Population Dynamics of a Reintroduced Asiatic Wild Ass (Equus Hemionus) Herd

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Ecological Applications is currently published by Ecological Society of America.

POPULATION DYNAMICS OF A REINTRODUCED ASIATIC WILD ASS (*EQUUS HEMIONUS*) HERD[1]

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Abstract. Reintroduction is the release of animals into an area where they were extirpated or have significantly declined. Little is known about the factors that determine the success or failure of ungulate reintroduction. We studied the dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) population for 10 yr (1983–1993) following the first successful release into the wild. A total of 14 adult females and 14 adult males were released into a nature reserve in the Negev Desert of southern Israel. Over this 10-yr span the female population has grown to only 16 adults. Reproductive success of reintroduced females was low in the first 5 yr following release (0.0–0.8 foals·female^{-1}·yr^{-1}), but increased to 0.5–1.0 foals·female^{-1}·yr^{-1} in the last 5 yr. Reproductive success of wild-born females ≥ 3 yr old was higher than that of reintroduced females of similar ages, and ranged from 0.5–1.0 foals·female·$^{-1}$yr^{-1}. Our study and data from the *E. hemionus* studbook suggest that young nonprimiparous females produced primarily males, while primiparous and old females produced primarily females. We attribute the low reproductive success following reintroduction to the stress caused by capture, transport, and release procedures; we consider the age-dependent progeny sex ratio within the framework of Trivers and Willard's (1973) maternal allocation hypothesis. We conclude that the slow growth of the female population was due to: (a) low reproductive success of females in the early years following reintroduction, and (b) a male-skewed progeny sex ratio among prime-aged reintroduced females. A simple stochastic Leslie matrix model suggests that high survival and improved reproductive success of reintroduced females at later stages of the study, and the reproductive success of wild-born females, make the population relatively unsusceptible to extinction from random demographic processes. In-depth knowledge of the dynamics of reintroduced populations is vital for the correct assessment of their viability. We offer suggestions for increasing the efficacy of future wild ass reintroductions.

Key words: Asiatic wild ass; Equus hemionus; *extinction; population dynamics; progeny sex ratio; random demographic processes; reintroduction.*

INTRODUCTION

Reintroduction is the release of captive animals into wild areas where they occurred in the past, and where they have significantly declined or were extirpated in historical times (Jungius 1985, Kleiman 1989). A reintroduction is considered successful only if it results in a self-sustaining population (Scott and Carpenter 1987, Griffith et al. 1989). Reintroductions of threatened or endangered species tend to fail more often than not (Griffith et al. 1989). This is especially true of mammals (Kleiman 1989). To improve the rate of success, the International Union for the Conservation of Nature and Natural Resources (IUCN) has recommended a four-phase reintroduction schedule: (1) a feasibility study to determine likelihood of success, (2) a preparation phase for selecting animals and release sites, (3) the release phase including selection of date and time for release, and (4) post-release monitoring

that evaluates the success of the release; it also recommends management steps for enhancing the success of current and future reintroductions (IUCN 1987). While much attention has been devoted to the first three phases, post-release monitoring has often been neglected (Ralls et al. 1992). Consequently, little has been learned about factors that determine the success or failure of reintroductions.

The success of a reintroduction depends on the reproductive success and survival of the population. This, in turn, is dependent on the species' natural rate of increase, its genetic attributes, and environmental conditions (Ballou and Ralls 1982, Griffith et al. 1989), and on stochastic variations in these factors (Shaffer 1981). Thus, monitoring should concentrate on survival and breeding success of individuals by age and sex, and the intrinsic and extrinsic variables that may affect them (Scott and Carpenter 1987, United Nations 1992). As data accumulate, the dynamics of the population and its determinants can be quantified, its present and future performance assessed, and management strategies recommended.

In this paper we report on the dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) population in Israel, from the time the herd was established in the wild in 1983 until 1993. We incorporate relevant wild ass and ungulate biological attributes in analyzing and modeling the dynamics of the population, and consider our findings with respect to future reintroduction attempts.

BACKGROUND

Asiatic wild ass are medium-sized equids weighing ≈200 kg as adults. Females live in open membership groups that wander through large territories defended by solitary males (Klingel 1977, Rubenstein 1989). Males are larger than females (Groves 1974) and intensively compete for territories (Berger 1981). Many males do not obtain territories, and often associate in bachelor herds. Females usually attain sexual maturity at age 2 and give birth for the first time at age 3 (Groves 1974). Gestation is 11 mo, at the end of which a single foal is born (Pohle 1972). Females survive up to 26 yr in captivity (Pohle 1992) and may give birth in consecutive years, but wild animals rarely reproduce after age 15 (Zhirnov and Ilyinsky 1986).

There are several distinct races of *E. hemionus* that fall into three size groups (Groves 1986): the two large Mongolian subspecies (*E. h. hemionus* and *E. h. luteus*), 110–130 cm at the withers; the mid-sized Turkmenian, Iranian, and Indian subspecies (*E. h. kulan, E. h. onager,* and *E. h. khur* respectively), 108–120 cm; and the small *E. h. hemippus,* ≈100 cm. The latter were endemic to the Middle East and were probably distributed from the foothills of Judea and Samaria in present-day Israel to the Euphrates region (Ducos 1975). The last sighting of a wild *E.h. hemippus* individual was in Syria in 1938, and the subspecies is now considered extinct (Groves 1986).

METHODS

Study animals

The population we studied originated from a breeding core established in Israel in 1968, by the Israel Nature Reserves Authority (INRA). The core was founded from six Persian wild ass (*Equus hemionus onager*) (three males, three females), followed by an addition of five animals (two males, three females) from the Turkmenian subspecies (*Equus hemionus kulan*) obtained from zoos in Europe. The animals were kept at the Hai-Bar Yotvata reserve (a 2-km² fenced compound) where they were allowed to interbreed. The herd, therefore, must be considered as *Equus hemionus* spp. (Pohle 1971–1992).

From 1982–1987 the INRA carried out four releases into the wild (INRA, *unpublished data*). All released animals were from the Hai-Bar Yotvata breeding core. The first release took place in 1982 and included only males. Documentation concerning this release (and oth-

ers) is limited, but suggests that the decision to release only males was due, partly, to an excess of males at Hai-Bar Yotvata. All these animals dispersed shortly after release. Some were found in the Arava valley after being shot along the Israel/Jordan borderline, but the fate of most of them is unknown. In 1983 a second attempt was made releasing eight animals (two males, six females). This release took hold, and was followed by a boost release in 1984 (two males, five females) and another in 1987 (five males, three females). All except two females (aged 6 and 17) were between the ages of 2 and 5 when released. The two older animals and one 5-yr-old died shortly after release.

Study area

The site selected for reintroduction was Makhtesh Ramon nature reserve. The reserve is a 200-km² erosional crater in the central Negev Desert of southern Israel. Steep cliffs surround the crater, except for a few narrow gorges and passes along its southern edge. Climate and vegetation phenology are strongly seasonal with hot, dry summers and cool, wet winters. Average rainfall for the years 1985–1993 was 57 mm, with large yearly fluctuations in precipitation and primary production (D. Saltz and D. I. Rubenstein, *personal observation*). Plant development usually peaks in late winter to early spring, and vegetation is dormant by June. Most growth is restricted to the seasonally dry riverbeds (wadis) that drain the crater. Free water is available year round from a single natural spring (En Saharonim) at the southeast margin of the crater. Natural and artificial (formed by mining activity) ephemeral ponds may hold runoff water as late as November.

All releases were made by INRA personnel. For releases during 1982–1984 the animals were transported in individual crates from Hai-Bar Yotvata to a fenced holding pen that included the En-Saharonim spring. Food, water, and shade were provided. The animals were kept in the pen for ≤3 mo and released by simply opening the gates. In the last release (1987) captive animals were transported from Hai-Bar Yotvata in trucks and released directly into the wild ("hard release," Griffith et al. 1989).

Field data collection

The population has been continually monitored by direct observation since the first release. During 1983–1987 the herd was monitored opportunistically by the INRA, and information for this period is based on communication with the local ranger, A. Cohen. We began an intensive and systematic study in 1988, at which time all reintroduced animals were of known sex and age, and were all individually identifiable by distinctive natural markings. One animal, a female released in 1984, was radio collared, but the transmitter failed 3 mo after release. Relocation of animals was by random visual searching with an off-road vehicle, tracking of spoor, and monitoring of water sources. We used 10 ×

50 binoculars and a 20×–50× spotting scope to identify individuals. During spring and summer (foaling and breeding season) monitoring took place 2–3 times/wk. Pregnancy was noticeable in its advanced stages, and the sex of the newborn foals was determined shortly after birth. Newborns usually received scars that permitted identification by 2 yr of age. Because female offspring remain with their mothers until their first parturition (at 3 yr of age) it was possible to identify them and to determine maternity. Young males, however, were chased from the herd by territorial males at 1–2 yr of age, and were often impossible to identify as adults.

Analysis

We used SAS (SAS Institute 1987) for all our statistical analyses, and considered differences significant at $P < 0.05$. We calculated reproductive success (RS) of individual females as the number of foals each female produced over a given number of years. We compared RS between reintroduced and wild-born animals using general linear models after performing an arcsine transformation, and weighting the data according to the number of years data were available for particular animals. To test for changes in RS over time we divided the number of years data were available on each female into two equal periods. In females for which we had an odd number of years we did not include the middle year. We calculated the RS of each reintroduced female in each time period, noted whether it increased or decreased, and tested the results with a sign test (Siegel 1956). Data on annual precipitation were available from 1985–1993. We correlated annual RS with annual precipitation in the year preceding parturition and with annual precipitation in the year preceding conception. RS was arcsine transformed before we did the correlations. We defined progeny sex ratio (PSR) as the ratio males born : females born. We calculated PSR for five age groups: 2–3, 4–6, 7–9, 10–12, and >13, and tested deviations in PSR with chi-square or Fisher's exact test (depending on sample size).

We constructed a life table for females using data from the reintroduced herd. We calculated RS and PSR for dams based on six age groups: 2, 3, 4–6, 7–9, 10–12, and >13. For each dam in each age group we calculated RS as the number of progeny divided by the number of years data were available for the dam in the age group. Mean RS per age group was calculated weighting RS by the number of years data were available for each dam. RS was then adjusted accordingly by the PSR for that age group to determine the number of females produced. Because of limited numbers, we were unable to construct a survival curve. Instead we used the survival curve of zebra (*Equus burchelli*) provided by Spinage (1972).

We compared our demographic findings with data from the world wild ass studbook published by the Berlin Zoo (Pohle 1971–1992), and from other literature (Zhirnov and Ilyinsky 1986). The studbook documents births and deaths of wild ass in zoos and wildlife sanctuaries throughout the world, by subspecies. Birth data include the gender of the foal, date of birth, location, and mother identification that permits the determination of her age. From these data we calculated postnatal survival and PSR as a function of maternal age. We did not estimate age-specific RS from the world studbook because it may be artificially manipulated rather than naturally determined.

Modeling

We used Monte Carlo Leslie matrix simulations to predict the future growth of the population and extinction probabilities arising from random demographic processes. This technique does not consider density-dependent responses (and, therefore, requires no estimates of carrying capacity) and projects an exponential growth. Consequently, the Leslie matrix is adequate only for short-range projections of populations at the lower end of their growth curve. In this study we had no estimate of carrying capacity, the population was small, and density effects were therefore presumed minimal.

The model was based on the life table constructed for the reintroduced herd. Pulses were 1 yr. Simulations were stochastic with the probability of producing a female and surviving varying as random binomials around the mean values found in the wild population and literature. Specifically, the program generated two random uniforms between 0 and 1 (one for reproduction and one for survival) for each individual in each pulse (Simberloff 1988). If the first generated value was less than the survival rate given to that specific age group, the female in the model survived to the following year. Similarly, if the second random number was smaller than the probability of an adult female in that age group producing a female offspring, the female in the model produced a female offspring. Environmental stochasticity and genetic effects were not incorporated in the model owing to insufficient data. We ran the model 1000 times (Harris et al. 1987), producing a range of growth curves, and calculated extinction probability due to random demographic processes.

RESULTS

Reproduction and survivorship

In August 1993, there were 16 adult females, 3 2-yr-old females, 4 female yearlings, and 9 female foals. In the 10 yr since the first successful reintroduction (1983), 66 foals had been born in the wild, of which 24 were second and third generation. The RS of reintroduced females ranged from 0.50–0.78 foals·female^{-1}·yr^{-1} ($\bar{X} = 0.57$, $n = 11$ animals), and increased with time since reintroduction in 8 animals, and remained unchanged in the other 3 ($P = 0.004$, sign test). For 6 reintroduced females for which at least
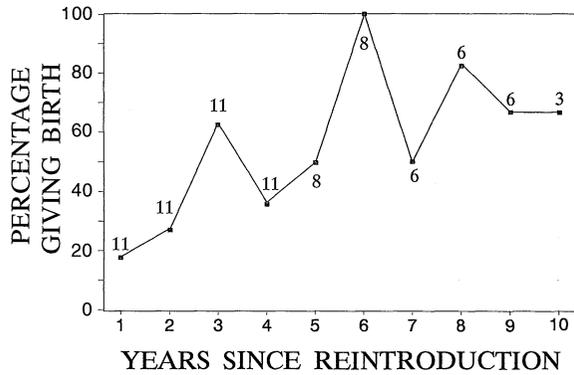
FIG. 1. Percentage of adult (≥3 yr old) reintroduced wild ass females giving birth as a function of time since reintroduction. Numbers by data points represent sample size.

FIG. 2. Percentage of adult (≥3 yr old) reintroduced wild ass females giving birth as a function of their age. ———— = reintroduced females, - - - - - = native-born females. Numbers by data points represent sample size.

9 yr of data were available, RS increased from 0.27 ± 0.67 foals·female^{-1}·yr^{-1} (mean ± 1 SD) in the first 5 yr to 0.74 ± 0.46 foals·female^{-1}·yr^{-1} in the following 4–5 yr (P = 0.0144, t test after arcsine transformation and weighted by the number of years). Only 2 of 11 (18%) animals produced an offspring in the year following their release. Since successfully reintroduced females were all roughly the same age (ages 2–5), the effects of age and time since reintroduction are collinear (Figs. 1 and 2).

Only 1 of 12 wild-born females produced an offspring at age 2. Seven gave birth for the first time at age 3, and 2 at age 4. Similarly, only 3 of 215 kulan and 5 of 117 onager dams listed in the studbook produced an offspring at age 2. RS of wild-born females aged 3–6 was higher (P < 0.0001, t test after arcsine transformation and weighted by the number of years) than that of reintroduced females of the same age groups (0.81 ± 0.33, n = 9; and 0.19 ± 0.33 foals·female^{-1}·yr^{-1}, n = 11, respectively).

We found no correlation between the percentage of adult females (≥3 yr old) giving birth each year and annual rainfall in the year before parturition (P = 0.453 for all dams, and P = 0.361 for reintroduced dams only). Similarly there was no correlation between the percentage of adult females giving birth each year and annual rainfall in the year before conception (P = 0.065 for all dams, and P = 0.212 for reintroduced dams only).

Overall PSR was 1.54 and did not deviate from the expected 1:1 (40 males vs. 26 females, P = 0.085, normal approximation of the binomial). Variance across age, using four age groups (ages 2–3, 4–6, 7–9, 10–12, and >13), was significantly greater (P = 0.017, Fisher's exact test) than expected, given the overall PSR. Mid-age groups produced most of the males (Fig. 3). Six of eight primiparous females produced daughters, while six of these produced a second time and gave birth to males only (P = 0.009, Fisher's exact test).
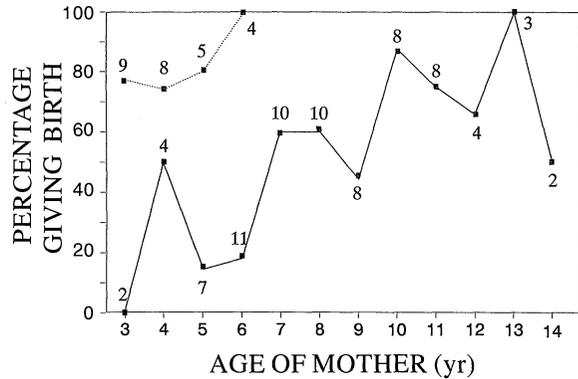
We found 417 and 677 births of onagers and kulans,

respectively, to dams of known age in the world studbook. In both cases PSR was not significantly different from 1:1 (PSR = 1.17, P = 0.116; and PSR = 1.05, P = 0.441, for onagers and kulans, respectively). Also variance across ages was not significantly greater than expected (P = 0.192, chi-square = 6.09, 4 df; and P = 0.762 chi-square = 1.857, 4 df, for onagers and kulans, respectively). However, age-related PSR patterns were similar to the Ramon herd (Fig. 4), with PSRs in the 4–12 age groups being significantly male skewed for both onagers and kulans (P = 0.007, PSR = 1.35, n = 275; and P = 0.040, PSR = 1.16, n = 550, respectively, using a one-tailed test. The one-tailed test is justified because we were testing for deviation from 1:1 in the same direction of the Ramon herd). Onager and kulan females producing an offspring for the first time at age 2 or 3 had more females in their primiparous birth than the subsequent birth (in onagers 7 males, 14 females vs. 14 males, 7 females, P = 0.031, using a one-tailed test; in kulans 10 males, 16 females vs. 17 males, 9 females, P = 0.048, using a one-tailed test). By contrast, no such pattern was
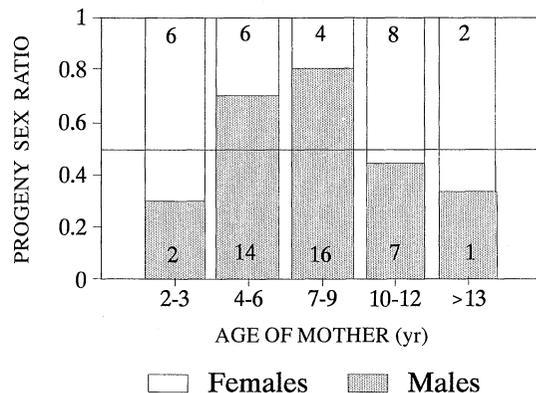

FIG. 3. Progeny sex ratio (males/females) in the Ramon wild ass herd as a function of mother's age. Numbers in bars represent sample size.
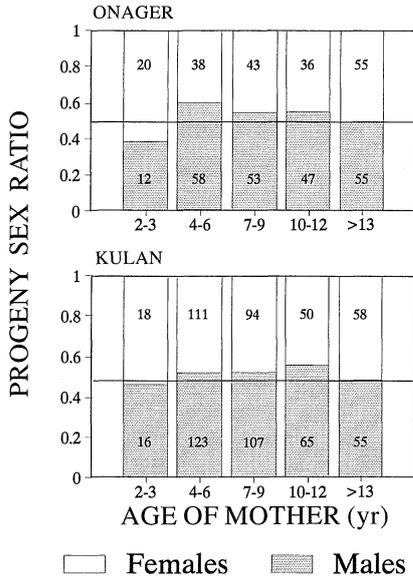
FIG. 4. Progeny sex ratio (males/females) of wild ass onager and kulan subspecies as a function of mother's age (from studbook data). Numbers in bars represent sample size.

TABLE 1. Life table for females reintroduced into the Ramon reserve and their wild-born daughters. $1 - q_x$ is the probability of an average female of age x surviving to age ($x + 1$), l_x is the probability that an average newborn female will survive to age x, and m_x is the number of female offspring produced by an average mother at age x. R_0 is net reproductive rate.

	Reintroduced females				Wild-born daughters			
Age	$1 - q_x^*$	l_x	m_x	$l_x m_x$	$1 - q_x^*$	l_x	m_x	$l_x m_x$
0					0.95	1.00	0.00	0.00
1					0.95	0.95	0.00	0.00
2	0.95	1.00	0.00	0.00	0.95	0.90	0.08	0.07
3	0.95	0.95	0.00	0.00	0.95	0.86	0.56	0.45
4	0.90	0.90	0.08	0.06	0.90	0.81	0.24	0.18
5	0.90	0.81	0.08	0.06	0.90	0.73	0.24	0.16
6	0.90	0.73	0.08	0.05	0.90	0.66	0.24	0.14
7	0.09	0.66	0.10	0.06	0.90	0.59	0.10	0.05
8	0.90	0.59	0.10	0.05	0.90	0.53	0.10	0.05
9	0.90	0.53	0.10	0.05	0.90	0.48	0.10	0.04
10	0.90	0.48	0.40	0.17	0.90	0.43	0.40	0.16
11	0.90	0.43	0.40	0.16	0.90	0.39	0.40	0.14
12	0.90	0.39	0.40	0.14	0.90	0.35	0.40	0.12
13	0.90	0.35	0.50	0.16	0.90	0.31	0.50	0.14
14	0.67	0.31	0.50	0.11	0.67	0.28	0.50	0.10
15	0.67	0.21	0.50	0.07	0.67	0.19	0.50	0.07
16	0.00	0.14	0.00	0.00	0.00	0.13	0.00	0.00
R_0				1.14				1.87

* Based on survival of zebras (Spinage 1972).

found in females that were primiparous at ages 4 or 5 ($P = 0.832$ and $P = 0.743$, respectively). The distribution of PSRs across age groups in the Ramon herd was not significantly different from onager studbook data ($P = 0.106$, chi-square $= 6.16$, 3 df).

Data on adult survival are limited. We believe that three females (aged 5, 6 and 17) that disappeared immediately following the release, died of causes related to the reintroduction process. Of the other reintroduced females, three more died between the ages 7 and 9. Of nine wild-born females that reached adulthood one died at age 6 as a road-kill. Of the 66 foals born in the wild 4 (6%) died during their first year. Three of these were males that disappeared within 3 mo of birth and presumably died of natural causes. One female foal was a road-kill. Based on the studbook 27% (67 males, 45 females) of onager foals and 21% of kulan foals (83 males, 62 females) died during their first year. In both cases the sex ratio of foals that died did not differ from the PSR at birth ($P = 0.286$ and $P = 0.200$, respectively).

Life table and simulations

Because of differences in their RS, we constructed separate life tables for reintroduced and wild-born females (Table 1). Based on the literature, we assumed females 16 yr of age and older made no contribution to reproduction and did not include these ages in the life table. R_0 (net reproduction rate) of wild-born females was 1.87, as compared with 1.14 for reintroduced females. Based on our Leslie matrix simulations, probability of extinction due to random demographic processes alone is <0.1% in the next 100 yr (no extinctions in 1000 simulations). The simulations predict an expected population size of 250 adult females within 20 yr (Fig. 5). Using the same parameters and starting with the population that existed 2 yr after the first females were reintroduced, only 12 of 1000 simulations (1.2%) ended in extinction. Starting with the population that existed in 1988 (5 yr after the first females were reintroduced), none of the 1000 simulations ended in extinctions. However, if we calculate RS and PSR for the first 5 yr (1983–1988), we find that RS = 0.15 foals·female⁻¹·yr⁻¹ and PSR = 1.0 for all age groups (data is insufficient for a breakdown by age); and R_0 = 0.95, indicating an unviable population.
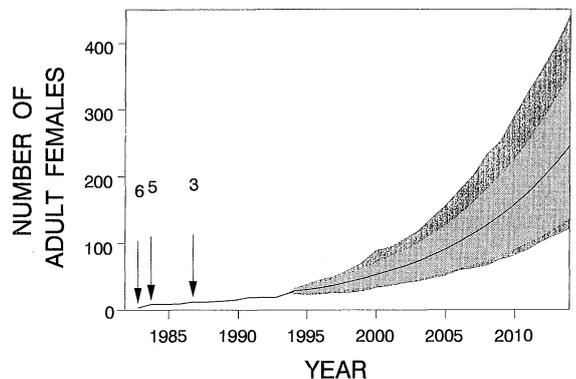

FIG. 5. Number of adult (≥ 3 yr old) females as a function of time in the reintroduced Ramon wild ass herd. Arrows indicate the number of adult females reintroduced. Curve after 1993 is simulated using a stochastic Leslie matrix design. Light shaded area shows ± 2 SD, dark shaded area shows the minimum and maximum values from 1000 simulations.

DISCUSSION

Although presently the Ramon herd is small, its susceptibility to extinction due to random demographic processes alone is minimal. Even at earlier stages its susceptibility to extinction from such processes was minor. Yet today, there are only 16 adult females, 2 more than the number released in the wild in the past 10 yr. Why has the population grown so slowly? Our findings suggest two proximate causes: (1) low RS of reintroduced females in the early years following release, and (2) a male-skewed PSR. We will consider these factors as follows.

RS following reintroduction

RS in the last 3 yr of the study averaged 0.75 foals·female^{-1}·yr^{-1}. This is high. By comparison, the RS of kulans in the Gobi National Park refuge was estimated at 0.66 foals·female^{-1}·yr^{-1} (Zhirnov and Il-yinsky 1986), and that of kulans in Badkhiz Reserve in Turkmenistan was estimated between 0.4 and 0.5 foals·female^{-1}·yr^{-1} (V. Kuznetsov, *personal communication*). By contrast, RS in the years following release into the wild was low. A similar pattern was also documented in introduced wild ass on Barsakelmes Island in the Aral Sea (Zhirnov and Ilyinsky 1986). What caused the low RS? We offer several explanations that are not necessarily mutually exclusive:

1) An Allee effect (Allee 1931). Density-dependent models of population growth often assume that RS decreases as population density increases. This may not always be the case. Allee (1931) hypothesized that in very small populations RS may be positively correlated with population density, i.e., the maximum potential reproductive success is realized at some number greater than one pair, and below this number RS declines. For example, in social ungulates, individuals in small herds may spend more time being alert for predators, thus spending less time feeding and consequently reducing their RS.

2) Inbreeding depression. Decreased RS is documented in several inbred populations of ungulate species (Ballou and Ralls 1982). The Ramon herd has gone through potential bottlenecks, the first being the founder group of Hai-Bar Yotvata, and the second the reintroduction itself. Furthermore, only 7 of the 31 males that reached adulthood have held territories and reached breeding status (D. Saltz and D. I. Rubenstein, *unpublished data*), reducing effective population size considerably. Thus, reduced RS due to inbreeding depression is plausible. However, the increase in RS of released females over time, the high RS of wild-born females, and the high postnatal survival suggest this is not so.

3) Long-term effects of the reintroduction process. The process of removing an animal from its former home range and transporting it to a new unknown area is undoubtedly stressful (O'Bryan and McCullough 1985, Chivers 1991). This may be especially true of captive-reared animals. Reintroductions of captive-reared animals have a lesser chance of succeeding than translocation of wild-caught animals (Griffith et al. 1989). The low RS following reintroduction may be a response to the stress caused by the removal of the animals from Hai-Bar Yotvata and to change in environment.

4) Carryover effects from Hai-Bar Yotvata. For reasons not understood, RS at Hai-Bar Yotvata is lower than that of the Ramon herd and ranges between 0.3 and 0.4 (Sinai 1994). It is possible that whatever the causes of the low RS at Hai-Bar Yotvata, they continued to have an impact on the animals for several years following release.

5) Age effects. Because all reintroduced females were roughly the same age (2–5 yr), the increase in RS over time can be explained by age. However, high RS of 3–6-yr-old wild-born females suggests this not to be the case.

Male-skewed PSR

Overall PSR was markedly skewed toward males (although it did not deviate significantly from 1:1 at $P \leq 0.05$). Omitting 1993, the PSR was 2.21 (>2 males for each female born, $n = 53$, $P = 0.009$). By contrast, PSR from studbook data and other sources (Solomatin 1964, Zhirnov and Ilyinsky 1986) ranged from 1.07 and 1.25, and did not significantly differ from 1:1 in those cases where sample size was available. Age-dependent PSR combined with the specific age structure of the reintroduced herd is the apparent cause for male-skewed PSR in the Ramon herd. Because all females were 2–5 yr old when released, over the next 5–8 yr most females were in the "male-producing age." Consequently, few females were recruited into the population in the years following release. With time, the age structure of the female population should become skewed toward the older age groups, which should cause a shift in PSR from male skewed to female skewed. As expected, in 1993, 9 of 13 births were female—a complete turnaround from the PSR in previous years.

We explain the age-dependent PSR patterns in wild ass in the context of Trivers and Willard (1973) who hypothesized that: to the extent that maternal investment can influence the RS of the offspring, mothers should invest more in the gender with the higher variance in RS. In polygamous and sexually dimorphic ungulates, males clearly have higher RS variance than females. If maternal investment influences offspring RS, females of these species should invest more in male offspring. The increased cost of rearing males would give a fitness advantage to those females that produce males when in better than average condition. Various factors, which may be indicative of favorable maternal condition, have been correlated with male-biased PSR in ungulates. These include: dominance in red deer

(*Cervus elaphus*; Clutton-Brock et al. 1988); age and breeding status in American bison (*Bison bison*; Green and Rothstein 1991, Rutberg 1986); age in Grevy's zebra (*Equus grevyi*; Hayward 1987); age in Peary and barren-ground caribou (*Rangifer tarandus pearyi,* and *R. t. groenlandicus*; Thomas et al. 1989); body mass in reindeer (*R. t. tarandus*; Kojola and Eloranta 1989); age in domestic sheep (*Ovis aries*; Kent 1992); and body mass and litter size in mule deer (*Odocoileus hemionus*; Kucera 1991). However, several studies have presented results that do not conform to the Trivers and Willard (1973) hypothesis. Skogland (1986) reported that reindeer had a male-biased prenatal sex ratio on poor habitat, and a female-biased prenatal sex ratio on good habitat. Dominance in bighorn sheep (*Ovis canadensis*) was associated with female-biased sex ratio at birth (Festa-Bianchet 1991), and white-tailed deer (*Odocoileus virginianus*) on restricted diets gave birth to more males than females (Verme 1985). Ad hoc explanations, such as local resource competition (Caley 1987) and timing of insemination (Verme and Ozoga 1981), were offered to explain these exceptions to the predictions of the Trivers and Willard (1973) model.

Each adult female in the Ramon herd produced at least one offspring during the 10-yr study, with RS ranging from 0.2 to 1.0 foals·female^{-1}·yr^{-1}. By contrast, only 7 of 31 (22%) adult males have held territories, and, thereby had access to breeding females (D. Saltz and D. I. Rubenstein, *unpublished data*). Thus, variance in RS among males is greater than among females, and the conditions required for the Trivers and Willard (1973) hypothesis are fulfilled. Wild ass mothers should, therefore, invest more in male offspring than in female offspring. The difference in cost of rearing a male or female is probably most pronounced during lactation (Oftedal 1985). Because gestation is 11 mo long in wild ass, habitat condition at conception is unlikely to be indicative of habitat condition during lactation, especially in variable desert environments. Consequently, because environmental cues are poor predictors with respect to PSR, wild ass dams rely on cues that are less variable over time, such as social status or age, in adjusting maternal investment. As in many ungulates, dominance in the Ramon herd is correlated with age (D. Saltz and D. I. Rubenstein, *unpublished data*). The high RS in the Ramon herd (as compared with other wild ass populations) suggests it is at low ecological density and good physical condition. We hypothesize that under such conditions intraspecific competition would be minimal. Dominance would play a minor role in determining condition and reproductive performance of dams, and age alone may be a sufficient determinant of PSR.

Future growth and carrying capacity

According to our model, the population exhibits a certain lag interval preceding a period of rapid growth.

Our simulations and the birth record of 1993 suggest that the rapid growth period is imminent or has already begun. The growth rate projected by the model (a population of 250 adult females within 20 yr) appears high, but agrees with the growth of translocated wild ass populations in Meana-Chaacha Nature Reserve, Turkmenistan. That herd was founded in 1978 with 14 animals (5 males, 9 females) translocated from Badkhiz reserve, followed by boosts in 1983 (9 animals: 3 males, 6 females) and 1985 (9 animals: gender unknown) (T. Rotaru, *personal communication*); as of September 1993 the herd consisted of 250 adult females, subadults, and foals (D. Saltz, *personal observation*).

Whether the Ramon population will reach 250 adult females depends on the carrying capacity of the area, of which we have no present estimate. Wild ass are dependent on free water during the summer months and in the Makhtesh Ramon Reserve they restrict their movements to the vicinity of the few water sources. Thus, the first signs of overgrazing will appear on the herd's summer range. Consequently, we are monitoring the habitat within the wild asses' daily movement range from the summer water sources.

Environmental and genetic stochasticity

The only stochastic environmental factor we monitored was annual precipitation. We found no relation between annual precipitation and RS. Wild ass are hardy animals that exist under a wide range of environmental conditions (Groves 1974, Zhirnov and Ilyinsky 1986), surviving on low-quality forage and in extreme temperatures. Although environmental stochasticity undoubtedly affects RS and survival of wild ass to some extent, we believe this effect is limited. The exclusion of environmental stochasticity from our model is, therefore, expected to have a minor impact on our estimates of population growth and extinction probability. Free water is one environmental factor that can have a significant impact on wild ass population dynamics (Zhirnov and Ilyinsky 1986). Although En-Saharonim provides water year round, the amount of water available varies from year to year, and at times the wild ass must dig to obtain it. To guarantee a sufficient water supply at all times we established an artificial water source near the En-Saharonim spring.

Our model also does not consider genetic stochasticity. Although the high RS suggests little or no inbreeding depression, the genetic variability of the reintroduced population is presumably low (although the original crossbreeding of two subspecies [May 1991] may have increased genetic variability in the Hai-Bar Yotvata founder population). Although theory and empirical data suggest that demography plays a bigger role than genetics in determining the existence of small populations (Lande 1988), the herd's ability to respond to pathogens and environmental changes may be much reduced.

Conclusions

The ultimate measure of success in reintroduction is the establishment of self-sustaining wild populations (Scott and Carpenter 1987). However, a good assessment of the success of a reintroduction requires detailed knowledge of age-dependent RS and survival. This requires close monitoring of the reintroduced population, combined with knowledge from other sources. A poor understanding of the dynamics of the population can result in poor analysis and erroneous conclusions regarding the population's status and likely fate. This study demonstrates the importance of a detailed postrelease monitoring program. For example, had we calculated R_0 at early stages of the reintroduction (e.g., years 1983–1987), and ignored the difference in RS between the reintroduced and wild-born females, we would have concluded the population is not viable.

Low ecological density and an age structure consisting mainly of prime-aged females are characteristic of ungulate reintroductions (Leader-Williams 1988, Stanley Price 1989). Our study suggests that such releases may result in a male-skewed PSR, thereby lowering population growth rate and increasing the population's susceptibility to stochastic processes.

Although our study population appears safe from extinction due to random demographic processes, the reintroduction of prime-aged females probably delayed attainment of full potential RS for ≥ 9 yr since release. Could a different release strategy increase RS and decrease PSR following reintroduction, enabling the release of fewer animals and a more cost-effective program? Our results suggest that this can be achieved by releasing 1-yr-old subadult females. Subadults may have lower fidelity to their former home range and may be more adaptable to new environments (see review by Stanley-Price 1989), minimizing post-release mortality and RS depression. Also, young females are expected to produce mostly females in their primiparous birth, thereby accelerating population growth. However, in the absence of adults, subadults may exhibit delayed RS after release (Stanley-Price 1989), and may tend to disperse (Jameson et al. 1982). A possible solution may be an initial release of prime-aged females, followed by boost releases of subadults once the herd is established.

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