CHAPTER 5

SPATIAL DISTRIBUTION

Introduction

Individual animals within a population use distinctive ranges or territories in the pursuit of their routine activities. Both the nature of these areas and the population's pattern of dispersion vary widely between species. However, each is determined by the underlying resource distribution (Brown 1975).

The range concept was first described by Burt (1943) who called it a home range which was "that area traversed by the individual in its normal activities for food gathering, mating and caring for young." It is increasingly being referred to simply as a range and its use as range use. A literature survey by Samuel & Fuller (1996) showed that the size of an animal's range can depend on the amount of resources available (Brown 1964), the distribution of these resources (Ford 1983), the preferred habitat type (Gese, Rongstad & Mytton 1988), the population density (Cooper 1978) and the risk of predation (Covich 1976). Among non-territorial species some parts of the range are rarely visited. The upper limits in this case are probably set by disadvantages which the animal is likely to experience if it frequents areas with which it is unfamiliar (Mace, Harvey & Clutton-Brock 1983). Wacher (1986) investigated the relationship between range size and annual rainfall in the genus *Oryx*, and found that the Arabian oryx in Oman used the largest ranges as they were found in the area of lowest primary productivity. This negative relationship between the range size of a female and the mean rainfall pattern is predicted through the known relationship between the rainfall and primary production above the ground in arid and semi-arid areas (Rosenzweig 1968; Noy-Meir 1973; Coe, Cumming & Phillipson 1976; Seely & Louw 1980), as well as the relationship between range size and the energy requirements of a species (McNab 1963).

In a study on small mammals, McNab (1963), showed that range size was related to body weight. Similar studies have also been done across samples of bird species (Armstrong 1965; Schoener 1968). Mace *et al.* (1983) reviewed various recent studies and found that they either demonstrated or confirmed that range size is related to body size and diet in a variety of animal groups, including primates (Milton & May 1976; Clutton-Brock & Harvey 1977a, b) and North American mammals (Harestad & Bunnell 1979). Despite all the cited studies, no conclusion has been reached on McNab's (1963) prediction that energetic requirements will determine range size (Mace *et al.* 1983). In addition to the predictions of energy requirements and range size, Stanley Price (1989) described the Arabian oryx as an "explorer species", indicating that in such species the range size increases throughout a lifetime. This is comparable to moose *Alces alces* (Linnaeus, 1758) which range widely in search of food in their short-lived successional habitats (Geist 1971). The aim of this part of the study was to describe the range use patterns of the reintroduced Arabian oryxes, and to address the following key questions:

- Are there any differences in the dispersal patterns of the Arabianoryxes from the B-generation, C-generation and the Mahazat as Sayd Protected Area or between the adult and subadult male and female oryxes?
- Do dispersal distances from the release site become asymptotic with time, or doreleased animals disperse increasingly further from the release site with time?
- Is there any seasonal pattern in which the different Arabian oryx groups use their range, and if there are seasonal differences in the range use patterns, what are these differences attributed to?
- To what extent do seasonal ranges overlap?
- Is it possible to distinguish a core area of the range that is used by the Arabian oryxes during all seasons?

Methods

Dispersal

Dispersal refers to the relatively large-scale movements of animals, but there appears to be no universally accepted definition (White & Garrot 1990). The definition given by these authors states that dispersal is a one-way movement of individuals from their natal site or an area that is occupied for a period of time. This definition was used in the present study with the natal site being replaced by the release site in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia.

In the database, which was collected over the 23-month monitoring period, there are specific north-south coordinates at every observation of any particular animal. For the purposes of this analysis these coordinates were sorted by date from the first to the last observation of each individual oryx. The dispersal distance from the release site was calculated for each set of north-south coordinates for each individual oryx for the entire data set using the relevant option in the Ranges V analysis package (Kenward & Holder 1995). The individual dispersal distances thus obtained were then used to calculate a mean dispersal distance from the release site for each group of oryx, for different periods after release. Collectively these means are referred to as the mean dispersal distances of the various oryx groups during a specified time, for example, the mean monthly dispersal distances of the C-generation oryxes for the first 12 months after release. In determining the mean monthly dispersal distances from the release site for the different groups of oryxes the data were corrected according to the time of release of the different individual animals in each group. In other words, when two adult male oryxes were released 3-months apart, the data for the first month in the desert would contain the coordinates of each individual animal's first month in the desert.

The trends in the dispersal distances from the release site with increasing time in the wild were investigated using linear regression analysis. Pearson's correlation coefficient was used to investigate the relationships between the composition of release groups and their dispersal from the release site. Subsequently the correlation between the proportion of adult males in the release groups and the mean annual dispersal distances of those groups were, for example, investigated. Single factor ANOVA was used to determine whether any significant differences existed between the mean dispersal distances of the various oryx groups. When such differences were found Student's t-test was used to test for differences between the means of specific oryx groups. In all analyses the significance level was set at $P \leq 0.05$.

Range use

The intuitive original definition of a home-range (Burt 1943) has been superseded by a statistical definition where the range is defined as some fixed percentage, usually 95%, confidence interval obtained from the animal's utilisation distribution function (Van Winkle 1975). The utilisation distribution function refers to the usual two-dimensional, relative frequency distribution of an animal's location over time. The utilisation distribution of an animal is usually specified in terms of a bivariate model. The utilisation distributions either have a predetermined form (Calhoun & Casby 1958; Jennrich & Turner 1969; Don & Rennols 1983) or not (Ford & Krumme 1979; Dixon & Chapman 1980; Anderson 1982).

There are three approaches that are frequently used in the analysis of range data (Worton 1987). The first approach is based upon estimators derived from peripheral points of the range, such as minimum area convex polygons* (Mohr 1947). The second approach assumes a parametric model, such as the bivariate normal for x- and y-coordinates (Jennrich & Turner 1969; Koeppl, Slade & Hoffmann 1975; Dunn & Gipson 1977), while the third, more recent approach determines the utilisation distribution by non-parametric procedures (Dixon & Chapman 1980; Anderson 1982; Worton 1989). The second and third approaches mentioned above are referred to as probabilistic methods, as these approaches attempt to assess an animal's probability of occurrence at each point in space (Harris, Cresswell, Forde, Trewhella, Woollard & Wray 1990). The non-parametric range use estimation methods tend to have lower precision than the parametric methods because fewer assumptions are made to develop an estimate (White & Garrot 1990).

A detailed discussion of the various analytical techniques in range estimation falls outside the scope of this work. Recent reviews of the different techniques available in range estimation include those done by Jaremovic & Croft (1987), Worton (1987) and Harris *et al.* (1990). However, the most frequently used minimum convex polygon method (Mohr 1947), and the more recent kernel methods (Worton 1989) which is used in this study, will be discussed briefly to illustrate the main differences between these two techniques.

In polygon methods the peripheral locations of an animal are joined by some connecting rule to determine the size of the range used. The simplest method uses a minimum convex polygon (Mohr 1947; Bearder & Martin 1980), which is a polygon with all its internal angles smaller than 180°. The polygon is called a minimum because it is the smallest area convex polygon that encloses all the location points (Worton 1987). Although one of the earliest techniques of range calculation, the minimum convex polygon method still is the one that is most frequently used (Voigt & Tinline 1980; Harris *et al.* 1990). The advantages of this technique are simplicity, flexibility of shape and ease of calculation (White & Garrot 1990). It can also be used to compare results with earlier studies. However, the technique has a number of disadvantages. Firstly, the range boundary encompasses all the fixes, including those occasional fixes well beyond the main area of activity. This means that the range size is strongly influenced by peripheral fixes, and the range area can include large areas that are never or seldom visited by the animal. There is also no indication of the intensity of range use (Worton 1987; Harris *et al.* 1990). Secondly, the range estimates are highly correlated with the number of observations used, especially for small sample sizes (Worton 1987). It has also been shown that within limits the range estimate increases as the number of locations increase (Jennrich & Turner 1969). Under the assumption of bivariate normality for the x- and y-coordinates, the range therefore seldom has an asymptote when plotted against the number of observations for most studies (Worton 1987).

The kernel methods, as described by Worton (1989) free the utilisation distribution estimate from parametric assumptions and provide a means of smoothing locational data to make more efficient use of them. These methods have well-understood consistent statistical properties and are widely used in both univariate and multivariate probability density estimation (Rosenblatt 1956; Cacoullos 1966). The kernel estimator can be viewed as follows: a scaled-down probability density function, the kernel, is placed over each data point. The estimator is then constructed by adding the *n* components. Therefore, the kernel estimator will have a higher density where there is a concentration of points, than where there are few points. The resulting estimate is a true probability density function. The amount of variation in each component of the estimate is controlled by the smoothing constant. A possible disadvantage of this technique is that relatively minor changes to the smoothing parameters have a large effect on the overall range size estimates (Harris *et al.* 1990). Based on the smoothing parameters used, two types of kernel estimators can be distinguished. The first are the fixed kernel estimators, where the smoothing parameters are of fixed value over the plane. The second type is called the adaptive kernel estimators. In the latter improved type of kernel estimators, the smoothing parameter is varied so that areas with a low concentration of points have a higher smoothing factor (h-value) than areas with a high concentration of points (Worton 1989). In practice it has been found that the approach of least squares cross-validation provides a reliable, objective method of estimating the smoothing constant (Silverman 1986). It has also been found that the adaptive kernel estimator is best suited in analysis where accuracy in the tails of density distributions is important (Worton 1989).

Tracking data are three-dimensional. Therefore, the closer in time two locations are taken the less likely they are to be statistically independent (White & Garrot 1990). Independence between successive observations is an implicit assumption in most statistical analysis of animal movements (Hayne 1949; Calhoun & Casby 1958; Jennrich & Turner 1969; Worton 1987), yet this assumption is rarely addressed by ecologists (Anderson 1982; Don & Rennolls 1983). Because frequent successive observations will tend to be positively correlated, sample variances of locations will be underestimates of the true values, and statistical estimates of range size will underestimate the true size of the range by an amount related to the covariance between successive observations (Swihart & Slade 1985). Auto correlation of the animal's consecutive locations must therefore be considered if the animal's movement patterns was not sampled randomly (White & Garrot 1990). More recently, however, it has been shown that the assumption of independence among sequential locational observations for non-parametric range analysis techniques, such as the kernel estimator, is not relevant (De Solla, Bonduriansky & Brooks 1999). These authors have also shown that the elimination of autocorrelation* reduces the accuracy of the range analysis and that it destroys biologically important information.

In the present study the seasonal range sizes of oryxes were calculated for those individual animals with sufficient observations by means of the non-parametric kernel analysis technique. The minimum number of fixes accepted in the range calculations of an individual oryx was 10. The effect of increasing observations on the range size was investigated through a Pearson's correlation coefficient and linear regression. The seasonal ranges calculated for individual oryx were used to calculate the mean seasonal range sizes for the different groups of Arabian oryx, for example, the B-generation animals and oryx males. Single factor ANOVA tests were used to test for significant differences in the mean range sizes. If such differences were found, finer scale analysis was done by means of Student's t-test to determine where the significant differences in the mean range sizes were located.

Each individual range was investigated to determine whether it became asymptotic. A range reaches an asymptote when additional locations result in a minimal increase in range size and is calculated by plotting the range size against the number of locations (Stickel 1954; Hawes 1977). The effect that the inclusion of non-asymptotic ranges had on the calculation of the mean seasonal ranges of the different Arabian oryx groups were investigated by means of Student's t-test. In all analyses the significance level was set at $P \leq 0.05$.

Results and discussion

Mean monthly dispersal

The mean monthly dispersal distances of all the released Arabian oryxes during the first 12 months after release are graphically illustrated in Figure 8. The mean monthly dispersal distance of the oryx population as a whole increased continuously during the first 12 months after release. This relationship between the mean monthly dispersal distances and the time in the wild was significant ($R^2 = 0.8334$; $P = 0.00003$) for this group during the first year of monitoring after release. The mean monthly dispersal distances of the animals from the different release groups ranged between 11.0km (Figure 9, release 1) and 30.4km (Figure 10, release 4) during the first month after reintroduction. Although the mean monthly dispersal distances from the release site became asymptotic within a few months after release, all the release groups once again showed an increase in their mean monthly dispersal distances from the release site towards the end of the first year of monitoring. This later increase resulted in a positive relationship between time spent in the wild and the mean monthly dispersal distances for the oryxes from five of the six release groups during the first year of monitoring after release. This relationship was, however, only significant for the oryxes from the third ($R^2 = 0.692$; $P \leq 0.05$), fifth ($R^2 = 0.853$; $P \leq 0.05$) and sixth ($R^2 = 0.870$; $P \leq 0.05$) release groups (Table 1). There was a negative relationship between the mean monthly dispersal distances from the release site and the time spent in the wild for the animals from the first release.

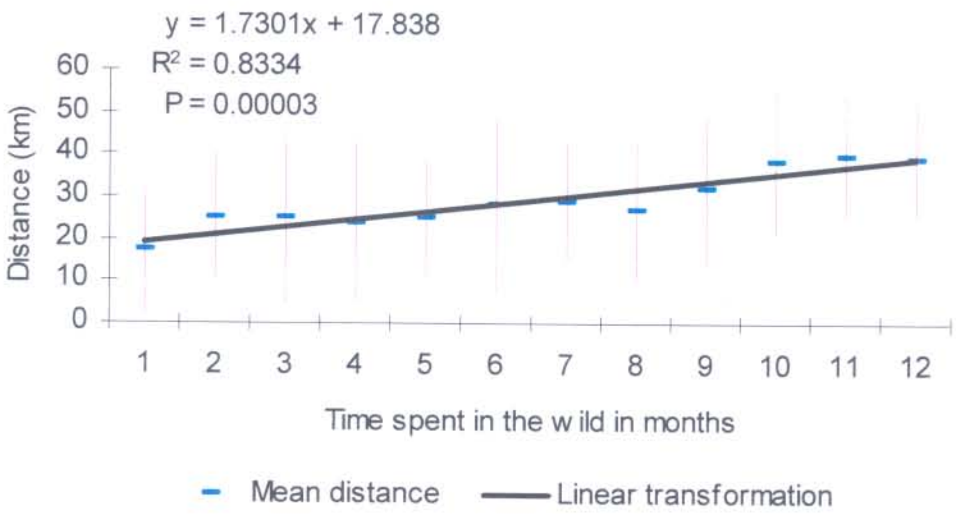


Figure 8: The relationship between the mean monthly dispersal distances (± 1 SD) of all the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia and the time spent in the wild for the first 12 months after release. The linear regression of the mean monthly dispersal distances against increasing time is significant ($R^2 = 0.8334$; $P = 0.00003$).

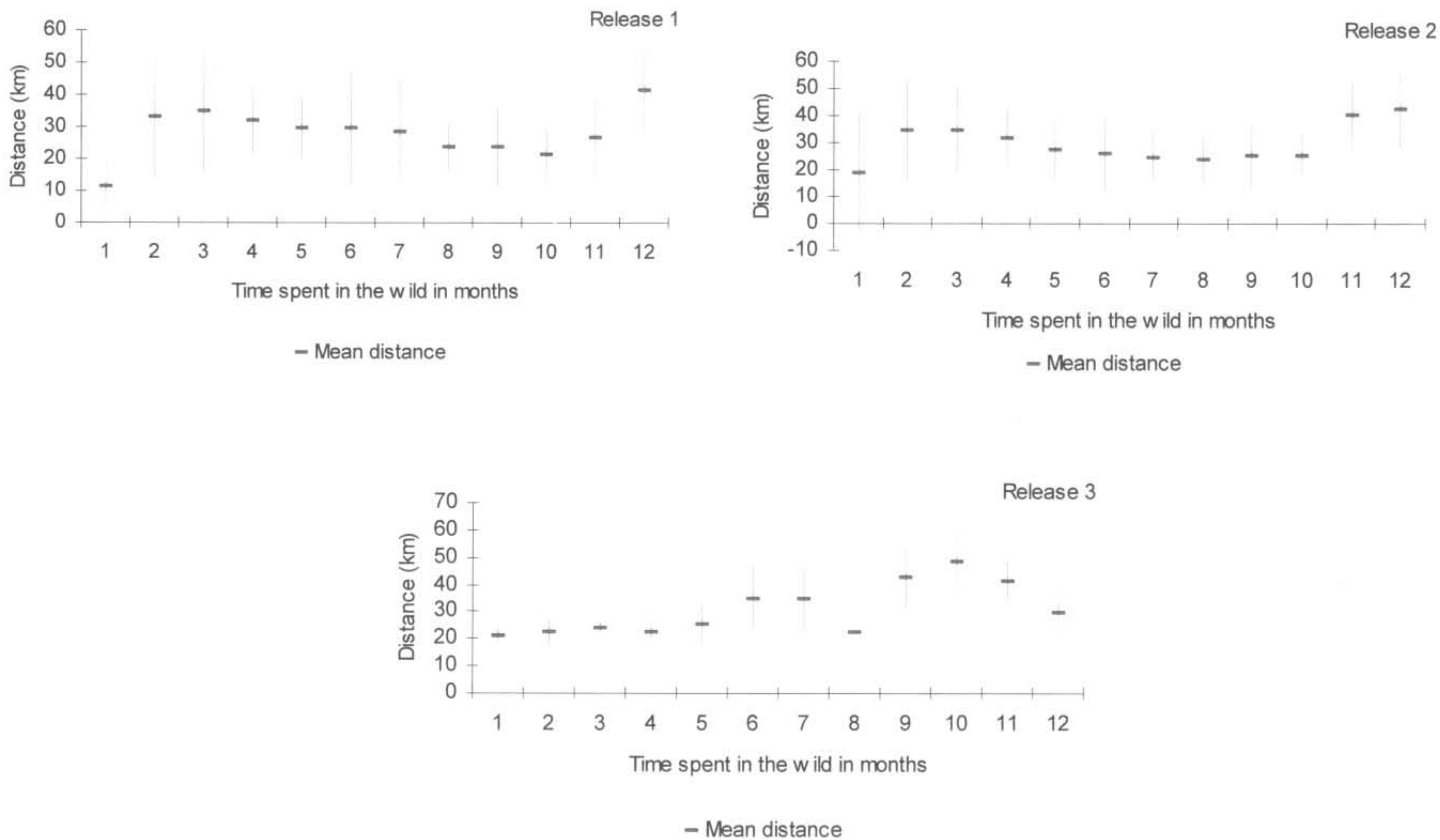


Figure 9: The mean monthly dispersal distances (± 1 SD) from the release site for the Arabian oryxes from the first three releases into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March to June 1995, for the first 12 months of monitoring after release.

It was also found that the mean monthly dispersal distances of the oryxes, irrespective of their origin, increased during the first year of monitoring (Figure 11). The relationship between time in the wild and the mean monthly dispersal distances from the release site was significant for the C-generation oryxes (R^2 = 0.877; $P \leq 0.05$) and those animals from the Mahazat as Sayd Protected Area (R^2 = 0.490; $P \leq 0.05$). The positive relationship between time spent in the wild and the mean monthly dispersal distances from the release site was not significant for the B-generation animals during the first 12 months after release. The mean monthly dispersal distances of the subadult male and female oryxes, as well as those of the adult male and female oryxes, during the first year after reintroduction, are presented graphically in Figure 12. The adult female oryxes dispersed furthest from the release site during this time, reaching a mean monthly dispersal distance of 44.9 km from the release site during the sixth month after release. Despite this, the relationship between time spent in the wild and the mean monthly dispersal distances from the release site was weakest for this age and sex class during the first 12 months of monitoring (Table 1). The data for both the subadult male oryxes (R^2 = 0.736; $P \leq 0.05$) and the subadult female oryxes (R^2 = 0.864; $P \leq 0.05$) showed a strong positive relationship between time in the wild and the mean monthly dispersal distances from the release site during this time. These two relationships were significant. Although the mean monthly dispersal distances of the adult male and female oryxes increased with time, these relationships were weaker than those of the subadult oryxes and were not significant during the first 12 months of monitoring.

Mean annual dispersal

No significant differences (F=2.18; d.f. = 5; $P \geq 0.05$) could be found between the mean annual dispersal distances of the different release groups after 12 months of monitoring. In addition, the proportional composition of the release groups in terms of age and sex class as well as origin had little effect on the mean dispersal distances of the release groups during the first year of monitoring. Based on Pearson's correlation coefficient non-significant, negative correlations between the mean annual dispersal distances of the different oryx release groups and the proportion of both the adult males (r = -0.609; d.f. = 4; $P \geq 0.05$) and the subadult females (r = -0.529; d.f. = 4; $P \geq 0.05$) in each release group were found during the first year of monitoring. In contrast, positive, but non-significant correlations existed between the proportion of adult female (r = 0.101; d.f. = 4; $P \geq 0.05$) and subadult male (r = 0.589; d.f. = 4; $P \geq 0.05$) oryxes in the release groups and the mean annual dispersal distances of the release groups from the release site during the first year after release. The proportion of animals from the Mahazat as Sayd Protected Area in the release groups was positively correlated (r = 0.159; d.f. = 4; $P \geq 0.05$) with the mean annual dispersal distance from the release site, while a negative correlation (r = -

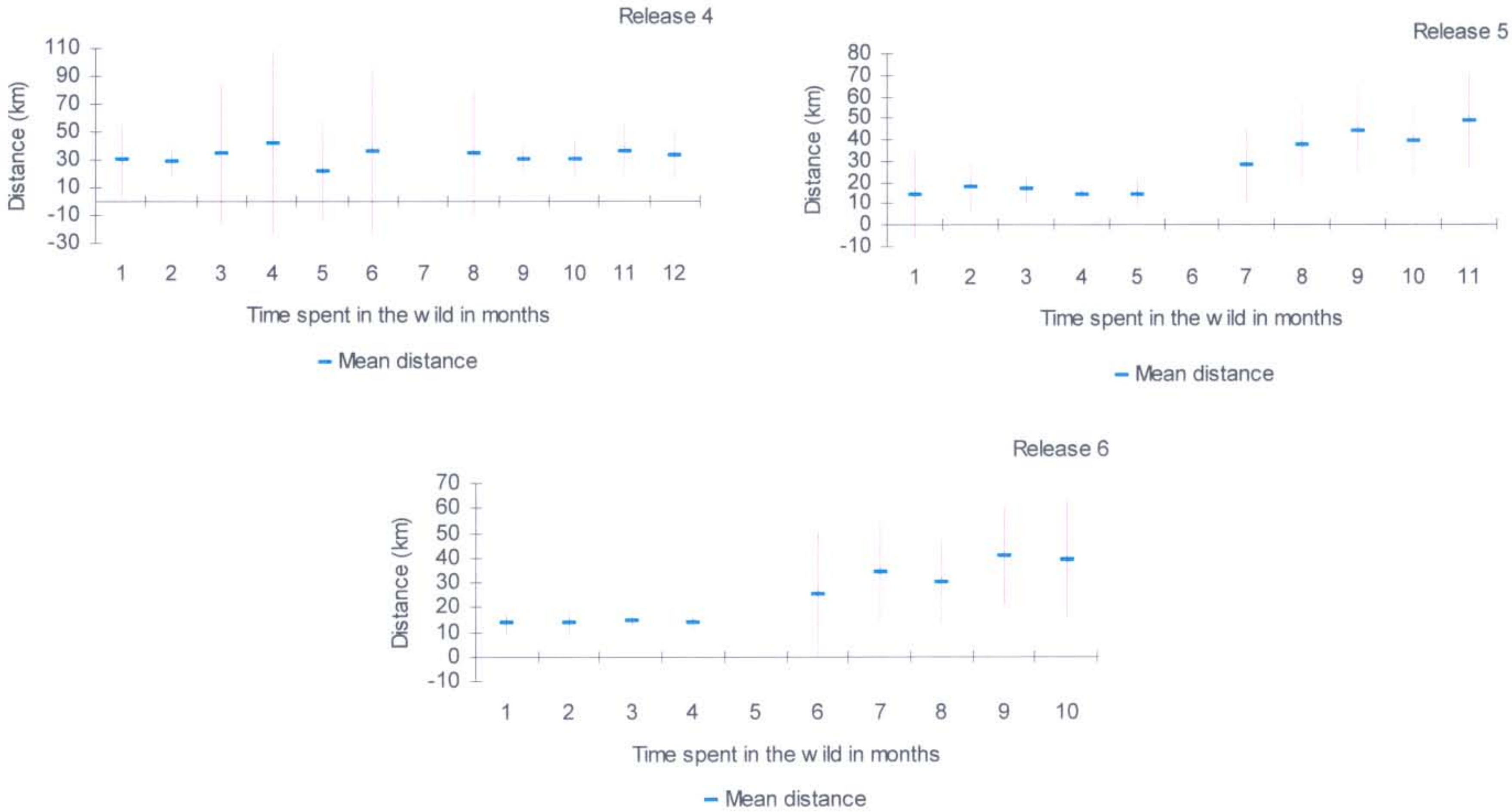


Figure 10: The mean monthly dispersal distances (± 1 SD) from the release site for the Arabian oryxes from the last three releases into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March to May 1996, for their entire monitoring period. There were no observations made during September 1996.

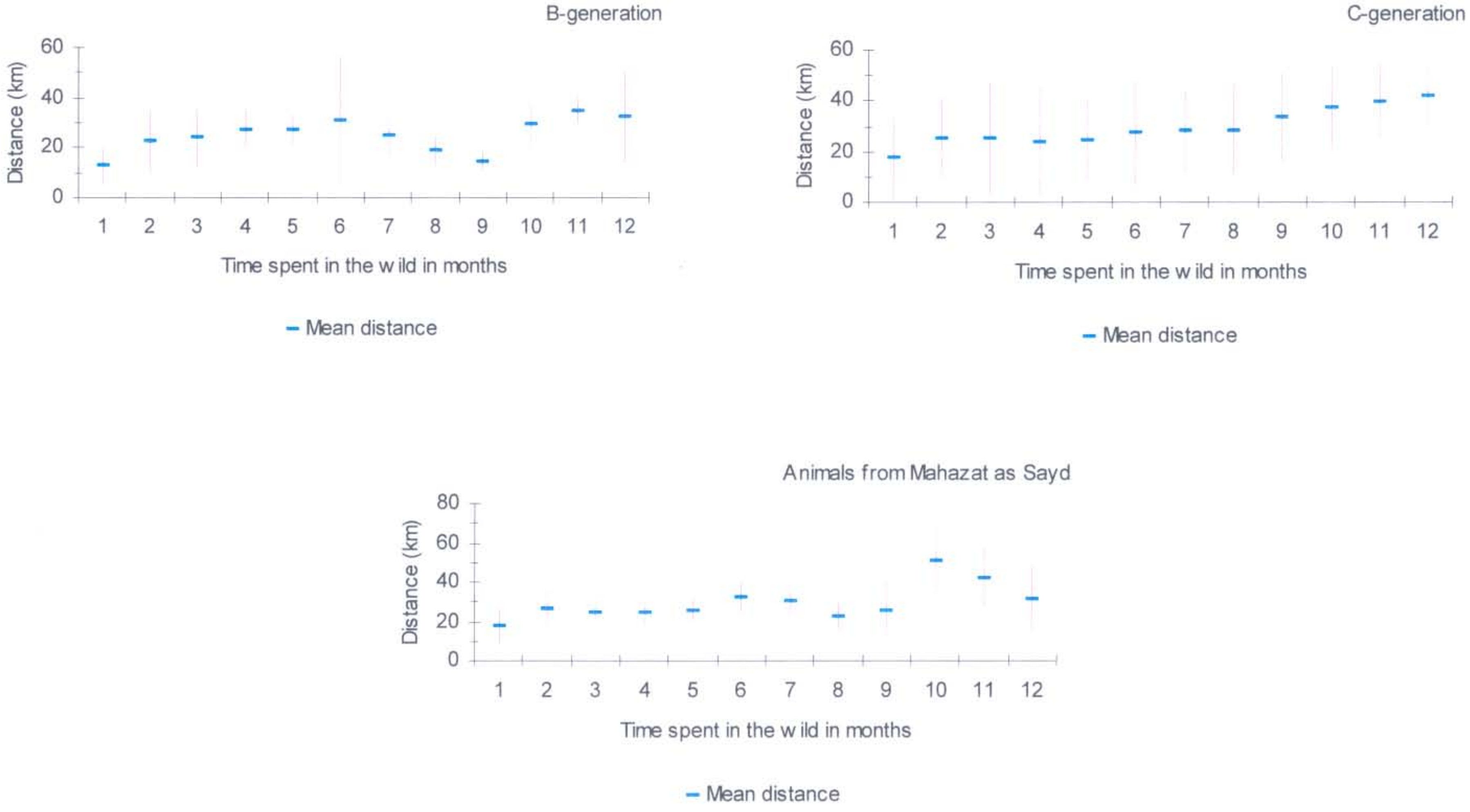


Figure 11: The mean monthly dispersal distances (± 1SD) from the release site for the Arabian oryxes of different origin as observed for the first 12 months after release in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia.

0.112; d.f. = 4; $P \geq 0.05$) existed between the mean annual dispersal distances of the release groups during the first year of monitoring and the proportion of C-generation oryxes in the release groups. These weak, non-significant correlations suggest that the composition of the release groups in terms of age and sex class as well as origin had little effect on the dispersal of the release groups during the first 12 months of monitoring.

There are significant ($F = 7.75$; d.f. = 3; $P \leq 0.05$) differences in the mean annual dispersal distances from the release site of the oryxes for the different age and sex classes during the first year of monitoring. In comparing the mean annual dispersal distances of the different Arabian oryx age and sex classes during this period it was found that the adult male oryxes were the common denominator in all instances where significant differences existed. The differences were significant when comparing the mean annual dispersal distances of the adult male oryxes during the first 12 months with that of the adult female oryxes ($t = -4.57$; d.f. = 1147; $P \leq 0.05$), the subadult female oryxes ($t = -4.83$; d.f. = 2753; $P \leq 0.05$) and the subadult male oryxes ($t = -3.74$; d.f. = 1735; $P \leq 0.05$) respectively. These negative values indicate that the mean dispersal distance of adult male oryxes from the release site was significantly smaller than that of any other age and sex class after one year of monitoring. There were also significant ($F = 6.855$; d.f. = 2; $P \leq 0.05$) differences in the mean annual dispersal distances of the oryxes of different origin from the release site during the first 12 months after release. Both the animals from Mahazat as Sayd ($t = 3.805$; d.f. = 1066; $P \leq 0.05$) and the C-generation ($t = 3.476$; d.f. = 3727; $P \leq 0.05$) oryxes had significantly larger mean dispersal distances from the release site during the first 12 months after release, than did the B-generation oryxes. No significant differences were found in the mean annual dispersal distances of the B- and C-generation oryxes.

The mean annual dispersal distance from the release site of all of the different oryx groups, except that of the second release group, decreased between years (Figure 13). It is not clear why the mean annual dispersal distance of the animals from the second release did not show this decrease from 1995 to 1996. Significant decreases in the mean annual dispersal distances from the release site was observed for the oryxes from the first ($t = 6.97$; d.f. 1700; $P \leq 0.05$), and third ($t = 6.22$; d.f. = 1184; $P \leq 0.05$) release groups between years. Significant decreases in the dispersal distances from the release site were also observed for the B-generation ($t = 3.06$; d.f. = 449; $P \leq 0.05$) and the C-generation oryxes ($t = 3.037$; d.f. = 4093; $P \leq 0.05$) as well as those animals from the Mahazat as Sayd Protected Area ($t = 5.02$; d.f. = 943; $P \leq 0.05$). Consequently the mean annual dispersal distance of all the oryxes grouped together decreased significantly ($t = 5.49$; d.f. = 5489; $P \leq 0.05$) between the 1995/6 and 1996/7 monitoring periods.

Entire monitoring period

The mean monthly dispersal distances of the various oryx groups monitored over the entire 23-month monitoring period are illustrated graphically in Figures 14 to 16. A negative relationship exists between time spent in the wild and the mean monthly dispersal distances from the release site for various groups of oryx (Table 1) when the data are analysed for the entire monitoring period. This relationship was, however, only significant for the oryxes from the first release group ($R^2 = 0.260$; $P \leq 0.05$). No other relationships between time spent in the wild and the mean monthly dispersal distances, whether positive or negative, were significant during this period.

During the 23-month monitoring period there was a positive correlation ($r = 0.841$; d.f. = 1; $P \geq 0.05$) between the proportion of C-generation oryxes in the release groups and the mean dispersal distances of these groups from the release site. A negative correlation ($r = -0.873$; d.f. = 1; $P \geq 0.05$) existed between the proportion of animals obtained from the Mahazat as Sayd Protected Area in the release groups and the mean dispersal distances from the release site. Neither of the latter two correlations were significant, however, indicating that group of origin had little effect on the mean dispersal distance of the various release groups during the 23-month monitoring period. Too few B-generation oryxes were in the different release groups to allow testing for correlations between the proportion of B-generation animals in these three release groups and the mean dispersal distances from the release site during the first 12 months of post-release monitoring.

A strong negative, but non-significant correlation ($r = -0.961$; d.f. = 1; $P \geq 0.05$) was found between the proportion of adult female oryxes in the release groups and the mean dispersal distances of those groups from the release site during the entire monitoring period. The correlation ($r = -0.555$; d.f. = 1; $P \geq 0.05$) between the proportion of adult males in the release groups and the mean dispersal distances from the release site was also negative, and not significant. Over the 23-month monitoring period the mean dispersal distances of the adult male oryxes from the release site was significantly ($t = -5.59$; d.f. = 1968; $P \leq 0.05$) less than that of the adult female oryxes. No comparative test could be done with the subadult oryxes, as there were none in the population that could be located regularly. As far as the different groups of origin are concerned, the B-generation oryxes had the smallest mean dispersal distance from the release site after 23-months in the wild (Table 1). This distance was significantly less than that of the C-generation ($t = -5.01$; d.f. = 4544; $P \leq 0.05$) and the Mahazat as Sayd ($t = -4.28$; d.f. = 1394; $P \leq 0.05$) animals' mean dispersal distances over this period. Similarly, the oryxes from the Mahazat as Sayd Protected Area had a significantly ($t = -2.13$; d.f. = 5038; $P \leq 0.05$) smaller

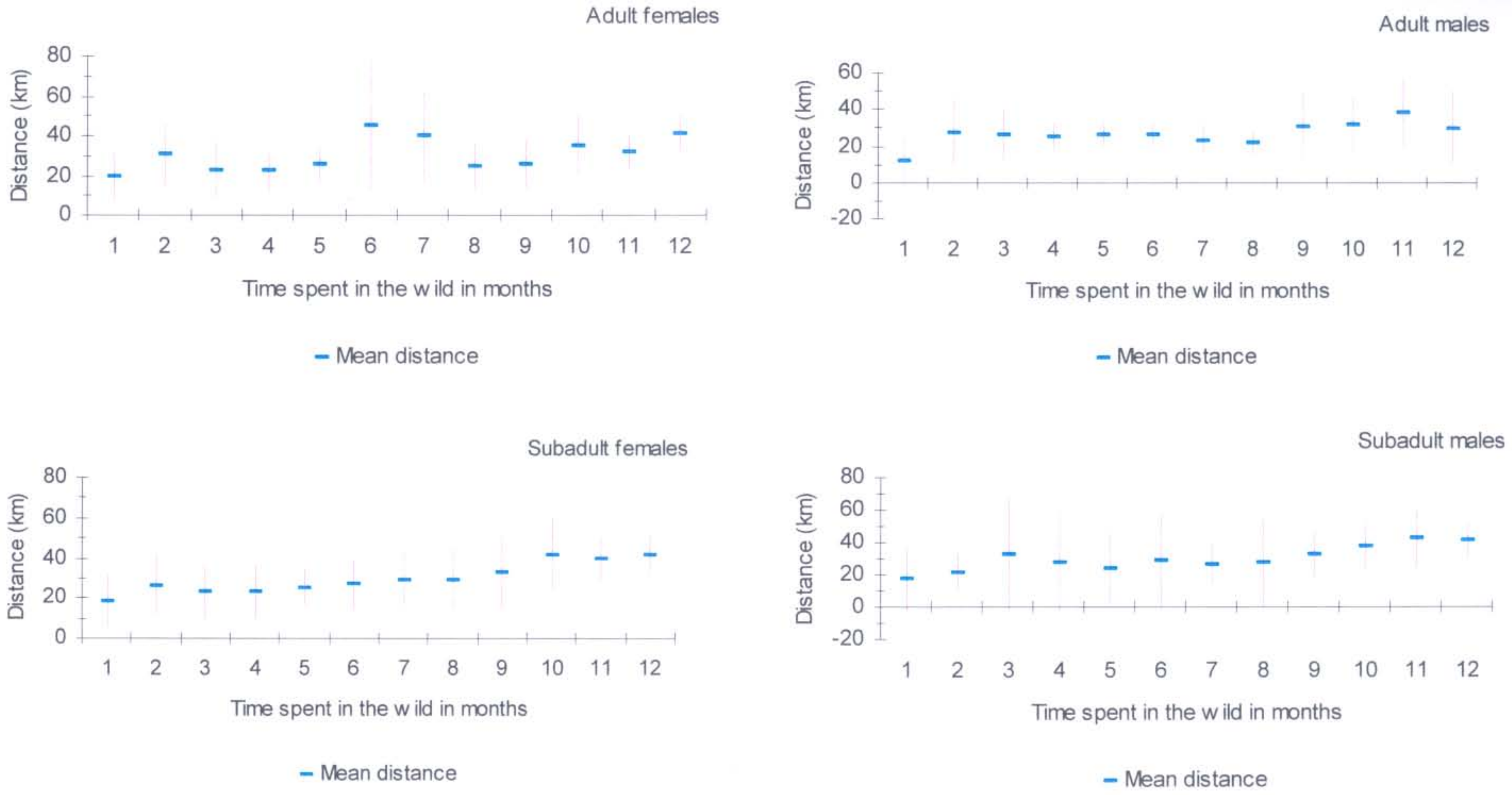
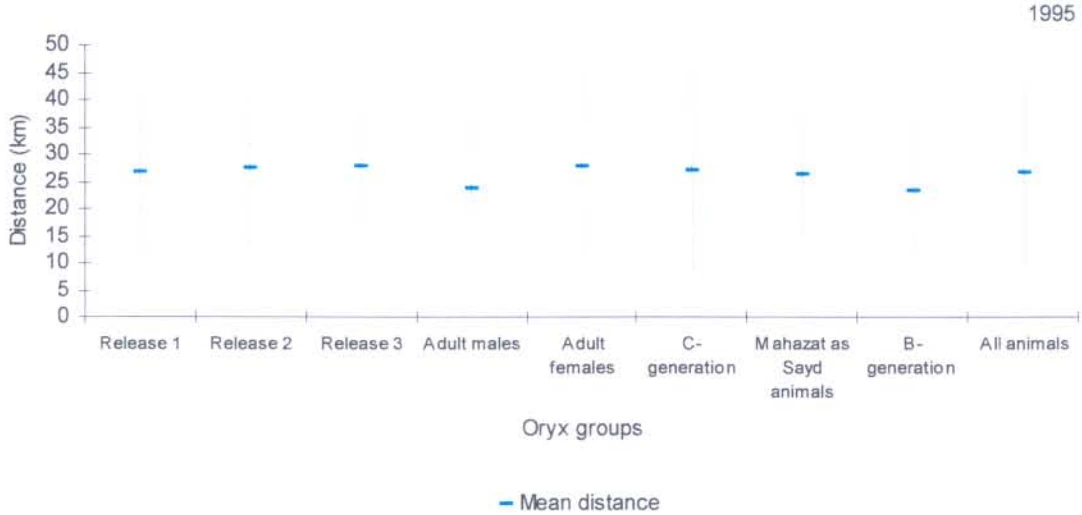


Figure 12: The mean monthly dispersal distances (± 1 SD) of the different Arabian oryx age and sex classes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997, during their first 12 months after release.



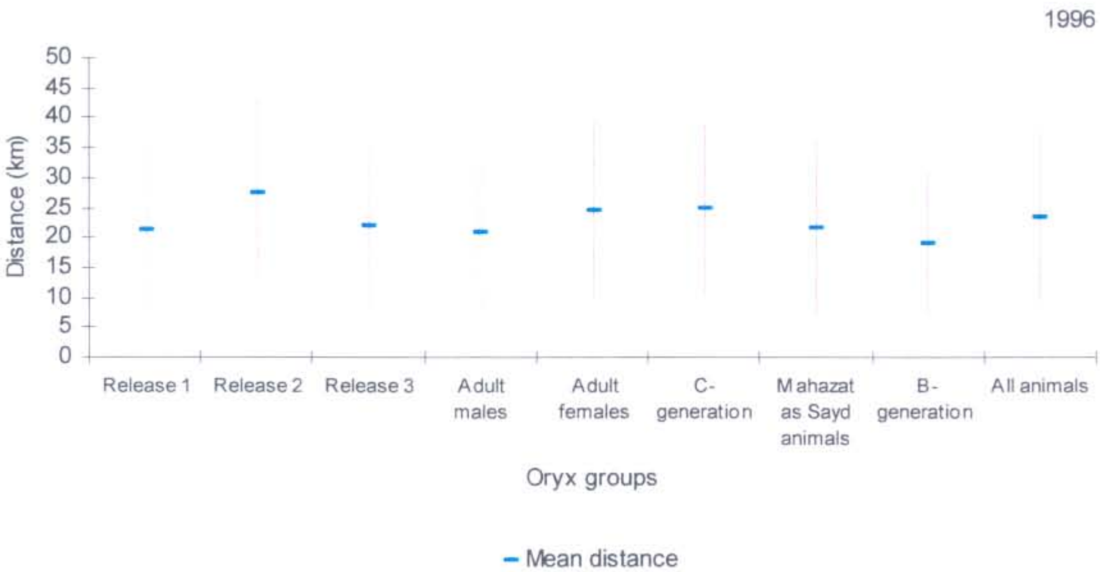


Figure 13: The mean annual dispersal distances (± 1 SD) from the release site for the different groups Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, in two successive years of monitoring after release.

Table 1: The regression analyses of the mean monthly dispersal distances (km) from the release site for the different of Arabian oryx groups in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, with increasing time in the wild (significant values are indicated in yellow). The n column indicates the number of oryxes in the sample.

ORYX GROUP	REGRESSION OVER 12-MONTH PERIOD					REGRESSION OVER 23-MONTH PERIOD				
	n	R^2	P	Slope	Mean distance	n	R^2	P	Slope	Mean distance
Release 1	12	0.008	0.786	-0.18	26.5	11	0.260	0.013	-0.69	24.9
Release 2	9	0.013	0.736	0.24	27.5	9	0.000	0.982	0.01	27.5
Release 3	10	0.692	0.001	2.44	27.7	9	0.001	0.925	0.04	26.8
Release 4	10	0.001	0.931	0.06	30.9	-	-	-	-	-
Release 5	9	0.853	0.000	4.20	24.8	-	-	-	-	-
Release 6	16	0.870	0.000	4.05	22.3	-	-	-	-	-
Adult males	8	0.486	0.117	1.21	23.0	28	0.110	0.122	-0.32	22.2
Adult females	8	0.267	0.085	1.19	27.9	34	0.428	0.344	-0.25	26.0
Subadult males	21	0.736	0.000	1.82	26.4	-	-	-	-	-
Subadult females	29	0.864	0.000	1.97	27.0	-	-	-	-	-
B-generation	4	0.175	0.175	0.78	23.3	4	0.061	0.256	0.23	22.1
C-generation	55	0.877	0.000	1.91	26.3	54	0.032	0.418	-0.21	26.6
Mahazat as Sayd animals	7	0.490	0.011	2.26	26.4	6	0.023	0.494	-0.22	25.3
All oryxes	66	0.833	0.000	1.73	24.9	64	0.576	0.270	-0.25	26.0

mean dispersal distance from the release site after 23-months in the wild, than did the C-generation oryxes.

The initial response of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area, seems to have been one of quick dispersal from the release site as indicated by the mean dispersal distances from the release site during the first month after release. This is further emphasised by the mostly positive relationship between the time spent in the wild and the mean monthly dispersal distances from the release site for 93% of the oryx groups during the first 12months of monitoring. The significant nature of 57% of these relationships further illustrates the quick dispersal from the release site. This is in accordance with the results of studies done in Oman (Tear 1995).

The mean dispersal distances of the reintroduced Arabian oryxes, irrespective of the group composition, do not continue to increase with increasing time spent in the wild. After 23 months spent in the wild, the mean dispersal distances of the different Arabian oryx groups were all less than 30.0 km from the release site, ranging between 22.2 and 27.5 km. Similar observations were made by Tear (1995) who analysed 8 years of data. Interestingly, there is a significant decrease in the mean annual dispersal distances of all the Arabian oryx groups, with the exception of the animals from the second release, between the first 12-month monitoring period and the remaining 11-month post-release monitoring period. The reason for this is not clear but it could be related to the knowledge gained by the animals during their first year in the protected area, which in turn resulted in better utilisation of the area during the second year. It is probably also related to the fact that the animals released during the second year of this project encountered other oryxes soon after release, unlike many of the animals reintroduced during the first year.

Group composition in terms of age and sex class as well as origin seems to be unimportant in predicting the mean dispersal distances of the different release groups from the release site over the first 12-months after release. The same holds true for the 23-month monitoring period, with the exception of the adult female oryxes. The strong correlation observed between the proportion of adult females in the release groups and the mean dispersal distances definitely suggests that an increasing proportion of adult females in a release group would result in lower mean dispersal distances. Unfortunately the relationship between the proportion of subadult male and female oryxes and dispersal distance from the release site could not be determined for the entire study period. Tear (1995), however, stated that dispersal distances from the release site decreases with increasing age.

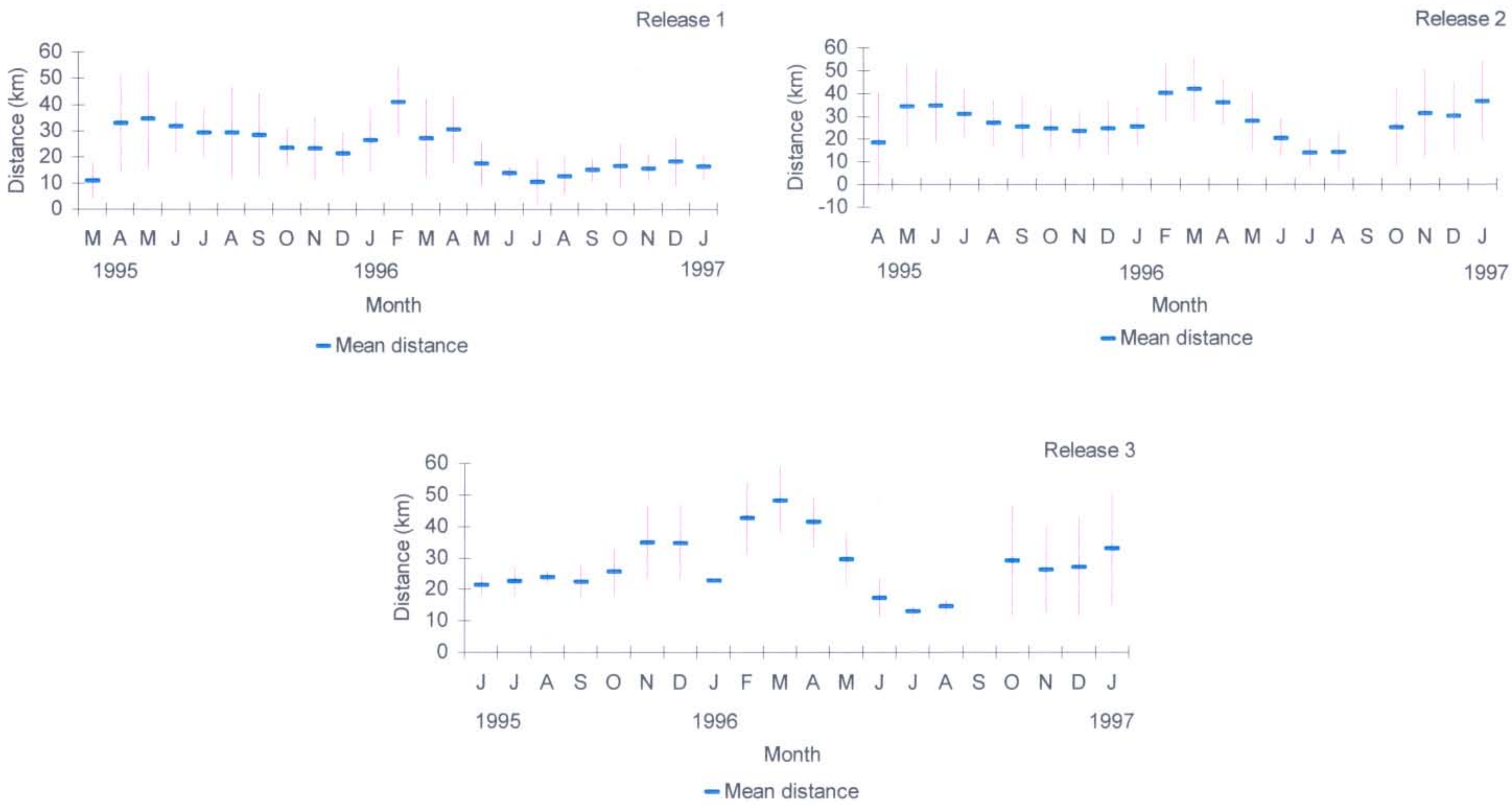


Figure 14: The mean monthly dispersal distances (± 1 SD) of the first three release groups of Arabian oryxes reintroduced into the ‘Uruq Bani Ma’arid Protected Area of the Kingdom of Saudi Arabia from the day of release to February 1997. No data are available for the animals from the second and third release groups during September 1996.

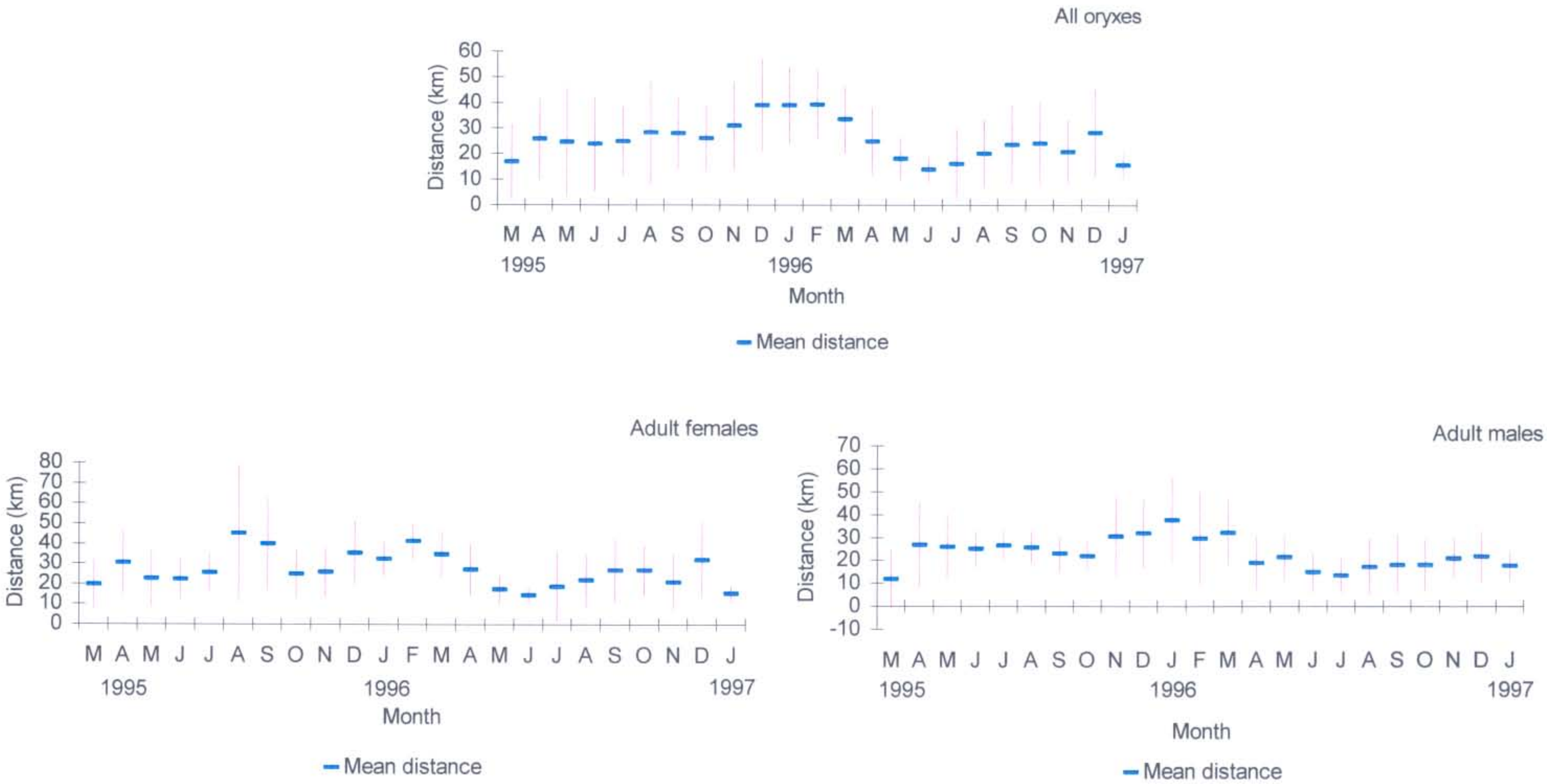


Figure 15: The mean monthly dispersal distances (± 1 SD) of all the Arabian oryxes combined as well as the different oryx age and sex classes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

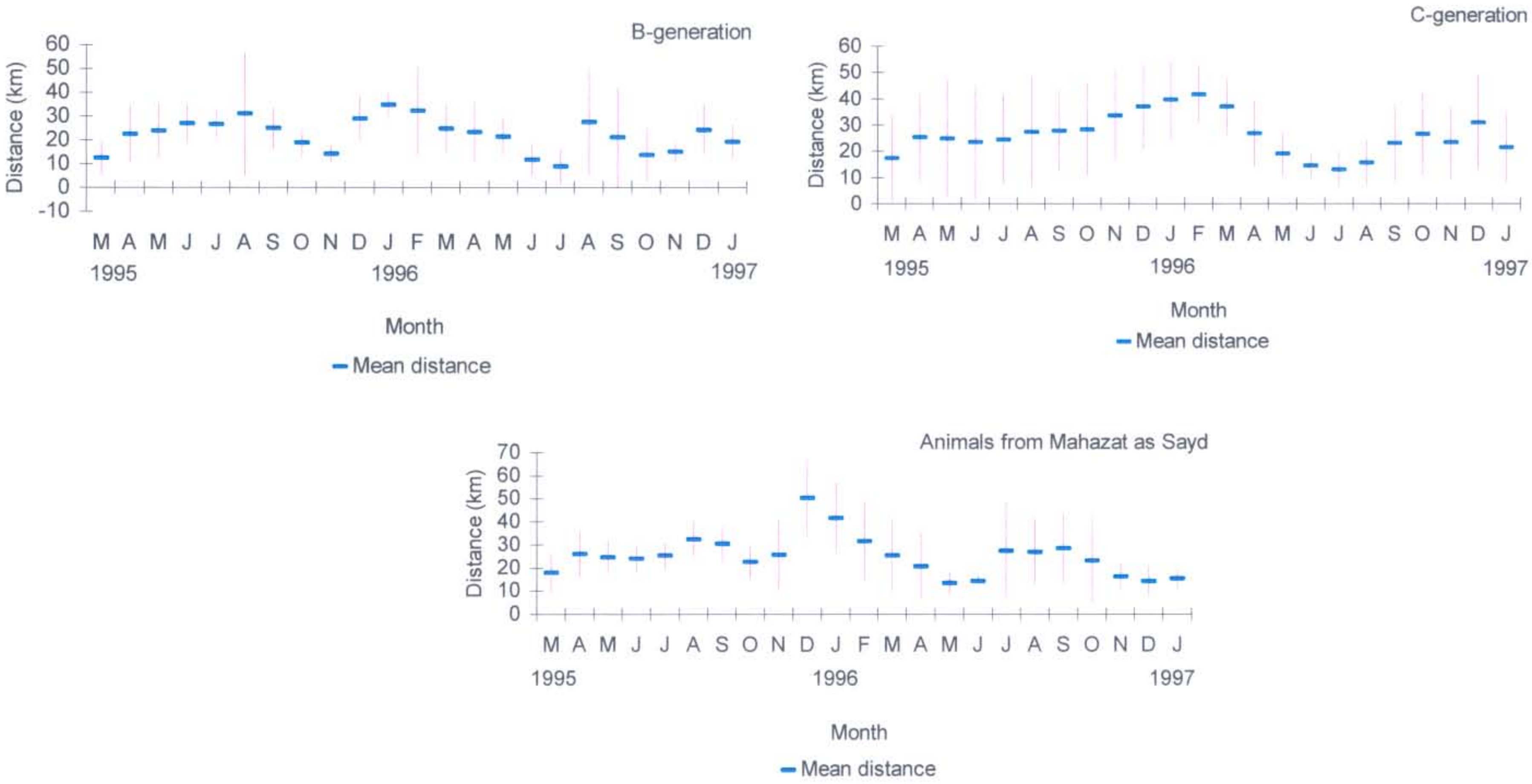


Figure 16: The mean monthly dispersal distances (±1 SD) of the Arabian oryx groups of different origin reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March to February 1997.

In the present study the quick dispersal of the Arabian oryxes from the release site was accomplished without any management to that effect. It is well known that the provisioning of both food and water can either create release site fidelity or encourage dispersal in release groups (Stanley-Price 1989). Rather, the observed quick dispersal of the oryxes from the release site is attributed to the widespread rain that fell in the area during 1995 and the subsequent investigation of the protected area by the oryxes after release. Rainfall is the most important determinant in the range use patters of the Arabian oryxes in Oman (Spalton 1995; Corp, Spalton & Gorman 1998) while the effect of rainfall on the dispersal patterns of the Arabian oryx has also been recognised before (Tear 1995).

Seasonal range use

The seasonal distribution of all of the Arabian oryx observations after release into the 'Uruq Bani Ma'arid Protected Area is illustrated graphically in Figure 17 for the seasons combined across years. No observations were made of any oryx west of the most western boundary of the protected area during the study period. The range areas shown to the west of the most western boundary of the protected area (Figure 18) are therefore a result of the analysis technique used.

The seasonal range use patterns of the Arabian oryxes, based on all the seasonal observations of all the animals, differed between the two years of monitoring. Based on the 95% use level of the kernel analysis the animals used their largest range of 2755.4 km² during the summer of 1995, while their smallest range of 759.0 km² was used during the autumn of that year. The same pattern was observed in the 50% core use areas during 1995 (Figure 19). During 1996, however, the smallest ranges for both the 50% core use and the 95% use level were used during the summer months, indicating a possible change in the ranging behaviour of the reintroduced animals. The data on the mean seasonal ranges used by the different groups of Arabian oryxes during the study period are presented in Tables 2 and 3. There are no significant differences in the mean seasonal range sizes of any of the oryx groups when those mean range sizes with, and those without the non-asymptotic ranges are compared statistically. In addition, no significant relationship was found between an increasing number of observations of the individual animals and the range size of those animals for the 50% core use or the 95% use ranges (Figure 20). Consequently all ranges were included in subsequent calculations, as long as each range was based on at least 10 observations. Examples of asymptotic* and non-asymptotic seasonal ranges are illustrated in Figure 21. The seasonal core use 50% ranges used by the groups of different origin during 1995 and 1996 are illustrated in Figure 22 while the seasonal 95% use areas used during such time are illustrated in Figure 23.

The smallest mean range size that was calculated for any of the oryx groups of different origin was the 11.8 $km^2 \pm 2.6$ (1SD) used by the animals from the Mahazat as Sayd Protected Area during autumn 1996. The largest mean seasonal range of 167.5 $km^2 \pm 128.8$ was used by the same group of animals during spring 1995. The mean 95% use areas used by the oryx groups of different origin ranged between 103.6 $km^2 \pm 93.7$ as used by the Mahazat as Sayd animals during the winter of 1996, to the range of 1824.2 $km^2 \pm 2266.4$ as used by the C-generation animals the spring of 1995. The large standard deviations associated with these mean range size values are indicative of the large degree of variation observed in the range use patterns of the individual animals within each of the groups of different origin. For example, the seasonal 50% core use ranges used by the individual animals within the groups of different origin ranged between 1.1 (n=15 observations) and 493.0 km^2 (n=30 observations) during the monitoring period of 2 years.

Based on the 50% core use areas, the C-generation oryx and the animals from the Mahazat as Sayd Protected Area used their largest mean seasonal ranges during spring in 1995 and 1996. In contrast, the B-generation animals used a mean seasonal range of 20.8 km^2 during spring of 1995, while their mean summer range was calculated as 68.7 km^2 during the same year. The small seasonal range used by the B-generation animals during spring of 1995 is partly attributed to the small sample size, and partly to the fact that one of the animals was an adult male. This male initially stayed in close proximity of the pre-release enclosures – an area where he was often observed - thereby contributing extensively to the small range size during spring 1995. At the 95% range use level, the pattern in terms of mean range size per season was clear during 1995, when each of the oryx groups of different origin used their largest seasonal range during spring. During 1996, however, the oryx groups of different origin used their largest mean 95% use areas during either spring or autumn. In such cases no significant difference existed between the mean 95% ranges used by a particular group of oryxes in spring and autumn. A definite decrease in range size was observed from spring to summer for the C-generation oryxes, and for those animals from the Mahazat as Sayd Protected Area, before increasing again from summer to autumn. These differences were often significant (Table 4) and occurred during both years of the study period. The fact that the B-generation oryxes exhibited a different, ill-defined range use pattern during this time is thought to be due to the small sample sizes associated with this group of oryx. Due to these small sample sizes, the differences between the mean range sizes used by the B-generation oryxes during summer and autumn could not be calculated for 1996, as too few observations were made of the majority of B-generation oryxes during autumn.

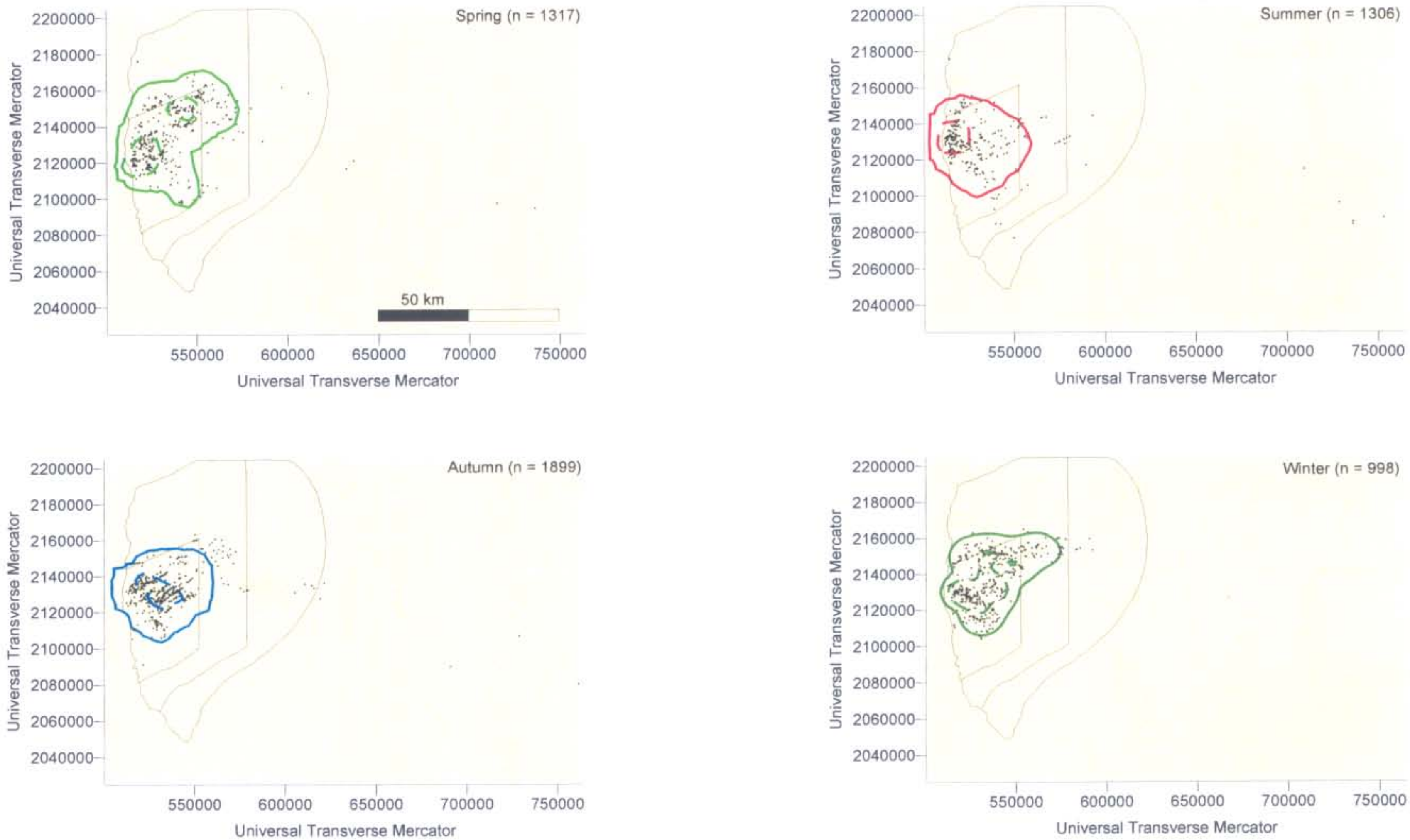


Figure 17: The seasonal distribution of all the Arabian oryx observations made in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the study period from March 1995 to February 1997. The seasonal ranges based on the 50% core use (dashed line) and the 95% use (solid line) Kernel analysis are also indicated.

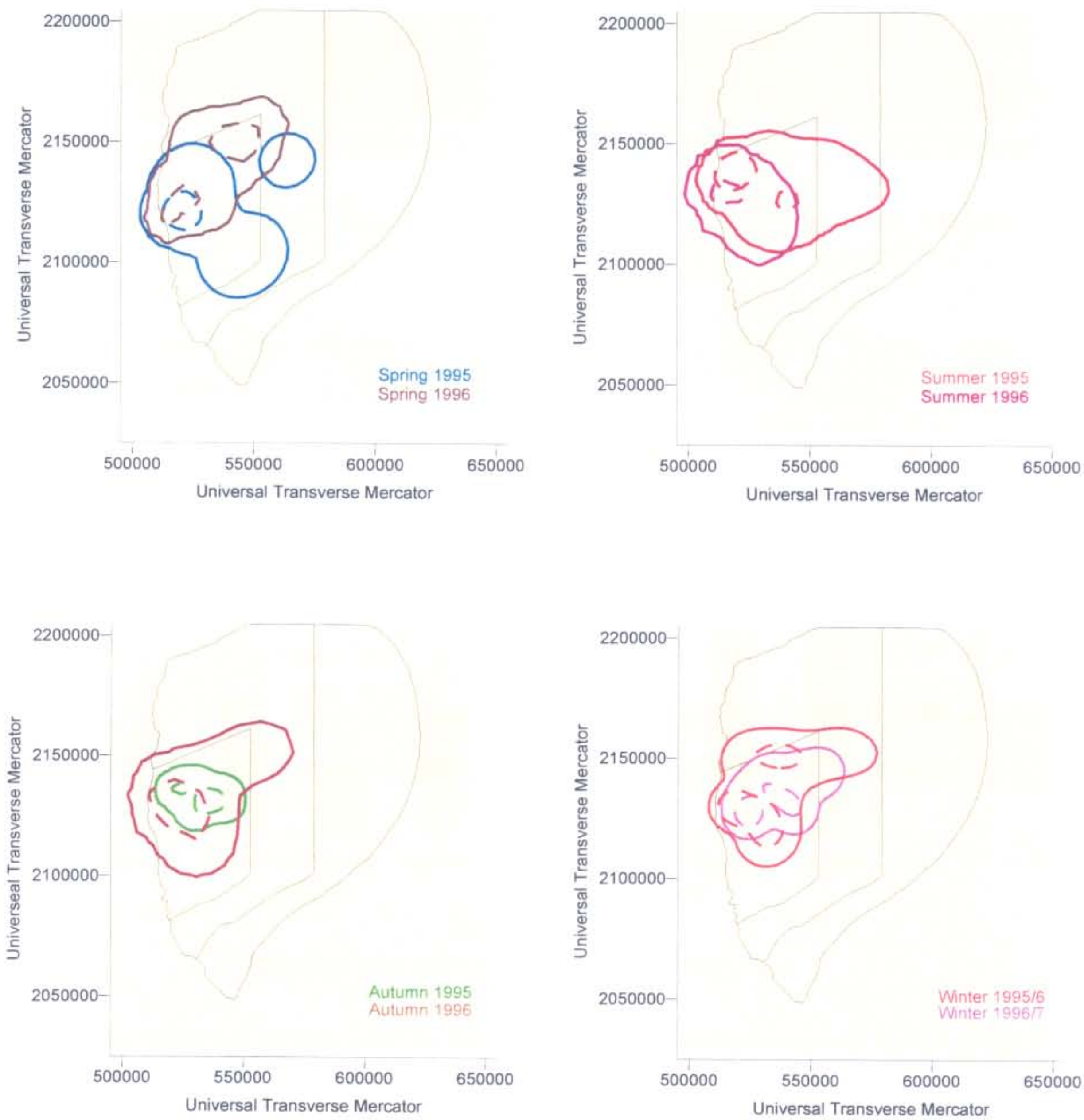


Figure 18: The annual seasonal ranges used by the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the study period from March 1995 to February 1997. The 50% core use areas are represented by the dashed lines and the 95% use areas by the solid lines.

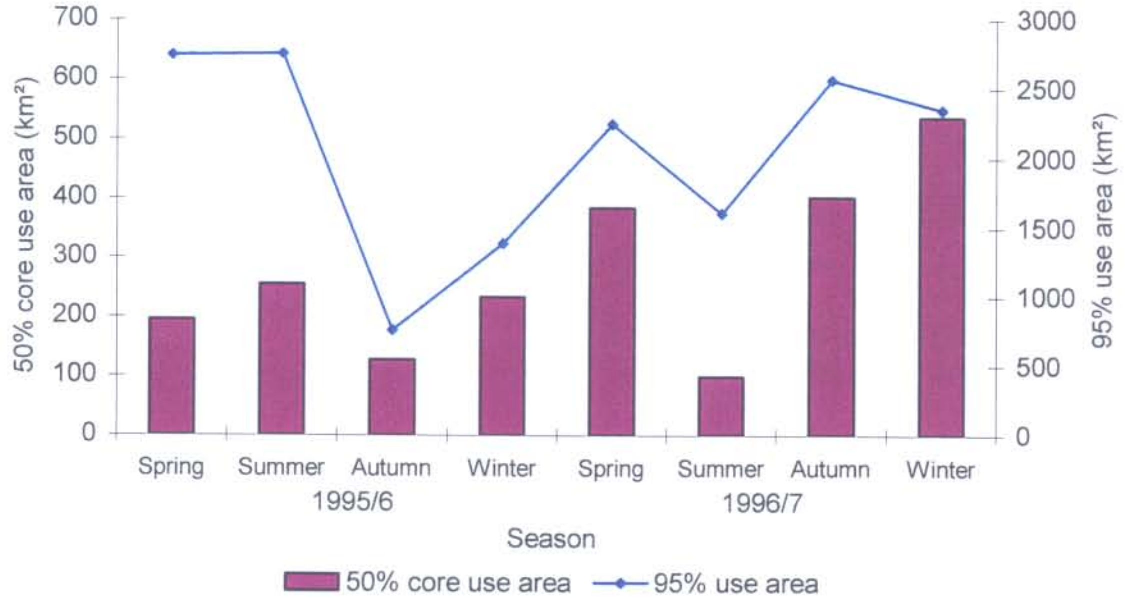
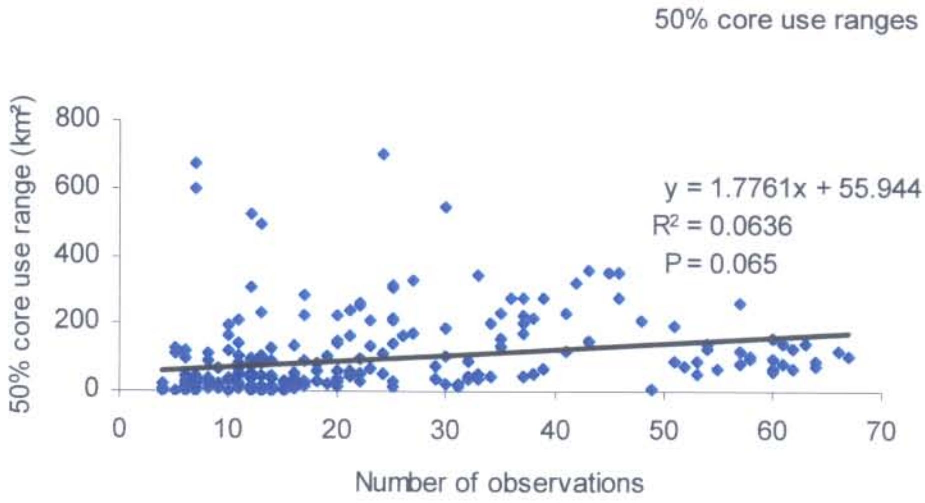


Figure 19: The seasonal ranges used by the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.



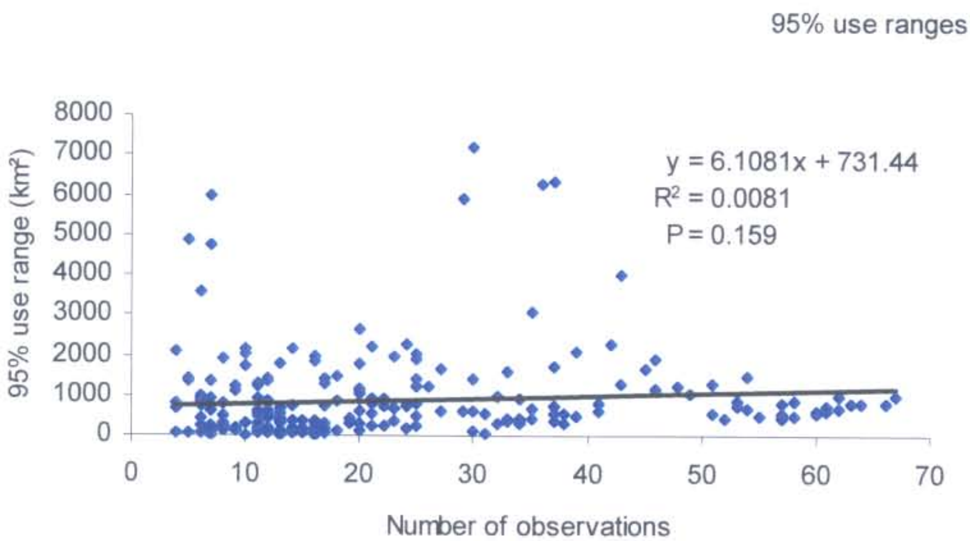


Figure 20: The relationship between the increasing number of observations and the 50% core use and 95% use range sizes of individual Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. The data are pooled for all individuals and all seasons.

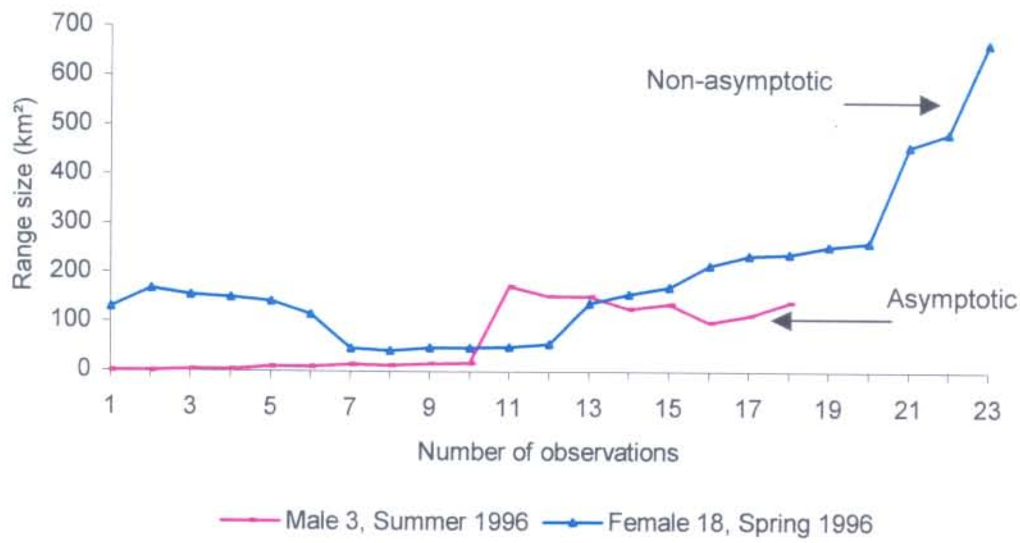


Figure 21: The relationship between the increasing number of observations of a particular Arabian oryx and the range size of that animal, as calculated through incremental area analysis, to illustrate the difference between the asymptotic and non-asymptotic ranges.

Table 2: The mean seasonal 50% core use and 95% use range sizes (km²) of the Arabian oryx groups of different origin with and without those ranges which are not asymptotic, as calculated for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. N column indicates the number of ranges.

GENERATION OR ORIGIN	YEAR	SEASON	N	MEAN RANGE		ASYMPTOTIC RANGES AT		MEAN RANGE		P-VALUE	
				50%	95%	50%	95%	50%	95%	50%	95%
B-generation	1995	Spring	2	20.8	1629.7	0	2	-	1629.7	-	-
		Summer	3	68.7	463.3	3	3	68.7	463.3	-	-
		Autumn	3	62.8	448.0	3	3	62.8	448.0	-	-
		Winter	3	24.4	424.1	3	1	24.4	-	-	-
	1996	Spring	2	162.2	713.9	2	2	162.2	713.9	-	-
		Summer	2	74.5	268.4	2	2	74.5	268.4	-	-
		Autumn	0	-	-	0	0	-	-	-	-
		Winter	2	63.0	530.7	1	2	-	530.7	-	-
C-generation	1995	Spring	16	112.7	1824.2	5	16	168.8	1824.2	0.291	-
		Summer	14	49.7	559.4	14	14	49.7	559.4	-	-
		Autumn	21	78.0	1288.8	17	19	78.9	1330.9	0.462	0.473
		Winter	20	72.4	398.0	10	13	66.0	520.9	0.401	0.253
	1996	Spring	35	77.4	671.5	35	35	77.4	671.5	-	-
		Summer	42	19.6	205.7	35	39	15.4	205.0	0.142	0.492
		Autumn	7	51.9	700.9	7	7	51.9	700.9	-	-
		Winter	38	71.7	430.8	27	30	49.4	382.5	0.114	0.345
Mahazat as Sayd Animals	1995	Spring	3	167.5	722.5	1	1	-	-	-	-
		Summer	7	42.6	309.1	7	7	42.6	309.1	-	-
		Autumn	7	64.7	444.2	6	6	63.0	427.9	0.436	0.346
		Winter	5	60.3	522.2	3	3	32.5	683.4	0.238	0.293
	1996	Spring	6	52.7	714.9	4	4	53.8	859.6	0.482	0.247
		Summer	5	19.6	252.1	4	4	18.0	246.3	0.412	0.479
		Autumn	2	11.8	795.3	1	2	-	795.3	-	-
		Winter	3	36.4	103.6	1	3	-	103.6	-	-

Table 3: The mean seasonal 50% core use and 95% use range sizes (km²) of the male and female Arabian oryxes with and without those ranges which are not asymptotic, as calculated for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. N column indicates the number of ranges.

GENDER	YEAR	SEASON	N	MEAN RANGE		ASYMPTOTIC RANGES AT		MEAN RANGE		P-VALUE	
				50%	95%	50%	95%	50%	95%	50%	95%
Male oryx	1995	Spring	10	104.9	1604.0	4	10	165.3	1604.0	0.331	-
		Summer	11	59.2	676.4	11	11	59.2	676.4	-	-
		Autumn	13	76.9	901.2	10	13	78.7	901.2	0.442	-
		Winter	12	79.9	515.3	7	8	64.1	657.5	0.323	0.307
	1996	Spring	20	75.3	602.6	20	20	75.3	602.6	-	-
		Summer	18	17.3	208.3	16	16	15.7	222.5	0.367	0.416
		Autumn	2	68.2	1006.7	2	2	68.2	1006.7	-	-
		Winter	16	83.6	413.8	12	14	61.9	435.3	0.275	0.448
Female oryx	1995	Spring	11	118.0	1688.6	2	9	101.2	1841.7	0.417	0.433
		Summer	13	42.3	303.4	13	13	42.3	303.4	-	-
		Autumn	18	71.1	1100.2	16	15	70.1	1165.6	0.450	0.460
		Winter	16	54.1	353.8	9	9	42.4	433.7	0.281	0.275
	1996	Spring	24	80.4	751.6	22	22	83.2	781.3	0.431	0.429
		Summer	31	24.5	215.7	25	29	20.4	205.4	0.262	0.374
		Autumn	7	35.8	640.5	6	7	39.5	640.5	0.452	-
		Winter	27	60.0	411.8	17	21	39.0	321.5	0.089	0.266

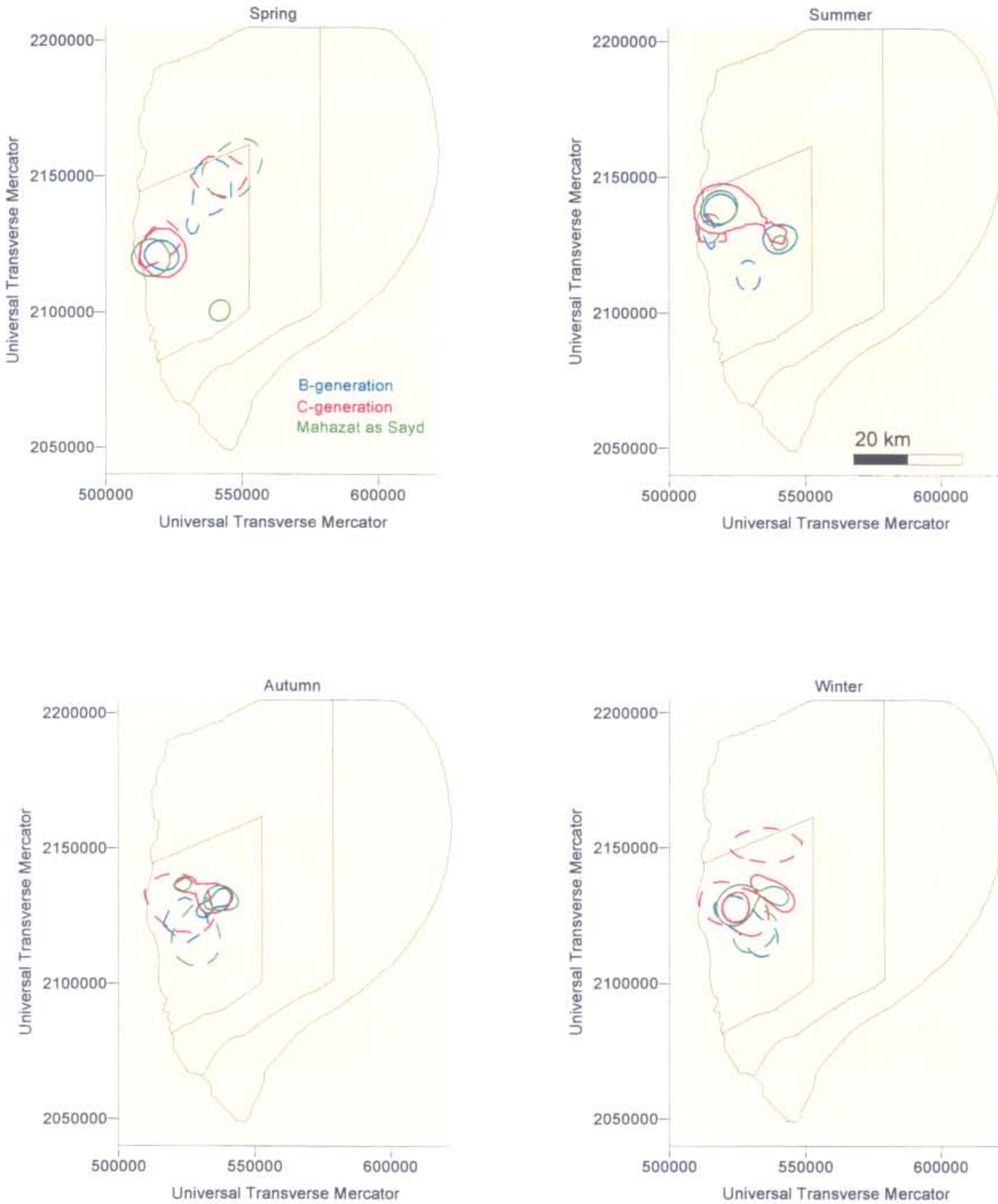


Figure 22: The seasonal 50% core use areas for 1995/6 (solid lines) and 1996/7 (dashed lines) of Arabian oryxes of different origin, reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

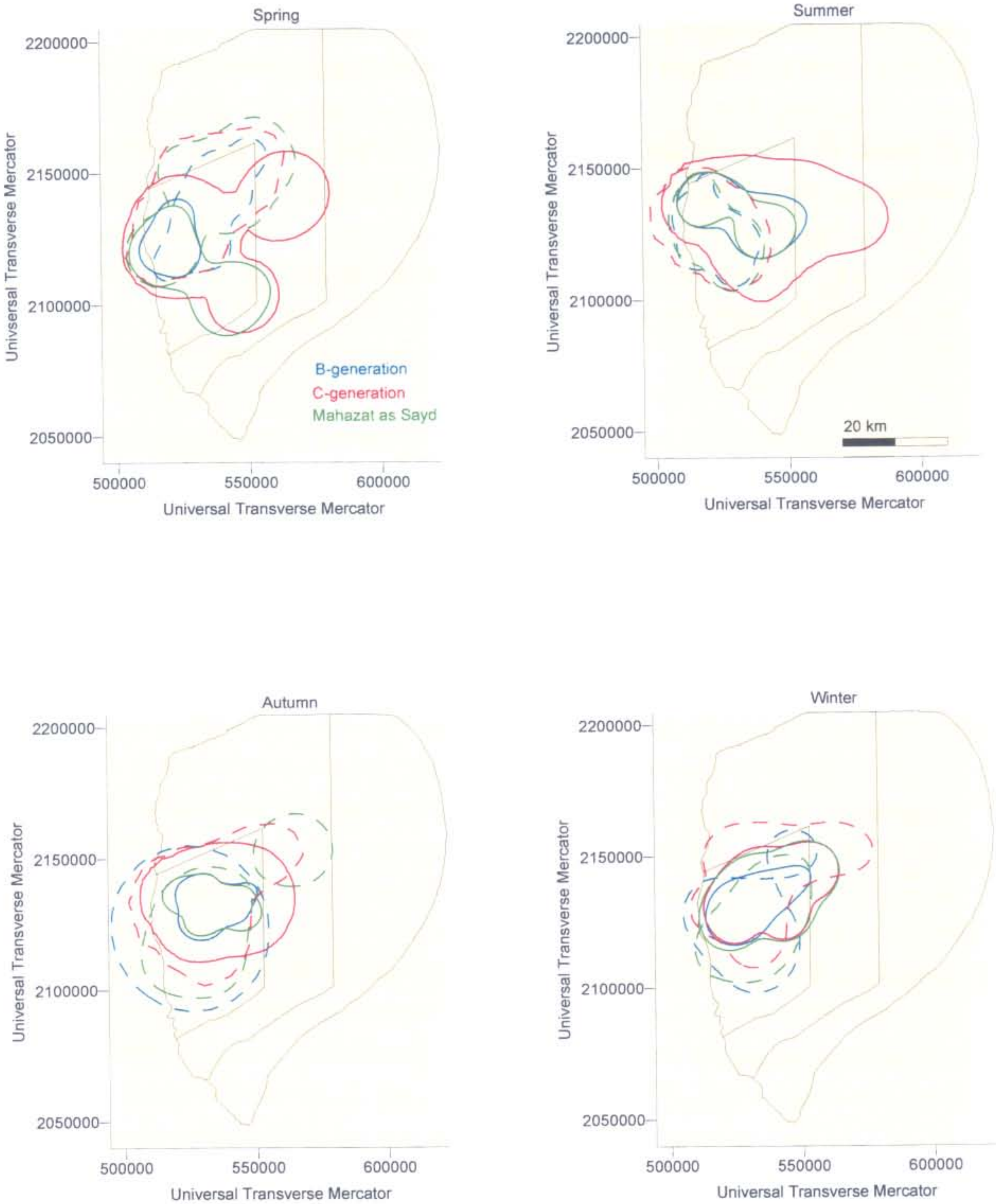


Figure 23: The seasonal 95% use areas for 1995/6 (solid lines) and 1996/7 (dashed lines) of Arabian oryxes of different origin, reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

The mean seasonal ranges used by the Arabian oryx groups of different origin showed significant changes in size between 1995 and 1996 (Table 5). The general trend was for the 1996 seasonal ranges to be smaller than that used during the same season of 1995. The B-generation oryx were the only group to show significant increases in their mean seasonal range sizes from 1995 to 1996. These increases in the mean range sizes for the B-generation oryxes were in the 50% core use areas, and were observed during spring and winter. As before, the different pattern in terms of range use as shown by the B-generation oryxes could probably be attributed to the small number of B-generation oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area, and the subsequent small sample sizes. The differences in the mean autumn ranges of the B-generation oryxes during 1995 and 1996 could not be calculated due to too few observations of these animals during autumn 1996.

Most interesting, though, were the decreases in the mean 50% core use areas and the 95% use areas used during summer by the C-generation oryx and the animals from the Mahazat as Sayd Protected Area from 1995 to 1996. The decrease in the 50% core use areas from summer 1995 to summer 1996 was significant for both the C-generation animals and those oryx from the Mahazat as Sayd Protected Area (Table 5). The decrease in the 95% use areas between the summer of 1995 and that of 1996 was only significant for the C-generation oryxes.

No clear pattern could be found between the mean seasonal range sizes of the male and the female oryxes during the study period. The mean seasonal ranges of the oryx males were, for example, not consistently larger or smaller than those used by the oryx females during the same seasons. For the oryx females, the smallest mean 50% core use and 95% use areas were recorded during the summer months of 1995 and 1996. A similar pattern in the 50% core use areas was observed for the oryx males. The smallest mean 95% use areas, as used by the oryx males in 1995 and 1996 was recorded during autumn and summer respectively. There were no significant differences between the mean seasonal ranges used by the male and female oryxes for either the 50% core use or the 95% use seasonal ranges during any season and year, with the exception of the mean 95% use ranges during summer 1995. During this season the mean seasonal 95% use range used by the oryx females was significantly smaller ($t = 1.87$, $df = 11$, $P = 0.044$) than the mean 95% use range of the Arabian oryx males during the same season. The reasons for this are not clear.

In the Mahazat as Sayd Protected Area it has been reported that the ranges used by the female Arabian oryxes tend to be larger than those used by the males (Van Heesnik & Ismail 2000). This difference was attributed to the higher nutritional demands of the females during pregnancy and lactation. In Southern Africa's Kgalagadi Transfrontier Park, Knight (1991) concluded that

Table 4: The mean seasonal range sizes (km²) calculated for Arabian oryx groups of different origin during the different seasons of 1995 and 1996, as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Only those ranges where significant differences were recorded are tabulated.

ORYX GROUP	YEAR	COMPARISONS MADE				RANGE	t-TEST	D.F.	P-
		Season	Range	Season	Range	USE			VALUE
B-generation	1995	Spring	20.8	Autumn	62.8	50%	3.18	3	0.025
	1995	Autumn	62.8	Winter	24.4	50%	2.73	4	0.026
	1996	Spring	162.2	Winter	63.6	50%	26.91	1	0.012
C-generation	1995	Spring	112.7	Summer	49.7	50%	2.06	18	0.027
	1995	Summer	49.7	Autumn	78.0	50%	2.63	26	0.007
	1995	Spring	1824.2	Summer	559.4	95%	2.15	17	0.023
	1995	Spring	1824.2	Winter	398.0	95%	2.47	16	0.012
	1995	Autumn	1288.8	Winter	398.0	95%	2.05	22	0.026
	1996	Spring	77.4	Summer	19.6	50%	5.88	44	0.000
	1996	Summer	19.6	Winter	71.7	50%	3.27	41	0.001
	1996	Spring	671.5	Summer	205.7	95%	5.12	39	0.000
	1996	Spring	671.5	Winter	430.8	95%	2.03	70	0.023
	1996	Summer	205.7	Winter	430.8	95%	2.72	43	0.005
Mahazat as Sayd Animals	1995	Summer	42.6	Autumn	64.7	50%	2.81	11	0.008
	1996	Spring	52.7	Autumn	11.8	50%	3.30	5	0.011
	1996	Spring	52.7	Summer	19.6	50%	2.54	6	0.022
	1996	Spring	714.9	Summer	252.1	95%	2.91	7	0.011
	1996	Spring	714.9	Winter	103.6	95%	3.94	6	0.004

Table 5: The mean seasonal range sizes (km²) calculated for the Arabian oryx groups of different origin in consecutive years, as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Significant differences are indicated in yellow.

ORYX GROUP	SEASON	RANGE AREA 1995	RANGE AREA 1996	RANGE USE	t-TEST	D.F.	P-VALUE
B-generation	Spring	20.8	162.2	50%	14.35	1	0.022
		1629.7	713.9	95%	0.60	1	0.327
	Summer	68.7	74.5	50%	0.16	2	0.443
		463.3	268.4	95%	0.91	3	0.915
	Autumn	62.8	*	50%	-	-	-
		448.0	*	95%	-	-	-
	Winter	24.4	63.0	50%	3.74	2	0.030
		424.1	530.7	95%	0.46	2	0.344
C-generation	Spring	112.7	77.4	50%	1.15	18	0.133
		1824.2	671.5	95%	2.01	16	0.031
	Summer	49.7	19.6	50%	3.20	17	0.002
		559.4	205.7	95%	2.21	14	0.020
	Autumn	78.0	51.9	50%	1.16	7	0.143
		1288.8	700.9	95%	1.10	23	0.141
	Winter	72.4	71.7	50%	0.04	53	0.486
		398.0	430.9	95%	0.25	40	0.403
Mahazat as Sayd Animals	Spring	167.5	52.7	50%	1.52	2	0.134
		722.5	714.9	95%	0.02	3	0.491
	Summer	42.6	19.6	50%	3.71	10	0.002
		309.1	252.1	95%	0.54	10	0.302
	Autumn	64.7	11.8	50%	7.82	7	0.000
		444.2	795.3	95%	0.46	1	0.362
	Winter	60.3	36.4	50%	0.67	5	0.266
		522.2	103.6	95%	2.33	5	0.034

* No observations of these animals were made during this season

there was no significant difference between the size of the mean seasonal ranges used by male and female gemsbok, or those used by the male and female blue wildebeest.

The ranging behaviour of the male and female oryxes in the present study is, however, still developing. It is therefore likely that similar patterns to that described by Van Heesnik and Ismail (2000) could develop. For example, Tear (1992) suggested that the influence that age and sex differences has on range use patterns develops over time. In comparing the range use of male and female oryxes in Oman in two distinct periods before and after 1986, it was found that before 1986 the male oryxes used larger monthly areas than did the females, while the reverse was true for the period after 1986. This change in range use patterns developed because of a shift in the social system because more males may have become territorial as a result of the many smaller herds that were being established (Tear 1992).

In the present study the oryx males showed no clear pattern in terms of their mean seasonal range sizes during 1995 and 1996. During 1995 the largest mean 50% core use area for the male oryxes was recorded during spring. During 1996, however, the largest mean 50% core use seasonal range for this group was recorded during winter. There were no significant differences in the mean seasonal 50% core use areas of male oryxes ($F = 0.57$, $df = 3$, $P = 0.639$) during 1995. During 1996, however, significant ($F = 2.73$, $df = 3$, $P = 0.053$) differences were found in the mean seasonal 50% core use areas of male oryxes. During 1996 the mean 50% core use area for oryx males during summer was significantly smaller than both the mean winter and spring 50% core use areas (Table 6). The mean seasonal 50% core use areas of the oryx females differed significantly during 1995 ($F = 5.49$, $df = 3$, $P = 0.002$) and 1996 ($F = 6.14$, $df = 3$, $P = 0.001$). The largest mean seasonal 50% core use range of female oryxes in 1995 was the 118.0 km^2 range, that was found during spring. This range was significantly larger than the mean ranges calculated for the oryx females during summer, autumn and winter 1995. The mean seasonal 50% core use area recorded for the oryx females during summer 1995 was smaller than any of the other mean 50% core use areas of that year, and significantly so when compared to autumn of that year. During 1996 the largest mean seasonal 50% core use area for female oryxes were again recorded during spring. This mean range of 80.5 km^2 was significantly larger than the mean ranges used by the oryx females during the summer and autumn of that year. In addition, the mean summer 50% core use range of the oryx females was significantly smaller than the mean 50% core use range of this group during winter.

The mean 95% use ranges of the oryx males also showed no clear pattern during 1995 and 1996. The mean seasonal 95% use areas used by the oryx males did not differ significantly during 1995 ($F = 1.21$, $df = 3$, $P = 0.319$). Significant differences were, however, found for this group during 1996 ($F = 5.19$, $df = 3$, $P = 0.003$). During the latter year the mean 95% use range used by the Arabian oryx males during summer was significantly smaller than that used by the same group of animals during spring and winter. The oryx females showed significant differences in their mean seasonal 95% ranges during both 1995 ($F = 3.37$, $df = 3$, $P = 0.025$) and 1996 ($F = 6.39$, $df = 3$, $P = 0.001$). The largest mean 95% use area recorded for the oryx females during 1995 was during the spring. This range of 1688.6 km^2 was significantly larger than that recorded for the females during either summer or winter of the same year. A similar pattern was observed during 1996. The largest mean seasonal 95% range use of oryx females during 1996 was again during the spring and it was significantly larger than that used by the same group during the summer and winter. In addition, the mean 95% use of range in the summer by the females was significantly smaller than the area used by those females during the winter of 1996 (Table 6).

The mean seasonal 95% range use areas of the Arabian oryx females in this study are larger than the ranges used by the fringe-eared oryx. In East Africa it has been found that the female and non-territorial male fringe-eared oryxes use ranges of between 250 and 300 km^2 (Wacher 1986). In the Kgalagadi Transfrontier Park in southern Africa the largest seasonal ranges used by the female gemsbok were 287 km^2 during winter in a period of drought (Knight 1991). The fact that the 95% use ranges of the Arabian oryx females during the spring and autumn are generally larger than those of the other oryx types are indicative of the lower rainfall in the 'Uruq Bani Ma'arid Protected Area, and the known relationship between rainfall and primary productivity (Coe *et. al.* 1976).

The most striking characteristic of the range use patterns of the Arabian oryx males and females is the definite decrease in the size of the mean ranges used by the animals from spring to summer. This decrease in the mean range size from spring to summer and the subsequent increase from summer into autumn can be seen in both the 50% core use areas and the 95% use ranges. This pattern has also been observed in the Arabian oryx groups of different origin. The observed changes in the mean seasonal range sizes of these oryx groups is thought to be due to a combination of, factors. Firstly there is a definite shift in the ranges used by the different groups of animals as indicated by their mean seasonal positions (Figure 24). This shift in range is characterised by a westward movement from spring into summer, which is again followed by an eastward movement away from the escarpment during autumn. Secondly there are significant differences in the mean distances moved by the Arabian oryxes ($F = 15.69$, $df = 3$, $P = 0.000$) during the different seasons. These differences are characterised by a decreased mobility of the animals during summer, when compared with the other seasons (Figure 25).

Table 6: A comparison of the mean seasonal range sizes (km^2) of male and female Arabian oryxes during the different seasons of 1995 and 1996, as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Only those ranges that differed significantly are tabulated.

GENDER	YEAR	COMPARISONS MADE				RANGE USE	t-TEST	D.F.	P-VALUE
		Season	Range	Season	Range				
Females	1995	Spring	118.0	Summer	42.2	50%	3.06	12	0.005
		Spring	118.0	Autumn	71.1	50%	1.92	11	0.040
		Spring	118.0	Winter	54.1	50%	2.29	17	0.017
		Summer	42.2	Autumn	71.1	50%	3.31	25	0.001
		Spring	1688.6	Summer	303.4	95%	2.44	10	0.017
		Spring	1688.6	Winter	353.8	95%	2.34	10	0.021
		Summer	303.4	Autumn	1100.2	95%	1.92	17	0.036
		Autumn	1100.2	Winter	353.8	95%	1.78	18	0.046
Males	1996	Winter	83.6	Summer	17.3	50%	2.15	15	0.024
		Summer	17.3	Spring	75.2	50%	4.46	22	0.000
Females	1996	Spring	80.5	Summer	24.5	50%	4.71	34	0.000
		Spring	80.5	Autumn	35.8	50%	2.00	10	0.036
		Summer	24.5	Winter	60.0	50%	2.62	35	0.006
		Spring	751.6	Summer	215.7	95%	4.64	25	0.000
		Spring	751.6	Winter	411.8	95%	2.28	47	0.013
		Summer	215.7	Winter	411.8	95%	1.98	29	0.028

The mean distance moved by the oryxes in successive observations (pooled for 1-10 days apart) during summer was 5.4 km. This was significantly smaller than that observed for the animals during spring ($t = 5.85$, $df = 2001$, $P = 0.000$), autumn ($t = 2.28$, $df = 1838$, $P = 0.001$) and winter ($t = 3.54$, $df = 1473$, $P = 0.000$). This decreased mobility of the Arabian oryxes during summer corresponds well with the decrease in the diurnal activity observed elsewhere (Chapter 8) and is attributed to the ambient temperature and the subhabitat structure in the summer ranges (Chapter 6).

It would therefore seem that the general trend in range use, as observed during the study period, is one where the animals range widely during spring. During the hot summer months, however, the majority of the animals move westwards, back to the escarpment area where trees and especially shrubs, which provide sufficient shade, are freely available. In addition the animals also become less mobile in the summer, in that they do not range as widely as they do during the other seasons. Consequently the range sizes are smaller during summer. The fact that the animals once again roam over larger areas after summer is possibly triggered by lower temperatures and may also be due to decreasing food availability in the escarpment areas, and the response of vegetation in other subhabitats to the changing temperatures (Chapter 6).

The ranges used by the different groups of animals during spring are, however, exaggerated during both years. This is due to the fact that five of the six releases during the 2-year study period took place during spring. Earlier it has also been shown that there is an initial quick dispersal from the release site and that a positive, linear relationship initially exists between time since release and the distance of the animals from the release site. Nevertheless, the decrease in the size of the ranges used from spring to summer probably is a true reflection of the ranging behaviour of the animals.

In general, the mean seasonal ranges used by the Arabian oryx males and females during 1996 were smaller than those used by the same group of animals during the same period of the preceding year (Table 7). Significant decreases in the mean seasonal ranges used by the Arabian oryx males and females were, however, only observed when the respective ranges used during summer 1995 were compared with those used during summer 1996. This has also been observed earlier when dealing with the oryx groups of different origin. This observed decrease in the mean seasonal range sizes between 1995 and 1996, where sample sizes are of sufficient size, is thought to be due to the experience gained by the animals during their time spent in the wild. In addition, the good environmental conditions during 1996 and further rain in the area then, excluded the necessity for the oryxes to range widely in search of grazing. The latter suggests that the range sizes of the Arabian oryxes decreased due to increased food quantity and quality. This has been shown for the Arabian oryxes in Oman, and particularly for those animals that were found in the areas there where rain occurred (Corp, Spalton & Gorman 1998). A similar response to rainfall has also been reported for both the gemsbok and the blue wildebeest in the Kgalagadi Transfrontier Park of Southern Africa, where ranges generally decreased with increasing rainfall (Knight 1991).

The increasing experience gained by the reintroduced animals since their release into the area enabled the animals to use the area optimally based on their increasing knowledge of the area. As the experience gained increases it is therefore expected that even "better" use of the area will be made in the future. This does not, however, mean ever-smaller seasonal range sizes. Stanley-Price (1989) concluded that the reintroduced Arabian oryx in Oman navigated accurately and that they remembered places, possibly even to the scale of individual trees and grazing areas, after limited experience and exposure. Furthermore the ability to reach a specific destination by different routes showed that the animals were at all times aware of their relative position in their habitat. Another possibility is that separations of some individuals from a given herd later in the study period resulted in a search for other oryxes in collectively known areas, as was the case in Oman (Stanley Price 1989). This may indicate that factors such as experience gained and greater group stability probably acted in unison.

Seasonal range fidelity

The seasonal 50% core use area fidelity of the Arabian oryxes of different origin ranged between 0 and 46% in consecutive seasons (Table 8). There were, however, no significant differences in the seasonal range use fidelity of these groups of different origin, based on their seasonal 50% core use areas.

Based on the seasonal 95% use ranges of the Arabian oryx groups of different origin, significant differences ($F = 4.360$, $df = 2$, $P = 0.025$) were found in their mean seasonal range fidelity when comparing their range during autumn 1995 with that of winter 1995/6. During this time it was found that the mean seasonal range fidelity of the C-generation oryxes were significantly higher ($t = 4.05$, $df = 13$, $P = 0.001$) than that of the animals from the Mahazat as Sayd Protected Area. There were no other significant differences in the mean seasonal range overlap as displayed by any of the oryx groups of different origin and during any of the seasons.

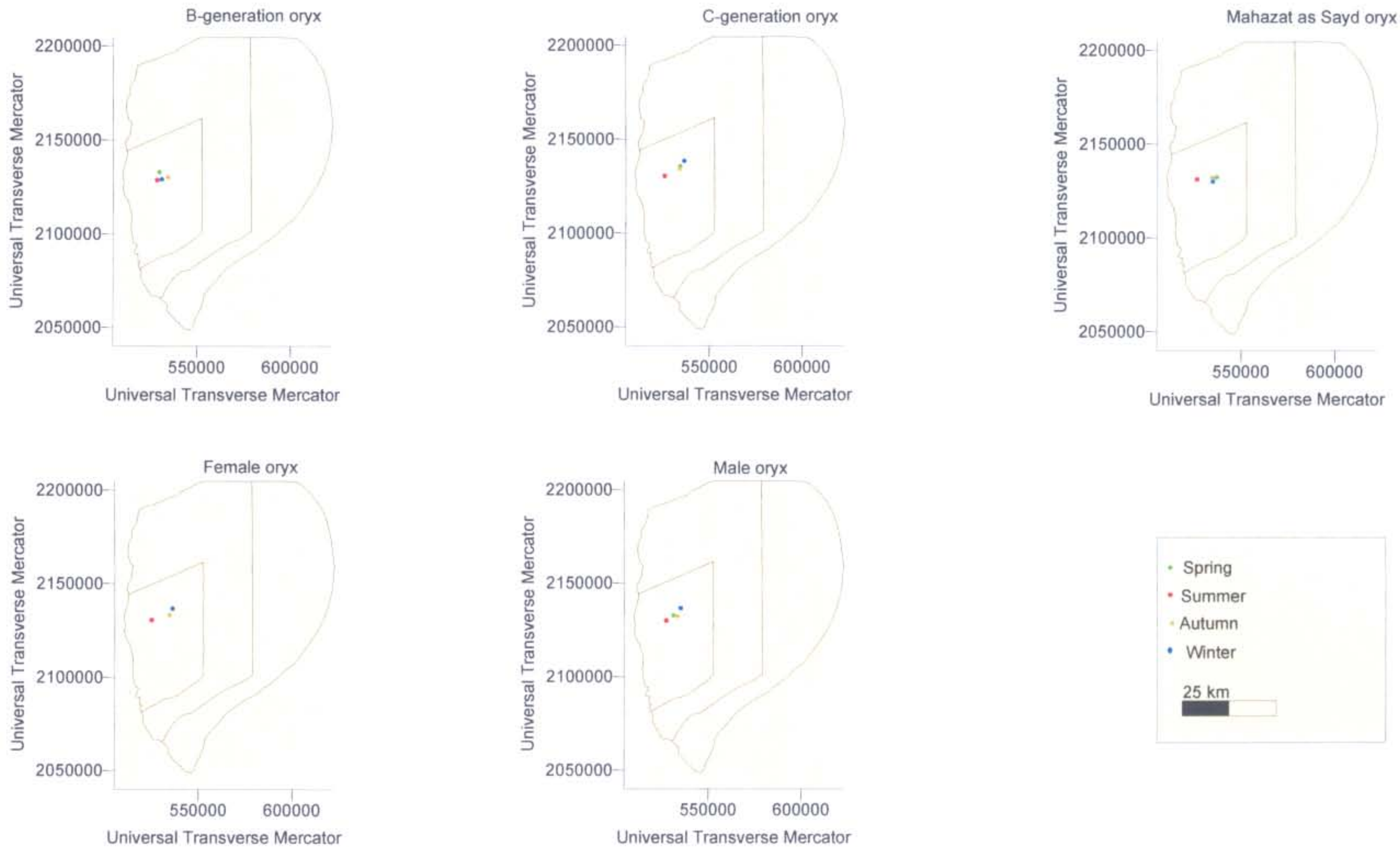


Figure 24: The mean seasonal distribution of different groups of oryx, combined over the 2-year study period as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

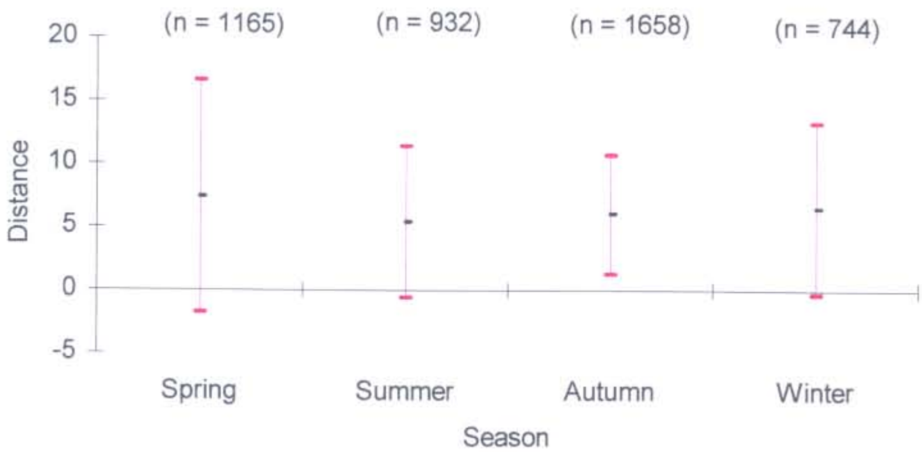


Figure 25: The mean (± 1 SD) seasonal distances (km) moved by the reintroduced Arabian oryxes in successive observations, 1-10 days apart, as observed in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. All the data are pooled across the years.

Table 7: The mean seasonal range sizes (km²) calculated for Arabian oryx males and females in consecutive years, as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Significant differences are indicated in yellow.

GENDER	SEASONS COMPARED	RANGE AREA 1995	RANGE AREA 1996	RANGE USE	t - TEST	D.F.	P-VALUE
Male oryx	Spring	104.9	75.2	50%	0.60	10	0.280
		1604.0	602.6	95%	1.34	9	0.107
	Summer	59.2	17.3	50%	4.09	13	0.001
		676.4	208.3	95%	2.34	11	0.019
	Autumn	76.9	68.2	50%	0.18	1	0.443
		901.2	1006.7	95%	0.13	2	0.455
	Winter	79.9	83.6	50%	0.10	24	0.459
		515.3	413.8	95%	0.52	20	0.304
Female oryx	Spring	118.0	80.5	50%	1.44	14	0.086
		1688.6	751.6	95%	1.62	11	0.067
	Summer	42.2	24.5	50%	2.07	26	0.025
		303.4	215.7	95%	1.77	19	0.047
	Autumn	71.1	35.8	50%	1.74	7	0.063
		1100.2	640.5	95%	0.87	21	0.196
	Winter	54.1	60.0	50%	0.31	35	0.379
		353.8	411.8	95%	0.48	41	0.316

The female oryxes displayed both the lowest and the highest levels of mean seasonal range fidelity when comparing the mean range overlap of male and female oryxes in consecutive seasons (Table 9). Between spring and summer 1995 there was no overlap in the 50% core use areas of the female oryxes. Between autumn 1996 and winter 1996/7, however, the mean range fidelity of this group of animals was 35.8%. The mean seasonal range fidelity of the male oryxes ranged between 0.2% and 20.6%, for the 50% core use areas. There were no significant differences in the mean seasonal range fidelity, of the 50% core use areas, of the oryx males when compared to that of the oryx females. For the 95% use seasonal ranges, the highest mean range fidelity for both the male and female oryxes were recorded from autumn 1995 to winter 1995/6. No significant differences in the mean seasonal range fidelity, of the seasonal 95% use ranges of the male and female oryxes, were recorded. The mean seasonal range overlap based on the seasonal 50% core use areas used by the groups of different origin, during 1995 as compared with 1996 were low, and no significant differences were recorded.

For example, there was no overlap in the 50% core use areas of any of the groups of different origin when comparing the ranges used during summer 1995 with those of summer 1996. This indicates a shift in the core use areas of these groups during summer, from 1995 to 1996. This shift in the core use areas within a season, but between years, was also observed during the other seasons and for all the groups of different origin, although less pronounced. There were significant differences in the mean seasonal range fidelity of the oryx groups of different origin when comparing their 95% use ranges of the same season during consecutive years. The B-generation animals showed significantly ($t = 7.31$, $df = 11$, $P = 0.000$) higher fidelity to their winter range of 1995/6 during 1996/7, than did the C-generation animals to their winter 1995/6 range during winter 1996/7. The mean 95% use range fidelity of the animals from the Mahazat as Sayd Protected Area was also significantly ($t = 2.96$, $df = 2$, $P = 0.012$) larger than that of the C-generation oryxes when comparing the winter 1995/6 and winter 1996/7 ranges.

There was little mean seasonal range overlap for the seasonal 50% core use areas of the male and female oryxes in consecutive years. The male oryxes showed virtually no mean seasonal range overlap (<1.0%) in consecutive years. Although the values were still low, the female oryxes showed slightly higher mean seasonal range fidelity in consecutive years than did the oryx males. Based on the 50% seasonal core use areas, the mean seasonal range fidelity of the Arabian oryx males and females in consecutive years did not differ significantly. Similarly no significant differences were found in the mean seasonal range fidelity of the male and female oryxes, in consecutive years, when looking at the seasonal 95% use

Table 8: The mean seasonal range fidelity of the Arabian oryx groups of different origin reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, from March 1995 to February 1997. Significant differences are indicated in yellow.

SEASONS COMPARED	RANGE USE TYPE	MEAN PERCENTAGE RANGE OVERLAP			F	D.F.	P-VALUE
		B-generation	C-generation	Mahazat as Sayd animals			
Spring 1995 & Summer 1995	50%	0.0	11.1	0.0	-	-	-
Summer 1995 & Autumn 1995	50%	3.2	3.7	12.7	2.390	2	0.115
Autumn 1995 & Winter 1995/6	50%	0.0	13.8	24.3	0.841	2	0.444
Winter 1995/6 & Spring 1996	50%	1.0	2.2	0.0	0.207	2	0.815
Spring 1996 and Summer 1996	50%	6.8	1.3	0.1	1.315	2	0.283
Summer 1996 & Autumn 1996	50%	-	3.2	18.0	2.266	1	0.176
Autumn 1996 & Winter 1996/7	50%	-	28.5	46.0	0.356	1	0.569
Spring 1995 & Summer 1995	95%	45.5	26.5	0.0	0.856	2	0.451
Summer 1995 & Autumn 1995	95%	53.8	44.8	45.2	0.152	2	0.860
Autumn 1995 & Winter 1995/6	95%	55.6	72.1	38.0	4.360	2	0.025
Winter 1995/6 & Spring 1996	95%	48.9	16.3	22.5	1.603	2	3.443
Spring 1996 and Summer 1996	95%	43.9	23.9	27.6	0.363	2	0.699
Summer 1996 & Autumn 1996	95%	-	17.2	52.1	1.798	1	0.222
Autumn 1996 & Winter 1996/7	95%	-	43.7	50.0	0.026	1	0.877
Spring 1995 & Spring 1996	50%	0.0	0.0	33.3	-	-	-
Summer 1995 & Summer 1996	50%	0.0	0.0	0.0	-	-	-
Autumn 1995 & Autumn 1996	50%	-	0.0	14.3	-	-	-
Winter 1995/6 & Winter 1996/7	50%	3.4	0.5	8.5	2.040	2	0.169
Spring 1995 & Spring 1996	95%	43.9	24.0	8.7	0.822	2	0.456
Summer 1995 & Summer 1996	95%	21.3	29.0	27.4	0.050	2	0.951
Autumn 1995 & Autumn 1996	95%	-	30.6	13.5	0.456	1	0.569
Winter 1995/6 & Winter 1996/7	95%	37.1	6.5	51.2	5.534	2	0.018

Table 9: The mean seasonal range fidelity of Arabian oryx males and females reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, from March 1995 to February 1997

SEASONS COMPARED	RANGE USE TYPE	MEAN PERCENTAGE RANGE OVERLAP		t-TEST	D.F.	P-VALUE
		Males	Females			
Spring 1995 & Summer 1995	50%	12.5	0.0	-	-	-
Summer 1995 & Autumn 1995	50%	3.8	8.3	1.153	20	0.263
Autumn 1995 & Winter 1995/6	50%	6.8	18.8	1.362	23	0.186
Winter 1995/6 & Spring 1996	50%	4.0	0.3	0.951	8	0.369
Spring 1996 and Summer 1996	50%	3.2	0.2	1.461	13	0.168
Summer 1996 & Autumn 1996	50%	0.2	8.2	1.451	6	0.197
Autumn 1996 & Winter 1996/7	50%	20.6	35.8	0.606	2	0.606
Spring 1995 & Summer 1995	95%	27.9	17.7	0.480	12	0.640
Summer 1995 & Autumn 1995	95%	46.5	45.6	0.083	16	0.935
Autumn 1995 & Winter 1995/6	95%	61.3	65.1	0.368	21	0.716
Winter 1995/6 & Spring 1996	95%	31.4	13.8	1.378	9	0.201
Spring 1996 and Summer 1996	95%	32.6	20.8	1.020	24	0.320
Summer 1996 & Autumn 1996	95%	6.5	32.0	1.708	7	0.131
Autumn 1996 & Winter 1996/7	95%	50.0	43.7	0.120	1	0.925
Spring 1995 & Spring 1996	50%	0.0	11.1	-	-	-
Summer 1995 & Summer 1996	50%	0.0	0.0	-	-	-
Autumn 1995 & Autumn 1996	50%	-	6.7	-	-	-
Winter 1995/6 & Winter 1996/7	50%	0.1	3.4	1.417	10	0.187
Spring 1995 & Spring 1996	95%	19.6	27.0	0.547	17	0.591
Summer 1995 & Summer 1996	95%	26.9	27.8	0.060	12	0.953
Autumn 1995 & Autumn 1996	95%	-	22	-	-	-
Winter 1995/6 & Winter 1996/7	95%	31	13.1	1.341	10	0.209

ranges as used by these animals during such time. Both the Arabian oryx males and females showed similar levels of seasonal range fidelity in consecutive years. These levels of range fidelity were, however, still low. The lack of significant differences in the mean seasonal range fidelity of the male oryxes when compared to the females is not surprising as the male and female oryxes showed similar patterns of range use throughout this study. It is, however, expected that differences in range use patterns, and consequently range fidelity, between male and female oryxes will be manifested with increasing time in the wild. In Oman, for example, it was found that the influence that age and sex had on range use patterns only developed over time, and that it was likely that these differences involved learning (Tear 1992).

Based on the seasonal ranging behaviour of the oryxes, especially the contraction of the range during summer, it is expected that the greatest seasonal range fidelity will occur during the summers of consecutive years. The fact that this did not happen is indicative of the exploratory phase that the animals find themselves in. It has been suggested that range fidelity in elk *Cervus elaphus* Linnaeus, 1758 may be advantageous due to the knowledge that it provides of the seasonal availability of resources (Edge & Marcum 1985). Due to the highly variable environment of the current study area, conditions are not necessarily similar in the same general area or subhabitat during a particular season in consecutive years or even from one season to another (Chapter 6). As for elk, the shift in the seasonal ranges used by the oryxes and the subsequent low range fidelity observed in the present study is indicative of the adaptability of the oryxes and their flexible social structure, both of which encourage range shift (Shoesmith 1979).

Despite the low levels of seasonal range fidelity shown by the oryxes, the results suggest that the patterns of range use of these animals were closely associated with specific subhabitat features that were preferred and, which are essential to the animals on a seasonal basis. Such seasonal subhabitat preferences indicate that the animals do not use the protected area and the habitat therein in a haphazard way. These seasonal differences in ranging behaviour have also been observed in the fringe-eared oryx (Wacher 1986) and gemsbok (Mills & Retief 1984; van der Walt, *et al.* 1984; Knight 1991), while large-scale seasonal migrations, which are linked to habitat conditions, have been observed in the scimitar-horned oryx (Gillet 1969 In: Wacher 1986). The ways in which the Arabian oryxes use their habitat are further explored in Chapter 6.

Conclusions

During the current study the release of the Arabian oryxes into the wild was characterised by quick dispersal of all of the release groups from the release site. This was primarily due to the good environmental conditions that existed then and the fact that no attempt was made to create release site fidelity amongst these animals. During the first 12 months after release the dispersal of the release groups was characterised by a positive relationship between time spent in the wild and distance from the release site. The distance from the release site increased consistently during this time. After 12 months in the wild the adult male oryxes had dispersed significantly less than did the adult females or the subadult males and females. Nevertheless, the mean dispersal distance of all the groups of oryx in terms of origin, release group and age-and-sex class, stabilised at less than 30 km from the release site after a 1-year period.

The proportion of C-generation animals in the release groups resulted in a positive relationship between time spent in the wild and dispersal distance from the release site. In contrast, the proportion of animals from the Mahazat as Sayd Protected Area in the release groups resulted in a negative correlation between dispersal distance and time spent in the wild, over the entire monitoring period. Neither of these relationships was significant, however. Therefore group of origin seems to be unimportant in influencing the mean dispersal distances of the different release groups when looking at dispersal over the entire monitoring period. The proportion of both male and female oryxes in the release groups resulted in negative correlations between time spent in the wild and dispersal distance during the entire monitoring period. The correlation between the proportion of females in the release groups and the mean dispersal distance over the entire study period explained three times more of the variation than did the correlation between the proportion of males in the release groups and the mean dispersal distance from the release site. Nevertheless no significant differences were found between the proportion of males or females in the different release groups and the mean dispersal distances from the release site of the release groups. The proportion of males and females in the release groups was therefore unimportant in determining dispersal distance from the release site.

The most striking characteristic in the seasonal range use patterns of the oryx groups of different origin and the male and female oryxes is the decrease in the mean seasonal range size from spring to summer, followed by an increase in the mean seasonal range size from summer to autumn. These changes in the mean seasonal range size are associated with a shift in the seasonal ranges of the animals. In addition the animals are less mobile during the summer months than during any of the other seasons.

The mean seasonal ranges used during the second year of the study were smaller than those used during the previous year. This is attributed to rain that fell in the area, but it also suggests that the animals are making increasingly better use of their environment as experience is gained. It further suggests greater group stability during the second year of the study period.

The lowest levels of mean seasonal range fidelity were observed in the seasonal 50% core use areas of all of the oryx groups. Seasonal range fidelity was higher for all groups at the 95% use ranges, but seldom higher than 50% fidelity. The low levels of mean seasonal range fidelity indicate that the reintroduced Arabian oryxes are in an exploratory phase.

The part of the study area that seems to be of primary importance to the reintroduced Arabian oryxes is the wadi-incised escarpment area on the western edge of the 'Uruq Bani Ma'arid Protected Area. Results indicate a definite westwards shift in the ranges of the reintroduced animals during summer. Due to this the summer refuge status of the escarpment area is vital because the wadis there are a major subhabitat for ensuring the survival of the animals in the area.