that locations within the park differ in greenness, and so in relative vegetation quality and quantity. Area Rigjamshid, more than areas Dehvazir and Einaljalal, has the highest average NDVI value and ground measurements of plant abundance also show that area Rigjamshid supports the highest average biomass (Hemami and Momeni 2013). Not surprisingly, densities and group sizes of females both with and without juveniles are highest in Rigjamshid.

Similar correlations between plant abundance and group size are found in other Asiatic wild ass populations (Henley et al. 2006; Sundaresan et al. 2007). Since the density of females with foals (juveniles) generally increases as NDVI values increase, it is likely that the need to acquire large quantities of high-quality forage leads to the disproportionate use of Rigjamshid by this class of females for much of the year. Only during spring (March–May) when grass is growing everywhere does the preference for Rigjamshid vanish for females with juveniles.

The overall distribution of onagers is independent of distance to water, most probably because watering points are distributed almost equally inside the QNP. This accords with observations of kulans *(Equus hemionus kulan*) in the Bukhara Reserve (Bahloul et al. 2001). Nevertheless, juveniles and females with foals tend to be located near water. This accords with observations of lactating females in other fission–fusion equids, such as onagers in the Negev desert (Rubenstein 1994) and Grevy's zebras *(Equus grevy)* in the semi-arid regions of Kenya (Rubenstein 1986).

Females with young foals come into post-partum oestrus and, like cycling females without young, are reproductively active (Rubenstein 1994). Hence the most able and dominant males should position themselves to increase their chances of mating with females tied to water and those coming to water at irregular intervals (Rubenstein 2010). Since Persian onager females with young are found in areas with the highest NDVI values and close to water, it is not surprising that sightings of 'lone' males are rarely seen in these locations; territorial males near water should always be with females, some of which will be those with young and others who will be coming to water from afar to drink. Instead, during the mating season territorial males that are seen alone should be the more subordinate males found in areas Dehvazir and Einaljalal, which is where most cycling females are also found. Vegetation in these areas is of intermediate quality. Studies on Grevy's zebras and other onagers (Rubenstein 1986, 1994; Ginsberg 1989; Sundaresan et al. 2007) suggest that females without young occupy areas controlled by mid-ranking males, some of which will be temporarily alone. Females often move to these areas to seek large quantities of vegetation and to minimize competition with higher densities and larger groups of females with juveniles that remain near water. Our observations on the composition and location of groups by relative size further support this interpretation. In the future, noting the exact locations of territorial and non-territorial males will provide important data for assessing the veracity of this notion.

The results of onager habitat use in QNP can contribute to their management and conservation in arid ecosystems of Iran. Reintroduction programmes of onagers from QNP to other protected areas are under study by the Department of Environment. Our findings indicate not only that overall habitat use is affected by weather, but also that the availability of quality food and water play significant roles, especially since the need and use of these key resources varies by onager sex and reproductive state. In general, hill-valley habitats are used by onagers in severe weather conditions in QNP. Therefore, future translocations of onagers to new habitats require that prospective sites include these habitats. The presence of large herds of females with their juveniles near water and in areas with high-quality vegetation within QNP shows that both adequate water resources and high-quality food must be abundant in any future locations because recruitment and population growth depend on large numbers of healthy females able to rear their young to independence. In contrast, our findings reveal that males can use the parts of QNP containing poorer food and water conditions. Hence, choosing future sites that maximize female survival and fecundity must take precedence if new populations of onagers are to be sustained.

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