
The Effect of Space-Use Patterns of Reintroduced Asiatic Wild Ass on Effective Population Size

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Abstract: *Empirical data on behavior, such as space-use patterns, are important to the success of animal reintroductions. We studied space-use patterns in a growing population of Asiatic wild ass (Equus hemionus) reintroduced into the Ramon erosion cirque in the Negev desert, Israel. Between 1988 and 1995 we used direct observation to determine the location and association of males and females. All adult females and dominant males were individually recognized. Home ranges of dominant males overlapped little, suggesting that in this population males are territorial. After the first release of males and females into the wild, only one territory was established, and it covered most of the 20,000 ha of the cirque. After 6 years the number of male territories increased as the number of males in the population increased, and average territory size decreased. Male territories were near permanent and ephemeral water sources, but the water sources were at the peripheries of the territories and were not centers of activity. When there was only one territorial male, female home ranges were almost entirely within the territory. As male territory size decreased, so did the spatial association of females with a single male. During the breeding season, males spent more time in close association with female groups, adopting what may temporarily appear to be a harem breeding strategy. Although demographic and environmental factors pose a greater threat to small populations, our data support the hypothesis that in small, reintroduced populations of territorial, polygynous species, effective population size (N_e) may be dangerously small. Our data suggest that this situation may last for several years until new males are recruited into the population. Thereafter, rapid male turnover and female use of several male territories may ameliorate this problem. We found no relationship between male turnover rate and female reproductive success. The establishment of more male territories is key to increasing N_e and should be the basis for planning reserves for territorial, polygynous species.*

Efecto de los Patrones de Uso del Espacio en el Tamaño Poblacional Efectivo en Asnos Asiáticos Silvestres Reintroducidos

Resumen: *Datos empíricos de conductas, tales como los patrones de uso del espacio, son importantes en el éxito de las reintroducciones de animales. Estudiamos los patrones de uso del espacio en una población en crecimiento de asnos asiáticos silvestres (Equus hemionus) reintroducidos en la depresión por erosión Ramon en el desierto de Negev, Israel. Utilizamos observaciones directas entre 1988 y 1995 para determinar la ubicación y asociación de hembras y machos. Las hembras adultas y los machos dominantes fueron reconocidos a nivel individual. Los rangos de hogar de los machos dominantes se sobrepusieron poco, sugiriendo que en esta población los machos son territoriales. Después de la primera liberación de machos y hembras en el ambiente silvestre, solo un territorio fue establecido, y cubrió la mayoría de las 20,000 Ha de la depresión. Después de seis años, el número de territorios de los machos se incrementó al incrementarse el número de machos en la población y el promedio del tamaño territorial disminuyó. Los territorios de los machos estuvieron cercanos a fuentes de agua permanentes y efímeras; sin embargo, las fuentes de agua estuvieron en las periferias de los territorios y no fueron los centros de actividad. Cuando solo hubo un macho territorial, los*

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rangos de hogar de las hembras estuvieron casi en su totalidad dentro del territorio. Cuando el tamaño del territorio de los machos disminuyó, el tamaño de la asociación espacial de las hembras con un solo macho disminuyó también. Durante la temporada de reproducción los machos pasaron más tiempo en cercana asociación con los grupos de hembras, adoptando lo que temporalmente aparenta ser una estrategia reproductiva de harén. A pesar de que los factores demográficos y ambientales representan una amenaza mayor para las poblaciones pequeñas, nuestros datos sustentan la hipótesis de que, en poblaciones reintroducidas pequeñas, de especies polígamas territoriales, el tamaño poblacional efectivo (N_e) puede ser peligrosamente pequeño. Nuestros datos sugieren que esta situación podría durar por muchos años hasta que nuevos machos sean reclutados hacia la población. Es por ello que una tasa de incorporación rápida de machos y el uso de varios territorios de machos por hembras podría aminorar este problema. No encontramos una relación entre la tasa de incorporación de machos y el éxito reproductivo de las hembras. El establecimiento de más territorios de machos es clave para el incremento de N_e y debería ser la base de la planeación de reservas para especies polígamas territoriales.

Introduction

Although reintroductions are an important part of world conservation efforts (World Conservation Union 1998), knowledge of the biology of reintroduced populations remains limited. Successfully reintroduced populations are initially small and have a positive growth rate, but most studies in conservation biology have been restricted to populations of either rare but stable species or declining species. Furthermore, although the volume of theoretical and empirical data concerning the deterministic and stochastic factors threatening small populations is impressive (Allee 1931; Shaffer 1981), little is known about how these factors are affected by and interact with the behavior and sociobiology of the species (Clemmons & Buchholz 1997; Sutherland 1998). Wildlife reintroduction efforts are generally concentrated on preparation and implementation (Ralls et al. 1992), with little attention to post-release monitoring (Beck et al. 1994). Consequently, empirical data are lacking on behavioral aspects, such as space-use patterns, considered important to the success of a reintroduction (Durant & Mace 1994; Beissinger 1997).

Knowledge of behavior patterns may be especially important in reintroduced social, polygynous species, in which a few dominant males obtain most of the breeding opportunities. In such cases, the demographic and genetic factors that play a critical role in the dynamics of small populations may be strongly affected by changes in behavior and space-use patterns that occur as the population increases. For example, in reintroductions where only a few animals are released, a single male may out-compete all other males for access to females. Consequently, a single male will mate with all females, making the genetically effective population size (N_e) considerably smaller than the actual number of animals released (Nunney 1993). If post-release reproductive success is low (Saltz & Rubenstein 1995; Novellie et al. 1996) or if the dominant male has low fertility, many years may pass before that male is replaced, exposing the population to increased demographic and genetic stochasticity.

We monitored the space-use patterns of reintroduced Asiatic wild ass (*Equus hemionus*) from the time the herd was established in 1983 until 1995. We describe the development over time of male home ranges and reproductive strategies and corresponding female movement patterns and consider our findings in the context of the conservation of small but growing (reintroduced) populations.

Animals and Study Area

The Asiatic wild ass is a mid-sized equid (approximately 200 kg) inhabiting arid environments. Once common throughout western Asia, the wild ass has been extirpated throughout much of its range with the advent of modern firearms. There are several subspecies (for review see Saltz & Rubenstein 1995). The subspecies endemic to the Middle East (*E. b. hemipus*) became extinct at the beginning of the twentieth century (Groves 1986). In 1982, the Israel Nature Reserves Authority began reintroducing Asiatic wild asses from a permanent breeding core founded in 1968 from six animals from the Persian subspecies (*E. b. onager*) and five animals from the Turkemen subspecies (*E. b. kulan*). The core was established shortly after these adjacent populations were separated into two subspecies (recent genetic studies suggest that this separation is erroneous) (A. Oakenfull, personal communication).

The site selected for reintroduction in Israel was Mahtesh Ramon, a nature reserve established within an unusual anticlinal erosion cirque (Fig. 1) in the Negev highlands (lat 30°35'N, long 34°45'E). The area of the cirque is about 20,000 ha. It is elongated, running 40 km southwest to northeast, with a maximum width of 10 km. It is drained by the Ramon dry riverbed, which exits on the eastern side of the southern rim. The north rim of the cirque consists of a sheer 200-m drop. The cirque floor tilts downward toward the northeast, so the rim elevation ranges between 800 and 900 m and the cirque

floor ranges from approximately 800 m at the southwest edge to about 400 m in the northeast basin. The southern rim is less steep, with an elevation of about 510 m, and it has several openings. Annual rainfall ranges from about 95 mm in the southwest basin to 40 mm in the northeast basin and is restricted to the fall and winter (Ward et al. 1993). A single permanent water source, En-Saharonim, exists in the Ramon riverbed near its exit from the cirque. Several natural and artificial (from mining activity) ephemeral ponds exist in the center of the cirque and sometimes hold water from winter floods until July. In addition, an artificial water source was constructed for the reintroduced animals 1 km west of En-Saharonim.

Asiatic wild asses are polygynous. Male spatial organization and breeding strategy are currently unclear, but males of other equid species are either territorial or protect a harem, depending on the social and physical environment (Rubenstein 1986). If female assemblages are temporary but their movements are predictable, males will defend a territory. Territorial males that defend an exclusive home range are often found alone, patrolling their territory, and are not necessarily associated with a specific group of females (Maher & Lott 1995). Permanent-membership equid societies evolve when resources are uniformly distributed and feeding competition is low (Rubenstein 1986). When females live in permanent-membership groups, males will form a long-term association with and defend a specific group of females, or harem, against other males. In such harem-based societies, male home ranges may overlap with other males and their harems. Feh et al. (1994) concluded that Mongolian Asiatic wild asses (*E. b. luteus*) have a harem-based society, but they live in arid environments where re-

sources are limited, movements are predictable, and females live in open-membership groups (Klingel 1977). Thus, males are expected to be territorial, especially when the population is small (Rubenstein 1986).

Females usually attain sexual maturity at age 2 and give birth for the first time at age 3 (Groves 1974). A single foal is born after 11 months of gestation. Females may give birth in consecutive years (Zhirnov & Ilyinsky 1986). Parturition is seasonal, with most births occurring in May and June. Post-partum estrus usually occurs within a few weeks after parturition. Based on our observations, juvenile females remain with their mother for 2–3 years. Dominant males expel yearling males from the maternal herd, who then join bachelor herds. Little is known about the dynamics of bachelor herds.

Methods

Between 1982 and 1987, 28 animals (14 males and 14 females) were released in Makhtesh Ramon. The first release in 1982 included only five males. All of these animals dispersed immediately after release, and none survived (Saltz & Rubenstein 1995). In 1983 two males and six females were released. The males were 3 and 4 years old and were named Randa and Gandolf, respectively. This release succeeded (females remained in Makhtesh Ramon and produced offspring) and was followed by a release of two males (3 and 4 years old) and five females in 1984. The last release in this area was in 1987 and included five males (four 4-year-olds and one 3-year-old) and three females. Except for two females, aged 6 and 17, that died shortly after their release, all females were between 2 and 5 years old. Until 1989, reproductive success was low and population growth was slow (Saltz & Rubenstein 1995). Thereafter, reproductive success increased, and the population was estimated at over 100 animals in 1997. Currently, the reintroduced population has had little effect on the vegetation in the cirque (Saltz et al. 1999).

Of the animals reintroduced between 1982 and 1984, only one female from the 1983 release was radiocolored. In 1987, all animals were numbered with freeze marks. Wild-born animals were not marked. All females and all unmarked reintroduced males were readily recognizable by natural markings. Female foals remained with their mother until age 2 or 3; during this period natural markings, such as scars, are accrued. Regular monitoring of the population and careful updating of pictorial identification charts enabled identification. This was not the case for male foals; because they were expelled from the herd by the dominant male by the time they were 1 year old, few if any identifying scars were noted before expulsion. Without close association with their mothers, it was almost impossible to identify individual males when they returned as dominant males (except those that had

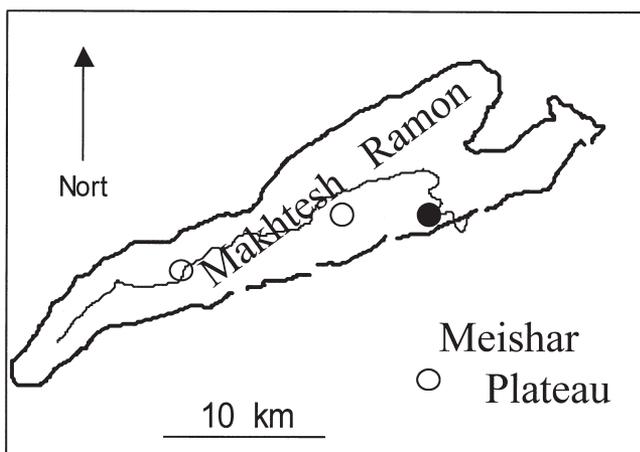


Figure 1. The Makhtesh Ramon study area. The thick line delineates the cliffs of the cirque, and the thin line is the Ramon dry riverbed. Open circles are ephemeral water sources; the filled circle is the En-Saharonim spring.

early scars or birthmarks). Thus, the genealogy of adult males born in the wild was, in most cases, unknown.

From 1982 to 1987 the Makhtesh Ramon ranger carried out post-release monitoring with periodic surveys to record the presence and reproductive success of all animals in the cirque. From 1988 to 1992 and in 1995 we monitored the herd intensively. In 1993 the population was surveyed and monitored for 10 days (in July and August), and in 1994 only reproductive success was noted.

We concentrated on movement patterns and association between males and females during the foaling and breeding season (April–September). Monitoring was done by systematically scanning the cirque 2–3 days per week from April to September. Each day, a different part of the cirque was randomly selected and scanned. Animals that we sighted were characterized according to group composition: (1) dominant males alone, a dominant male being defined as a male that appears to have regular and exclusive access to females and acts to maintain this exclusivity; (2) groups of females and young accompanied by a dominant male; (3) groups of females and young accompanied by one or more bachelor males (males that were sighted with females only once or twice); (4) groups of females and young unaccompanied by a dominant male or bachelor males; and (5) bachelor groups without females. Dominant and bachelor males are easily distinguishable. Dominant males are alert to human intruders (on foot or in a vehicle) but will generally stand their ground. They will turn and face the intruder until the human is within 50–100 m. Bachelors, on the other hand, roam in a group with other bachelors, are sensitive to human intruders, have large flight distances (>1 km), and will run at the first sight of humans.

Once animals were sighted, their location was recorded. Then, if the group was not a bachelor group, all animals were identified. Because of their large flight distances, we were unable to identify individuals in bachelor groups. We monitored female groups for at least 3 hours and collected behavioral data before searching for another group.

We analyzed the location data to determine dominant male home ranges, to assess whether males adopt a territorial or harem strategy, and to determine how female space-use patterns relate to male movements. Because female group composition changes on a daily basis, we calculated the home range of each individual separately. To ensure that locations were independent, we used only one location per animal per day.

To describe male home ranges, we used the Kernel estimator (Worton 1989) with the fixed-kernel option in the Ranges-V software. This is a robust technique that gives a good description of the animal's use intensity (utilization distribution) and center(s) of activity within its home range. These are depicted graphically by isopleths (isolines describing areas with equal location density). The Kernel estimator, however, requires a large

sample size. We calculated the home range of each dominant male from all locations during the study. If a major shift in the home range of a specific male was evident during the study, we carried out a separate analysis for each period.

To assess female space-use patterns in relation to those of males, we calculated the amount of overlap between each female and each dominant male for each of the foaling/breeding seasons. Because of the differences in sample size available for each male in each foaling/breeding season and the relative unimportance of the utilization distribution for this analysis, we used the more general and more robust bivariate normal technique (Jennrich & Turner 1969) to depict the home range of males. The bivariate normal calculates a home range by assuming that the animal's location in space is distributed normally along two axes (x and y) with a single center of activity. With Ranges-V software, we then determined the 90% density distribution line for each male and the fraction of sightings of each female that fell within it. We used a 90% density distribution to minimize home-range inflation by outliers. We considered the relative use of male home ranges by a female as the fraction of all locations obtained for that female which fell within the male's home range. We then categorized the overlap between each possible male-female pair as low, 1–25%; moderate, 25–50%; high, 50–75%; or very high, 75–100% (pairs with no overlap were excluded).

We assessed shifts of females among male home ranges by comparing changes in the overlap of female locations and male home ranges between years. For each female we determined the male with which she had the maximum overlap in a specific season, based on the number of her locations in each male's home range. A female was considered to shift between males if her maximum overlap changed from one male to another.

We tested whether a change in the male that a particular female was most associated with (compared with the previous season) had an effect on the reproductive success of the female in the following season. We considered a change in association as either a takeover by a new dominant male or a shift of the female's home range causing a change in the identity of the male with whom she had the greatest overlap.

Results

Male Space-Use Patterns

Shortly after the 1983 release, Gandolf expelled Randa and appeared to establish a home range on the east side of the cirque near the site of release. Over the next year, Gandolf's movements and those of the females expanded to include most of the cirque. The males released in 1984 and in 1987 disappeared shortly after their release and

were not seen again. (A. Cohen, local ranger, personal communication).

In the summer of 1988, when the intensive study began, Gandolf was still the only dominant male in the cirque, with a center of activity adjacent to the northern rim in the center of the cirque (Fig. 2a). At the end of July 1989, a second male (Napoleon) took over the eastern side of the cirque, and Gandolf's home range and center of activity shifted westward (Fig. 2b). In early spring of 1991, Napoleon disappeared after losing his home range to a new male named Triang. At the same time, a fourth male named HT established a home range in the western part of the cirque, taking over the western side of Gandolf's home range (Fig 2c). Consequently, Gandolf's home range became even smaller. A fourth home range was established in late 1991 by a male (Hector) born in Makhtesh Ramon in 1989 on the Meishar plain about 10 km south of the cirque. In 1992 two new

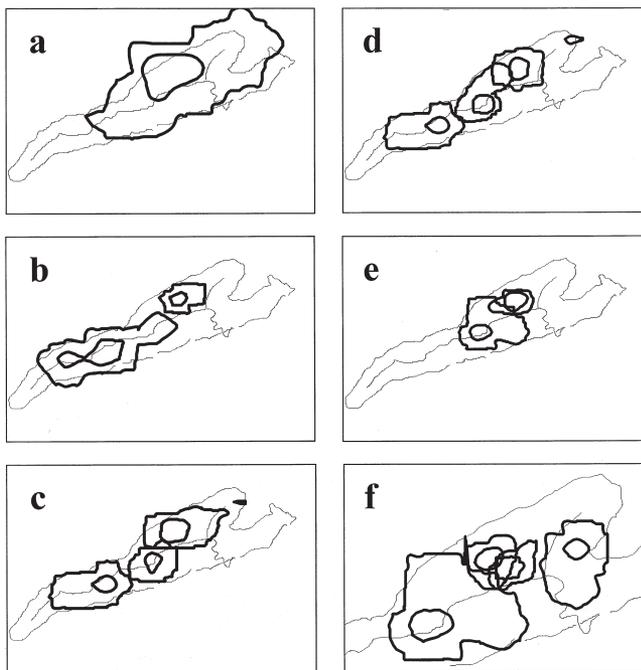


Figure 2. Male home ranges of the Asiatic wild ass as depicted by the Kernel estimator (heavy lines) superimposed on the Makhtesh Ramon study area (light lines). Isopleths (see text) are from the inside-out 30% and 90%. Home ranges are (a) Gandolf until 1989; (b) 1990, Gandolf (west) and Napoleon (east); (c) 1991, HT (west), Gandolf (center), and Triang (east); (d) 1992, HT (west), Gorby (center), and Cut (east and including isolated circle at northeast corner of the cirque); (e) 1993, HT moved to the center of the cirque between Gorby and Cut (data are insufficient to present Cut's home range); (f) 1995 close-up and the center and east end of the cirque, Gorby (center), Put (east), and between them Questa (center-north) and Richard (center-south).

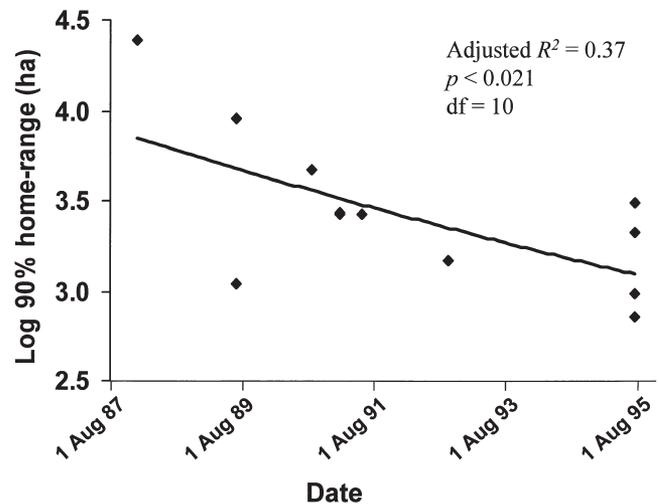


Figure 3. Male home-range size in hectares, calculated by the 90% isopleth using the Kernel method, as a function of date following release. Each point is the home range of one male as calculated at the time he was first sighted. If a major shift occurred in the home range with the appearance of another male, home-range size was recalculated and the second value was used. Regression line based on linear regression after log transformation.

males, Gorby and Cut, replaced Gandolf and Triang, respectively (Fig 2d). Gorby initially appeared at the northeast corner of Gandolf's home range and, after several weeks, took over entirely. In 1993 HT shifted his home range to the center of the cirque between Gorby and Cut (Fig 2e). In 1995 Gorby maintained his home range, but HT and Cut disappeared and three new males took their place: Richard, Questa, and Put (Fig. 2f). Overall, male 90% home range size declined significantly ($p < 0.021$, linear regression after log transformation), from 24,700 ha while Gandolf was the only dominant male in the cirque in 1988-1989 to $1,720 \pm 1090$ ha ($n = 4$) in 1995 (Fig. 3).

The fate of the reintroduced males that did not hold territories and territorial males that were deposed is unknown. None of the freeze-marked males released in 1987 ever held territories. Shortly after they were displaced, deposed territorial males were often sighted once or twice at the periphery of their home ranges, and then they disappeared.

Dominant males were often found either patrolling, resting at high points where part of the territory could be well observed, or following females. Occasionally, two dominant males would be found standing and facing each other along the boundary line between their respective home ranges. The movement patterns of dominant males varied with time of year. During the height of the breeding season (June), dominant males were often sighted with females (Fig. 4). In contrast, in earlier and

later months males were generally sighted alone ($p = 0.032$, second-degree polynomial regression), often while patrolling their home range.

Although water is probably the most critical resource in this region, individual male home ranges were not set up around water sources. Most water sources were located at the periphery of the home ranges and were used by several dominant males (Figs. 1 & 2). Certain males traversed other males' home ranges to get to water. We have two observations of such males being located by the resident male and chased away. Males were rarely found in the vicinity of water and were never sighted with the females near the water.

Bachelor males avoided entering existing dominant-male home ranges and were sighted mostly on peripheries and as far as 70 km from the cirque. Bachelor herds usually had 2–20 animals and were rarely sighted within male home ranges (<10 sightings over the entire study period). We sighted bachelors in association with females only once, and the dominant male was not present. Sightings of lone bachelors were rare. In most cases these bachelors were subadult males recently displaced by a territorial male. Bachelors were never sighted together with dominant males.

Male Recruitment

Reproductive success was low during the first several years after the reintroduction began, and progeny sex ra-

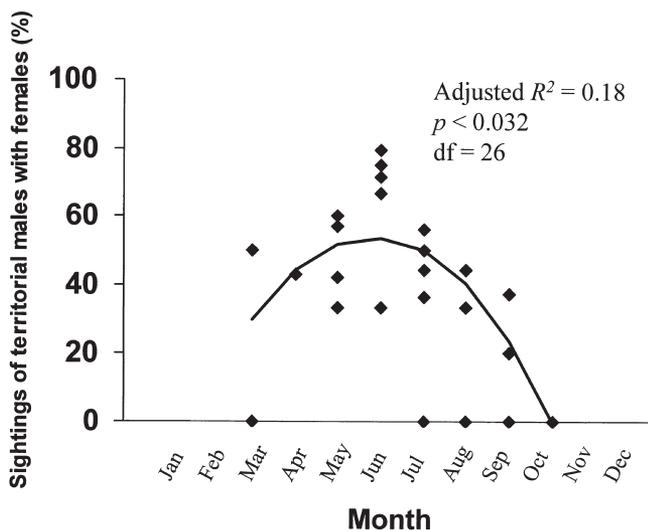


Figure 4. The association of territorial males with females as determined by the proportion of male sightings in which the male was accompanied by females. Each point is the percentage of all sightings per male per month. Only cases in which a male was sighted four times or more in 1 month are included. Regression line is a second-degree polynomial in which each point is weighted by the number of sightings.

tio was male-skewed (Saltz & Rubenstein 1995) until 1992. Thus, between 1985 and 1995 a total of 47 male foals were born, of which 43 survived to 1 year. In contrast, 37 females were born during this period, 20 of them between 1993 and 1995.

During the breeding season, dominant males continually harassed yearlings, eventually forcing them to leave their mothers and the female group. Thereafter, the yearlings roamed the peripheries of dominant-male home ranges and joined bachelor groups. Because bachelors were rarely sighted, we were unable to identify them individually and consequently have no data on their survival during this period. We were unable to determine at what age bachelors return to challenge the dominant males.

Male-Female Home-Range Overlap and Association

Between April and September, female movements were dictated by water sources (unpublished data). During this time, lactating females moved between grazing areas and water sources on a daily basis. Females tended to associate with conspecifics that had overlapping home ranges, with fission and fusion occurring on a daily basis. Based on the presence of dominant males in the cirque (Figs 2a–f), we analyzed female space-use patterns in six different periods: up to July 1989, July 1989 until the end of the summer of 1990, and spring and summer of 1991, 1992, 1993, and 1995.

When Gandolf was the only dominant male in the cirque, most female sightings (96% to 100%) fell within his home range. In 1990 when Napoleon took over part of Gandolf's territory, overlap was bimodally distributed, with the intermediate overlaps (25–75%) being less frequent (Fig. 5). Eight of 12 females had a high overlap (>72%) with Gandolf, and 4 exhibited a high overlap with Napoleon. Over time this distribution changed, with most females having a maximum overlap of <50% with any one male ($\chi^2 = 29.1$, $p = 0.004$, $df = 12$). The reproductive success of females that experienced a change in dominant male was 0.66 foal per female ($n = 33$), compared with 0.64 foals per female ($n = 56$) among females experiencing no change ($p = 0.82$, $\chi^2 = 0.052$, $df = 1$).

On several occasions males were sighted trying to herd females. This was done when females were moving to or from water and were approaching the edge of the male's home range. Males attempted to herd the females back toward the center of their home range by placing themselves between the females and the outer edge of the home range and lifting their heads in a threatening gesture. These attempts were never successful, and the females simply bypassed the male.

Discussion

Successful reintroductions offer a unique opportunity to study an important aspect of conservation—the biology

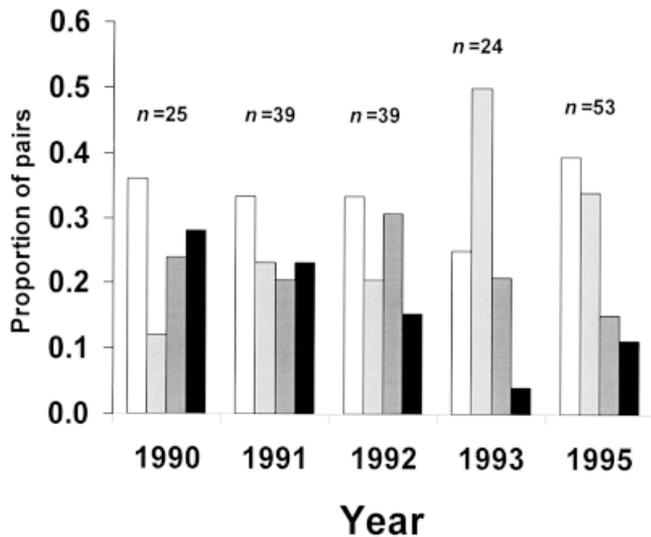


Figure 5. Proportion of all male-female pairs with overlapping home ranges in a given year that fall into each category (see text for details on calculation of percent overlap). Overlap categories include low (1–25%), white; moderate (25–50%), light gray; high (50–75%), dark gray; and very high (75–100%), black. Numbers above the bars of each year are the total number of overlapping pairs.

of small, increasing populations (Sarrazin & Barbault 1996). Our results indicate that in such populations space-use patterns may change dramatically over a relatively short period of time, during which there are only modest changes in the absolute size of the population.

Male Asiatic wild asses reintroduced into Makhtesh Ramon cirque exhibit exclusive use of their home range with respect to other males. Although sightings of actual combat and active defense were few, the expulsion of juvenile males from the home range and the general avoidance of these home ranges by bachelor groups and other males suggest that these areas are also defended. We conclude that male Asiatic wild asses in our study population are territorial.

As the number of males controlling territories increases, females may either (1) exhibit high fidelity to a specific male or (2) roam freely between different male home ranges. If females exhibit fidelity to a specific male, the proportion of female sightings that overlap with male home ranges should be distributed bimodally—each female exhibiting high overlap with one male and low overlap with all other neighboring males—with no intermediate overlaps. If females do not exhibit fidelity to a specific male, overlaps would be mostly in the middle and low ranges. In our study, as the number of territories increased, female fidelity to a single male decreased. Furthermore, female groups fissioned and fused on a daily basis. Thus, we conclude that Asiatic wild asses in our study population do not protect harems.

In contrast, Feh et al. (1994) concluded that Mongolian Asiatic wild asses (*E. b. luteus*) exhibit a harem-type behavior. The discrepancy may be real and may result from different conditions in Mongolia, such as higher densities or a different distribution of resources, that would render territories undefendable. Feh et al. (1994) did not individually identify males, and their observations were made between June and August, when females are in estrus. Our results indicate that during this period territorial males spend more time with female groups. This is not a harem protection strategy, however, but simply a male strategy of following estrus females in his territory to enhance his mating probability.

For several reasons, it is unlikely that any of the unmarked, reintroduced males other than Gandolf had held territories. First, in a reintroduction carried out in the Paran riverbed 50 km south of Makhtesh Ramon (Sinai 1994), the dominant male in the reintroduced group was displaced immediately by a 4-year-old male born in Makhtesh Ramon. This suggests the existence of a “resident advantage” (Krebs 1982). Second, displaced territorial males never returned to hold a territory, suggesting that, once displaced as adults, males do not attain territorial-male status again. Third, two territorial males born in the wild and identifiable as adults were young (≤ 4 years old) when they became territorial. Thus, the three unmarked males reintroduced in 1983 and 1984 would have suffered from three disadvantages: they were displaced as adults, they were non-native, and they were relatively old (≥ 8 years old) when Gandolf began losing parts of his territory. The failure of the five freeze-marked males released in 1987 to secure territories lends further support to this hypothesis.

The increase in the number of territory-holding males and the associated decline in territory size as the number of males in the population increased both indicate that intruder pressure is important in shaping the spatial organization of males. Similar results were found in other vertebrate species (Stamps 1994). Surveys we conducted in 1996–1999 indicate that the process is continuing as the population continues to grow. In 1996 and 1997, new territorial males were sighted in the southeastern lobe of the cirque, the southern portion of Hector’s territory in the Meishar plateau, and the west side of the cirque originally occupied by HT. In 1998 and 1999, six and nine males (respectively) exhibiting territorial behavior were sighted in various parts of the cirque. The males were sighted alone or with female groups and in different geographic regions of the cirque.

Effective Population Size

The social system of a species is expected to have considerable effects on effective population size (Primack 1993). The presence of a single territorial male in the reintroduced population during the first 6 years of the re-

introduction greatly reduces N_e . In species with nonoverlapping generations, if one male does all the breeding N_e can not exceed 4, regardless of population size ($N_e = 4r(1-r)N$, where r is the proportion of males and N is total population size; Nunney 1993). As generation time increases, however, N_e approaches $N/2$.

Asiatic wild asses have a relatively long generation time (7.4 years; Saltz & Rubenstein 1995). Thus, we used the equations developed by Nunney (1993) for calculating N_e in polygynous species with nonrandom mating and overlapping generations. In 1989 there were 12 breeding animals with only 1 male. Because of the non-normal age structure, reproductive success was male-skewed (2:1; Saltz & Rubenstein 1995), and we assumed that male survival was similar to that of females (0.9/year). Based on equation 18a from Nunney (1993), we calculate that $N_e = 4.1$. Although N_e can exceed 4 with only one breeding male, the contribution of additional females is marginal. For example, doubling the number of females to 22 would increase N_e to only 6.3.

In 1995 there were 40 breeding animals with five territorial males, and age structure was more normal; as a result, sex ratio at birth was approximately 1:1 (unpublished data). If we assume that the female survival rate remained unchanged and the adult male survival rate declined because of increased competition for territories to somewhere between 0.8–0.3/year, then according to equation 17b from Nunney (1993) N_e would be 19.0 for a male survival rate of 0.8/year and 25.0 for male survival rate of 0.3/year (Fig. 6).

Although other stochastic factors are considered a greater threat to small populations (Nunney & Campbell 1993), the low N_e in relation to total population size contributes significantly to the loss of genetic variability in the reintroduced population and, if possible, should be minimized by active management. Appropriate management depends on identifying the causes of the problem. We postulate that the extended presence of a single breeding male in the Makhtesh Ramon population was the result of four factors:

- (1) A small number of animals was released in 1983 (2 males and 5 females), enabling Gandolf to take over the entire herd and maintain control over it with little effort (i.e., only one competitor and few females to protect).
- (2) In later releases, Gandolf already had the “resident advantage” and, because the population was still small, he was able to maintain his dominance.
- (3) Due to low reproductive success in the first 4 years of the reintroduction (Saltz & Rubenstein 1995), few males were recruited, so competition for territories and intruder pressure remained low.
- (4) Asiatic wild asses are fully grown only at age 3, so young males are not expected to challenge territorial males before they are at least 3 years old. The

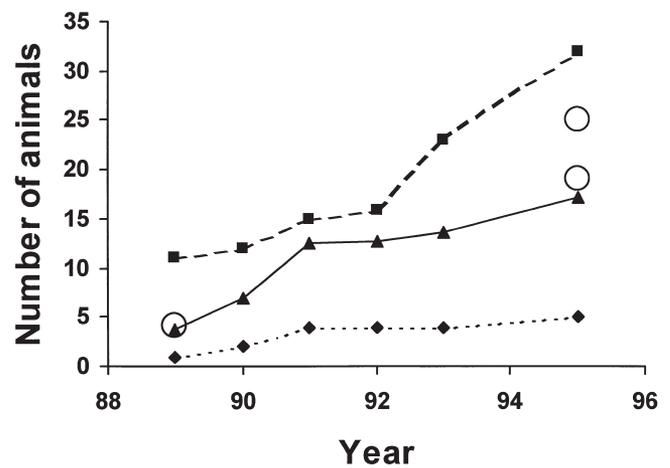


Figure 6. Number by year of adult females (squares), territorial males (diamonds), and genetically effective population size (N_e) based on nonoverlapping generation (triangles). Circles represent N_e calculated for territorial polygynous species with overlapping generations (in 1989 assuming a difference in recruitment between the sexes and in 1995 assuming differences in survival between the sexes, with female survival being 0.9/year and male survival being 0.8/year [lower circle] and 0.3/year [upper circle]).

first males were born in the wild in 1985. Thus, no native-born males could challenge Gandolf before 1988.

Given these conditions, several possible actions can be taken to increase the number of breeding males. Managers may be able to artificially increase male turnover by removing the dominant male. We found no correlation between male turnover and reproductive success, but the question remains of whether the possible cost—reduced reproductive success as a result of male turnover (Berger 1983)—outweighs the benefits of an increased male turnover rate.

The simultaneous or sequential release of animals to different areas will result in at least one territory in each release site. This technique also has the advantage of reducing the effect of environmental stochasticity, but it would greatly increase the cost of reintroduction because of the need to erect several habituation enclosures. In the case of sequential releases, we recommend that new release sites be outside the existing range of the previously released populations to prevent the displacement of new males by resident offspring of the dominant males from the previous releases. The release sites, however, should be located to enable eventual genetic flow among them.

Carrying out a single release of a large number of males and females will make the defense of a large territory costly and could lead to the establishment of several territories. The disadvantages of this method are (1) the

absence of knowledge regarding the number of animals needed to ensure that more than one territory is established and (2) the monetary and logistical effort required for such large releases.

Releasing a herd with many male yearlings creates a large pool of potential future challengers. Although these yearlings will be displaced immediately upon release, they are expected to return within 2 years to challenge those males holding a territory.

Because of the advantage of resident males and the low probability of displaced adult males attaining territorial status, we believe that repeated releases of adult males in the same area, as conducted in this reintroduction, are not feasible. The release of more females may also have limited advantages because, as long as the number of released females is small enough for a single male to control all of them, N_e will increase little.

Reserve Design

In populations where few males breed with many females, an increase in the number of females has a limited impact on N_e (Nunney 1993). Consequently, in polygynous species the number of males is key to achieving a genetically viable population. In the case of territorial polygynous species, more males may mean more territories. Thus, reserve design for such species must account for territoriality and territory characteristics.

Water is a critical resource in deserts and is an important determinant in the space-use patterns of Asiatic wild asses. During lactation, mothers must drink daily (personal observations) and can travel up to 20 km in each direction for this purpose, crossing several male territories in the process. Females spend only a few minutes at a watering site, presumably to minimize the risk of predation. Because water sources in this region are point sites serving many other animals, including predators and other conspecifics, and because females spend little time in their vicinity, the cost of defending them relative to the benefit may be unacceptably high. Thus, to enhance fitness, males are expected to set up territories in the vicinity of the water source or within a certain radius from water along female travel routes, but not to defend the water source itself. In our study, water sources were always on the periphery of several male territories and were shared by these males and by males in territories farther away. We conclude that although desert water sources are limited and critical to the existence of Asiatic wild ass populations, a considerable number of male territories and female home ranges can be established around a single water source. A similar pattern was found in the feral ass population of Death Valley (Moehlman 1974) and in Grevy's zebra (*Equus grevyi*; Ginsberg 1988; Rowen 1992). A single water source supporting a population within a radius of 20 km translates into an area of 120,000 ha (area = $\pi r^2 \times 100$).

If average territory size is 2000 ha, then a single water source can support a maximum of 60 territories, depending on other characteristics of the habitat and terrain. If we assume, based on the number of territorial males and adult females in the Ramon cirque, that the average number of females controlled by a single male is seven, then N_e for this population is roughly $60 \times 4 = 240$. If a minimum viable population should have an effective size of 5000 (Lande 1995), then at least 24 such reserves are required to ensure the population's long-term existence.

Behavior and social structure are seldom considered in population viability analyses. Growing reintroduced populations offer an excellent opportunity to study the effects of behavior and social structure on population viability. Our study demonstrates that the social structure of Asiatic wild asses is an important component of its viability, mostly in terms of N_e . Space-use patterns and behavior may change rapidly as small populations increase, and with season. Consequently, detailed, long-term knowledge is required to correctly characterize these patterns. These data can then be used to specify the reserve characteristics necessary to support a viable population.

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Literature Cited

- Allee, W. C. 1931. Animal aggregations: a study in general sociology. University of Chicago Press, Chicago.
- Beck, B. B., L. G. Rapaport, M. R. Stanley Price, and A. C. Wilson. 1994. Reintroduction of captive-born animals. Pages 265–286 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative conservation: interactive management of wild and captive animals. Chapman and Hall, New York.
- Beissinger, S. R. 1997. Integrating behavior into conservation biology: potential and limitations. Pages 23–47 in J. R. Clemmons and R. Buchholtz, editors. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom.
- Berger, J. 1983. Induced abortion and social factors in wild horses. *Nature* 303:59–61.
- Clemmons, J. R., and R. Buchholz. 1997. Problems and issues. Pages 3–22 in J. R. Clemmons and R. Buchholtz, editors. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom.

- Durant, S. M., and G. M. Mace. 1994. Species differences and population structure in population viability analysis. Pages 67-91 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman and Hall, New York.
- Feh, C., T. Boldsookh, and C. Tourenq. 1994. Are family groups in equids a response to cooperative hunting by predators? The case of Mongolian kulans. *Revue Ecologie (Terre Vie)* **49**:11-20.
- Ginsberg, J. R. 1988. Social organization and mating strategies of an arid adapted equid: the Grevy's zebra. Ph.D. dissertation. Princeton University, Princeton, New Jersey.
- Groves, C. P. 1974. *Horses, asses and zebras in the wild*. Ralph Curtis Books, Hollywood, Florida.
- Groves, C. P. 1986. The taxonomy, distribution, and adaptation of recent equids. Pages 11-51 in R. H. Meadow and H. Uerpman, editors. *Equids in the ancient world*. Ludwig Reichert Verlag, Weisbaden, Germany.
- Jennrich, R. J., and F. B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* **22**:227-237.
- Lande, R. 1995. Mutation and conservation. *Conservation Biology* **9**:782-791.
- Klingel, H. 1977. Observation on social organization and behavior of African and Asiatic wild asses (*Equus africanus* and *Equus hemionus*). *Zeitschrift für Tierpsychologie* **44**:323-331.
- Krebs, J. R. 1982. Territorial defence in the great tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology* **11**:185-194.
- Maher, C. R., and D. F. Lott. 1995. Definition of territoriality in the study of variation in vertebrate spacing systems. *Animal Behavior* **49**:1581-1597.
- Moehlman, P. D. 1974. Behavior and ecology of feral ass (*Equus asinus*). Ph.D. dissertation. University of Wisconsin, Madison.
- Novellie, P. A., P. S. Miller, and P. H. Lloyd. 1996. The use of vortex simulation models in a long term program of reintroduction of an endangered large mammal, the Cape mountain zebra (*Equus zebra zebra*). *Acta Oecologia* **17**:657-671.
- Nunney, L. 1993. The influence of mating systems and overlapping generations on effective population size. *Evolution* **47**:1329-1341.
- Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* **8**:234-239.
- Primack, R. B. 1993. *Essentials in conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Ralls, K., R. A. Garrott, D. B. Siniff, and A. M. Starfield. 1992. Research on threatened populations. Pages 197-216 in D. M. McCullough and R. H. Barrett, editors. *Wildlife 2000: populations*. Elsevier Applied Science, New York.
- Rowen, M. 1992. Mother-infant behavior and ecology of Grevy's zebra. Ph.D. dissertation. Yale University, New Haven, Connecticut.
- Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. Pages 282-302 in D. I. Rubenstein and R. W. Wrangham, editors. *Ecological aspects of social evolution*. Princeton University Press, Princeton, New Jersey.
- Saltz, D., and D. I. Rubenstein. 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. *Ecological Applications* **5**:327-335.
- Saltz, D., H. Schmidt, M. Rowen, A. Karnieli, D. Ward, and I. Schmidt. 1999. The feasibility of applying remote sensing techniques for assessing grazing impacts in hyper-arid environments. *Journal of Range Management* **52**:500-507.
- Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. *Trends Ecology and Evolution* **11**:474-478.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* **31**:131-134.
- Sinai, J. 1994. A program for assembling a herd from a large herbivore breeding core for the purpose of reintroduction: the Asiatic wild ass *Equus hemionus* in Hai-Bar Yotvata. M.S. thesis. Hebrew University of Jerusalem, Israel.
- Stamps, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior* **23**:175-232.
- Sutherland, W. J. 1998. The importance of behavioral studies in conservation biology. *Animal Behavior* **56**:801-809.
- Ward, D., L. Olsvig-Whittaker, and M. Lawes. 1993. Vegetation-environment relationships in a Negev Desert erosion cirque. *Journal of Vegetation Science* **4**:83-94.
- World Conservation Union. 1998. Guidelines for re-introductions. Reintroduction Specialist Group, World Conservation Union/Species Survival Commission, Gland, Switzerland, and Cambridge, United Kingdom.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* **70**:164-168.
- Zhirnov, L. V., and V. O. Ilyinsky. 1986. Wild-ass. Pages 68-79 in V. Y. Sokolov, editor. *The Great Gobi National Park: a refuge for rare animals in the central Asian deserts*. Center for International Projects, GKNT, Moscow.

