POPULATION GROWTH OF MOUNTAIN GAZELLES Gazella gazella REINTRODUCED TO CENTRAL ARABIA

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(Received 8 June 1996; revised version received 12 November 1996; accepted 12 November 1996)

Abstract
Captive-born mountain gazelles were reintroduced to Hawtah Reserve in central Saudi Arabia from 1991 to 1995. This study describes the survival, reproduction and changing number of gazelles within the population during the first four years of the programme. The mortality rate was highest during the first month after release, but 69–73% of gazelles survived for ≥1 year and 58–59% survived for ≥2 years. Weaned gazelles <2 years-of-age had the highest survival rate during the first year after release. The mean annual survival rate for gazelles which survived their first month of freedom was 78%. Predation was a major mortality factor and older gazelles were particularly vulnerable. Rainfall was seasonal, but calves were born throughout the year, with peaks in the number of births during spring and autumn. Females often produced two calves annually. All calves were singletons. The exponential rate of increase (r) of a subpopulation during two years after the last release was 0.275 on a yearly basis. In a wadi protected from domestic livestock, the density of gazelles remained constant after reaching ca. 15 gazelles km⁻². By the end of 1994, the estimated number of gazelles in the reserve was 165, more than twice the number released during the previous four years. An important lesson for all reintroductions is that predators can be a major problem even when uncommon. Recommendations are given for selecting gazelles for release during future reintroductions. © 1997 Published by Elsevier Science Ltd

Keywords: reintroduction, gazelles, Arabia, survival, reproduction.

INTRODUCTION
Populations of large mammals in Saudi Arabia have declined dramatically since the First World War as a result of excessive hunting and habitat degradation, the latter due mainly to overgrazing by domestic livestock (Alwalaie, 1989). Saudi gazelles Gazella (dorcas) saudiya are extinct in the wild and few wild mountain gazelles Gazella gazella and sand gazelles Gazella subgutturosa survive, occupying limited parts of their former geographical ranges (Thouless et al., 1991). Species which recently became extinct in all or part of their range are being reintroduced to reserves which lie within their former range (Büttiker & Grainger, 1989).

The first formal reintroduction programme in Arabia was the release of Arabian oryx Oryx leucoryx in Oman, where the reintroduced population was closely monitored (Stanley Price, 1989; Spalton, 1992). In the past, many other reintroductions were poorly monitored and documented (Short et al., 1992). The main reason for monitoring is to determine the causes of any problems which a reintroduced population experiences while establishing itself so that the management of future releases, in the same area or elsewhere, can be modified if necessary in order to improve the chances of success, or to reduce the financial costs (Stanley Price, 1991).

The reintroduction of mountain gazelles into central Saudi Arabia was a joint project by the Zoological Society of London and the National Commission for Wildlife Conservation and Development (NCWCD). This was the first time that ungulates had been reintroduced into an area of Saudi Arabia where domestic livestock and large mammalian predators were present. Dunham et al. (1993) described the origins of the gazelles and preparations for their release. This paper describes the survival and reproduction of these gazelles and the resulting changes in population number and density during the first four years of the reintroduction. Mountain gazelles are small antelopes (adult body mass 18-25 kg), formerly common on the Arabian peninsula and northwards into Israel (Baharav, 1974; Harrison & Bates, 1991). They are mixed feeders, but prefer to graze (Baharav, 1981).

STUDY AREA
Hawtah Reserve is 150 km south of Riyadh in central Saudi Arabia (approximately 23°30′N & 46°30′E).
Mean annual rainfall is ca. 50 mm (Habibi & Grainger, 1990), but annual rainfall (July–June) is very variable, ranging between 18 and 123 mm in the four years 1991–1995. Precipitation is confined mainly to winter and spring (November–April) and occasionally there are brief but heavy hailstorms. Frost may occur during winter. Summer is dry and very hot (daily maximum temperatures > 40°C).

The reserve covers ca. 2000 km² and comprises a gently undulating, stony, limestone plateau, 800-1100 m asl, which is deeply incised by several major wadi systems. Plant standing crop is very low on the plateau, but greater in the wadis where Acacia bushes dominate the vegetation. Some 1200 domestic camels Camelus dromedarius feed in the reserve and sheep Ovis aries and goats Capra hircus forage in some wadis, but all receive water and supplementary food from their owners. The reserve also contains ca. 250 Nubian ibex Capra ibex nubiana (Habibi, 1994). Potential predators of gazelles include wolves Canis lupus, feral dogs C. familiaris, red foxes Vulpes vulpes and migratory eagles. Local residents report that the last mountain gazelles of the original population were shot by hunters in about 1970. Today, NCWCD rangers are responsible for preventing hunting in the reserve.

The only sections of the reserve which were protected from camel foraging are the fenced heads of three wadis, namely Ghaba, Ghafar and Jida. The first two are adjacent and join downstream of the fences. They form part of the Wadi Matham system (Fig. 1), which is not used by sheep or goats. During February 1992, the mean density of camels in the unfenced section of this wadi system was 5 km⁻². Wadi Jida is > 20 km southwest of the other fenced wadis. The fences exclude camels, but permit the movement of ibex and gazelles. Plant standing crop in fenced wadis is noticeably greater than in unfenced, but otherwise similar, wadis. Heavy rainfall causes widespread flooding in the wadis, but water is found in the river beds for only the few days after rain. In Wadi Ghaba, there is a perennial spring and, in both Ghaba and Ghafar, there is a seep with surface water for several months after rain. A water trough is provided for gazelles throughout the year in each fenced wadi.

**METHODS**

**Release of the gazelles**

Seventy-one gazelles in eight groups were released into the fenced wadis from January 1991 until June 1993 (Table 1). A ninth group was released during May 1995, after completion of most of the fieldwork reported here, and is not referred to again in this paper. The gazelles were captive-born at the King Khalid Wildlife Research Centre, which is 200 km north of the reserve and has a similar climate. Some females were pregnant when released. The age of the gazelles was known, except for the oldest ones, whose minimum age was known. A radiocollar was fitted to 28 gazelles and all were fitted with a plastic eartag, whose colour, shape, size and position permitted animals to be individually recognised. Most gazelles had been fitted with a small metal eartag during captivity and these tags were not removed prior to the releases. Gazelles born in the reserve were generally distinguished by the absence of a tag. Two released gazelles lost both their metal and plastic tags, but they remained recognisable from the shape of the tear in their ear. On the basis of body size and horn

![Fig. 1. An outline of the Matham wadi system in Hawtah Reserve, showing the locations of the camel fences in wadis Ghaba and Ghafar, and the sections of Wadi Ghaba (dotted) and Wadi Matham (crosshatched) for which separate density estimates were calculated.](image-url)
length and shape, wild-born gazelles were assigned to one of four age/sex classes: adult males, adult females, yearling males and juveniles (Table 1).

**Monitoring**

Intensive monitoring followed the releases and the reserve was visited on 396 days from January 1991 to December 1994. The number of daily visits per calendar month, summed over the four years, averaged 33 ($SD = 9$, $n = 12$ months), ranging from 19 during July to 45 during April. Additional visits were made during 1995. The location, age, sex and identity of all gazelles seen were noted when possible. Gazelles were observed through binoculars or a 30× telescope to check for an ear tag. Deaths and disappearances of gazelles were noted. NCWCD rangers reported gazelles seen in unusual locations. The four-week period during which a female gave birth was determined from the condition of her udder, swollen during early lactation, and by estimating the calf’s age when it was first seen with her.

**Data analysis**

**Survival of released gazelles**

The survival rate of released gazelles was calculated in two ways: (1) as the percentage of gazelles known to have survived for a given time period (annual survival rate = 100 * $(N_t/N_i)^{1/t}$, where $N_i$ is the initial number of animals and $N_t$ is the number known to be alive after $t$ years); (2) using the computer program JOLLY (version 24/1/91) (Pollock et al., 1990). This calculates survival rates from capture-recapture data using the Jolly-Seber model. The release of a gazelle was analogous to its initial capture, marking and release and a subsequent sighting of that animal was analogous to its recapture. Months represented sampling periods and the months during which individual gazelles were seen were noted for the first 71 animals freed (i.e. the first eight groups). Data were available for 48 months in the period January 1991 to June 1995. Initial analyses revealed that the mortality rate of gazelles was relatively high during the first month after their release and so Model 2 within JOLLY was the most biologically appropriate model. Mortality rates were compared using a two-tailed Fisher exact probability test or Chi-square test (Siegel & Castellan, 1988).

**Reproduction**

Seasonal variation in the frequency of births was studied using data for calves born to 25 released females which were regularly observed during one to three complete years after release. Data collected during the six calendar months immediately following their release were not used in this part of the analysis, in order to exclude calves conceived in captivity. (The gestation period is ca. six months (Baharav, 1983).) For five females which were <6 months-of-age when released, the study period commenced during the month following their first birthday. A non-parametric correlation (Siegel & Castellan, 1988) was used to test for a relationship between the duration of the inter-calving interval and the mother’s age, because the age of older females was known only approximately.

**Number of gazelles**

The number of gazelles without functioning radiocollars was estimated from the numbers of marked and untagged gazelles seen each day, using the Petersen estimate for mark-recapture data (Caughley & Sinclair, 1994). A mean estimate and 95% confidence limits were obtained for each calendar month by combining the daily estimates using the joint hypergeometric maximum likelihood estimator, utilizing the formula given by White and Garrott (1990). The mean duration of the period for which data were combined to provide these monthly estimates was 18 days ($SD = 9$, $n = 38$). Each month, the number of animals with a functioning radiocollar was added to the mean estimated number of gazelles.

### Table 1. Size and composition of nine groups of mountain gazelles released into three wadis in Hawtah Reserve in central Saudi Arabia from 1991 to 1995

<table>
<thead>
<tr>
<th>Group</th>
<th>Date of release</th>
<th>Site of release</th>
<th>Adult males</th>
<th>Adult females</th>
<th>Yearling males</th>
<th>Juveniles 0–6 m</th>
<th>Juveniles 7–12 m</th>
<th>Group total</th>
<th>Year/wadi total</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>16 Dec 90 a</td>
<td>Ghaba</td>
<td>1</td>
<td>10</td>
<td>2</td>
<td>2 F</td>
<td>1 M, 3 F</td>
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<td>– 11 Jan 91</td>
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<td>2</td>
<td>17 Jun 91</td>
<td>Ghaba</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1 F</td>
<td>6</td>
<td>29</td>
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<tr>
<td>3</td>
<td>22 Jul 91</td>
<td>Ghaba</td>
<td>4</td>
<td>0</td>
<td>0</td>
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<tr>
<td>4</td>
<td>24 Jan 92</td>
<td>Ghabar</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>1 M</td>
<td>8</td>
<td></td>
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<tr>
<td>5</td>
<td>6 May 92</td>
<td>Ghabar</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1 F</td>
<td>0</td>
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<td>6</td>
<td>3 Aug 92</td>
<td>Ghabar</td>
<td>1</td>
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<td>0</td>
<td>13</td>
<td>25</td>
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<td>7</td>
<td>11 May 93</td>
<td>Jida</td>
<td>1</td>
<td>10</td>
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<td>8</td>
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<td>9</td>
<td>13 May 95</td>
<td>Jida</td>
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<td>1 M</td>
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<td>13</td>
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<tr>
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<td></td>
<td>15</td>
<td>43</td>
<td>11</td>
<td>8</td>
<td>7</td>
<td>84</td>
<td>84</td>
</tr>
</tbody>
</table>

*a A few gazelles from group 1 escaped from the pre-release pen before it was opened during January 1991.*
without radiocollars, to estimate the total number of gazelles. Confidence intervals for this estimate were the same as for the estimated number of animals without radiocollars. When calculating Petersen estimates, marked gazelles were defined as released animals without a functioning radiocollar. When a transmitter stopped working (usually when the batteries were exhausted), that collared animal became a marked one for the purpose of calculating the Petersen estimate. The number of marked gazelles alive at the start of each month was determined retrospectively from subsequent sightings.

There was no movement of gazelles between Wadi Jida and Wadi Matham during this study and so the numbers of gazelles in these wadi systems were estimated separately. The total number of gazelles in the reserve was estimated by summing the estimates for the two wadi systems. A lower confidence limit for the combined estimate was calculated simply by summing the lower limits of the two separate estimates. The upper confidence limit was calculated similarly. Statistically speaking, this procedure will overestimate the confidence intervals. In practice, however, the calculated intervals may be closer to the real ones; when the assumptions of the Petersen method are not met (see below), the 95% confidence intervals calculated for the joint hypergeometric maximum likelihood estimator may be too small (Neal et al., 1993).

Visits to the reserve were concentrated on the Wadi Matham system and the vicinity of Wadi Jida. During the second half of the study, NCWCD rangers saw small numbers of untagged gazelles in other parts of the reserve. Thus, the population estimates will slightly underestimate the true population number.

The numbers of gazelles in each age/sex class were estimated monthly during 1993 and 1994 using the Petersen method. This method was also used to estimate the numbers of gazelles in two sections of the Wadi Matham system (Fig. 1): Wadi Ghaba upstream of the fence (area of wadi floor 2.7 km²); and central Wadi Matham, a section downstream of the Ghaba/Ghafar junction (area of wadi floor 6.5 km²). The area of each section was determined using the GIS package IDRISI (Eastman, 1993).

The exponential rate of increase \( r \) of the population in the Wadi Matham system was calculated as the slope of the regression line fitted to natural logarithms of the monthly estimates of the number of gazelles in this subpopulation from December 1992 to December 1994 (Caughey & Sinclair, 1994). The gazelles released into Wadi Jida and their offspring were excluded from the estimates for this calculation.

RESULTS

Survival of released gazelles

By the end of 1994, 19 of the first 71 gazelles released were dead and 12 had disappeared and, in the absence of evidence to the contrary, were assumed to have died soon after they were last seen. Of these 71 animals, 69–73% were alive one year after release (the precise date of death of three gazelles is unknown: two died and one disappeared 51–54 weeks after release) and 58–59% were alive two years after release. Data on survival >2 years after release are available only for animals freed early during the reintroduction: 56–65% of the 54 gazelles freed during 1991–1992 survived ≥3 years; and 45–48% of the 29 of these freed during 1991 survived ≥4 years.

The mortality rate during the first 12 months after release varied widely between years/wadis (Fig. 2). The mortality rate was often high during the first month following release and nine gazelles (13%), including three aged <1 month when freed, died during this period. During the first 54 weeks after release, the mortality rate amongst gazelles >3 years old when freed was nearly three times the mortality rate amongst younger animals (54% v. 19%; \( \chi^2 = 7.5, \) d.f. = 1, \( p = 0.006 \)) (Fig. 3). Within the older age group, the mortality rate amongst males (73%, \( n = 11 \)) was twice the rate amongst females (38%, \( n = 13 \)), but the difference was not significant (Fisher exact test, \( p = 0.12 \)). Animals aged 1–24 months when freed had the highest survival rate during the first year (94%, \( n = 31 \)).

During the second year after release, the survival rates of gazelles of all ages were greater than during the first year for animals of similar age (Fig. 3). This was due mainly to the high mortality rate during the first month after release. For gazelles which survived their initial month of freedom, the mean mortality rate for animals of all ages and both sexes during the next 23 months was 18–19% per annum. Not surprisingly, the second-year survival rate for non-juveniles declined with

![Fig. 2. Estimated survival of captive-born mountain gazelles after release in Hawtah reserve. Dashed lines refer to animals freed in Wadi Ghaha during 1991 (centre line), Wadi Ghafar during 1992 (upper) and Wadi Jida during 1993 (lower). The solid line is the mean for all these gazelles (n = 71). Vertical bars show maximum and minimum survival rates when the fate of some individuals is unknown during 1995 (towards the end of the study), or some dates of death were known only approximately (12 months after release).](image)
age, from 100% for animals aged one to two years to 71% for gazelles \( \geq 5 \) years old (Fig. 3).

Forty of the gazelles released into wadis Ghaba or Ghafar were alive at the end of 1992. During 1993, following a winter of above-average rainfall (99 mm), four (10%) died or disappeared. During 1994, following a winter of low rainfall (18 mm), three (8%) of the survivors died or disappeared.

Model 2 of JOLLY estimated the mean annual survival rate of released gazelles at 78%. This estimate excludes animals which died or disappeared within a month of release. Coincidentally, these gazelles which died soon after release accounted for much of the variation in survival rates between release wadis/years. The Model 2 estimate was slightly greater than the Model A estimate (76%; confidence limits 70% and 83%) which included all animals, but Model A was a poor fit to the data \( (\chi^2 = 19 \cdot 3, \ d.f. = 4, \ p = 0 \cdot 0007) \). JOLLY was unable to calculate confidence limits for the Model 2 estimate or to undertake a goodness-of-fit test. Nevertheless, 78% is probably the best estimate of the mean annual survival rate of released gazelles which survived their first month of freedom, because it is derived from data covering the entire observation period for each animal, not just one to two years.

Causes of mortality

Deaths during 1991–1992 were discussed by Dunham et al. (1993): seven gazelles died and one disappeared during 1992, probably owing to wolf predation. Since 1992, feral dogs killed two, possibly three, gazelles. An adult male died from septicaemia three months after release:

post-mortem examination showed that the skin had been punctured (N. Brown, pers. comm.), possibly by the horn of another gazelle. An adult female died three months after release when she became caught in a camel fence, probably after being chased by a predator or vehicle. Two juveniles of unknown sex, born in a pre-release pen, disappeared soon after being freed and three gazelles died of unknown causes 7, 13 and 18 months after release. Only two wild-born gazelles were found dead — a male \( ca \). nine months-of-age, found in Ghaba riverbed after a flash flood, and a newborn.

Predators were responsible for at least 32% of the mortality of released gazelles. At the end of 1991, 24 of the gazelles released that year were still alive; 12 were \(< 2 \) years-of-age when freed and 12 were \( \geq 3 \) years old. By June, a wolf had killed the above-mentioned eight gazelles, all \( \geq 3 \) years-of-age. Thus, older released gazelles were more likely to be killed than younger ones (Fisher exact test, \( p = 0 \cdot 0007 \)). The increased vulnerability of older gazelles to predation was a major reason for their greater mortality rate during the first year of freedom; when the deaths due to wolf predation were excluded from the data set, the first-year mortality rate of gazelles \( \geq 3 \) years-of-age when freed was not significantly different from that of younger animals \( (\chi^2 = 1 \cdot 0, \ d.f. = 1, \ p = 0 \cdot 31) \).

Reproduction

Released females gave birth to \( \geq 134 \) calves from March 1991 to December 1994, at least 107 of which were conceived in the wild. All offspring were singletons. Calves were born during all months of the year, but the number of births varied between months \( (\chi^2 = 21 \cdot 46, \ d.f. = 11, \ p < 0 \cdot 05) \) with two peaks, during late winter/spring (February-April) and late summer/early autumn (August-September) (Fig. 4). Adult females produced, on average, 1·54 offspring per year \( (n = 25 \) females

![Fig. 3. Survival of captive-born mountain gazelles: (solid histogram) during the first 54 weeks of freedom, in relation to their age at the time of release \( (n = 15, 19, 13, 12 \& 12 \) for the five classes, from left to right); and (shaded histogram) during the second year of freedom, in relation to their age at the start of that year \( (n = 12, 17, 9, 4, 7) \). There were no animals in the 5+ age-class during the first year or in the 0-1 age-class during the second year. Three gazelles died between 51 and 54 weeks after release, but their exact dates of death are unknown and so mortality is shown for two periods: 0–54 weeks after release (solid histogram); and 54–106 weeks after release (shaded histogram).](image)

![Fig. 4. Seasonal distribution of births in the reintroduced population of mountain gazelles. Data refer only to calves conceived in the wild and born to 25 adult females which were regularly observed for one to three years, starting \( \geq 6 \) months after release. The number of calves born was 82 or 83 (the exact birth date of one calf was unknown): \( n = 82 \cdot 5 \).](image)
observed for one year): 11 females produced one calf; 13 produced two calves; and one female produced one or two, but the exact birth date of one calf was unknown. For 19 females observed for \( \geq 2 \) years, the mean number of calves per female increased from 1.42 in the first year to 1.74 during the second: 42% of females produced two calves during the first year, increasing to 79% in the second (\( \chi^2 = 3.96, d.f. = 1, p = 0.046 \)). It is unclear whether this rise was related to the time interval since release, or to the age of the females, which were a year older during the second observation year. During three years of study, three females produced six calves each, five females produced five calves each and one female produced three calves. 

The mean interval between successive calves was 7.06 months (\( n = 31 \) females). Usually, the interval was six to seven months: 64% of intervals were of this duration when only the first inter-calving interval for each mother was considered, but the figure rose to 72% (\( n = 85 \)) for all recorded intervals (Fig. 5). A recorded inter-calf interval of 14 months was probably really two intervals of ca. seven months, with a birth having been undetected. The mean interval implies a mean rate of calf production of 1.70 (12/7.06) calves per female per year, which is similar to the observed rate of 1.74 during the second year of observation.

For females which produced at least three calves, the duration of the first recorded inter-calving interval was not correlated with the duration of the second (\( r = -0.076, n = 18 \), but was correlated with the mother’s age (\( r_S = 0.377, n = 31, p = 0.037 \)). This suggests that, on average, older females produce fewer calves per annum than younger females. During 1993, following a winter of above-average rainfall, four females (20%) produced one calf and 16 (80%) produced two single calves. During 1994, following a winter of below-average rainfall, six females (27%) produced one calf, 14 (64%) produced two calves and two females (9%) produced one or two calves (in each case, one calf was born during December or January). These translate to mean production rates of 1.80 and 1.68 calves per female during 1993 and 1994, respectively. The proportion of females which definitely produced two calves did not differ between the years (\( \chi^2 = 1.3, d.f. = 1, p = 0.4 \)).

Five females, aged 2, 3, 4, 7 and 8 months when freed, conceived in the wild and produced their first calf when aged 16, 12, 13, 18 and 23 months respectively. Two females born in the wild, probably during June-August 1991, produced their first calf in March 1993, giving 13–15 months as their age at first conception. During late 1993, two wild-born males aged 18–24 months replaced older, released males as territory holders.

**Number of gazelles**

The number of marked gazelles in the Wadi Matham subpopulation increased from 12 during early June 1991, to 28 during September 1992, to 33 during August 1993. Thereafter, it was 30–34. The number of marked gazelles in the Jida subpopulation declined from seven during August 1993 to five at the end of 1994.

By December 1994, the estimated number of gazelles in the population within the reserve had increased to 165 (confidence limits 152 and 185) (Fig. 6). The exponential rate of increase (\( r \)) of the Matham subpopulation during 1993 (\( r = 0.388, SE = 0.058 \)) was not significantly different from that during 1994 (\( r = 0.280, SE = 0.062 \)) (\( t = 1.271, p < 0.2 \)) and the mean exponential rate of increase on a yearly basis between December 1992 and December 1994 was 0.275 (\( SE = 0.025 \)). This is equivalent to a growth multiplier (\( \lambda \)) of 1.32 and any population increasing at this rate doubles in number about every 2.5 years. In contrast, the estimated number of gazelles within the Jida subpopulation remained approximately

![Fig. 5. Frequency distribution of the duration of the inter-calving interval in the reintroduced population of mountain gazelles (\( n = 85 \)).](image)

![Fig. 6. The increase in the total number of mountain gazelles in the reserve during the first four years of the reintroduction; mean monthly estimates with 95% confidence intervals. Histogram shows the number of animals released each month. Dashed line shows the estimated number of gazelles in the Jida subpopulation.](image)
constant during 1994, because the mortality rate was high and the numbers of births and deaths were about equal.

From May to June during 1992, 1993 and 1994, there were slight declines in the population estimate (Fig. 6) coinciding with decreases in the number of juveniles aged < 6 months in the Matham subpopulation (which made up most of the reserve's population). From May to June 1993, there were also declines in the numbers of large juvenile (> 6 months-of-age) and yearling males and, from May to June 1994, the numbers of yearling and adult males decreased. Although these declines are probably not statistically significant, their temporal consistency from one year to the next may indicate that some juveniles and non-territorial males dispersed from the Matham wadi system at the start of summer.

**Density**

The density of gazelles in the fenced section of Wadi Ghaba increased in 1991 as a result of releases and births, but declined during early 1992 after some animals were killed by a wolf and others moved into Wadi Matham, causing the density there to rise (Fig. 7). Density increased at a similar rate in both areas during the 1992–1993 winter and was approximately constant in Ghaba after August 1993. In contrast, density in Matham declined during the first part of both 1993 and 1994, as numbers of juveniles and males declined, but increased during the second half, and the overall trend was slowly upwards. Density in Ghaba averaged 15.1 gazelles km\(^{-2}\) (SD = 2.0, n = 15 monthly estimates) from August 1993 to December 1994, but peak density in Matham was less than half this, at 7.1 gazelles km\(^{-2}\) at the end of the study. If the mean mass of a gazelle was equal to that of an adult female (18 kg (Bahrain, 1974)), the mean biomass density of gazelles in Ghaba was 272 kg km\(^{-2}\).

**Population structure**

The reserve was estimated to contain 33 (20%) adult males, eight (5%) yearling males, 54 (33%) adult females and 69 (42%) juveniles during December 1994. The sum of these estimates for the age/sex classes (164) is close to the separate estimate of the total number of gazelles (165). Ten adult males and 30 adult females were released animals and the others were wild-born. The ratio of adult females to adult males in the reserve was 1:6:1 and for adult females to adult and yearling males was 1:3:1. The latter ratio was unchanged even when only wild-born gazelles were included. It is estimated that 15 (45%) of the adult males held a territory. Thus, assuming that at any given time the only males socially capable of mating were the territory holders, but that all adult females were breeding, the ratio of breeding females to breeding males was 3:6:1.

**DISCUSSION**

**Validity of population estimates using the Petersen method**

Several conditions must be met before the Petersen method of using mark-resighting data provides an accurate estimate of numbers (Caughley & Sinclair, 1994). The first, that marked individuals remain individually recognisable, was met, although a few tags were lost. The second is that no animal is born or immigrates during a sampling period. There were no gazelles locally before the study, thus immigration was zero, and the error due to births can be calculated from the number recorded during the average 18-day sampling period. Since adult females formed 33% of the population and each produced 1.74 calves per year, the potential error is 2.8% (33*1.74*18/365). The third condition is that no animal dies or emigrates. No gazelle was reported outside the reserve and so emigration was presumed to be zero. If the mean mortality rate of unmarked gazelles was similar to that of released animals (22%), then deaths during the average sampling period were 1.1% (22*18/365) of the population. Deaths counter the increase due to births and therefore the mean net change in population number during an average sampling period was < 2%.

The fourth condition is that marked and unmarked animals have the same, independent, probability of being seen. This assumption cannot be tested, because the sighting probability of unmarked (i.e. wild-born) animals could not be determined. If untagged gazelles had a lower sighting probability than marked ones, then the population estimate is less than the true number. Newborn gazelles do not always accompany their mother but often hide, and so their number may be underestimated. During an average month, juveniles < 1 month-of-age formed 4.7% (1.74*33*30/365) of the population, but the error was less, because some newborns were seen.

Heterogeneity of individual sighting probabilities within a population may bias the population estimate,
especially with small populations, but the bias is small (maximum ca. 8%) (Neal et al., 1993). Heterogeneity decreases the precision of the estimate and, on average, calculated 95% confidence limits include the true population number on 79% of occasions.

Thus, some assumptions of the Petersen method may have been violated and estimates may be less precise than the confidence limits suggest, but any errors are probably small compared to the population number when the study ended.

Reproduction, survival and density in Hawtah Reserve
The seasonality of births and the rate of calf production at Hawtah were similar to those found in other mountain gazelle populations. For example, in Lower Galilee and on the Farasan Islands, mountain gazelles also breed year-round (Baharav, 1983; Habibi, 1992). In Lower Galilee, birth numbers peak during spring and autumn and females often produce two single calves per year, with an inter-calf interval of 6-8 months. Age at first conception varies from 6-12 months in Lower Galilee to >18 months in Upper Galilee (Baharav, 1983), with gazelles at the King Khalid Wildlife Research Centre (N. Lindsay, pers. comm.) and Hawtah first conceiving at ca. 15 months.

A high mortality rate amongst juvenile and old animals and low mortality amongst young adults is a typical pattern amongst ungulates, e.g. Arabian oryx (Spalton, 1992). The mortality rate of gazelles at Hawtah (22%) is within the range for wild adult ungulates of 2-38% per annum (Owen-Smith, 1993). After increased protection from hunting, the density of mountain gazelles on the Farasan Islands increased 2.7-fold during 3-2 years (Habibi & Al Toun, 1993), equivalent to r of 0.315 on an annual basis, similar to the rate at Hawtah. The biomass density of gazelles in Wadi Ghaba, after being constant for >1 year, was within the range predicted from body size, using data from African ruminants (Owen-Smith, 1992).

These comparisons suggest that reproduction, survival, density and the rate of population increase at Hawtah are typical for gazelles and that the reintroduction has been successful so far. It is likely that the population will continue to increase and that gazelles will disperse into other wadis in the reserve. Once the gazelle population reaches carrying capacity, emigration will likely become one regulating factor, given the absence of any barrier to movement and the presence of suitable habitat outside the reserve. If this is the case, management will not be needed to control gazelle numbers within the reserve.

Effects of camel browsing and rainfall on food supply for gazelles
In most wadis in the reserve, the vegetation is heavily utilised by camels and the plant standing crop is much less than in the release wadis. The effect of camels on the density of gazelles that a wadi can support needs to be determined. The difference in gazelle densities between Ghaba and central Matham at the end of 1994 was probably due mainly to the presence of camels in Matham, but other factors cannot be ruled out at this stage. Even if it is conservatively assumed that the average camel-grazed wadi can support only half the maximum density of gazelles found in central Matham (i.e. 7/2 km²), the reserve, with >300 km² of wadis, can probably support >1000 gazelles.

One year of low rainfall had no detectable effect on the birth rate or survival of gazelles at Hawtah, although it remains to be seen what effect several successive years of low rainfall would have. Plant production in a wadi depends not only on direct rainfall, but also on run off from higher parts of the catchment. Thus, production is greater than would be predicted from direct rainfall (Coe et al., 1976). In addition, some moisture is stored in the subsoil of the wadi and is available to perennial plants with deep roots long after the rain fell. In consequence, plant growth and therefore food availability in a wadi are more consistent than rainfall, which varies temporally and spatially. This explains why gazelles can breed all year round at Hawtah.

Reintroduction of desert ungulates
Ungulates seem to be relatively easy to reintroduce, when compared to other mammalian orders (Griffith et al., 1989; Stanley Price, 1989; Gordon, 1991). Desert ungulates are considered particularly easy because they have few competitors or predators, tolerate a range of habitat conditions and eat a wide variety of plants. Furthermore, animals, such as desert ungulates, which become locally extinct because of persecution by man, should not be difficult to reintroduce because it is relatively simple to overcome this. Other factors which may cause local extinctions, for example the presence of an introduced predator or competitor, are often more difficult to eliminate (Caughley & Gunn, 1996). At Hawtah, the presence of rangers to prevent hunting, the absence of opposition to the reintroduction from local people and the protection of some areas of gazelle habitat from domestic livestock have all contributed to the initial success of the reintroduction.

Captive-bred animals sometimes have lower survival rates after release than wild-caught animals (e.g. otters Lutra lutra (Sjøasen, 1996)), but the survival rate of the captive-bred gazelles was relatively high. This is fortunate because, although wild populations of Arabian ungulates have declined, there are sizeable captive populations of some species.

Lessons for future gazelle reintroductions
During a reintroduction, it is important to select for release those individuals with a high probability of survival in the new environment. Unweaned gazelles should not be released; three freed at Hawtah, including two born in a pre-release pen, soon died. Births in a pre-release pen can be avoided by managing captive breeding
so that pregnant females are not near full-term when in the pen. Releasing pregnant gazelles increases the number of founders of the reintroduced population, if the females are pregnant by males unrelated to the animals being released. The ideal age group for release is probably weaned gazelles <2 years-of-age, which have a high survival rate. Gazelles >3 years old were particularly vulnerable to predators. Small samples may have obscured a real difference between the mortality rates of older males and females; adult male ungulates often suffer a higher mortality rate than females (FitzGibbon, 1990; Owen-Smith, 1993).

During the early years of a reintroduction, when gazelle numbers are small, predators may limit or even eliminate the population. It was not anticipated that predation would be a major cause of death amongst released animals at Hawta, because large carnivores are rare in Arabia, although the wolf is widely distributed (Gasperetti et al., 1985). In order to reduce the impact of predators on a reintroduced population, the number of animals should increase rapidly and this number will reach a safe level quicker if all animals associated for release are freed during a relatively short period. Although releases over many, rather than few, years is characteristic of successful reintroductions (Beck et al., 1994), the number of release years may simply reflect the number of animals freed, which is also greater in successful projects.

The lessons from this study have been applied in the planning of other gazelle reintroductions. During early 1995, 100 sand gazelles (98% being <3 years old) were released in the Uruq Bani Ma’arid Protected Area, on the western edge of the Empty Quarter in southern Arabia (Wacher, 1995). Pregnant females were freed well before the spring birth season and the females released close to the birth season were not pregnant. During January 1996, an additional 99 sand gazelles were released there.

ACKNOWLEDGEMENTS

NCWCD rangers are thanked for reporting gazelles seen outside the release wadis. Dr S. Albon, Dr F. Robertson, Dr R. Hammond and Miss A. Dixon commented on a draft of this paper. Mr N. Lindsay supplied a copy of his report on the reproductive parameters of captive gazelles at KKWRC and Dr J. Hines supplied a copy of the program JOLLY. The study was funded by the National Commission for Wildlife Conservation and Development.

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