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Short communication

Fission-fusion social structure of a reintroduced ungulate: Implications for conservation

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ABSTRACT

In a reintroduced population, the social behavior of the species can strongly affect the long-term viability of the population through its effects on movement, information flow, disease spread and the population's genetic variability. Therefore, information on the social behavior of a reintroduced population can contribute to conservation practices; however, its importance is often underestimated. The initial phase of the Asiatic wild ass's (*Equus hemionus*) reintroduction in Israel has been considered a success, and the population is currently estimated at more than 250 individuals. However, the current social structure of the population remained unknown. We aimed to study this important population trait and to provide helpful information for efficient conservation and management protocols. The study was based on direct observations that were conducted over four consecutive years, and on the analyses of groups' composition and female groups' stability. Female groups accompanied by males constituted only 5% of the total 659 observations, males were observed to be mainly solitary or in groups of various sizes, and females were organized in non-stable groups, indicating that the reintroduced population exhibits a fission-fusion social structure. Identifying the social structure for the species in the expanding Negev population of the Asiatic wild ass can assist in implementing future reintroductions and can contribute to effective management decisions aimed at protecting the species.

1. Introduction

Reintroductions have become a common tool in wildlife management and conservation (Soorae and Seddon, 1998; Lipsey and Child, 2007; Seddon et al., 2007). In the case of species extinction in the wild, particularly in keystone species whose activities affect many other organisms (Simberloff, 1998), the importance of reintroduction as an ecosystem restoration tool is even higher (Polak and Saltz, 2011; Armstrong and Seddon, 2008). Nevertheless, many reintroduction attempts fail (Fischer and Lindenmayer, 2000). This is because reintroduction success depends on various factors, including the initial population size released, demography parameters, the availability of natural habitats and the effective removal of the original cause of decline (Fischer and Lindenmayer, 2000; Ewen et al., 2012). Another factor that has often been neglected is the species' social structure (Seddon et al., 2007), which can influence the long-term viability of a reintroduced population by affecting the movement of individuals, population range expansion (Le Gouar et al., 2011), information flow, and disease spread (Manlove et al., 2014). Therefore, studying the social structure of reintroduced populations is highly important, and the findings can be directly translated into conservation practice and management plans (Anthony and Blumstein, 2000) and can aid in assessing the reintroduction status in terms of its success (Berger-Tal and Saltz, 2014). In social species, the formation of groups in a pattern that resembles that of established populations may be one indication for the reintroduction's success, while altered patterns of social behavior may result in reduced average fitness in the population, affecting the persistence of the entire population (Berger-Tal et al., 2011; Caro and Sherman, 2012). In this study, we focus on the social structure of the reintroduced Asiatic wild ass (*Equus hemionus*).

The Asiatic wild ass is an elusive, critically endangered species. It was once abundant in western Asia, including Israel's Negev Desert, but

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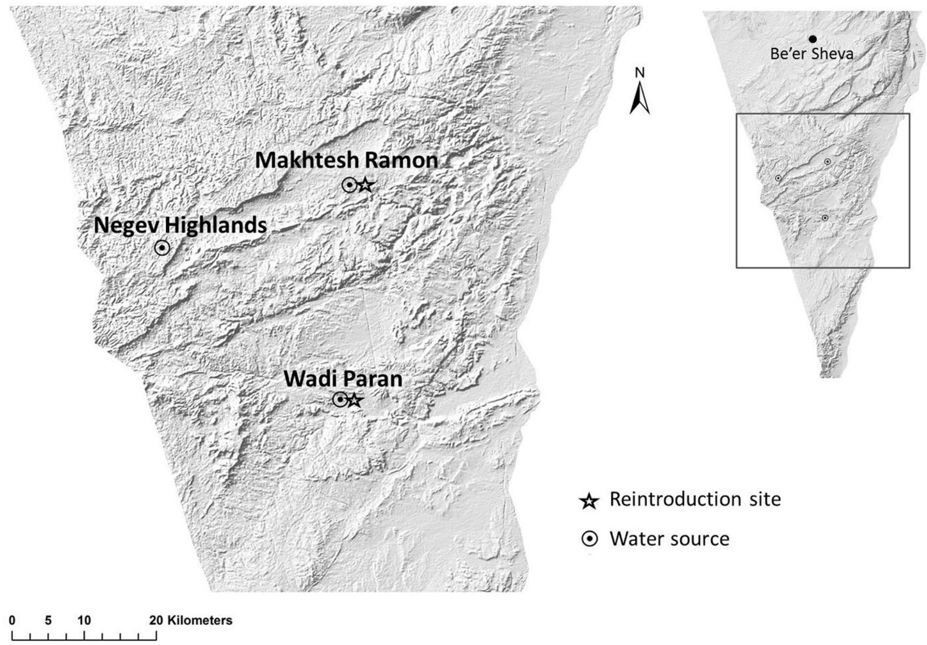

Fig. 1. Reintroduction sites and main water sources in the wild ass distribution range in the Negev Desert.

declined throughout its range due to hunting and habitat loss. The local subspecies, *E. h. hemippus*, endemic to the Middle East, became extinct in the early twentieth century. In 1968, a breeding core was established at the Hai-Bar Yotvata Reserve from 11 individuals belonging to the Iranian (*E. h. onager*, 3 M, 3 F) and the Turkmanian (*E. h. kulan*, 2 M, 3 F) subspecies (Saltz and Rubenstein, 1995). Between 1982 and 1993, *E. hemionus* ssp. (resulting from the mixture of the two subspecies) was reintroduced into the Negev Desert by the Israel Nature and Parks Authority (INPA); between 1982 and 1987, 28 individuals (14 M, 14 F) were reintroduced into Ein Saharonim, in Makhtesh Ramon, and between 1992 and 1993, 10 additional individuals (3 M, 7 F) were reintroduced into Wadi Paran, about 35 km south of Ein Saharonim (Fig. 1). The reintroduction procedure was well documented, and the reintroduced population was intensively monitored in the years following the reintroduction (Sinai, 1994; Saltz et al., 2006). During the late 1990s, the population naturally expanded its geographical range to the Northern Negev Highlands and the Arava Valley (Fig. 1). The initial phases of the wild ass reintroduction into the Negev have been considered a success: the population size increased from 38 to an estimated size of 250–400 individuals (Renan et al., 2015), the population's geographical range has expanded and the females' annual reproductive success was found to be high (at around 0.5, Speyer, 2012). However, the current social structure of the population, an important factor in the population's long-term persistence, was not known.

Equids are typically organized into one of two social organizations (Klingel, 1975). In “female defense polygyny” (here referred to as a “harem” structure), stable groups of females and their young live in strong association with usually one (occasionally two) dominant stallion, and non-dominant males live in separate all-male bachelor groups (Klingel, 1975; Boyd et al., 2016). This social organization characterizes three wild species (takhi, *Equus przewalskii*, plains zebra, *E. quagga*, and mountain zebra, *E. zebra*) and the feral horse (*E. caballus*). In “resource defense polygyny” (here referred to as a “fission-fusion” structure), females and their young tend to live in non-stable groups, and dominant males protect good quality territory rather than female groups. The dominant, territorial males are solitary, while the subordinate, non-territorial males live in unstable all-male bachelor groups (Klingel, 1975; Rubenstein, 1986; Moehlman, 1998a). This social organization characterizes three wild species (kiang, *E. kiang*, Grevy's zebra, *E. grevyi*, and the African wild ass, *E. africanus*) and the feral ass (*E. asinus*). The situation in the remaining species, the Asiatic wild ass, *E. hemionus*, will be discussed below.

The harem species inhabit more mesic habitats, while the fission-fusion species tend to live in semi-arid and arid habitats. This has led to the hypothesis that environmental factors determine which of the two basic social organizations will appear in equids (Klingel, 1975; Rubenstein, 1986): In relatively rich and homogeneous mesic landscapes, the lack of competition for resources among females enables the formation of stable and cohesive groups, allowing males to dominate mating opportunities when defending a specific female group. In poor and heterogeneous arid landscapes, competition over resources and the different physiological needs of females (e.g., lactating females need to drink more frequently than non-lactating females) break the groups' cohesiveness, leading females to live in fission-fusion groups (Rubenstein, 1986). This social structure also provides the opportunity to adjust the group size to the amount of resources in a specific area or in a particular season. Under this non-stable group condition, dominant males invest their energy in defending valuable territories that will attract females and increase their mating opportunities. Several studies on feral donkeys and horses have shown that differences in environmental conditions can change the social organization, even within the same species, causing a shift from the common social organization of that species (Rubenstein, 1981; Moehlman, 1998b). Potentially, this may also occur in wild equids who share with the feral equids the same social structures.

According to this environmental-effect-on-the-social-organization hypothesis, the Asiatic wild ass, which inhabits arid and semi-arid habitats, is expected to form a fission-fusion social system. However, this may not always occur, and there is an ongoing debate in the literature regarding the Asiatic wild ass's social structures (Boyd et al., 2016). Studies of Mongolian and Turkmenian wild asses (Bannikov, 1958; Rashek, 1973; Feh et al., 2001) described their social structure as harem. Conversely, studies of Iranian (Nowzari et al., 2013), Tibetan (Neumann-Denzau and Denzau, 2007; St-Louis and Côté, 2009) and Indian (Rubenstein et al., 2007; Sundaresan et al., 2007) wild asses, but also studies of Mongolian (Neumann-Denzau and Denzau, 2007; Kaczensky et al., 2008) and Turkmenian wild asses (Klingel, 1998; Neumann-Denzau and Denzau, 2007), described a fission-fusion structure and questioned the interpretation of previous observations. One way to explain these conflicting descriptions is to suggest that the

Asiatic wild ass has a high social plasticity that enables it to adapt its social system to environmental conditions (Moehlman, 2002; Feh, 2005).

A previous study by Saltz et al. (2000) on the reintroduced Asiatic wild ass population in Makhtesh Ramon, in the first years following the reintroduction, identified a few territorial males, female groups of varying compositions and separate bachelor groups, indicating a fission-fusion social structure. However, since that study, the population has expanded its geographical range significantly, and today most of the population inhabits the Northern Negev Highlands. This area is higher in elevation than the Makhtesh Ramon area (on average 930 m vs. 440 m, respectively), the average precipitation is higher (95 mm per year vs. 54 mm, respectively), and hence, the vegetation cover is larger (Danin et al., 1975). In addition, the Northern Negev Highlands area is considered to be part of the Irano-Turanian phytogeographical zone, which is characterized by cold winters, hot dry summers and dwarf-shrub steppe vegetation (Stern et al., 1986), while Makhtesh Ramon lies within the Saharo-Arabian and Sudano-Zambesian zones, which are characterized by warmer winters and hot summers with low annual rainfall rates, and the vegetation in this region is mainly restricted to wadis (Danin et al., 1975). According to the environmental-effect-on-the-social-organization hypothesis, this shift in the population distribution range to a richer, more predictable and more homogeneous landscape could reduce conflicts between individuals and the need for group flexibility; hence, it could promote group stability and a harem-type social structure.

In this study, we aimed to examine whether the shift in the population distribution range involved a change in the wild ass social structure from fission-fusion to harem. Such knowledge can aid in constructing efficient conservation and management protocols for the persistence of the wild ass in the Negev Desert.

2. Methods

2.1. Study population and data collection

The behavioral observations were made during the breeding seasons (between June and October) of four consecutive years (2010 – 2013) in the Northern Negev Highlands, the most populated activity center of the wild ass population in the Negev (Fig. 1). We conducted direct observations once or twice a week, during the afternoon till dusk, the peak activity hours (observations were ~5 h long). The animals were observed from a hiding place situated approximately 50 m from the water source. Two observers documented each encounter with the wild asses: one counted the number of individuals and identified their age (adult, sub-adult or juvenile) and sex using binoculars, and the other took close-up videos of the individuals using a video camera (Sanyo Xacti VPC-FH1 HD, x30).

2.2. Female individual identification

From the videos, a unique individual identification profile was built for every female with distinguishable natural markings, such as: coloration, tail length, moles, scars, missing hair in the mane, missing parts of the tail or the ears, etc. (following Van Dierendonck et al., 1996). For each of the profiles, an identification card was created showing left and right side and hind and front views. Then, using these identification cards, the profiles were searched for in all other videos for multiple observations. The assignment of an individual to an existing profile was done conservatively, only when three distinctive marks were recognized (similar to Feh et al., 2001).

2.3. Social structure analyses

Under the fission-fusion social structure, we expected to find non-stable groups composed of females and their young (only infrequently accompanied by one or two males), solitary males and all-male bachelor groups. Alternatively, under the harem-type social structure, we expected to find stable female groups with their young accompanied by one or two males and separate all-male bachelor groups. Solitary males or female groups with their young without a male were expected to be infrequently encountered.

To examine whether the wild ass population's social structure fits the fission-fusion or harem structure, analyses of group composition and female group stability were conducted. For the group composition analysis, only group observations in which all individuals were identified to the level of female, male, sub-adult or juvenile were included. Groups were divided by their type (following Saltz et al., 2000): solitary males, male bachelor groups, female groups with their young without males, and mixed groups (i.e., groups of females and young accompanied by one or more males); then the proportion of each group type was calculated.

In order to examine female group stability, we tested whether females stayed with the same group of females. Because we did not have identifications of all the females in the groups, we compared the size of the groups in which an identified female was observed and tested whether the female was seen in groups of a similar size throughout the year. For this aim, the average group size and standard deviation of group size were calculated for each identified female with multiple observations within the same year. Then, the mean of these standard deviations was compared to the mean standard deviation of a random arrangement of female group sizes. This random arrangement was made using 100,000 permutations of the observed group sizes of the identified females, partitioned according to the observation scheme (i.e., the number of observations per female was retained). For the permutation process, we used MATHEMATICA software (Wolfram, 1999). If females stayed with the same female group throughout the year, we would expect the mean of the standard deviations to be significantly different from the mean standard deviation of the random arrangement of female group sizes.

3. Results

3.1. Group composition

A total of 659 observations of wild ass groups and solitary wild asses, in which most of the individuals were identified to the age and the sex level, were recorded during 2010–2013 (97, 280, 116 and 288 observations in the years 2010, 2011, 2012 and 2013, respectively). In most observations (n = 544), all observed individuals were identified to the age and the sex level. Out of these, 268 observations were of solitary males, 100 of male groups, 148 of females with juveniles and only 28 observations (5.1%) were of mixed groups that included female majorities and one or two males (additional descriptive statistics of the group sizes are presented in Table 1). Besides solitary individuals, group size varied between 2 and 26 individuals. Males were observed to be mainly solitary or in groups of various sizes, while females were observed mainly in small to medium groups (Fig. 2a; for this classification, we split the mixed groups into female groups and male groups). When adult females were observed in a group of one, they were always

Table 1
Detailed descriptive statistics of group sizes of the 544 observations in which all individuals were identified to the age and the sex level. Juveniles were not included in the group sizes.

Group type	Number of groups (%)	Range	Median	Mean (SD)
♂ solitary	268 (49.3)	1	1	1 (0)
♂ group	100 (18.4)	2–25	3	4.85 (4.34)
♀ group	148 (27.2)	1–26	2	2.98 (3.15)
♀ + ♂ group	28 (5.1)	2–16	5	6.1 (4.05)
Total	544 (100)			

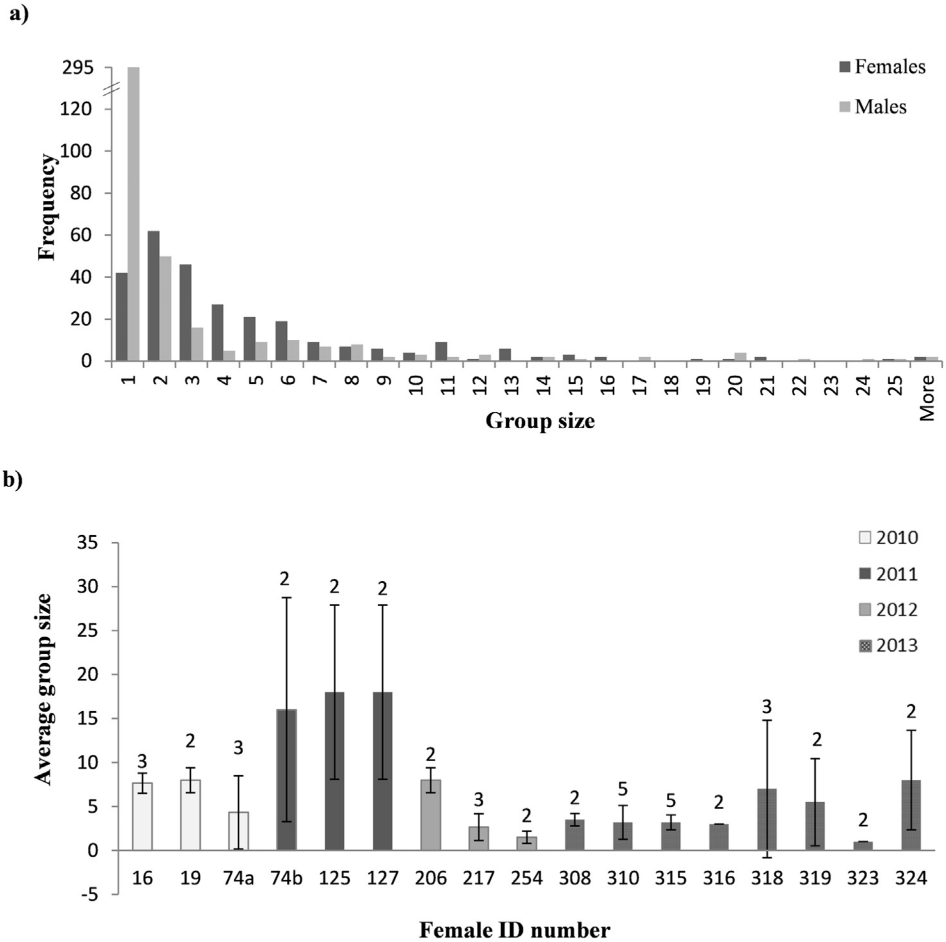

Fig. 2. Distributions and average size of the wild ass groups.
a) Distributions of male groups and female groups. Males were observed to be mainly solitary or in groups of various sizes, and females were observed mainly in small to medium groups. Juveniles were not included in the group sizes.
b) Average group size observed for each of the 16 females with multiple observations within the same breeding season (individual #74 had multiple observations during two consecutive years). Error bars represent SD, and the number of observations for each female is noted above each bar.

accompanied by their young.

3.2. Female groups' stability

A total of 103 individual female identification profiles were created during the four years of the study: 15 profiles in 2010 and 35, 33 and 20 profiles in the years 2011, 2012, 2013, respectively, with the aforementioned proviso that some of the females' profiles may have been assigned to "new" females in later years rather than connected to an already identified female. Out of the identified females, 16 females were observed more than once within the same year, and the highest number of multiple observations per female per year was five (females #310 and #315; Fig. 2b). Identified females were observed in groups of various sizes on different observation days (Fig. 2b), and the observed mean SD for group size in all identified females was 5.18. This mean SD falls within the random assignment of female group sizes (mean = 5.99, 95% CI = 4.26, 7.46, Appendix 1), indicating a non-stable female group composition.

4. Discussion

4.1. The social structure

The social structure of the reintroduced Asiatic wild ass in the Negev Highlands was an open question until this study began. Both the group composition and the non-stable group size of females indicate that the social structure of this population is fission-fusion. The high number of solitary male observations and the low number of female groups accompanied by males do not fit the harem social structure; instead they support the existence of a fission-fusion social structure. The high variance in female group sizes also supports the fission-fusion dynamic. These findings indicate that despite the spatial expansion of the wild ass into the Northern Negev Highlands, the social organization of the population has not changed from that of the small population during the years after the reintroduction onset (Saltz et al., 2000).

The existence of a fission-fusion society in the Northern Negev Highlands may indicate that although the Northern Negev habitat is a richer, more predictable and more homogeneous landscape than the Ramon habitat, the differences between the two habitat characteristics are not large enough to cause a significant change in the social structure. This interpretation does not reject the environmental-effect-on-the-social-organization hypothesis; rather, it suggests that our system is not suitable for testing this hypothesis. Nevertheless, the fission-fusion social structure in both Negev populations may indicate that, similarly to all other equid species that are characterized by one of the two social organization types, the Asiatic wild ass also lacks a high social plasticity, and that the species social structure is fission-fusion. This claim was made in a few recent studies of the wild ass population in Mongolia (Kaczensky and Walzer, 2002; Neumann-Denzau and Denzau, 2007), in which the authors observed a fission-fusion structure in the same populations that had previously been documented as having a harem social structure (Feh et al., 2001). It is possible that since Mongolian herds are extremely large (between 100 and 500 individuals) and flight distance is long, the early studies failed to identify the real group composition and to assess the group stability in the population. The "family" groups of stallions, mares and young that characterize only the harem structure, and which were described in the Asiatic wild ass by Feh et al. (2001), may be the result of associations between female groups and territorial males, which are relatively common in this species during the breeding season (Neumann-Denzau and Denzau, 2007, personal observations), rather than stable harem groups.

4.2. Conservation implications

A fission-fusion social structure can have both positive and negative effects on the sustainability of a reintroduced population. This social structure can be beneficial for the flexible exploitation of the heterogeneous landscape (Klingel, 1975; Lehmann et al., 2007), for the efficient exchange of social information (Aureli et al., 2008; Ramos-Fernández and Morales, 2014) and for the acceleration of gene flow among individuals (Altmann et al., 1996). However, this social structure could also speed disease transmission (Cross et al., 2004) and could increase juveniles' predation, as no dominant male continuously protects the females and their foals.

Identifying the population's social structure is important for the wild ass reintroduction project for three main reasons. First, the formation of a reintroduced population's social structure can serve as an indicator of reintroduction success (Berger-Tal and Saltz, 2014). The fission-fusion structure is more common than the harem social structure for this species (Kaczensky and Walzer, 2002; Neumann-Denzau and Denzau, 2007), and the fact that it was found in this expanding population is an indication of the project's success. Second, information on the wild ass's social behavior can assist in implementing future reintroductions, in terms of the composition of the groups to be released (size, age, sex) as the group composition can have a major impact on the viability, demography and the effective population size of the reintroduced population (Saltz, 1996; Seddon et al., 2007; Bell, 2016; Greenbaum et al., 2017).

The third reason for the importance of clarifying the social structure of the Negev population is its contribution to effective management decisions, e.g., the design of nature reserves and determination of artificial water points' distribution. Our previous genetic studies on the Negev wild ass population revealed a strongly polygynous mating system (Renan et al., 2015) in which the number of dominant breeding males is the limiting factor of the population variance effective size and not the demographic history of the population (Greenbaum et al., 2017). Since the fission-fusion structure is characterized by territorial polygyny (Klingel, 1975; Rubenstein, 1986; Moehlman, 1998a), the level of polygyny in the wild ass population may be influenced by the possible number of territories that can be formed within the species distribution range. In the Northern Negev Highlands, there is currently only one permanent artificial water source that supplies water during the breeding season months and has a major impact on individuals' space use patterns, daily movements and habitat selection (Davidson et al., 2013; Giotto et al., 2015; Ziv, 2016; Nezer et al., 2017). Because territorial males tend to establish their territories next to water sources to increase mating opportunities (Saltz et al., 2000), the existence of only a single water source in the entire area may limit the number of possible territories, leading to the observed strongly polygynous mating system. It is highly probable that increasing the number of permanent water sources in the Northern Negev Highlands would result in increased numbers of dominant males contributing to the population's gene pool, thus increasing the variance effective size of the population.

The existence of a fission-fusion social structure in the Northern Negev Highlands population, along with territorial strong polygyny, may have another potentially important effect that should be taken into consideration: Since dominant males are the main contributors to the population's gene pool, their strong site fidelity to their territory (Giotto et al., 2015; Ziv, 2016) can limit the level of gene flow among subpopulations and facilitate the development of a fine-scale genetic structure in the Negev's Asiatic wild ass population. Evidence of this population subdivision has already been found in recent studies (Gueta et al., 2014; Renan, 2014). If the resulting subpopulations are relatively small, this spatial genetic structure may accelerate drift and inbreeding, and hence, may dramatically reduce the genetic variation of each subpopulation. However, the fine-scale population structure may increase the variance effective size of the entire population (Chesser et al., 1993; Sugg and Chesser, 1994; Sugg et al., 1996; Templeton, 2006) and actually reduce the loss of genetic diversity in the overall reintroduced population. Further research is needed to examine the relationship between social structure, mating system and the fine-scale genetic structure of the Negev population and its implications for the population's future viability.

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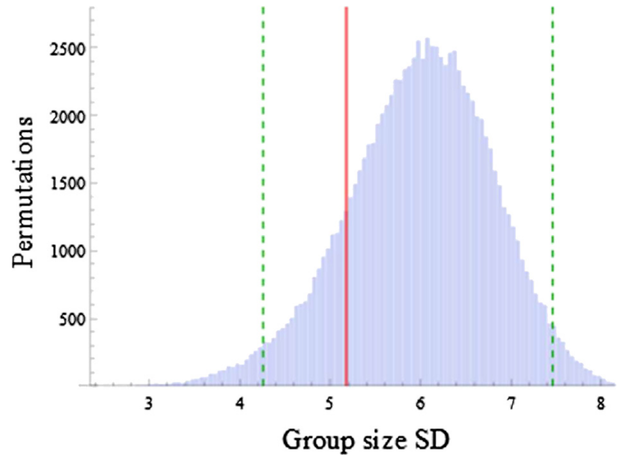
Author contributions box

SR developed the study approach, conducted most of the behavioral observations, analyzed the data and wrote the manuscript. ES, TB and AZ conducted many of the behavioral observations and helped in analyzing the data. GG helped in analyzing the data. SB, ART and AB contributed to the research design and conclusions and commented on the manuscript; AB and SB conceived the research framework.

Appendix 1



App. 1. Distribution of mean Standard Deviation results for 100,000 permutations of the observed group sizes of identified females. Dashed green lines indicate the 95% Confidence Interval of the distribution, red line indicates the observed mean Standard Deviation.

References

Altmann, J., Alberts, S.C., Haines, S.A., et al., 1996. Behavior predicts genes structure in a wild primate group. Proc. Natl. Acad. Sci. U. S. A. 93, 5797–5801.

Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. Biol. Conserv. 95, 303–315.

Armstrong, D.P., Seddon, P.J., 2008. Directions in reintroduction biology. Trends Ecol. Evol. 23, 20–25.

Aureli, F., Schaffner, C.M., Boesch, C., et al., 2008. Fission-fusion dynamics. Curr. Anthropol. 49, 627–654.

Bannikov, A., 1958. Zur Biologie des Kulans. Z. Säugetierkd. 23, 157–168.

Bell, B.D., 2016. Behavioral based management: Conservation translocations. In: Berger-Tal, O., Saltz, D. (Eds.), Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management. Cambridge University Press, Cambridge.

Berger-Tal, O., Saltz, D., 2014. Using the movement patterns of reintroduced animals to improve reintroduction success. Current Zoology 60, 515–526.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P., Saltz, D., 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behav. Ecol. 22, 236–239.

Boyd, L., Scorolli, A., Nowzari, H., Bouskila, A., 2016. Social organization of wild equids. In: Ransom, J.I., Kaczensky, P. (Eds.), Wild Equids: Ecology, Management, and Conservation. JHU Press, Baltimore, Maryland pp. 7.

Caro, T., Sherman, P.W., 2012. Vanishing behaviors. Conserv. Lett. 5, 159–166.

Chesser, R.K., Rhodes Jr, O.E., Sugg, D.W., Schnabel, A., 1993. Effective sizes for subdivided populations. Genetics 135, 1221–1232.

Cross, P.C., Lloyd-Smith, J.O., Bowers, J.A., Hay, C.T., Hofmeyr, M., Getz, W.M., 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. Ann. Zool. Fenn. 41, 879–892.

Danin, A., Orshan, G., Zohary, M., 1975. The vegetation of the Northern Negev and the Judean Desert of Israel. Israel Journal of Botany 24, 118–172.

Davidson, A., Carmel, Y., Bar-David, S., 2013. Characterizing wild ass pathways using a non-invasive approach: applying least-cost path modelling to guide field surveys and a model selection analysis. Landsc. Ecol. 28, 1465–1478.

Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J., 2012. Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, Oxford.

Feh, C., 2005. Relationships and communication in socially natural horse herds. In: Mills, D.S., SM, McDonnell (Eds.), The Domestic Horse: The Origins, Development and Management of its Behaviour. Cambridge Univ Pr, Cambridge pp. 83.

Feh, C., Munkhtuya, B., Enkhbold, S., Sukhbaatar, T., 2001. Ecology and social structure of the Gobi khulan *Equus hemionus* subsp. in the Gobi B National Park, Mongolia. Biol. Conserv. 101, 51–61.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biol. Conserv. 96, 1–11.

Giotto, N., Gerard, J.F., Ziv, A., Bouskila, A., Bar-David, S., 2015. Space-use patterns of the Asiatic wild ass (*Equus hemionus*): complementary insights from displacement, recursion movement and habitat selection analyses. PLoS One 10 (12), e0143279.

Greenbaum, G., Renan, S., Templeton, A.R., Bouskila, A., Saltz, D., Rubenstein, D.I., Bar-David, S., 2017. Revealing life-history traits by contrasting genetic estimations with predictions of effective population size. Conserv. Biol. http://dx.doi.org/10.1111/cobi.13068.

Gueta, T., Templeton, A.R., Bar-David, S., 2014. Development of genetic structure in a heterogeneous landscape over a short time frame: the reintroduced Asiatic wild ass. Conserv. Genet. 15, 1231–1242.

Kaczensky, P., Walzer, C., 2002. Przewalski horses, wolves and khulans in Mongolia. In: Report July 2002, . *http://www.takhi.org*.

Kaczensky, P., Ganbaatar, O., von Wehrden, H., Walzer, C., 2008. Resource selection by sympatric wild equids in the Mongolian Gobi. J. Appl. Ecol. 45, 1762–1769.

Klingel, H., 1975. Social organization and reproduction in equids. J. Reprod. Fertil. 23, 7–11 Supplement.

Klingel, H., 1998. Observations on social organization and behaviour of African and Asiatic wild asses (*Equus africanus* and *Equus hemionus*). Appl. Anim. Behav. Sci. 60, 103–113.

Le Gouar, P., Mihoub, J.-B., Sarrazin, F., 2011. Dispersal and habitat selection: behavioural and spatial constraints for animal translocations. In: Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J. (Eds.), Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, Oxford, UK Chapter 5.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. Evol. Ecol. 21, 613–634.

Lipsey, M.K., Child, M.F., 2007. Combining the fields of reintroduction biology and restoration ecology. Conserv. Biol. 21, 1387–1390.

Manlove, K.R., Cassirer, E.F., Cross, P.C., Plowright, R.K., Hudson, P.J., 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). Proc. R. Soc. B 281, 20142331.

Moehlman, P.D., 1998a. Behavioral patterns and communication in feral asses (*Equus africanus*). Appl. Anim. Behav. Sci. 60, 125–169.

Moehlman, P.D., 1998b. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. Appl. Anim. Behav. Sci. 60, 171–195.

Moehlman, P.D. (Ed.), 2002. Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan. World Conservation Union.

Neumann-Denzau, G., Denzau, H., 2007. Remarks on the social system of the Mongolian wild ass (*Equus hemionus hemionus*). Erforsch. biol. Ress. Mongolei 10, 177–187.

Nezer, O., Bar-David, S., Gueta, T., Carmel, Y., 2017. High-resolution species-distribution model based on systematic sampling and indirect observations. Biodivers. Conserv. 26, 421–437.

Nowzari, H., Hemami, M., Karami, M., Kheirkhah, Z.M.M., Riazi, B., Rubenstein, D.I., 2013. Habitat use by the Persian onager, *Equus hemionus onager* (Perissodactyla: Equidae) in Qatrouyeh National Park, Fars, Iran. J. Nat. Hist. 47, 2795–2814.

Polak, T., Saltz, D., 2011. Reintroduction as an ecosystem restoration. Conserv. Biol. 25, 424–427.

Ramos-Fernández, G., Morales, J.M., 2014. Unraveling fission-fusion dynamics: how subgroup properties and dyadic interactions influence individual decisions. Behav. Ecol. Sociobiol. 68, 1225–1235.

Rashek, V.A., 1973. Reproduction of the wild ass and its behavior during rutting time on the Barsa-Kelmes Island. Biulleten'.Otdel Biologicheskii 54, 9–18.

Renan, S., 2014. From behavioral patterns to genetic structure: The reintroduced Asiatic wild ass (*Equus hemionus*) in the Negev Desert. In: PhD Thesis. Ben-Gurion University of the Negev.

Renan, S., Greenbaum, G., Shahar, N., Templeton, A.R., Bouskila, A., Bar-David, S., 2015. Stochastic modelling of shifts in allele frequencies reveals a strongly polygynous mating system in the re-introduced Asiatic wild ass. Mol. Ecol. 24, 1433–1446.

Rubenstein, D., 1981. Behavioural ecology of island feral horses. Equine Vet. J. 13, 27–34.

Rubenstein, D.I., 1986. Ecology and sociality in horses and zebras. In: Rubenstein, D.I., Wrangham, R.W. (Eds.), Ecological Aspects of Social Evolution. Princeton University Press, Princeton, NJ, pp. 282–302.

Rubenstein, D.I., Sundaresan, S., Fischhoff, I., Saltz, D., 2007. Social networks in wild asses: comparing patterns and processes among populations. Exploration into the Biological Resources of Mongolia 10, 159–176.

Saltz, D., 1996. Minimizing extinction probability due to demographic stochasticity in a

reintroduced herd of Persian fallow deer *Dama dama mesopotamica*. Biol. Conserv. 75, 27–33.
Saltz, D., Rubenstein, D.I., 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. Ecol. Appl. 5, 327–335.
Saltz, D., Rowen, M., Rubenstein, D.I., 2000. The effect of space-use patterns of reintroduced Asiatic wild ass on effective population size. Conserv. Biol. 14, 1852–1861.
Saltz, D., Rubenstein, D.I., White, G.C., 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. Conserv. Biol. 20, 1402.
Seddon, P.J., Armstrong, D.P., Maloney, R.F., 2007. Developing the science of reintroduction biology. Conserv. Biol. 21, 303–312.
Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83, 247–257.
Sinai, Y., 1994. A program for selecting individuals from a breeding core for reintroduction - *Equus hemionus* in Hai-Bar Yotveta. In: M.Sc. Thesis. The Hebrew University, Israel.
Soorae, P.S., Seddon, P.J., 1998. Re-introduction Practitioners Directory. Published jointly by the IUCN Species Survival Commission's Re-introduction Specialist Group, Nairobi, Kenya, and the National Commission for Wildlife Conservation and Development, Riyadh, Saudi Arabia.
Speyer, E., 2012. Preservation of genetic diversity in a reintroduced population: the Asiatic wild ass in the Negev. In: M.Sc. Thesis. Ben-Gurion University of the Negev, Israel.
Stern, E., Gradus, Y., Meir, A., Krakover, S., Tsoar, H., 1986. Atlas of the Negev. Keter Publishing House, Jerusalem.
St-Louis, A., Côté, S.D., 2009. *Equus kiang* (Perissodactyla: Equidae). Mamm. Species 835, 1–11.
Sugg, D.W., Chesser, R.K., 1994. Effective population sizes with multiple paternity. Genetics 137, 1147–1155.
Sugg, D.W., Chesser, R.K., Dobson, S.F., Hoogland, J.L., 1996. Population genetics meets behavioral ecology. Trends Ecol. Evol. 11, 338–342.
Sundaresan, S.R., Fischhoff, I.R., Dushoff, J., Rubenstein, D.I., 2007. Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. Oecologia 151, 140–149.
Templeton, A.R., 2006. Population Genetics and Microevolutionary Theory. John Wiley and Sons, Hoboken, New Jersey.
Van Dierendonck, M.C., Bandi, N., Batdorj, D., Dügerlham, S., Munkhtsog, B., 1996. Behavioural observations of reintroduced Takhi or Przewalski horses (*Equus ferus przewalskii*) in Mongolia. Appl. Anim. Behav. Sci. 50, 95–114.
Wolfram, S., 1999. The Mathematica Book. Cambridge University Press.
Ziv, A., 2016. Males social behavior and space use patterns in the Asiatic wild ass (Equus Hemionus). In: MSc Thesis. University of the Negev, Ben-Gurion.