An ecological study of reintroduced Arabian oryx in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia

By

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ABSTRACT

This study was conducted in the 'Uruq Bani Ma'arid Protected Area, on the western edge of the 'Rub al Khali of the Kingdom of Saudi Arabia. The dispersal of different groups of Arabian oryx *Oryx leucoryx* (Pallas, 1777) was investigated, along with the seasonal range use patterns of the animals. The dispersal distances from the release site stabilised after a period of one year. The animals show seasonal differences in their range use patterns, associated with changes in their mobility. The dynamics of the relationship between the oryxes and their habitat were investigated. The structure and the condition of the vegetation, as well as some climatic variables were important determinants of seasonal habitat use. The diurnal activity patterns of the animals correspond with that characteristic of ungulates generally and the animals showed seasonal changes in their feeding preferences. The productivity of the population was high during the study period, with 34 live births, while six of the reintroduced animals died. Population viability analysis, however, shows that the population is vulnerable over the medium term (100 years) and that management should target the juvenile and especially adult females as they are keys to population growth and recovery.

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CHAPTER 1

INTRODUCTION

The demise of the Arabian oryx *Oryx leucoryx* (Pallas, 1777) in the Arabian Peninsula, and the subsequent rescue effort which led to the reintroduction of the species in Oman in 1982 has been well documented (Chapter 3). This rescue effort and the resulting reintroduction of the Arabian oryx into Oman has been hailed as one of the conservation success stories of the 20th century (Dixon & Jones 1988; Stanley-Price 1989; Spalton 1993).

Developments in Oman during the late 1990's have, however, indicated the susceptibility of such reintroduction projects even after nearly 20 years into a reintroduction project's life-span (Spalton, Lawrence & Brend 1999). If anything, these developments underline the need for involving various sectors, including the local communities in all conservation efforts. It also emphasises the need for long-term monitoring of the reintroduced populations and the establishment of various free-living populations of an animal type within any particular country, given that there are sufficient areas containing enough suitable habitat of sufficient quality for such populations.

The National Commission for Wildlife Conservation and Development (NCWCD) of the Kingdom of Saudi Arabia initiated this study on the reintroduction of the Arabian oryx into the unfenced 'Uruq Bani Ma'arid Protected Area of that Kingdom. This reintroduction was the next step, after a successful captive-breeding programme, for the National Commission for Wildlife Conservation and Development in fulfilling its mandate as specified by Royal Decree. This decree directed them to develop and restore the wildlife and natural resources of the Kingdom of Saudi Arabia (Joubert 1994). If successful, this reintroduction would give rise to only the second free-living Arabian oryx population in the Arabian Peninsula, and the only such population within the Kingdom of Saudi Arabia.

Concurrently with the Arabian oryx reintroduction project there were also reintroductions of two of the Arabian gazelle types into the 'Uruq Bani Ma'arid Protected Area. These reintroductions included in excess of 200 sand gazelles *Gazella subgutturosa marica* (Güldenstaedt, 1780) and more than 20 mountain gazelles *Gazella gazella gazella* (Pallas, 1766), thereby confirming the National Commission for Wildlife Conservation and Development's commitment to restoring the Kingdom's wildlife to its former glory.

The reintroduction of the Arabian oryx into the 'Uruq Bani Ma'arid Protected Area was not a mere replication of the process in Oman. Although much was learned from the Oman reintroduction, the approach taken in the present study was not to make any assumptions in advance on aspects of Arabian oryx ecology. No assumptions were for example made on the social organisation and the herd composition or the size of the "ideal" Arabian oryx herd. In addition no management action was taken to influence group composition, cohesion, dispersal from the release site, or even range size.

The title of this thesis states that it is an ecological study. This title is quite broad. In finalising the title the author was guided by the immediate needs and concerns of the National Commission for Wildlife Conservation and Development as far as the reintroduction of the Arabian oryxes was concerned. The fact that such a large proportion of the animals was fitted with radio-collars (Chapter 3) contributed to the collection of data on a wide range of topics. The aim of this study was not to re-write the books on Arabian oryx ecology. Rather, the aim was to assess the performance of a group of captive-bred animals, including some hand-reared individuals, that were mixed with wild born individuals from the Mahazat as Sayd Protected Area and then were reintroduced into their native, hyper-arid habitat in the Kingdom of Saudi Arabia.

In the following chapters some background information on the Arabian oryx and the Kingdom of Saudi Arabia are presented first, as it is considered essential for understanding the ecology of the species fully. The main part of this thesis, however, deals with the various aspects of the ecology of the reintroduced Arabian oryxes and includes chapters on the Arabian oryx range use, habitat use, feeding, activity, and productivity. In addition, population viability analysis is used to assess the reintroduction process and to predict the future of this population, given the assumptions made. Some management recommendations aimed at the effective management of the Arabian oryx in the Kingdom of Saudi Arabia are also made.

CHAPTER 2

STUDY AREA

Location and topography

The Kingdom of Saudi Arabia has a surface area of approximately 2.2 million km², and it occupies 80% of the surface area of the Arabian Peninsula. The country extends from 32° 15' N on the Jordanian border to 16° 30' S on the Yemen border. In the east and west the Arabian Gulf and the Red Sea respectively (Child & Grainger 1990) bound it.

The Arabian Peninsula is a huge crustal plate that is composed of ancient sedimentary and volcanic rocks. During Precambrian*[1] times long before the formation of the Red Sea, the Arabian Peninsula was still attached to Africa as part of the African (Nubian) Shield. Some 30 million years ago in the middle Tertiary* Period the Arabian plate split away from the African Shield along the Red Sea Trough. This separation of Arabia from Africa was accompanied by extensive volcanism along the western edge of the Arabian Peninsula (Chapman 1978a).

Today the Arabian Peninsula can be divided into two structural provinces. A western province, known as the Arabian Shield, is part of the Precambrian crustal plate and is composed of igneous and metamorphic rocks. Volcanism was widespread in western Arabia from the Tertiary Period to the recent past. Floods of basic lava poured out onto the surface of the shield (Chapman 1978a). The Arabian Shelf is the second of the two structural provinces. It lies east of the Arabian Shield and forms about two-thirds of the peninsula. Its foundation is part of the same Precambrian plate that makes up the Arabian Shield. When the crystalline rocks of the eastern extension of the Shield tilted progressively towards the northeast, they were inundated by a series of shallow seas that led to successive sedimentary deposits. These sedimentary rocks mostly consist of limestone, sandstone and shale, which dip gently eastward into a number of sedimentary basins ranging in age from the Cambrian* to the Pliocene* (Child & Grainger 1990).

[1] * Refers to terms that are included in the glossary.

Biogeography

The present position of the Arabian Peninsula dates back to 25 million years ago from the Miocene* Period. From the Precambrian to the Paleocene* Eras the peninsula was attached to Africa as part of the Nubian Shield (Child & Grainger 1990). From the end of the Cretaceous* Period until the end of the Oligocene* the fauna and flora of this landmass evolved their distinctive forms in relative isolation over a period of approximately 45 million years.

Until the Paleocene the African-Arabian landmass had been separated from Europe and Asia by the Tethys Sea. During the Eocene* and the Oligocene, however, this sea regressed and the Levantine land bridge formed between Eurasia and Africa through the Middle East. This land bridge formed one of five biogeographical filters that separated the terrestrial biogeographical* regions of the world. The Levantine land bridge is considered to be the most important nodal point in the distribution history of modern terrestrial species of the globe (Child & Grainger 1990).

The global fauna and flora are divided into eight terrestrial biogeographical realms, their provinces and lesser subdivisions. Portions of the Palearctic (Europe and Asia) and Afrotropical (Africa south of the Sahara) Terrestrial Realms are within the boundaries of Saudi Arabia. Elements of the Indo-Malayan Terrestrial Realm are also present in Saudi Arabia. In addition, the Kingdom of Saudi Arabia includes the Indo-Pacific Marine Realm. Saudi Arabia is therefore an area of great international biogeographic significance (Child & Grainger 1990).

The fauna and flora of the Arabian Peninsula are therefore a unique assemblage of elements with African, Eurasian and Indo-Malaysian affinities. There are also a number of endemic forms and passage migrants which further enrich the area. The resident biological complex is a product of the geological evolution of the peninsula and its more recent history of climatic change (Child & Grainger 1990). Several mammals from Saudi Arabia now occur, or have recently occurred, in all three of the Terrestrial Realms mentioned above. These include the honey badger *Mellivora capensis* (Schreber, 1776), the striped hyaena *Hyaena hyaena* (Linnaeus, 1758), the leopard *Panthera pardus* (Linnaeus, 1758), the cheetah *Acinonyx jubatus* (Schreber, 1775), the golden jackal *Canis aureus* Linnaeus, 1758 and the lion *Panthera leo* (Linnaeus, 1758). Other species like the Arabian oryx and the Cape hyrax *Procavia capensis* (Pallas, 1766) have an African origin. The presence of the Arabian tahr

Hemitragus jayakari Thomas, 1894 in the northern mountains of Oman confirms that there has been a land connection between Arabia and Asia in the past (Child & Grainger 1990). The vegetation of the Arabian Peninsula has been studied less intensively than that of all the other areas of southwest Asia (Kaul & Thalen 1979). General compilations, which include part of this area, are those by Mc Ginnies (1967), UNESCO-FAO (1969) and Zohary (1973). Some specific area studies have also been done by Vesey-Fitzgerald (1955, 1957 a, b), Popov and Zeller (1963) and Mandaville (1986; 1990).

The flora of Saudi Arabia has affinities with the Saharo-Arabian and the Sudano-Zambesian Floristic Regions (Takhtagan 1986 In: Child & Grainger 1990). The Saharo-Arabian Region with its desert and semi-desert forms is characterised by a low species diversity with ca.1500 plant species. The Saharo-Arabian Region is divided into the Saharan and the Egyptian-Arabian Floral Provinces. The latter province covers the largest part of extra-tropical Saudi Arabia. The Sudano-Zambesian Floral Region covers a vast area of Africa and Arabia and consists mainly of open woodland and savanna grassland.

Physiographic regions

According to Child and Grainger (1990) Saudi Arabia divides naturally into seven terrestrial physiographic* regions with 30 subregions, and two marine regions (Figure 1). The main terrestrial physiographic regions are the Tihama Coastal Plain and adjacent foothills, the Western Highlands, the Arabian Hinterland, the Cuesta Region, the Aeolian Sands, the As-Summan and Widyan Plateaus, and the Arabian Gulf Coastal Region. The two marine regions are the Red Sea and the Arabian Gulf.

The physiographic region that is of particular importance to the current study, and which includes the traditional distribution of the Arabian oryx in the Kingdom of Saudi Arabia, is the Aeolian Sands. Wind-blown sand covers 38% (855 000 km^2) of the Arabian Peninsula. The main areas of such sand are in the great basins of the Nafud and the 'Rub al Khali and in the low-lying areas between the cuestas of the sedimentary Najd (Child & Grainger 1990). In the north of the country the term Nafud refers to areas of deep sand and wind-built dunes and includes the Great Nafud (an-Nafud), Al Jafurah, the Ad-Dahna sand belt and a group of sand bodies along the western side of the Tuwayq escarpment (Chapman 1978b).

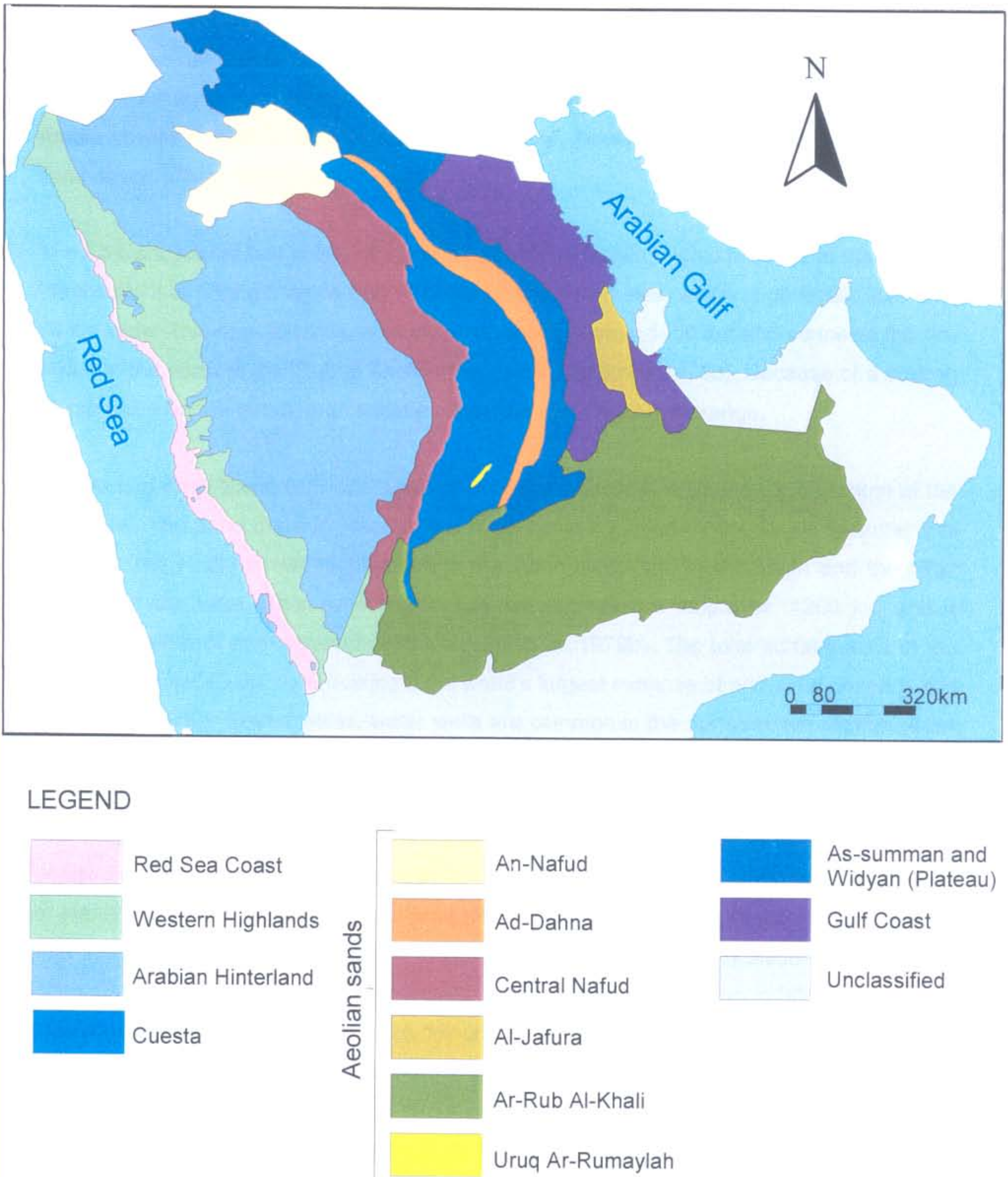


Figure1: The seven main terrestrial physiographic regions of the Kingdom of Saudi Arabia (Child and Grainger).

The sparsely vegetated An-Nafud Basin in the northwestern part of the peninsula is characterised by sands that are stained red-orange by iron oxide and occur in closely spaced crescentic dune ridges and linear dunes. This sand desert in the north of Saudi Arabia covers a surface area of some 57 000 km². No oases occur in the interior of this sand desert (Chapman 1978b)

The Ad-Dahna sand belt is one of the most distinctive physiographic features of the Arabian Peninsula. It is a long, narrow belt of shifting sand and dunes, which is generally less than 50 km wide. This area extends in an arc over approximately 1300 km and connects the An-Nafud in the north to the 'Rub al Khali in the south (Chapman 1978b). Because of a coating of iron oxide on the quartz grains these sands are also bright red-orange.

The 'Rub al Khali Basin or Empty Quarter as it is also called, is situated in the south of the peninsula. The sand there is present in a huge basin bounded by the Oman Mountains in the east, the Hadhramawt Highlands and the Aden Hinterland in the south and the Hijaz Plateau in the west. This sand region has an approximate length of 1200 km and a maximum width of approximately 650 km (Chapman 1978b). The total surface area of the 'Rub al Khali is 640 000 km² making it the world's largest expanse of arid sand desert (Child & Grainger 1990). Nevertheless, water wells are common in the northeastern section of the 'Rub al Khali.

The dunes of the 'Rub al Khali illustrate the variety of shapes present in all the sand areas of Saudi Arabia. The dunes in this area are crescent-shaped, dome-shaped, hook-shaped or star-shaped. Many of these dunes form long, single or parallel ridges also known as *'uruq* with a height of 100 m or more and a length of 20 to 200 km. Many of these dunes are also huge complex pyramids or sand mountains, which attain heights of up to 300 m (Chapman 1978b). The sands are red-orange in colour and have a medium to fine grain like those of the Great Nafud and the Ad-Dahna sand areas.

The sources of sand for the 'Rub al Khali have always been numerous. The primary source is from crystalline rocks exposed in the uplands of the peninsula. From there, the wadis* or river courses carry alluvium to the flood plains and the deltas in the lowlands of the peninsula, where aeolian processes winnow out the sand and transport it to the 'Rub al Khali Basin (Holm 1960). Shorelines of lakes and the sea are other potential primary sources of sand. Secondary sources of sand are the outcrops of sandstone which are found upwind from the dune fields, and the gravel plains in which unconsolidated clastic sediments are partly protected by a veneer of gravel, which often is a rich source of sand (Holm 1960). It is believed that the 'Rub al Khali Basin derives its sand from the highlands on three sides of it, as well as from the coastal dunes and beach deposits of the southern Persian Gulf (Holm 1960).

The prevailing wind therefore plays a major role in the distribution of the aeolian sand and its concentration in the Kingdom of Saudi Arabia. The wind regime of the Arabian Peninsula is complex in detail but rather simple in broad view. The region lies within the trade-wind belt of the Northern Hemisphere. Westerly winds from the Mediterranean Sea enter the region in the northwest, travel toward the Persian Gulf, and then swing south and southwest through the 'Rub al Khali Basin (Holm 1960).

There are several striking characteristics of the plant life in the 'Rub al Khali basin. The first is that the vegetation in the 'Rub al Khali Basin is widespread. Another characteristic is the close association of the vegetation with the sand. Approximately 90% of the 'Rub al Khali Basin is covered with sand. This sand has relatively good textural and moisture-storing properties when compared with some of the other desert soils in the world. These properties provide niches for at least a few hardy psammofiles throughout most of the basin. It is also notable that there is limited floristic diversity in the area with only approximately 20 plant species known from the main body of the sands (Mandaville 1986) and another 17 species which mostly occur on the outer margins of the sands.

Based on the present knowledge of the 'Rub al Khali, only a broad tentative classification of the vegetation of the area is possible. Mandaville (1986) described three basic plant communities (Figure 2). The first is the *Cornulaca arabica* community, which is distinguished by the presence of the endemic chenopodiaceous bush *Cornulaca arabica*. The next is the *Calligonum crinitum-Dipterygium glaucum* community, which is a rather poorly defined and variable complex that is mapped over large areas where other dominant plant species such as *Cornulaca arabica* and *Haloxylon persicum* are absent. The last is the *Haloxylon persicum* community, which is a rather clear-cut and conspicuous unit with a restricted, patchy distribution in a broad belt across the northern and northwestern edges of the sands.

In physiognomic* terms the vegetation of the 'Rub al Khali basin can be described as a diffuse but fairly evenly distributed sandy shrubland, which is interrupted in some parts by

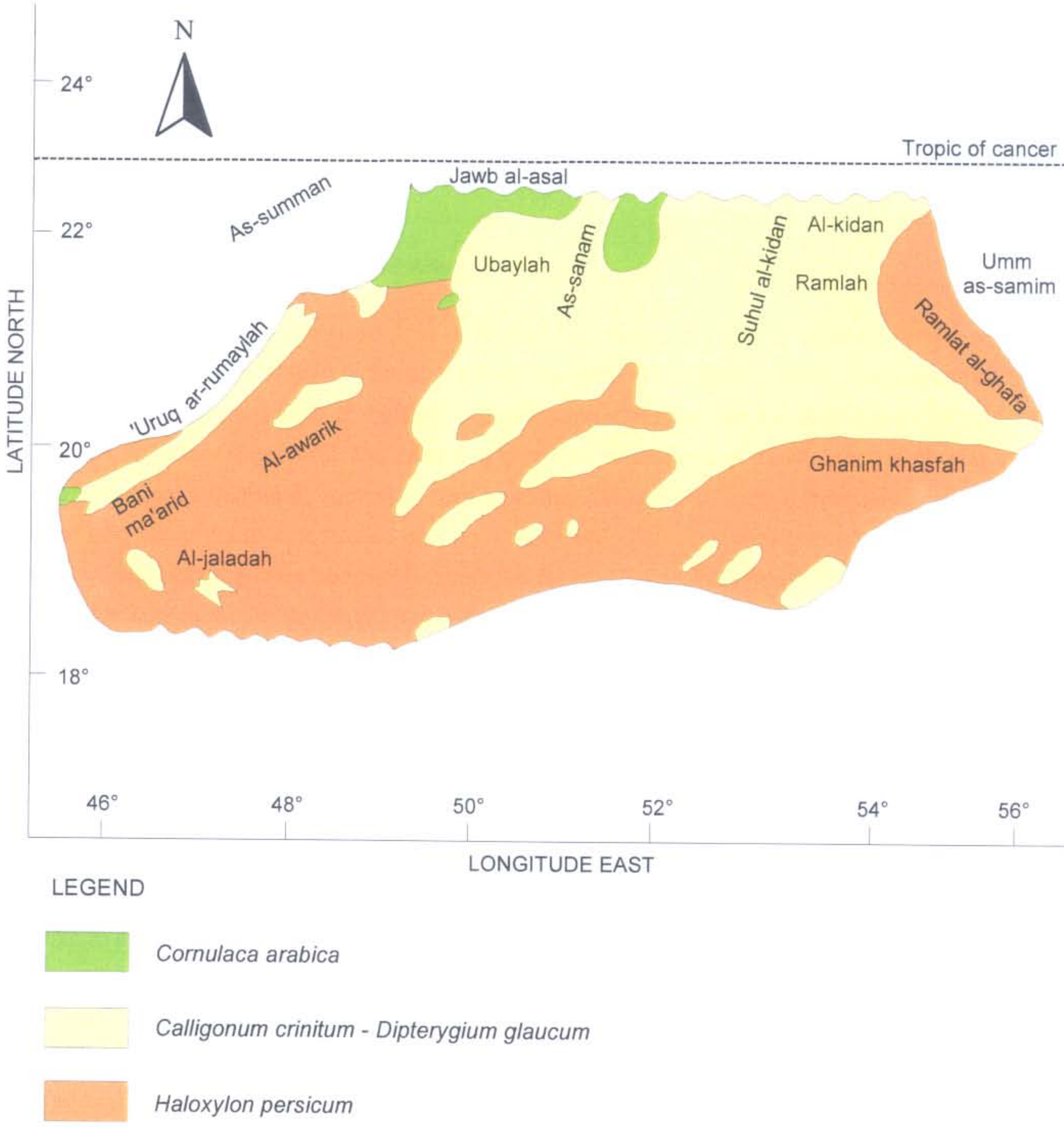


Figure 2: The major plant communities of the Rub' al-Khali (Mandaville 1986).

near-sterile inter-dune valleys. Trees are virtually absent except for a few individuals along the outer sand margins. It has also been noted that there is little seasonal variation in the general aspect of the plant cover. The main growth period for plants in the 'Rub al Khali is from March to June, but such growth depends on the amount of rain received. No spring annuals are found in the 'Rub al Khali basin (Mandaville 1986) because the infrequent rains do not seem to meet the cyclical moisture requirements of even these desert-adapted annual plants.

The 'Uruq Bani Ma'arid Protected Area

The 'Uruq Bani Ma'arid Protected Area is located approximately halfway between the cities of Wadi D'Awasir and Najran in Saudi Arabia. It lies within the Aeolian Sands Physiographic Region on the western edge of the Empty Quarter and it has the Tuwayq Escarpment as its western boundary (Figure 3). The protected area was proclaimed in 1994, and it is divided into three zones (Figure 4), namely a core protected area of 2400 km^2, a managed grazing zone of 5500 km^2 and a controlled hunting area of 4400 km^2. The core protected area and the managed grazing area corresponds with the Special Nature Reserve and Resource Use Reserve categories respectively, as defined by Child and Grainger (1990), while the controlled hunting area corresponds with the Controlled Hunting Reserve category.

The western edge of the 'Uruq Bani Ma'arid Protected Area is a limestone plateau which rises approximately 900 m above sea level and slopes gently to the east. A number of large wadis are incised into this plateau. The largest part of the protected area is covered by parallel sand dunes with a northeast-southwest orientation. These dunes are often more than 1 km wide and may be up to 152 m high. They merge at times to form mobile dunes close to the escarpment edge. The area between the parallel dunes consists of gravel plains interspersed with sand belts over the first 30 to 40 km, whereafter the gravel plains are replaced by sand. This produces a continuous undulating sand mass some 40 km or more away from the escarpment edge (Bothma & Strauss 1995).

Climate

An analysis of climatic data on a scale smaller than the whole Arabian Peninsula is difficult because insufficient data are available on the climatic conditions of any of the countries of

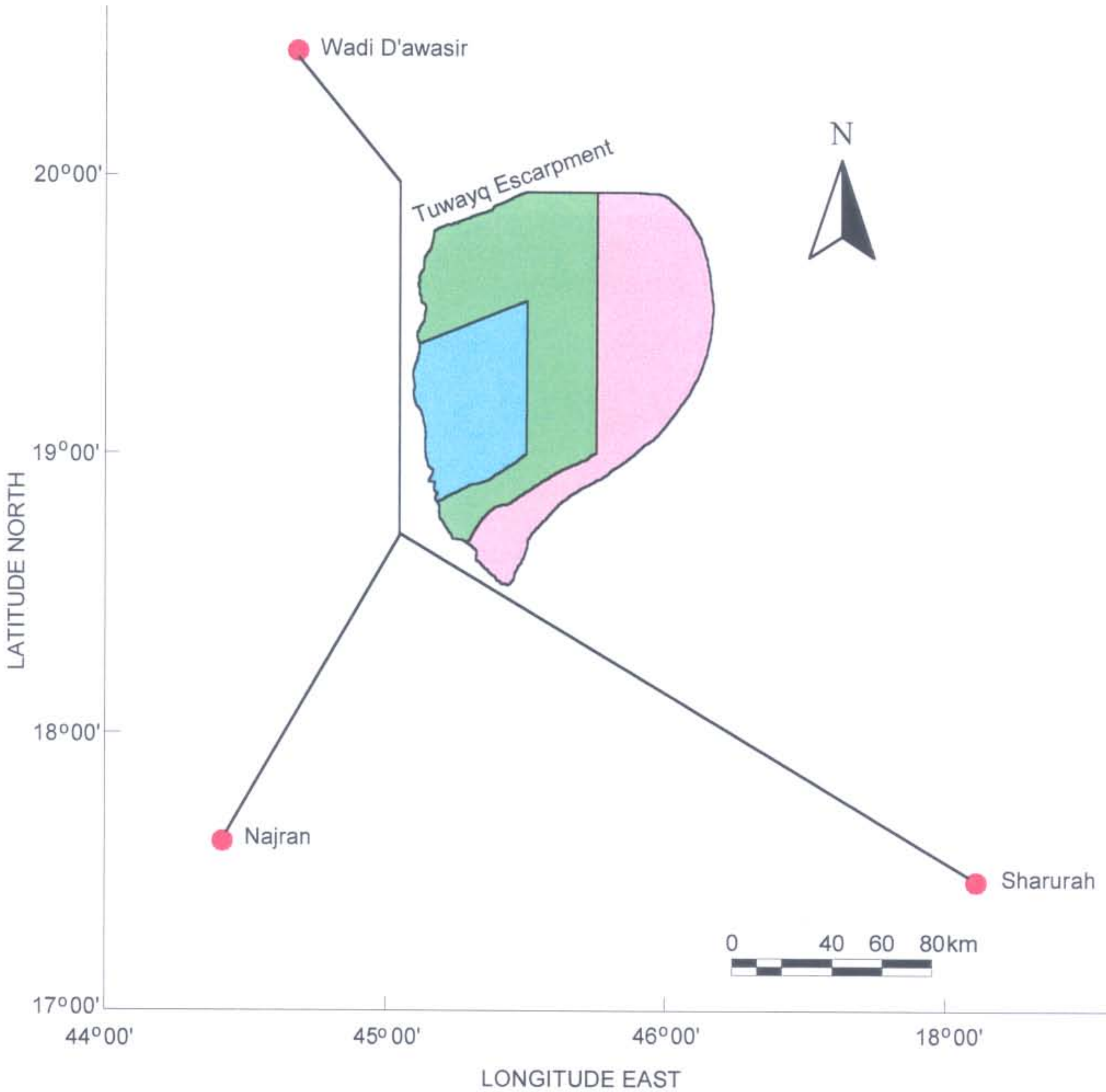


Figure 3: The location of the 'Uruq Bani Ma' arid Protected Area in the Kingdom of Saudi Arabia, in relation to three major towns (red dots). The different zones of the 'Uruq Bani Ma'arid Protected Area as indicated by the different colours above are explained in Figure 4.

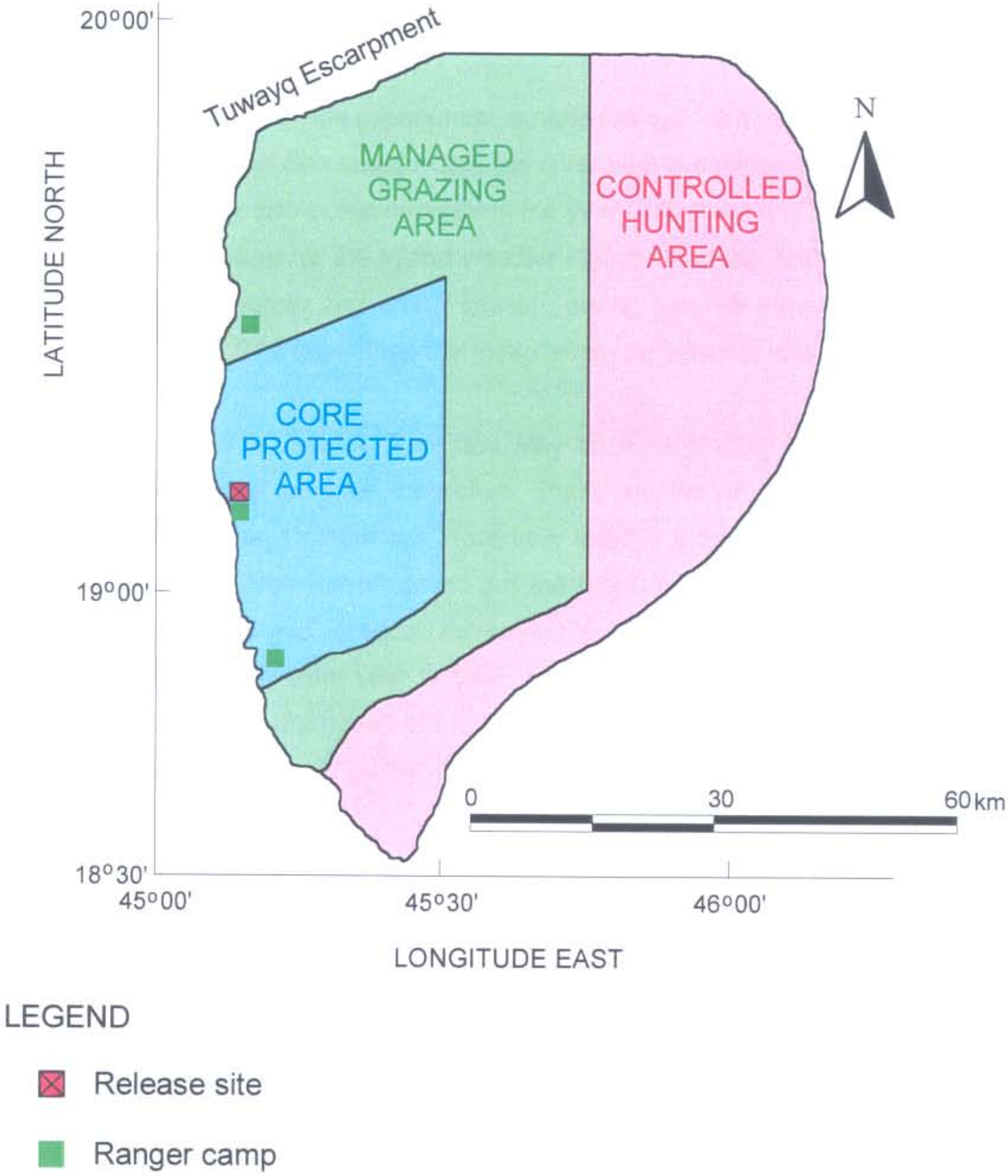


Figure 4: The 'Uruq Bani Ma' arid Protected Area of the Kingdom of Saudi Arabia showing some prominent features and the original release site of the reintroduced animals.

the peninsula (Taha, Harb, Nagib &Tartauny 1981). The climatic description that follows is therefore largely based on that given by Child and Grainger (1990). From this description it is clear that the subtropical high-pressure ridge which is part of the tropical circulatory system known as the Hadley Cell dominates the climate of Saudi Arabia. In the Equatorial Tropical Convergence Zone, this cell is characterised by rising air and clouds, with rain coming from the north. After rising to a height of 1400 m the air returns to the north, sinking as it does so to complete the Hadley Cell and to give rise to an extensive subtropical high pressure ridge which circles the globe (Child & Grainger 1990).

In general the Arabian Peninsula experiences a rapid change from summer to winter, except for the area along the Red Sea coast where the difference is small and the relative humidity of the air is more evenly distributed throughout the year (Schyfsma 1978). The ranges of the mean monthly temperature for the inland weather stations and the Arabian Gulf area show that there is a clear summer and winter season, during which the mean maximum winter temperature is about 7.5 °C lower than the mean minimum summer one.

In the Arabian Peninsula, March, April and May show a gradual increase in the mean monthly temperature until summer is reached. These months are therefore recognised as spring. During September, October and November there is a gradual decrease in the mean monthly temperature. These three months are therefore recognised as autumn (Schyfsma 1978). The timing of these gradual increases and decreases in the mean monthly temperature varies slightly from year to year, but when taken over a long period there is sufficient evidence for the distinction of the four seasons in the peninsula. The identification of the four seasons is confirmed by the changes in the relative humidity of the air (Schyfsma 1978).

Rainfall

Saudi Arabia lies within the subtropical ridge. This is an area of dry, stable and subsiding air. This ridge gives rise to hot, dry and near cloudless conditions, with 355 to 365 physiologically dry days per year (Child & Grainger 1990). During the summer the ridge is weaker than in the winter when it is displaced to the north. Disturbed tropical monsoon weather may then also occasionally reach the Kingdom of Saudi Arabia, bringing rain to the south of the country during the summer (Child & Grainger 1990).

The variability of the rainfall in deserts is well known. A way to measure this variability is to calculate the relative inter-annual variability (Wallén 1966). This is done by calculating the difference between the year-to-year mean rainfall figures, and expressing it as a percentage of the mean annual rainfall. For the majority of the weather stations in the Eastern Province of Saudi Arabia this figure ranges from 70 to 90%, which shows that this high degree of variation approaches the value of the mean itself (Mandaville 1990).

The annual rainfall in eastern Saudi Arabia declines from the north to the south, as does the annual rainfall in the 'Uruq Bani Ma'arid Protected Area, where the mean annual rainfall probably is less than 47 mm per year (Dunham, Robertson & Wacher 1995). Many parts of the 'Rub al-Khali may have several years without any rain. For example, during the early 1930's Philby reported that no rain had fallen in the northern margin of the sands near Wadi D'Awasir for several years (Carruthers 1935).

Temperature

The ambient temperatures in Saudi Arabia show considerable diurnal and seasonal fluctuations. The winters are cool to warm, with frost not being uncommon at night. Occasionally, snow falls in the north of the country at higher altitudes. The maximum summer temperatures tend to be above 40° C in general, while occasionally exceeding 50° C. The relative humidity of the air is generally low, except along the coasts where the days may be excessively hot and humidly oppressive (Child & Grainger 1990).

The 'Uruq Bani Ma'arid Protected Area is a new protected area in the Kingdom of Saudi Arabia. Therefore much climatic data are not available for the area (Bothma & Strauss 1995). Data are, however, available for the three towns surrounding the area.[2] These are the towns of Wadi D'Awasir, Sharurah and Najran. Following Walther (1979) the climatic data for these towns can be used to create a composite display of the expected monthly rainfall and the mean temperatures of each town (Figure 5) and consequently the study area. This display gives a useful impression of the seasonal march of aridity (Mandaville 1990). The ratio of temperature to rainfall is chosen so that the area between the curves provides an approximate indication of the water balance (excess or deficit) (Mandaville 1990).

The three diagrams show that the mean annual temperature of the three towns involved range from 25.5 to 29.4 °C, while the mean annual rainfall ranges from as low as 30 mm per

[2] Climatic data for a 5-year period (1989 to 1993) as supplied by the Meteorological and Environmental Protection Administration, Jeddah, Saudi Arabia.

year in Sharurah to 54 mm per year in Najran. It is also apparent that there is a water deficit in all three of these towns throughout the year. According to Mandaville (1986) the evapo-transpiration in as-Sulayil, a town approximately 150 km north of the protected area, was 5250 mm per year over a 9-year period. This evapo-transpiration rate strongly supports the current climatic data available for the three towns used.

Vegetation

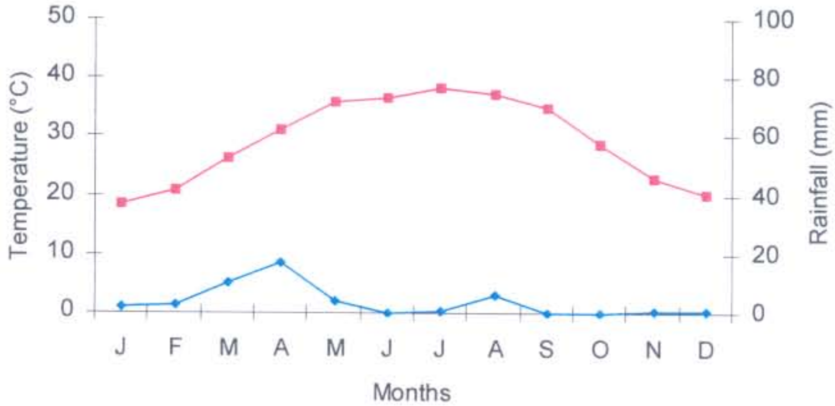
Based on the topography of the 'Uruq Bani Ma'arid Protected Area, several vegetation associations are distinguished (MEPA 1986; NCWCD 1987; NCWCD 1990), of which the sand and the escarpment associations are the two basic types (MEPA 1986; NCWCD 1987). The sand association can be divided into the vegetation of the dunes and the *shiquats*, the latter also being known as dune corridors. The *shiquats* consist of hard, compact lacustrine* deposits, lag* gravels adjacent to run-off sites, and fringing plains. The escarpment association can be subdivided into the escarpment gravel plains, which are mostly void of vegetation, the escarpment sand sheets, and the vegetation-rich wadis.

Various *Acacia* tree species dominate in the 'Uruq Bani Ma'arid Protected Area with *Acacia tortilis*, and *Acacia ehrenbergiana* especially abundant and *Acacia hamulosa*, *Acacia oerfota*, *Ziziphus spina-christi* and *Maerua crassifolia* also present. The shrub and herb layer consists of species such as *Calligonum crinitum*, *Leptadenia pyrotechnica*, *Tribulus arabicus*, and *Dipterygium glaucum*. Grass species commonly found in the protected area include *Panicum turgidum, Lasiurus scindicus*, *Stipagrostis plumosa, Centropodia fragilis* and *Pennisetum divisum* (Bothma & Strauss 1995).

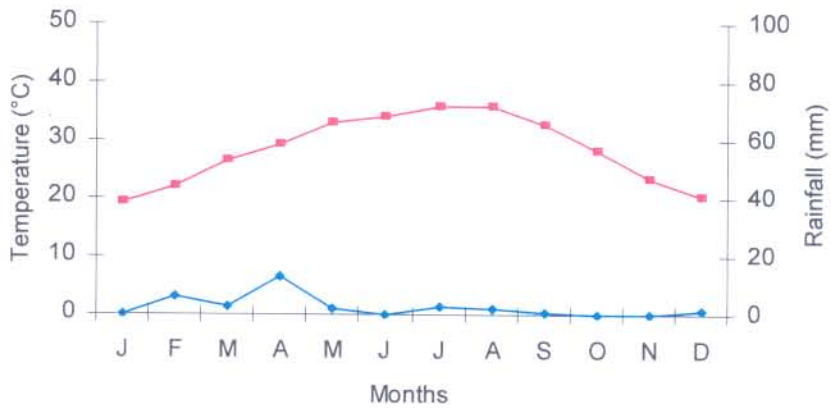
Based on the location of the 'Uruq Bani Ma'arid Protected Area and the vegetation in the area, this protected area is located mainly within the *Calligonum crinitum - Dipterygium glaucum* plant community, as defined by Mandaville (1986). The *Haloxylon persicum* and *Cornulaca arabica* communities also occur within the protected area (Figure 2).

Previous surveys conducted in the 'Uruq Bani Ma'arid Protected Area (MEPA 1986, NCWCD 1987; NCWCD 1990) concluded that the protected area has an appreciable habitat diversity, a vegetation that is less degraded than in other areas of Saudi Arabia, and that the protected area lies within the historical range of the Arabian oryx, all three of the native gazelle types and the ibex *Capra ibex nubiana* Linnaeus, 1758 (Büttiker &

Wadi D'awasir (701.02 m) 29.4°C 45.6 mm



Sharurah (724.65 m) 28.4°C 30.0 mm



Najran (1212.33 m) 25.5°C 54.0 mm

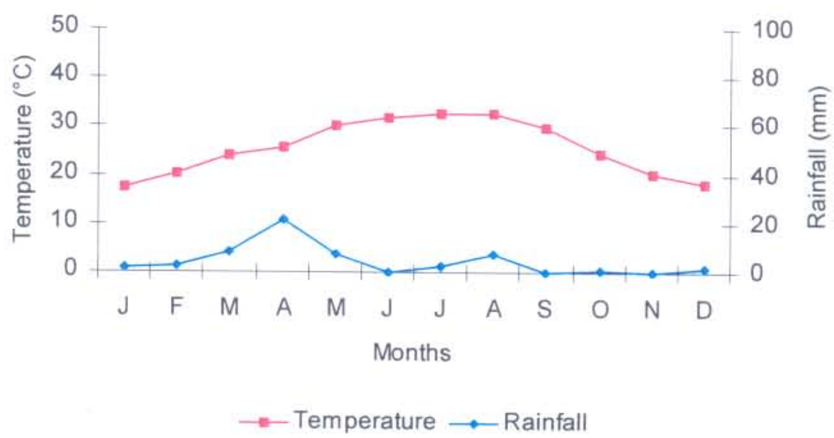


Figure 5: Walther diagram for three towns surrounding the 'Uruq Bani Ma'arid Protected Area in the Kingdom of Saudi Arabia. Figures at right of station name are, from left to right: station elevation in metres above mean sea level, mean annual temperature and mean annual rainfall. The red line depicts the mean monthly temperature and the blue line the mean monthly rainfall. The area in-between the graphs represent the period of moisture deficit.

Grainger 1989). There is therefore no question about the suitability of these herbivores for their reintroduction* into the 'Uruq Bani Ma'arid Protected Area.

CHAPTER 3

THE ARABIAN ORYX

Taxonomy

The Arabian oryx *Oryx leucoryx* is a member of the subfamily Hippotraginae of the family Bovidae of the order Artiodactyla (Skinner & Smithers 1990; Harrison & Bates 1991; Grubb 1993). The subfamily Hippotraginae contains three living genera. They are *Hippotragus*, *Addax* and *Oryx* (Gentry 1978; Grubb 1993). Within these genera six species are found, five of which occur on the African continent. All the members of the subfamily Hippotraginae are large, horse-like antelopes (Stanley-Price 1989). The most striking characteristic of this subfamily is that both the sexes have horns, which are long and either swing backwards from the head in a curve, or are straight. Distinctive facial patterns also occur in all the members of this subfamily (Roberts 1951; Skinner & Smithers 1990).

The sable antelope *Hippotragus niger* (Harris, 1838) and the roan antelope *Hippotragus equinus* (Desmarest, 1804) inhabit mixed woodland-grassland habitats in central, southern, and partially also into western Africa, while the addax *Addax nasomaculatus* (Blainville 1816) occurs in the Sahara desert (Stanley-Price 1989).

There are three species recognised within the genus *Oryx* (Grubb 1993). The distribution of the genus shows that it is historically associated with arid areas (Figure 6). In southern Africa, the gemsbok *Oryx gazella gazella* (Linnaeus, 1758) occurs in the Kalahari system. Towards eastern Africa, the beisa oryx *Oryx gazella beisa* is found in the arid areas of Somalia, while the fringe-eared oryx *Oryx gazella callotis* is found in an area adjacent to that of the beisa oryx, which is separated by the Tana River of Kenya. *Oryx gazella gallarum* is found in the Sudan and Ethiopia while *Oryx gazella annectens* occurs in Kenya and Somalia (Ansell 1972). In North Africa, the scimitar-horned oryx *Oryx damah* (Cretzschmar, 1827) is found in the Sahara desert (Stanley-Price 1989). The Arabian oryx *Oryx leucoryx* (Pallas, 1777) is the smallest of the *Oryx* species known to science, and the only one to occur outside the African continent (Stewart 1963; Loyd 1964; Harrison & Bates 1991).

Historical distribution and decline

The Arabian oryx formerly occurred throughout the desert regions of the Arabian Peninsula.

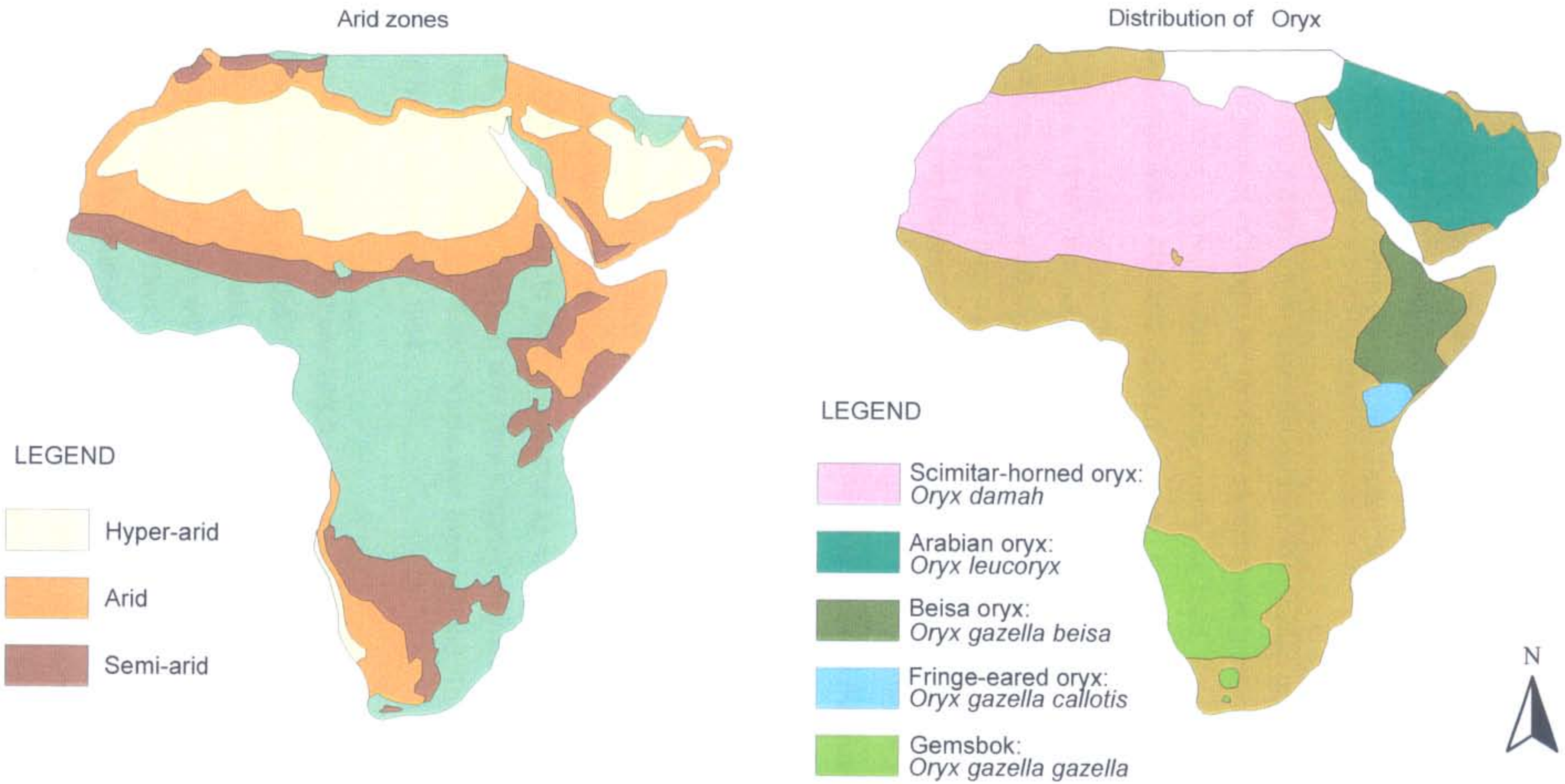


Figure 6: The distribution of the arid zones in Africa and Arabia (Unesco 1979) and the historical distribution of the genus *Oryx* in Africa and Arabia (Stanley-Price 1989).

The precise limits of its former northern range are not known (Harrison & Bates 1991). During the 1800's the Arabian oryx was still found over virtually the whole Arabian Peninsula, Sinai, Lower Palestine, Trans-Jordania and much of Iraq (Turkowski & Mohney 1971; Dolan 1975). It is doubtful whether the Arabian oryx ever occurred east of the Euphrates River into Iran (Talbot 1960; Dolan 1975; Harrison & Bates 1991).

Towards the middle of the nineteenth century, the Arabian oryx began to disappear from the northern parts of its range. By 1914 the situation was grave and only a few Arabian oryxes seem to have survived outside Saudi Arabia. In 1926, Colonel Cheesman noted that the Arabian oryx was a rare and rapidly diminishing species (Carruthers 1935).

During the 1930's the remaining Arabian oryxes in Saudi Arabia were divided into two populations, which were kept in their respective areas approximately 1100 km apart. These populations were in the Great Nafud in the north, and in the 'Rub al Khali basin in the south of Saudi Arabia (Figure 7). The ad-Dahna sand belt connects these two areas. Historically, this sand belt probably served as a migration route between the northern and southern Arabian oryx populations. The 'Rub al Khali was probably the main, and last stronghold of the Arabian oryx (Carruthers 1935).

In Jordan, a few animals survived until about 1930, but they were already being exterminated rapidly then (Dolan 1975). After World War II, the Arabian oryx numbers decreased drastically due to the automatic weapons and four-wheel-drive vehicles which entered the Arabian Peninsula (Loyd 1964). In the early 1950's for example, the pressure on the oryx had increased to such a level that as many as 300 vehicles were used in a single hunting foray (Dolan 1975). It was only a matter of time before the oryx population in the northern Nafud desert of Saudi Arabia was exterminated. The last set of oryx tracks in the Great Nafud was seen in 1954.

During 1960, between 100 and 200 Arabian oryxes remained in the 'Rub al Khali Basin, but little hope remained for their continued survival in the wild (Talbot 1960). As a result of the drastic decline in the Arabian oryx numbers, the Fauna and Flora Preservation Society of England, in conjunction with the International Union for Conservation of Nature (IUCN) launched "Operation Oryx" during 1962. This operation took place in the then Aden Protectorate (now southern Yemen) during 1962, and entailed capturing two males and a female Arabian oryx from the wild (Grimwood 1962; Shepherd 1966). In cooperation with the Zoological Societies of London and Arizona, and the then World Wildlife Fund (now called

LEGEND

Recorded historical limits of former distribution

Distribution circa 1945

Distribution in 1902: (known limits)

Figure 7: The historical distribution of the Arabian oryx in the Arabian Peninsula (Stewart 1963)

the World Wide Fund for Nature) and the Shikar-Safari Club, the three Arabian oryxes were shipped to the Phoenix Zoological Gardens in the United States of America. This group was supplemented with a female Arabian oryx from the Zoological Society of London, a female Arabian oryx from the private collection of the ruler of Kuwait, and two pairs of Arabian oryx from the late King Faisal of Saudi Arabia. This nucleus of nine animals became what was subsequently known as the "World Herd" (Dolan 1987).

Before the establishment of the "World Herd" little success was achieved in keeping the Arabian oryx under captive conditions. Dolan (1975) could find only 13 records of Arabian oryx calves being born in captivity between 1848 and 1946. The longevity of captive Arabian oryxes was poor during the years before the World War II, with a mean life expectancy of 5 years. The "World Herd", however, was so successful that the first group of Arabian oryx started to return to the Arabian Peninsula during 1978, when eight (sex ratio 1:1) were sent to Jordan over a period of 2 years. The first reintroduction of the Arabian oryx into the wild took place during 1982 in the unfenced Jiddat al Harasis area of Oman (Jungius 1982; Stanley Price 1986). During 1983, a further 31 Arabian oryxes were released into the 22 km^2 fenced Shaumari Reserve in Jordan (Fitter 1982; Dolan 1987).

Captive breeding programme in Saudi Arabia

Wildlife is an integral part of the Arabian culture. It is therefore natural that, when the Saudi Arabian Government became aware of the trend of overutilisation of its wildlife, it initiated several measures to rectify the situation. The National Commission for Wildlife Conservation and Development (NCWCD) was created in 1986, and was given the mandate to restore the Kingdom's natural heritage. In its endeavours to fulfil its mandate, the National Commission for Wildlife Conservation and Development has adopted a two-pronged approach. The first was to prepare a national systems plan, which identified areas worthy of protection according to a predetermined set of criteria. Secondly, the National Commission for Wildlife Conservation and Development initiated a captive-breeding programme of endangered native wildlife, with the purpose of providing animals for reintroduction into the protected areas (Joubert 1994).

The late King Khaled made part of his private farm and the game on it available for the captive-breeding programme of wildlife in Saudi Arabia. In 1987, the King Khaled Wildlife Research Centre was established on the farm. In 1986 a piece of land was also obtained near Taif for the captive breeding of the houbara bustard *Chlamydotis undulata macqueenii*.

The facilities erected there were named the National Wildlife Research Centre. At both the King Khaled Wildlife Research Centre and the National Wildlife Research Centre the most modern veterinary and animal husbandry equipment and expertise are being used (Joubert 1994).

A national strategy for captive breeding was adopted next. This strategy acknowledges the need for the captive-breeding programme to be based on sound scientific principles. The strictest veterinary quarantine measures are enforced within and around the facilities of both these breeding centres to prevent the spread of diseases between the animals within the centres, and to exclude possible infection from outside. It was decided to separate the breeding programme of the various endangered wildlife types. The breeding of the four native types of gazelle became the responsibility of the King Khaled Wildlife Research Centre. The 56 Arabian oryxes on the late King Khaled's farm at Thumamah were translocated to the National Wildlife Research Centre in 1986. Subsequently, this centre has focussed mainly on the captive breeding of the Arabian oryx and some avifauna, especially the houbara bustard (Joubert 1994).

Shortly after their arrival at the National Wildlife Research Centre in 1986, a tuberculosis outbreak reduced the Arabian oryx founder population (A-generation) from 56 to 37 animals (Greth, Sunnucks, Vassart & Stanley 1992). Subsequently, an antibiotic treatment of all the Arabian oryxes at the National Wildlife Research Centre was undertaken for a period of 9 months during 1987 (Flammand, Delhomme & Ancrenaz 1994; Greth, Flamand & Delhomme 1994). Since 1988, none of the bacteriological cultures taken from the oryxes that died at the National Wildlife Research Centre have shown any evidence of tuberculosis infection (Seddon, Ancrenaz, Ostrowski & Magin 1995). In addition, the following husbandry techniques were adopted to prevent the release of tuberculosis-infected oryxes into the protected areas.

Calves born into the infected herd are removed from their mothers directly after birth, and are reared by hand, to reduce the risk of horizontal tuberculosis infection (Flamand *et al.* 1994). These oryx calves are kept in small groups of up to four animals to prevent widespread infection if one of these animals were infected with the disease. The calves (B-generation) born from the infected herd are tested regularly for tuberculosis from the age of 2.5 months (Joubert 1994). When these tests are negative, the animals are considered as part of the "filter herd", the members of which join the breeding nucleus on reaching adulthood. These B-generation oryx represents the main herd for oryx production at the

National Wildlife Research Centre (Seddon *et al.* 1995). Calves produced from the breeding nucleus are called the C-generation, and are reared by their own mothers. They are free of tuberculosis.

The whole captive herd is tested periodically for tuberculosis (Ancrenaz, Ostrowski & Delhomme 1995a). Animals are only considered for reintroduction into the protected areas after two consecutive negative tuberculosis test results. In addition, all captive Arabian oryxes at the National Wildlife Research Centre are vaccinated annually against foot-and-mouth disease, rabies, pasteurellosis and rinderpest (Greth & Schwede 1993; Ancrenaz *et al.* 1995a).

The Arabian oryx captive breeding programme of the National Commission for Wildlife Conservation and Development has been so successful that from a founder herd of 37 animals, the national herd now numbers more than 400 individuals (Joubert 1994). In 1990, a first group of 17 Arabian oryxes was released into the fenced Mahazat as Sayd Protected Area near Taif. Since then, this original group has been reinforced with oryxes from several neighbouring countries, including Qatar and Bahrain. At present this population numbers approximately 340 animals (Seddon 2000).

The genetic management of the captive breeding programme at the National Wildlife Research Centre aims to maintain at least 90% of the genetic variation in the original population over a period of 200 years, and to produce animals that are genetically fit enough to survive in the wild. Missing or underrepresented genetic lineages are added by reintroducing wildborn animals caught in the Mahazat As Sayd Protected Area (Ancrenaz *et al.* 1995a).

The reintroduction of animals

Species become endangered through a population decline that can be attributed to various factors, including extensive poaching and habitat loss (Green & Rothstein 1998). Any attempt to re-establish a species in an area which it had previously occupied, is futile unless the factors causing its initial decline are properly addressed.

Different terms have been used to define the re-establishment of a species in an area formerly occupied by that species. These include reintroduction (IUCN 1987; Griffith, Scott, Carpenter & Reed 1989) and repatriation (Dodd & Siegell 1990; Novellie & Knight 1994). The terminology that is used here is in accordance with that of the IUCN (1987).

The reintroduction of organisms can be defined as the release of a plant or animal species into an area in which it was indigenous before its extermination by man or a natural catastrophe (IUCN 1987). Reintroductions should therefore only take place when the original causes of extinction have been removed, and where the habitat requirements of the species are satisfied (IUCN 1987; Griffith *et al.* 1989). Reintroduction is a powerful technique in conservation, especially in view of the increasing rate of species extinction and the impending reduction in overall biological diversity (Griffith *et al.* 1989). It can be used to increase the number of individuals, genetic variability and gene flow, and to redistribute populations to areas of optimal habitats (Franzmann 1988; Gripps 1991; Caughley 1994). Many reintroductions have been attempted in the world to date but the success rates have not always been acceptably high (Novellie & Knight 1994). This is so despite the fact that the procedures for a systematic reintroduction effort are clearly documented (Anderegg, Frey & Muller 1983; Jungius 1985; IUCN 1987). The following four phases (IUCN 1987) have been recognised as being essential in any reintroduction process and include most of the suggested procedures:

- A feasibility study to indicate the likelihood of a successful reintroduction
- The preparation stages where the release area is identified, animal sources are identified and logistical arrangements for the capture and transport of the animals are made
- The release phase
- A post release monitoring phase

Selection of Arabian oryxes for reintroduction

Sixty-six Arabian oryxes were selected for reintroduction into the 'Uruq Bani Ma'arid Protected Area during 1995 and 1996. This included four B-generation oryxes at a ratio of 1 female per male, 55 C-generation oryxes at a ratio of 1.12 females per male from the National Wildlife Research Centre, and seven free-ranging Arabian oryxes at a ratio of six females per male, from the Mahazat as Sayd Protected Area.

The choice of animals for reintroduction was based on two criteria. Firstly, the selected oryxes should contain a homogeneous genetic component of the founder population (A-generation) to avoid a genetic bottleneck, and secondly the selected animals should not be related directly to each other to decrease potential inbreeding (Ancrenaz, Delhomme, Anagariyah & Khoja 1994).

Two pairs of half-siblings were selected for release, however, as their genetic contribution could increase the genetic representation of the founder population (Ancrenaz *et al.* 1994). The four B-generation oryxes, which were all hand-reared, were included in the selection to diversify the age structure of the reintroduced population and to increase the genetic diversity of the population (Ancrenaz *et al.* 1994). Cytogenetic studies of the captive Arabian oryx population at the National Wildlife Research Centre revealed the presence of a chromosomal Robertsonian translocation, resulting from the fusion of chromosomes 17 and 19. This translocation is usually not expressed phenotypically, but a reduced fecundity in heterozygotes with this translocation has been recorded in cattle (Cribiu, Asmodé, Durant, Greth & Anagariyah 1990). None of the Arabian oryx with this chromosomal translocation was selected for reintroduction into the 'Uruq Bani Ma'arid Protected Area, following a meeting of the International Wild Arabian Oryx Advisory Panel in London, during 1990 (Vassart, Granjon, Greth, Asmodé & Cribiu 1991; Greth & Schwede 1993).

Translocation of the Arabian oryx

Because of their nervous disposition and aggressiveness, it is particularly difficult to transport members of the family Hippotraginae. High mortalities have been experienced in attempting to do so. Hofmeyr (1974) reported that immobilisation with etorphine was the safest way to transport the roan antelope *Hippotragus equinus*. More than 70 roan antelopes have subsequently been kept immobilised with etorphine for up to 5 hours while being airlifted.

During the translocation of the Arabian oryx that took place from the National Wildlife Research Centre to the Mahazat As Sayd Protected Area in 1992, the Arabian oryxes were kept under deep anaesthesia. It then became apparent that long-term anaesthesia on the Arabian oryx could only be performed safely for 5 to 6 hours (Ancrenaz 1994). Long-term anaesthesia was therefore not a desired technique for the translocation of the Arabian oryx from the National Wildlife Research Centre to the 'Uruq Bani Ma'arid Protected Area, a transfer which normally takes 9 hours to complete. It was therefore decided to use a combination of boma-training and long-term tranquillisers (neuroleptics) instead. Groups of four animals of similar age and size were placed in pre-transportation enclosures, 3 months before translocation. These enclosures consisted of an indoor pen of 5 x 3 m with wooden walls and a roof of shade cloth, and an outdoor pen of 6 x 10 m that was fenced with chain-link wire mesh. The outdoor pens were connected to an off-loading ramp, which was 2.5 m wide and 3 m long. The ramp was connected to a corridor that decreased in a funnel shape to a width of 1 m and a length of 8 m. The walls of the corridor were constructed from wire-mesh fencing that was covered with a tarpaulin. The mass crates, which were to be used for transportation, were made of wood, while the floors were covered with rubber mats. The crates were 2.5 m long x 2 m wide x 2 m high and could accommodate five Arabian oryxes each (Ancrenaz, Ostrowski, Delhomme & Greth 1995b).

During the first 6 weeks of the boma-training, each group of oryx was enclosed in the indoor pen for increasing periods of time ranging from 2 to 24 hours. Progressively, the Arabian oryx became accustomed to being moved into the corridor and the crates. Each group of oryx was driven around the National Wildlife Research Centre twice a week for periods varying between 30 minutes and 2 hours. After each drive the animals were released into the pre-transportation enclosures. A week before the translocation, each group of Arabian oryx was enclosed in the mass crates overnight on every second day (Ancrenaz *et al.* 1995b).

A long-term tranquilliser is a neuroleptic for which a single dose gives a therapeutically effective tissue concentration of drugs for at least a week (Lingjaerde 1973). The prolonged effect is achieved through one of four ways (Ebedes 1993):

- The slow release of the active ingredient from the injection site
- The slow but sustained absorption of the active ingredients or metabolites into the bloodstream
- The slow metabolism of the active drug in the tissues
- The slow elimination of the drug or its metabolites from the tissues and the bloodstream

Trilafon, which is a derivative of phenothiazine, is one such long-term neuroleptic. In South Africa, this neuroleptic has been used successfully on the roan antelope during a journey of 32 hours (Morkel 1992) duration, and it was selected for use on the Arabian oryxes. The Arabian oryxes were therefore injected intra-muscularly with 2.5 to 3.0 mg Trilafon per kg body weight 3 days before their translocation. The first signs of tranquillisation were observed 24 hours after injection. This rendered the animals subdued, while they remained before translocation. These enclosures consisted of an indoor pen of 5 x 3 m with wooden walls and a roof of shade cloth, and an outdoor pen of 6 x 10 m that was fenced with chain-link wire mesh. The outdoor pens were connected to an off-loading ramp, which was 2.5 m wide and 3 m long. The ramp was connected to a corridor that decreased in a funnel shape to a width of 1 m and a length of 8 m. The walls of the corridor were constructed from wire-mesh fencing that was covered with a tarpaulin. The mass crates, which were to be used for transportation, were made of wood, while the floors were covered with rubber mats. The crates were 2.5 m long x 2 m wide x 2 m high and could accommodate five Arabian oryxes each (Ancrenaz, Ostrowski, Delhomme & Greth 1995b).

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The tranquillised Arabian oryxes were enclosed in mass crates, each large enough to take five animals, and transported to within 150 km from the 'Uruq Bani Ma'arid Protected Area with a Hercules C-130 transport aircraft. From there the animals were transported to the protected area by road. The animals were relatively insensitive to stressful situations and did not develop any obvious or latent pathological problems following the 9-hour transportation (Ancrenaz *et al.* 1995b).

Upon arrival in the 'Uruq Bani Ma'arid Protected Area, the Arabian oryxes were off-loaded into temporary holding pens of 4.8 x 10 m each. The number of animals per pen varied. Water was provided *ad libitum* from the start, but dry alfalfa and hay was only provided as feed on the following morning. During their time in the temporary pens, 57 of the Arabian oryxes were fitted with radio-collars from either Telonics (n=38) or AVM (n=19), with an expected battery-life of 2.5 to 3 years each. All the radio-collars worked on the 164 MHz frequency. Numbered collars only were fitted on seven of the Arabian oryxes. The two calves that were reintroduced with their mothers were not collared. The Arabian oryxes were released from the temporary holding pens into a 4 ha enclosure, 5 days after arrival at their destination (Ancrenaz *et al.* 1995b). This enclosure was divided into two areas of 2 ha each. Alfalfa and hay were again supplied on a daily basis and water was available *ad libitum*. The Arabian oryxes were then given time to orientate themselves in the enclosures and to get used to eating the natural vegetation present in their environment.

Over the 2-year study period six releases of oryxes took place. The first was officiated by HRH Prince Sultan Bin Abdulaziz on 28 March 1995. During this release, the Arabian oryxes were driven out of the enclosure with vehicles. In the five subsequent releases, the oryxes were fed close to the release gates in the days preceding the release. On the day of release the alfalfa was placed outside the enclosure, opposite the gate. After an hour, the gates were opened. This meant that the normal feeding time of each morning was delayed by approximately an hour, whereafter the animals were left to leave the enclosure at their own pace and will. The animals were not immediately followed by vehicle, but were left to investigate the area without any disturbance. The oryxes were, however, located during the same afternoon with the aid of an aircraft (Bothma & Strauss 1995). The provision of food and water at the release site ceased on the day on which the oryxes were released into the 'Uruq Bani Ma'arid Protected Area.

The combination of boma training and the use of long-acting tranquillisers proved successful. During the 9-hour transportation by both road and air the animals were relatively insensitive to stressful situations and did not develop any obvious pathological problems (Ancrenaz *et al.* 1995b).

CHAPTER 4

METHODS

Introduction

The Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area were monitored from the day of the first release (28 March 1995) until 18 February 1997. During this time 156 hours were spent on aerial surveys in and around the protected area, culminating in 1267 aerial locations of the individual reintroduced Arabian oryxes. Ground surveys during the study period resulted in 4565 observations of different groups of oryxes.

All the data that were collected during the aerial and ground surveys were entered into a database constructed in such a way as to present data for each individual animal seen during each observation. For this to be effective each individual oryx released had to be individually identifiable and data had to be collected in a structured way.

The methods discussed here apply to the study in general. More specific methods of data collection, pertaining to various other aspects investigated during this study are addressed in the relevant chapters, as are the analysis techniques used.

Oryx identification

During the study period 66 Arabian oryxes were reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, all of which were individually identifiable. Of these, 86% (57 oryxes) were equipped with battery-operated radio-collars from either the Telonics Company in Arizona, USA (n = 38) or the AVM company (n = 19). In addition, numbered tags were fitted onto each radio-collar to further facilitate identification and to ensure positive identification in the event of radio-collar failure. The remaining nine Arabian oryxes reintroduced were not equipped with radio-collars. Of these, seven animals were fitted with numbered tags on a collar. The remaining two oryxes were approximately 3 months old at the time of release and were considered to be too young to be fitted with collars, as this would mean recapture at some future time to adjust or fit new radio-collars. These two animals were initially identified by their different facial and leg colour patterns, and later on the shape of their horns.

Neonates born into the reintroduced population were given unique identification numbers. Initially these oryxes could only be identified through their association with their mothers. If several neonates were found in a group, identification would be postponed until an animal could be positively identified through its association with its mother (e.g., when suckling). As the calves grew older, unique features such as the colour patterns on the face, side and legs, features of their tails, or the shape of their horns identified them.

The Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area were usually located by ground vehicle. In addition a Maule aircraft was available for 2 days every fortnight. This made it possible to locate all the reintroduced Arabian oryxes in a relatively short period of time. It also made the search for any "missing" oryxes easier. The procedure used for locating the Arabian oryxes on both the ground and from the air was similar. As the oryxes were free to roam around the protected area and group composition was not controlled, there was no way of determining which oryx would be located first or where it would be located during any particular day. It is therefore considered that, in general, the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area were located in a random way.

Data collection

Locating the oryxes from the ground

The radio-tracking of the Arabian oryxes from the ground was initially done with a Telonics TR2 receiver only. Later a TS1 scanner was coupled with the receiver. This allowed for each of the 57 unique radio-collar frequencies to be entered into the scanner, thereby facilitating quicker location of animals. Every time that either a given animal or herd was located on the ground through radio-tracking or visual observation, the following variables were recorded:

Herd characteristics

All the animals present were counted and identified individually by the tag number or other distinguishing features. The age and sex structure was also determined in this way. The sex of any new-born oryx was determined if the opportunity presented itself.

Physical condition

This was judged according to the method used by Riney (1960), based upon the external appearance of the individual. The physical condition of an animal is an indication of the current state of the veld, the availability of suitable food, the quality and digestibility of the food and the general health of the animal (Ebedes 1996). A similar technique, which seems to have been based on the above-mentioned technique, was also developed for the gemsbok (Hamilton, Buskirk & Buskirk 1977) in Namibia and it was used to subjectively measure the nutritive level of an animal. Berry (1980) also used the same technique in studies on blue wildebeest *Connochaetes taurinus* (Burchell, 1823) in the Etosha National Park of Namibia.

In the present study the physical appearance of all the Arabian oryxes were judged on the degree to which the skeletal details of its body were visible externally. Points were thus awarded on the same basis as used by Berry (1980) on the blue wildebeest. They were:

1. Excellent: the hindquarters are well rounded, no ribs show, and the general appearance of the animal, its posture and coat sheen are excellent
2. Good: the hindquarters are rounded, but the ribs show slightly through the hide
3. Fair: the hindquarters are angular in appearance and the ribs are well defined externally
4. Poor: the pelvic bones are prominent and the ribs protrude
5. Degraded: all the skeletal details are clearly visible externally and the rump is concave. The general appearance, posture and coat condition of the animal are degraded

Subhabitat

The types of subhabitat in the 'Uruq Bani Ma'arid Protected Area were distinguished on topographical features. The type of subhabitat in which an oryx or herd of oryxes was found was coded numerically. These codes were subjectively given for each subhabitat and its subdivisions, where applicable. The numerical codes and the types of subhabitat distinguished were:

1. Dune
2. *Shiqquat* or dune street
    - 2.1. Gravel plain
    - 2.2. Sand sheet
    - 2.3. Pan at dune foot
3. Escarpment plateau
    - 3.1. Gravel plain
    - 3.2. Sand sheet
    - 3.3. Wadi

Vegetation condition

The condition of the vegetation at each location was assessed for three aspects. These were the overall greenness of the vegetation, the condition of the grasses and annual plants present, and the condition of the shrub and tree layer.

In terms of the overall degree of greenness, the vegetation was coded as:

1. Mostly white with a slight green tint
2. Mostly green with a white-brown tint
3. Fully green

A subjective numerical code was used to assess the grasses in the area where oryxes were observed. This assessment was made in terms of the phenology of the grass as well as the percentage of green material in the grass layer. The percentage crown cover of the grass layer was also estimated. The density of the trees and shrubs was estimated as the number of trees or shrubs per hectare, and were then entered into one of five density categories. The degree of greenness of the trees and shrubs was recorded as for the grasses and annual plants based on the percentage of green material present.

At each observation the grass layer was categorised into one of the following categories based on the growth stage observed:

0 = No grass present

1 = Sprouting

2 = Intermediate: the grass is mature but not flowering

3 = Mature, flowering grass

4 = Dormant

The following categories were recognised for the percentage ground cover of the grass layer:

0 = No cover

5 = 1 to 5% cover

20 = 6 to 20% cover

>20 = More than 20% cover

The tree and shrub densities were estimated as follows:

0 = No trees / shrubs

5 = 1 to 5 trees / shrubs per hectare (100 m^2)

10 = 6 to 10 trees / shrubs per hectare

15 = 11 to 15 trees / shrubs per hectare

>15 = More than 15 trees / shrubs per hectare

The following categories were used to estimate the percentage of green material in the grass layer and in the trees and shrubs.

0 = No grass / tree / shrubs

25 = 1 to 25% green material

50 = 26 to 50% green material

75 = 51 to 75% green material

100 = 76 to 100% green material

Locating oryxes with the help of an aircraft

Radio-tracking from the aircraft was done with the use of a Telonics TS1 scanner and TR2 receiver. An antenna was fitted to each wing of a Maule 6 aircraft. Radio signals could be monitored on both antennae simultaneously or on each one separately with the help of a cockpit-mounted left-right switch. Initially, standard transects were flown in a north-south direction across the protected area, at a height of 457 m (1 500 ft) above ground level. As the protected area became better known, however, the pilot was requested to fly to the areas known to be frequented by the oryxes first.

The reception of a radio signal indicated the presence of a specific oryx in a certain area. Therefore, once a signal was received, it was determined from which antenna, left or right, it was the loudest, whereupon the pilot was requested to turn to that side. This process was repeated until the aircraft flew over the specific animal. It was, however, still necessary to locate each oryx visually to determine the subhabitat used, the condition of the area, the density of the trees and shrubs and the percentage ground cover. The categories used for recording these variables were the same than that used during the ground surveys. The only variable recorded on the ground, and not during aerial surveys, was the phenology of the grass layer. An added advantage of visually locating the animal being radio-tracked was the plotting of accurate GPS locations.

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.

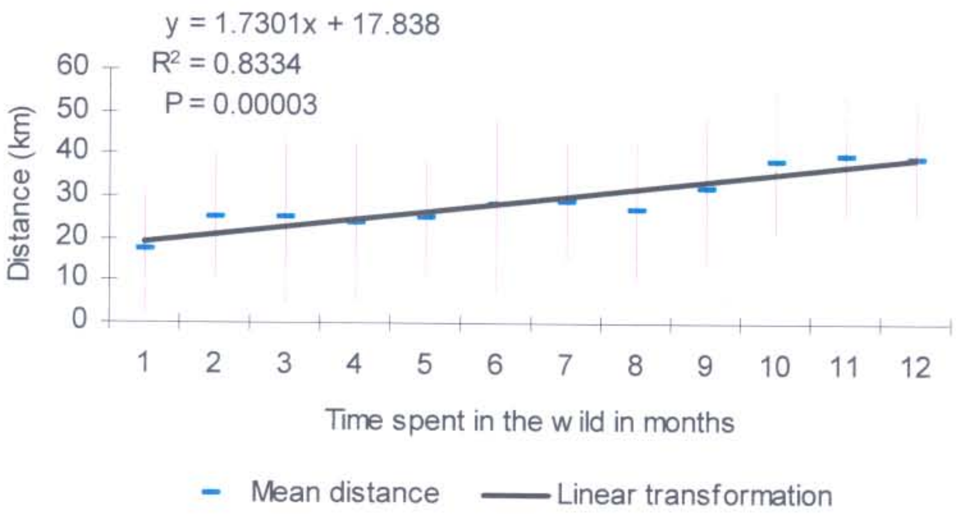


Figure 8: The relationship between the mean monthly dispersal distances (± 1 SD) of all the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia and the time spent in the wild for the first 12 months after release. The linear regression of the mean monthly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

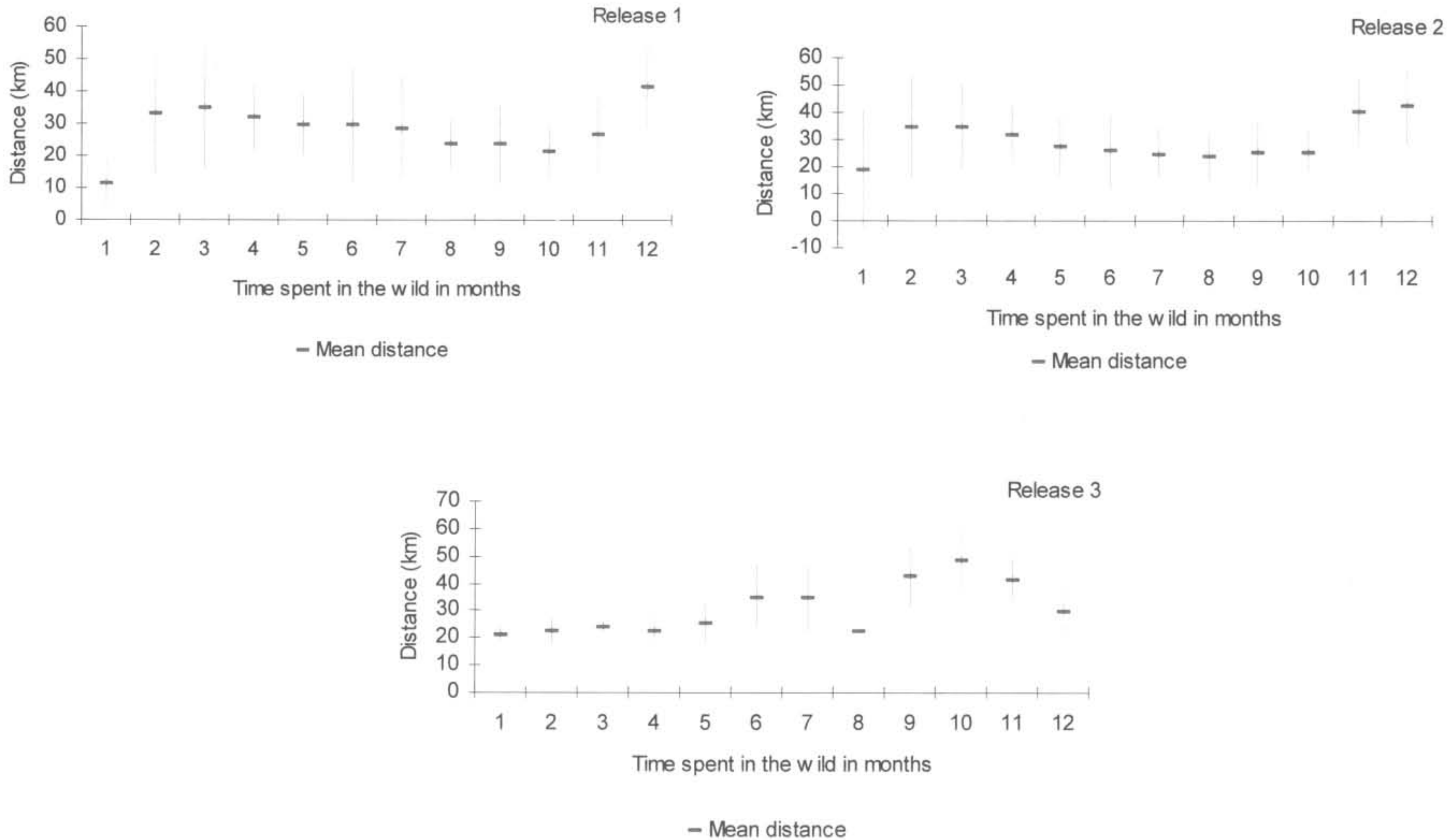


Figure 9: The mean monthly dispersal distances (± 1 SD) from the release site for the Arabian oryxes from the first three releases into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March to June 1995, for the first 12 months of monitoring after release.

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 = -

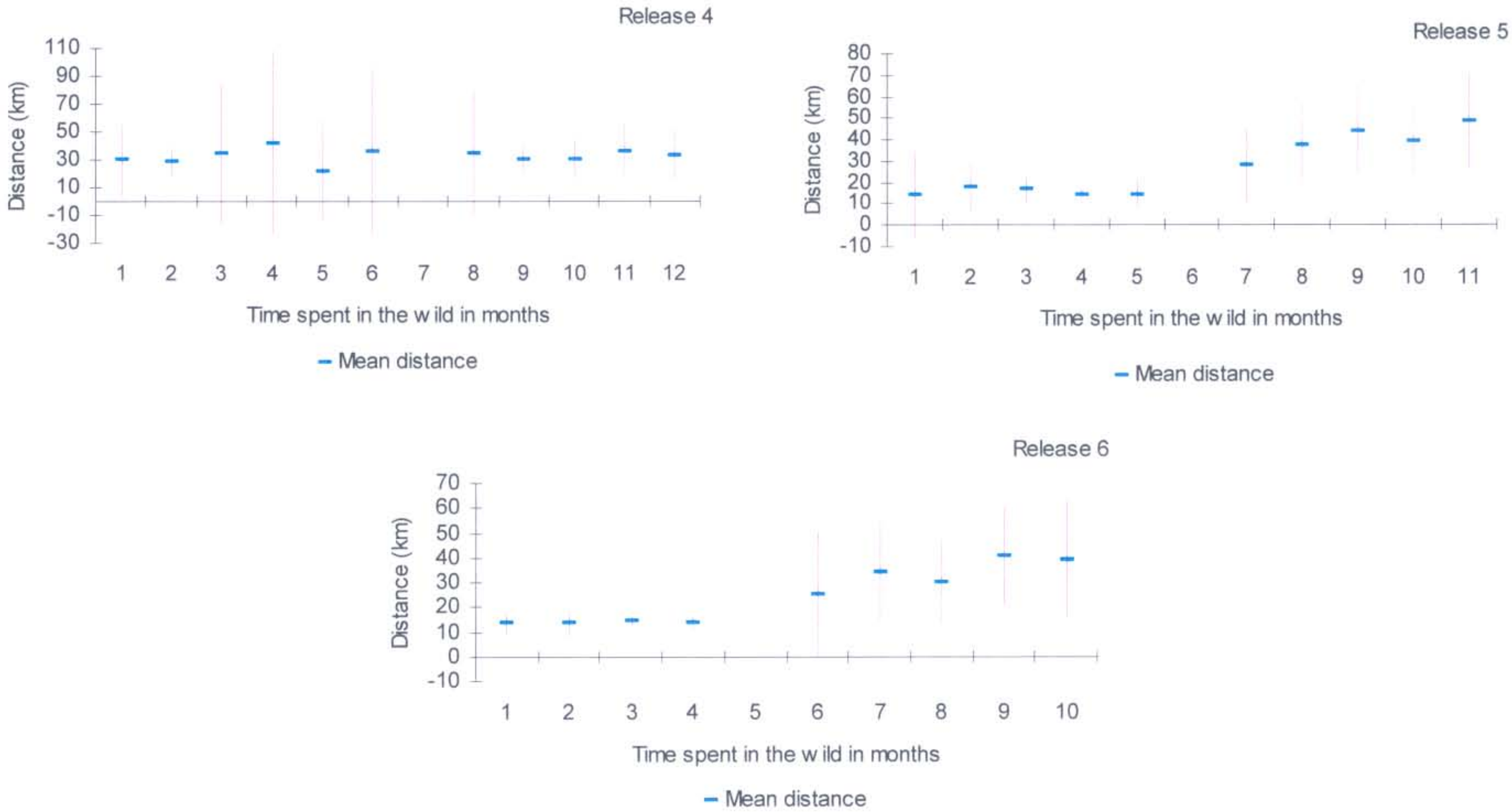


Figure 10: The mean monthly dispersal distances (± 1 SD) from the release site for the Arabian oryxes from the last three releases into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March to May 1996, for their entire monitoring period. There were no observations made during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

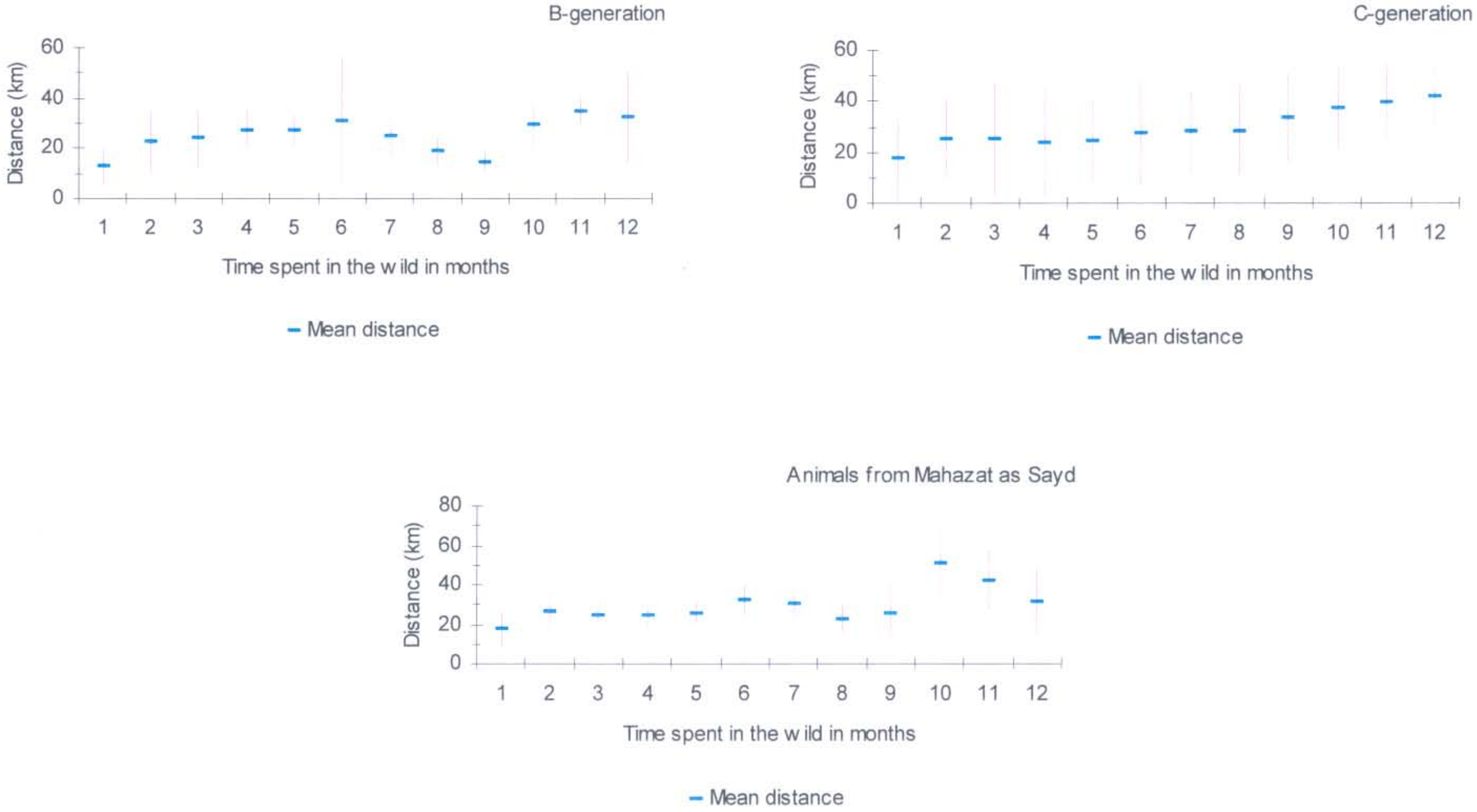


Figure 11: The mean monthly dispersal distances (± 1SD) from the release site for the Arabian oryxes of different origin as observed for the first 12 months after release in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia.

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

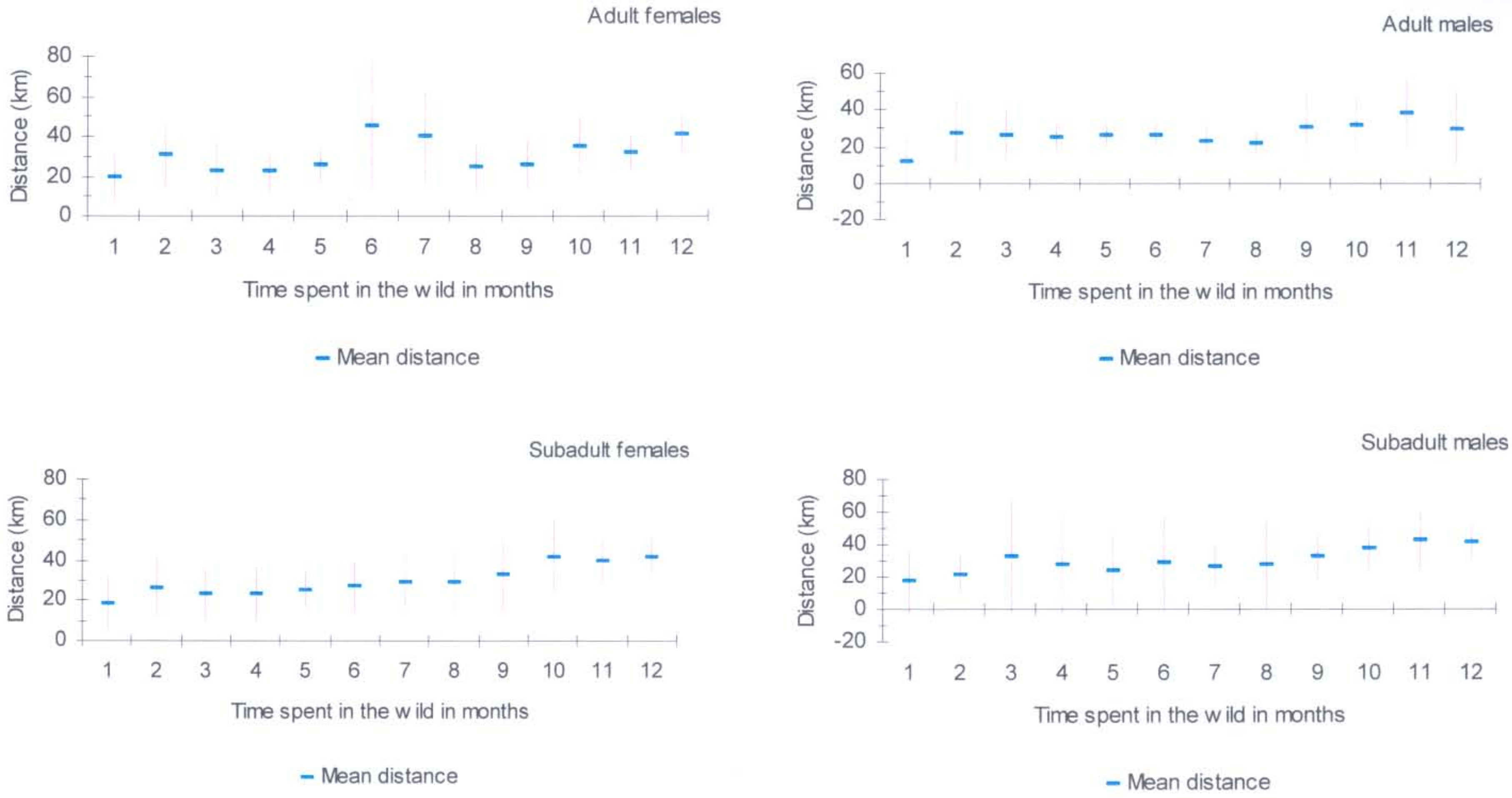


Figure 12: The mean monthly dispersal distances (± 1 SD) of the different Arabian oryx age and sex classes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997, during their first 12 months after release.

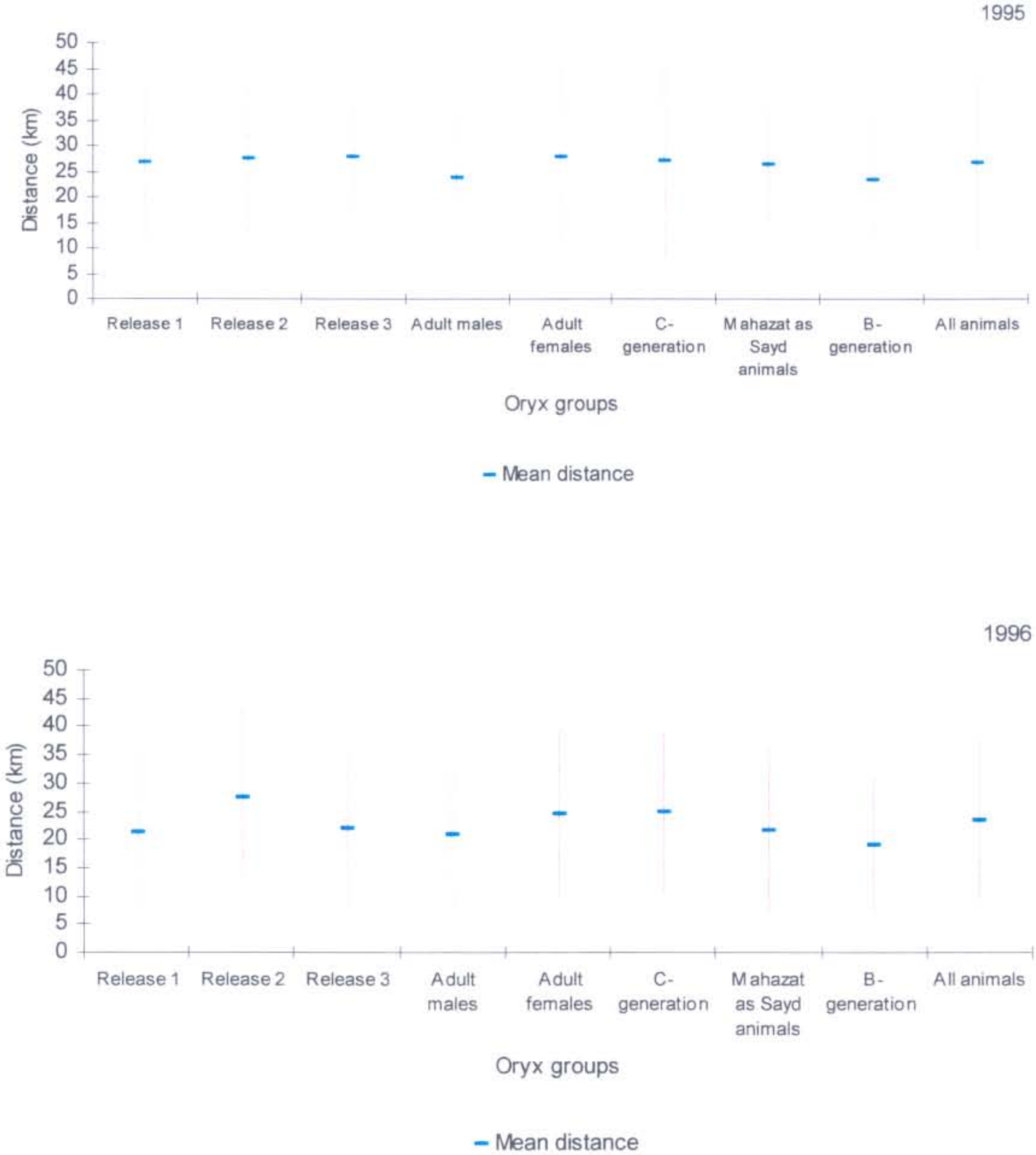


Figure 13: The mean annual dispersal distances (± 1 SD) from the release site for the different groups Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, in two successive years of monitoring after release.

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.

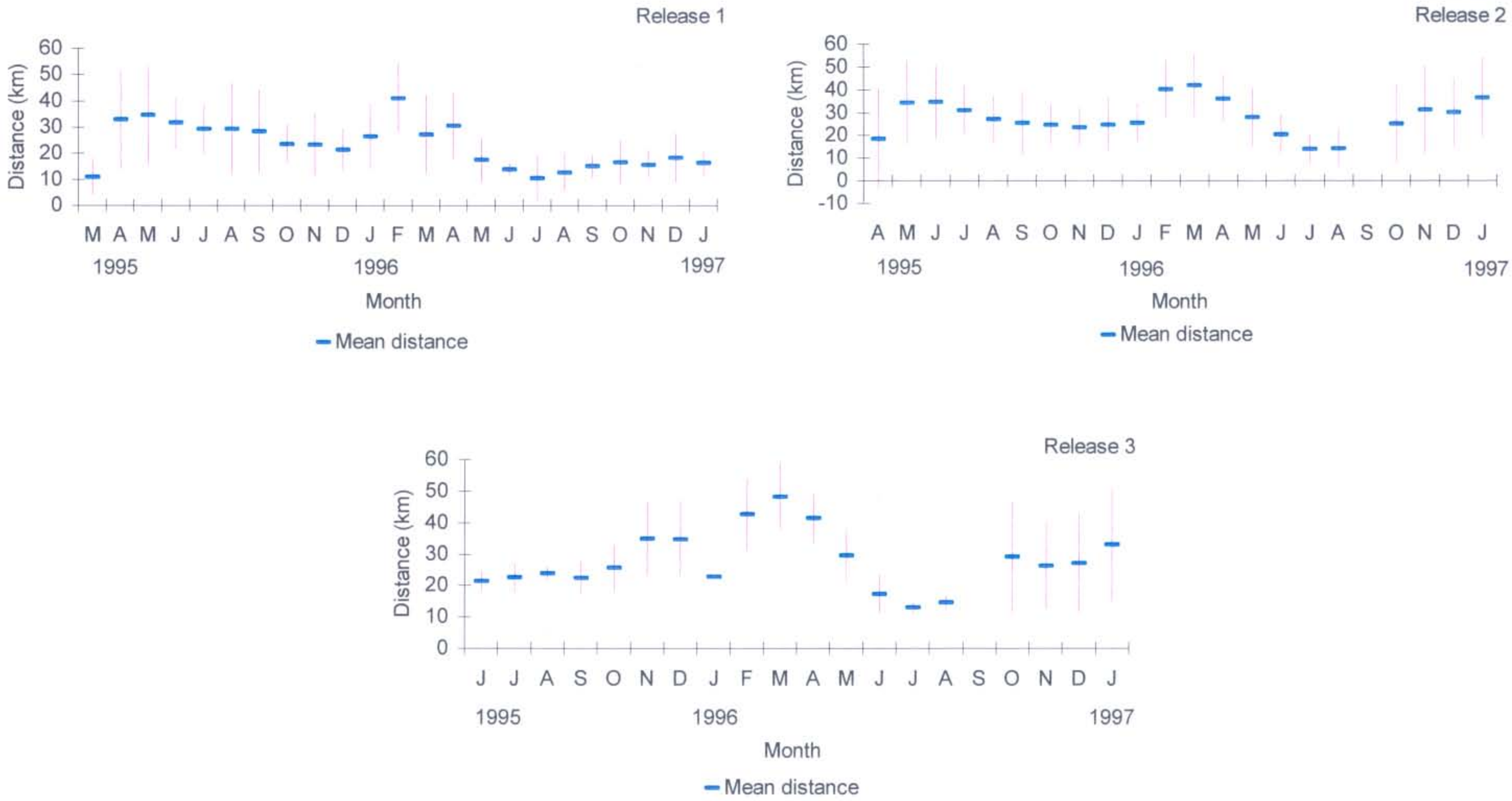


Figure 14: The mean monthly dispersal distances (± 1 SD) of the first three release groups of Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from the day of release to February 1997. No data are available for the animals from the second and third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

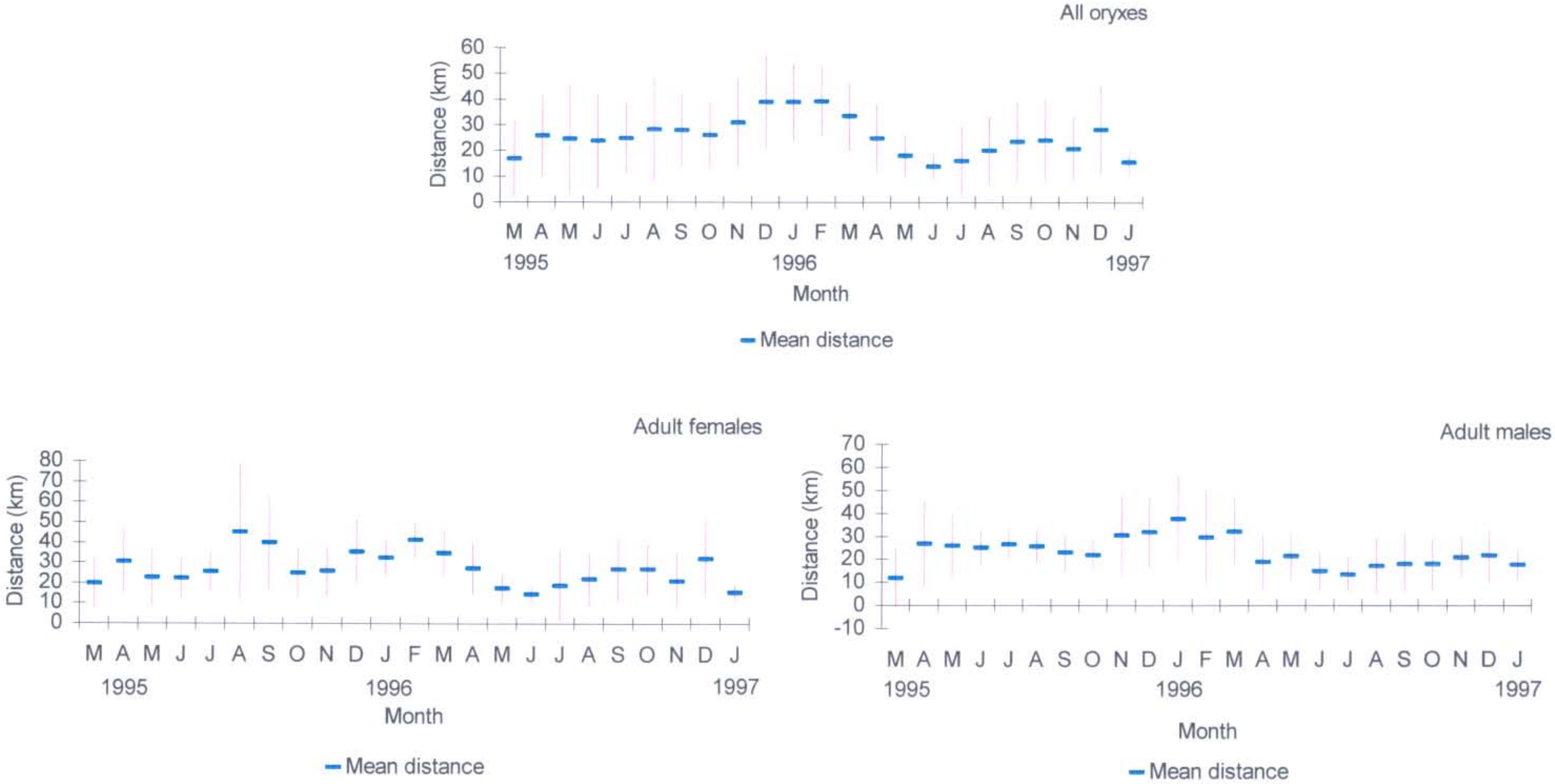


Figure 15: The mean monthly dispersal distances (± 1 SD) of all the Arabian oryxes combined as well as the different oryx age and sex classes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

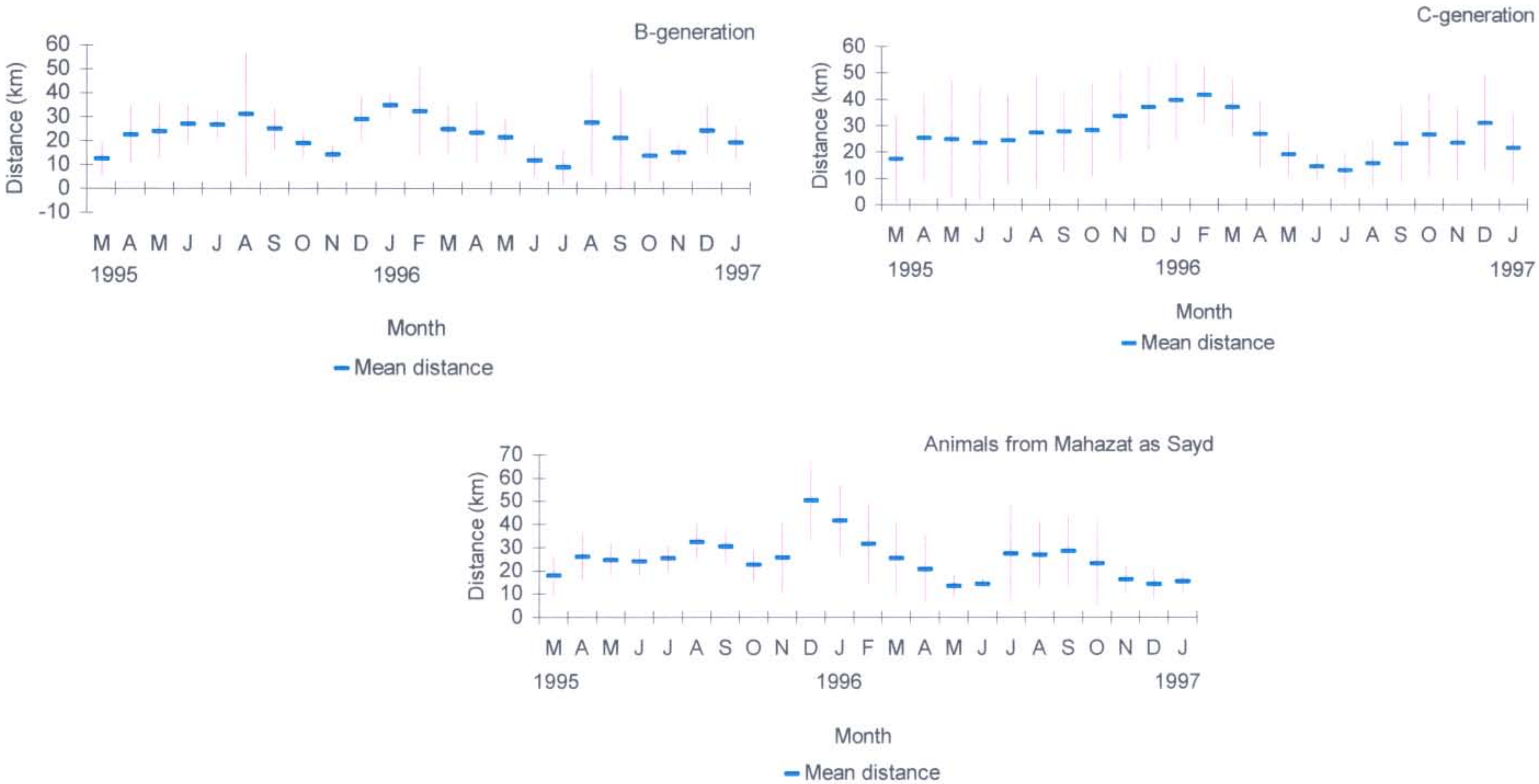


Figure 16: The mean monthly dispersal distances (±1 SD) of the Arabian oryx groups of different origin reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March to February 1997.

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.

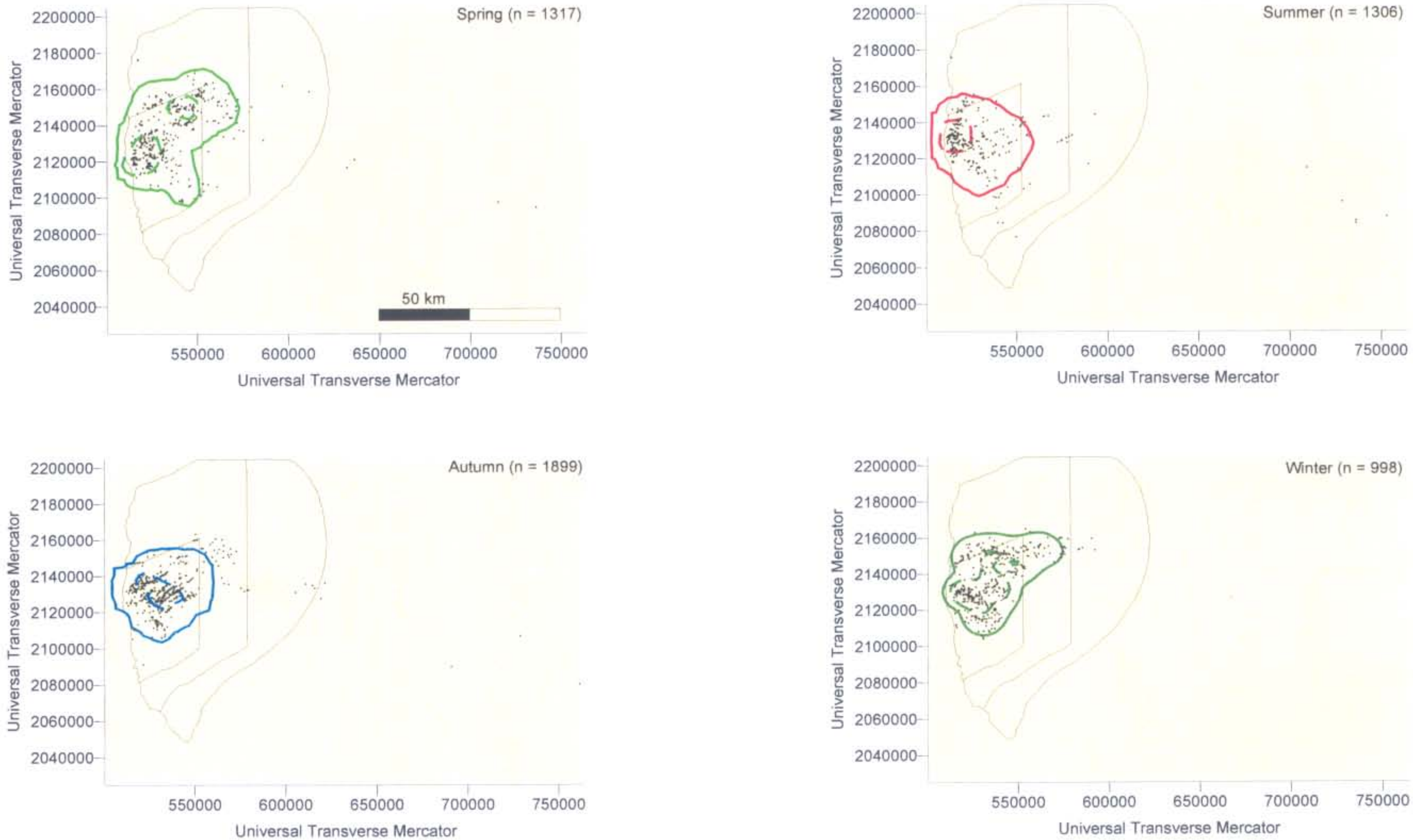


Figure 17: The seasonal distribution of all the Arabian oryx observations made in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the study period from March 1995 to February 1997. The seasonal ranges based on the 50% core use (dashed line) and the 95% use (solid line) Kernel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

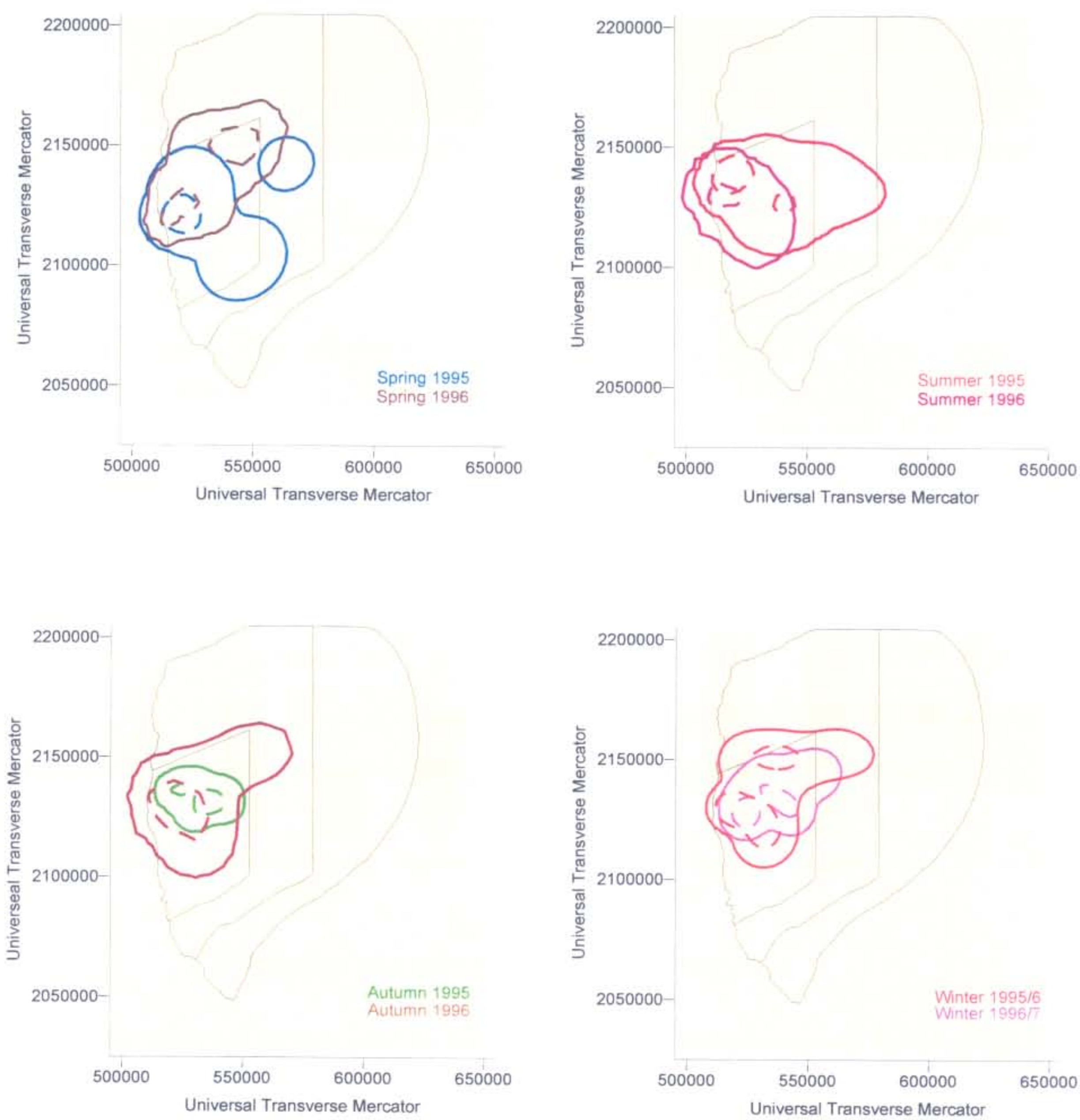


Figure 18: The annual seasonal ranges used by the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the study period from March 1995 to February 1997. The 50% core use areas are represented by the dashed lines and the 95% use areas by the solid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

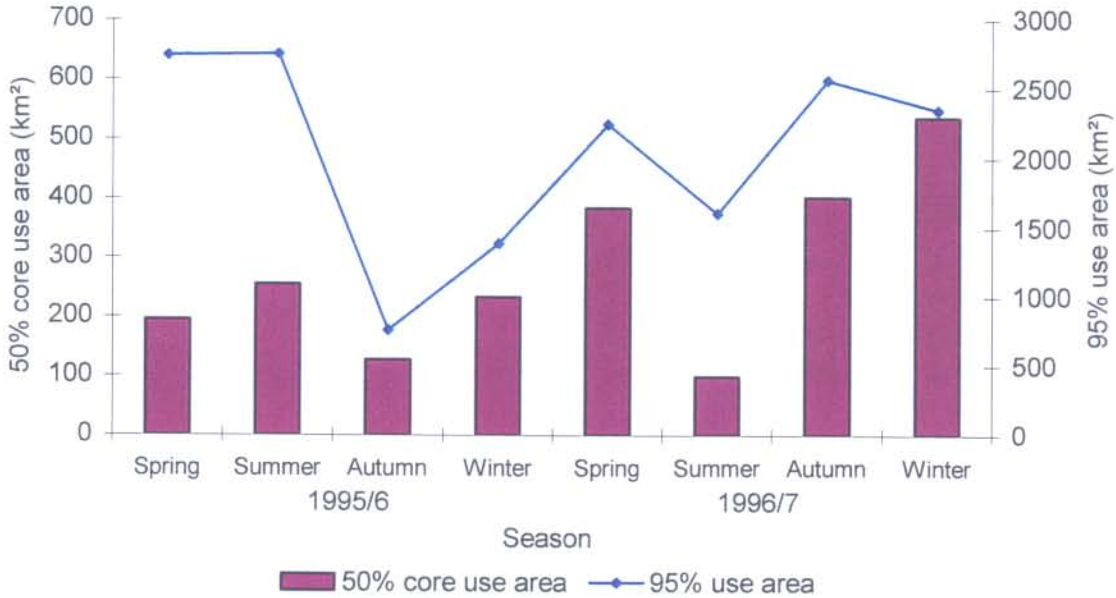
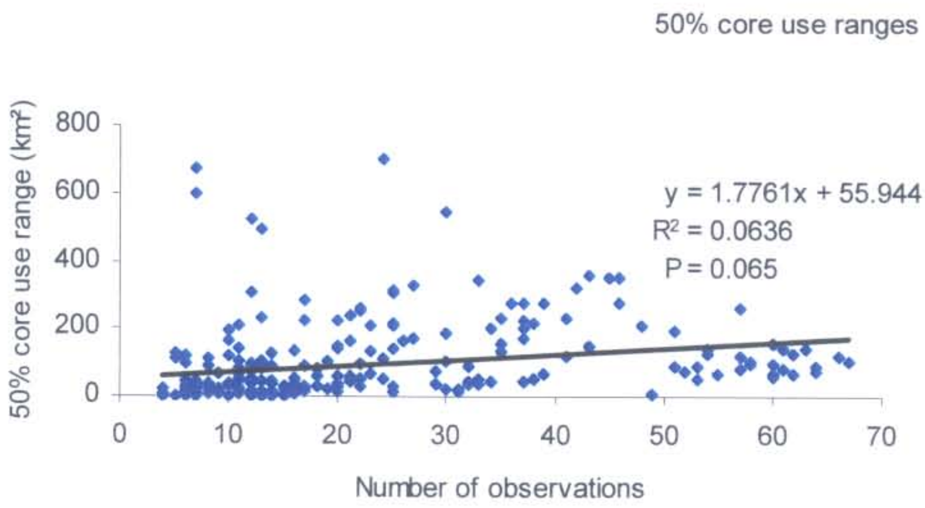


Figure 19: The seasonal ranges used by the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.



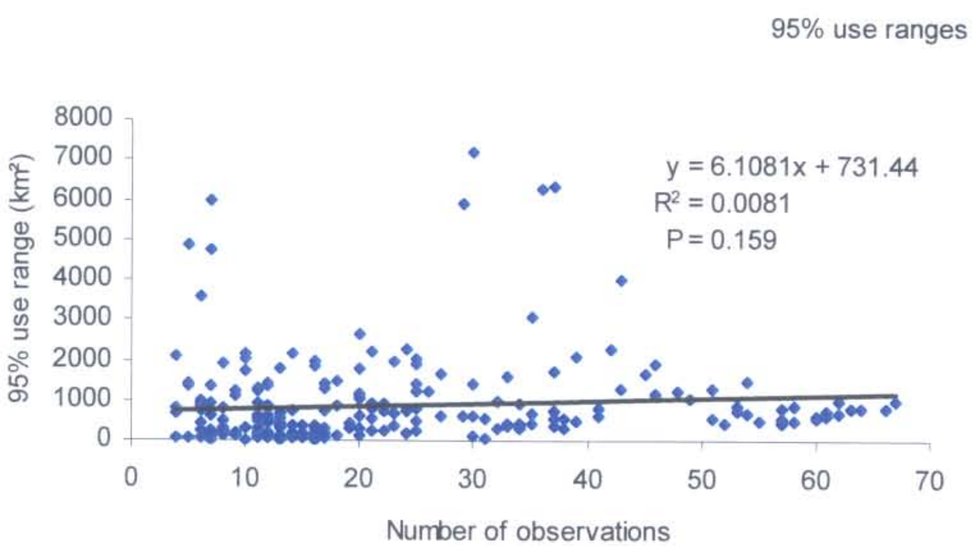


Figure 20: The relationship between the increasing number of observations and the 50% core use and 95% use range sizes of individual Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. The data are pooled for all individuals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

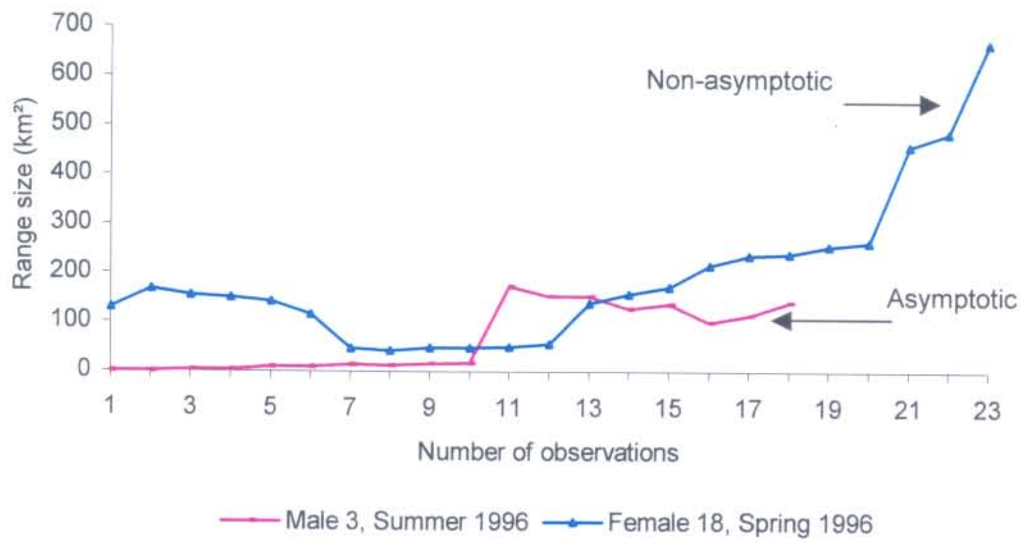


Figure 21: The relationship between the increasing number of observations of a particular Arabian oryx and the range size of that animal, as calculated through incremental area analysis, to illustrate the difference between the asymptotic and non-asymptotic ranges.

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

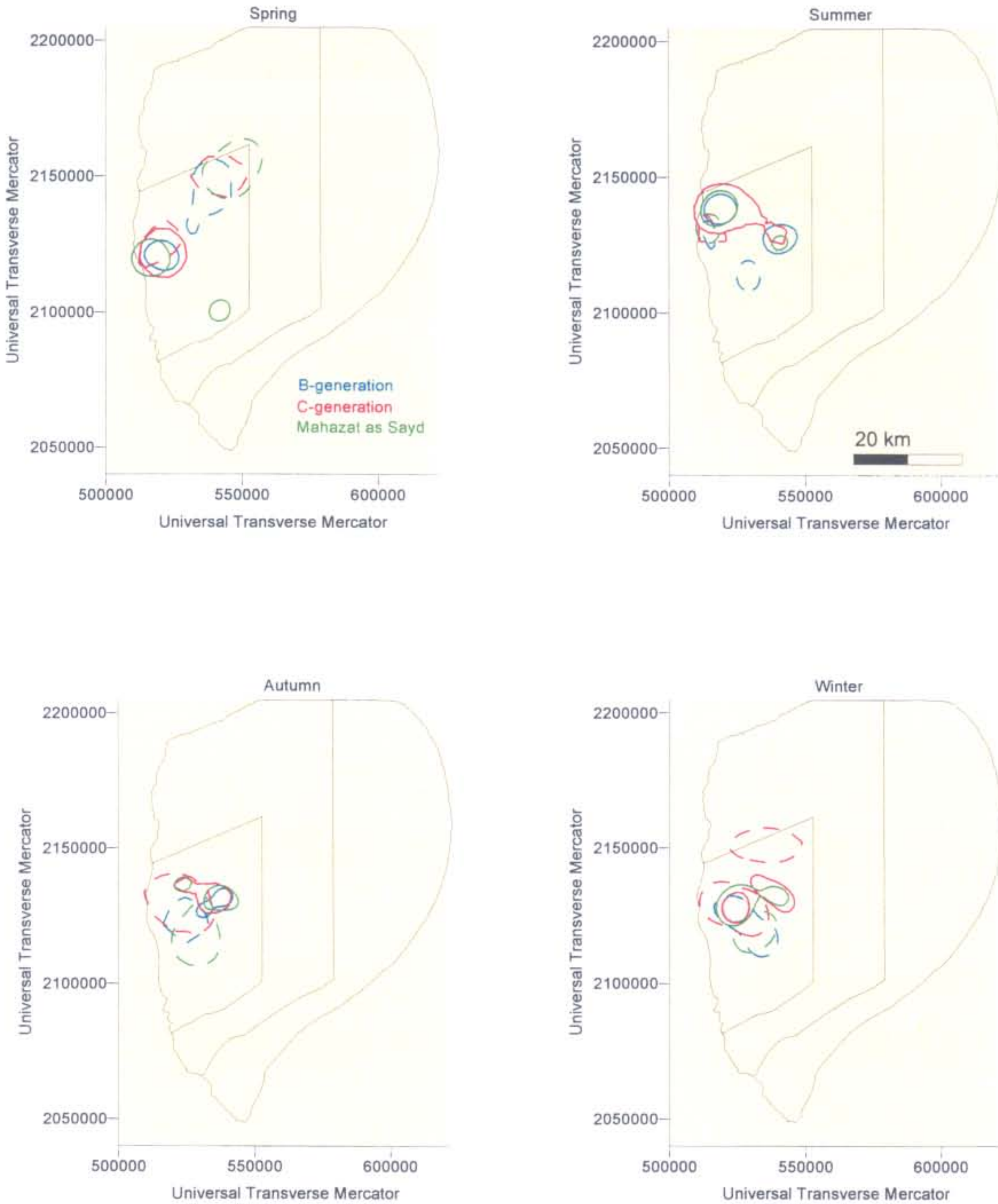


Figure 22: The seasonal 50% core use areas for 1995/6 (solid lines) and 1996/7 (dashed lines) of Arabian oryxes of different origin, reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

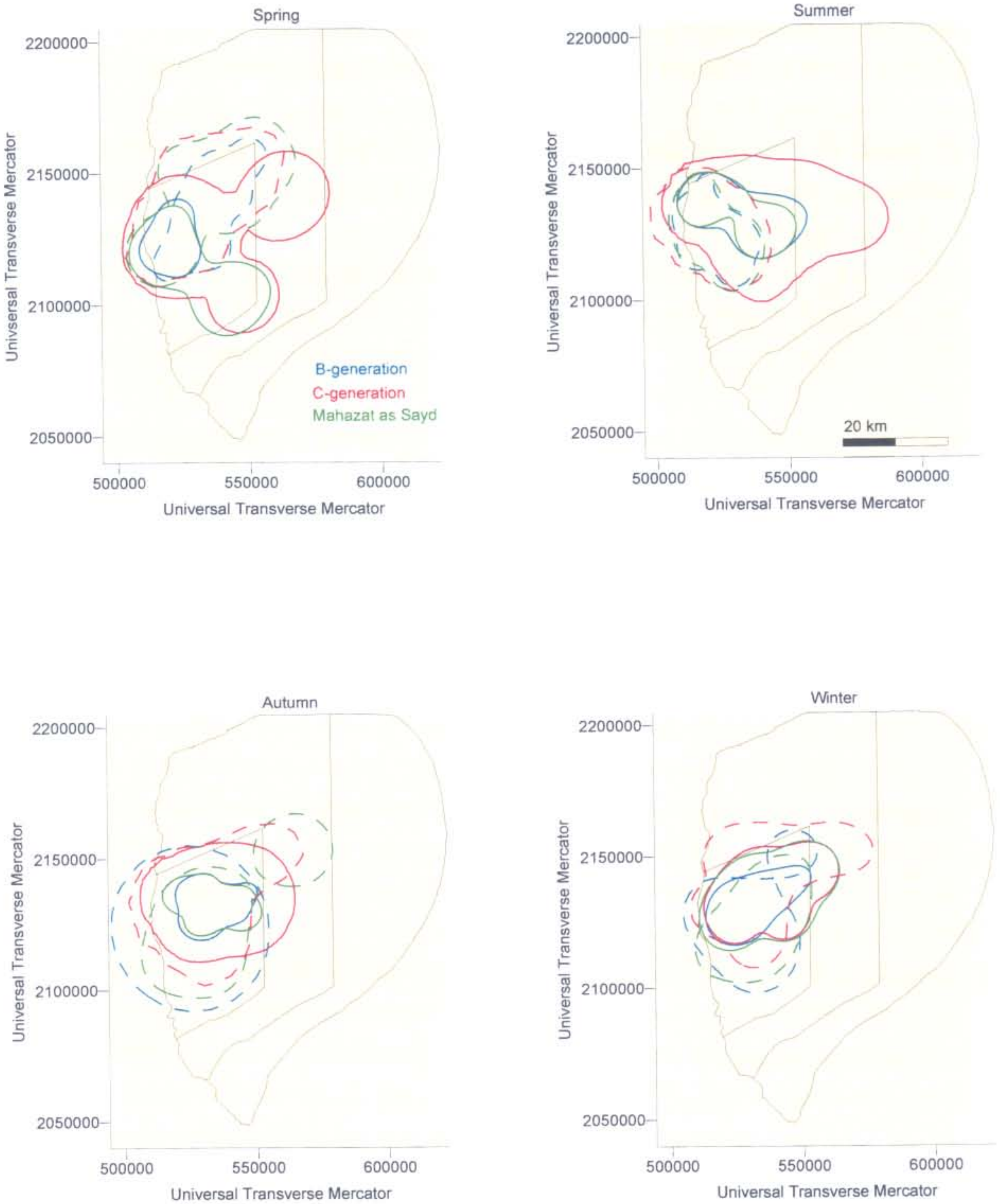


Figure 23: The seasonal 95% use areas for 1995/6 (solid lines) and 1996/7 (dashed lines) of Arabian oryxes of different origin, reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

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		RANGE USE	t-TEST	D.F.	P-VALUE
		1995	1996				
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 (km²) 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.

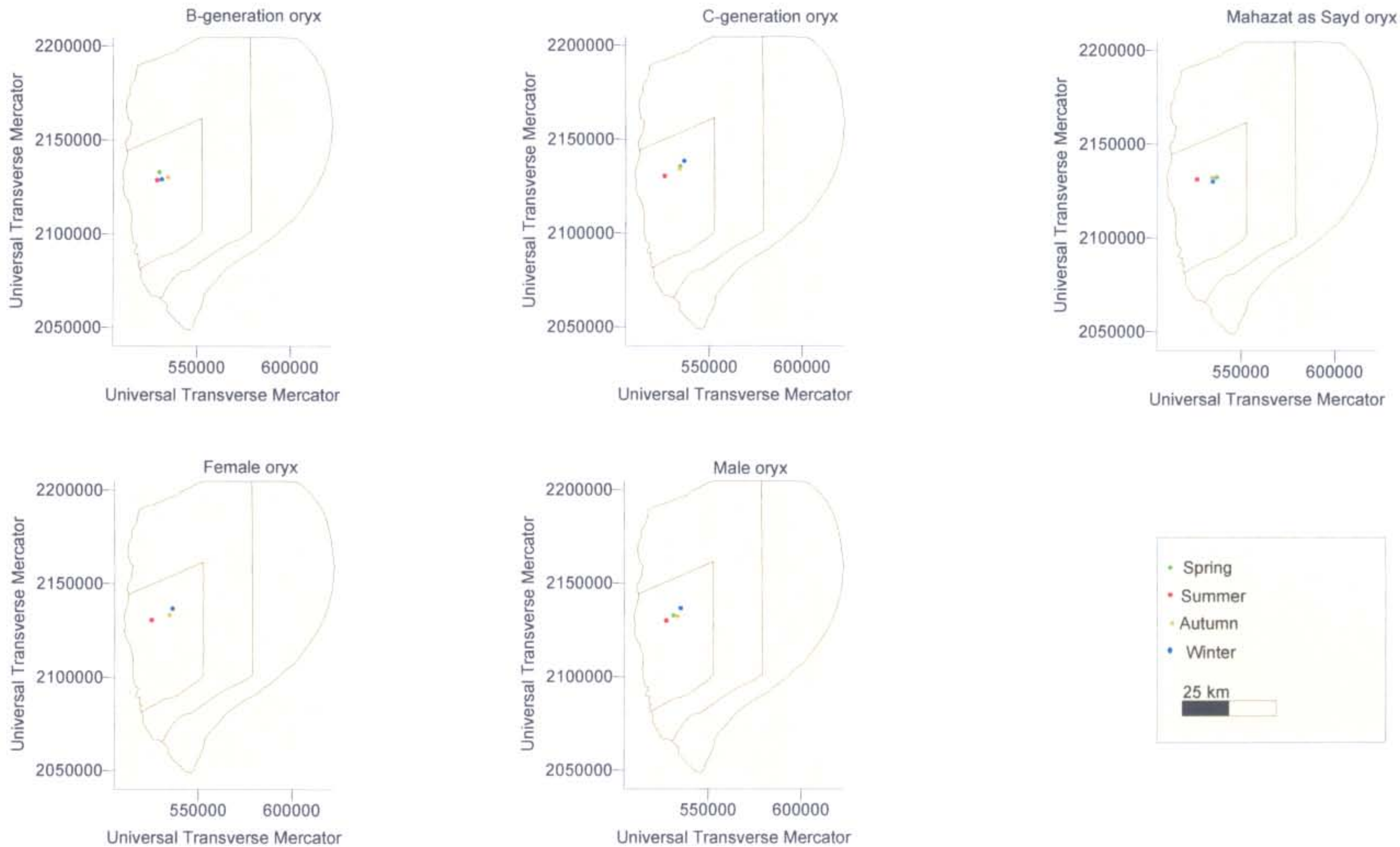


Figure 24: The mean seasonal distribution of different groups of oryx, combined over the 2-year study period as observed for the animals reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

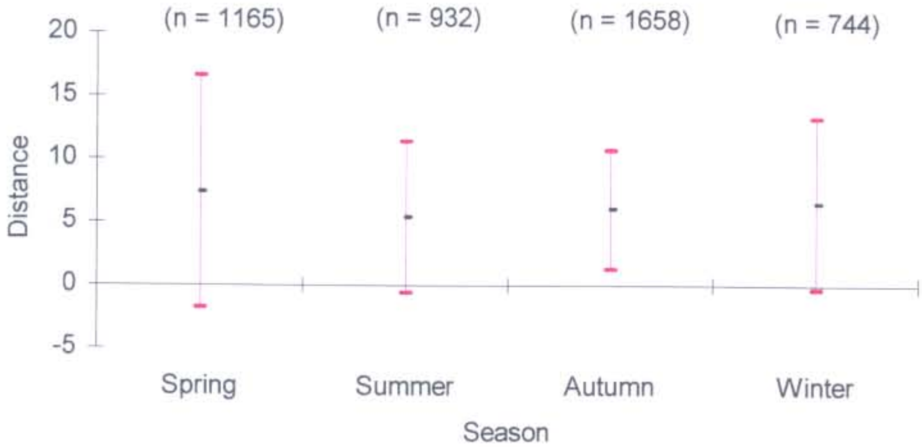


Figure 25: The mean (± 1 SD) seasonal distances (km) moved by the reintroduced Arabian oryxes in successive observations, 1-10 days apart, as observed in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. All the data are pooled across the years.

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.

CHAPTER 6

HABITAT UTILISATION

Introduction

The use that an animal makes of its environment includes its habitat and the associated variety of subhabitats it occupies. Therefore the subhabitat preferences of any animal are central to the study of animal ecology (Johnson 1980; Ben-Shahar & Skinner 1988; White & Garrot 1990). A habitat can be defined as the area that contain all the abiotic and biotic components necessary to an organism to sustain all of its requirements (Fabricius 1989; Joubert 1996). Habitats are composed of geomorphological characteristics such as topography, geological formations and soil types as well as the associated vegetation (Joubert 1996). Habitat can be regarded as a multivariate complex with the distribution of any specific organism in it being a function of the distribution of one or more biotic or physical community factors (Hirst 1975).

The degree of dependence of a ruminant on a certain habitat is determined by the availability of the ruminant's preferred food, the minimum size of the area for daily and seasonal activities (range use), the absence of extreme competition, the availability of cover, the opportunity for reproduction and the freedom to escape unnatural climatic extremes (Pienaar 1974). The fact that a species is invariably associated with a certain habitat or its elements indicates that the minimum requirements for the existence of the species are met in such a habitat (Riney 1982). In water dependent organisms the presence or availability of water plays an important role in subhabitat preferences (Engelbrecht 1986; Joubert 1996). It is the physical structure of the subhabitat that is the decisive factor when water and food is available in more than one place. Animals also show preferences for certain topographical features such as slopes, level territory or features brought about by geological formations like escarpments and rocky outcrops. In addition, soil types may also have an influence on the areas used. The geomorphological characteristics of any habitat can be regarded as unchangeable because changes normally take place slowly and over long periods (Joubert 1996). Plant species composition and vegetation structure is the two components that form an important part of an organism's habitat. The plant species, which constitute the vegetation, will determine whether or not the food source is sufficient. Similarly, the vegetation structure also plays an important part in determining if the habitat is suitable, through for example the availability of shelter and good visibility (Joubert 1996).

A number of reasons for the subhabitat preferences shown by animals have been found. These include the rate of forage production and the degree of vegetation utilisation (Wentzel, Bothma & Van Rooyen 1991). The availability of food at certain height classes (Sauer, Theron & Skinner 1977; Pellew 1983; Owen-Smith & Cooper 1989), the height of the grass layer (Ferrar & Walker 1974; Grobler 1981; Smuts 1982) and the plant phenology (Novellie 1983; Kok & Opperman 1985; Engelbrecht 1986) are also important factors in determining subhabitat use. All these factors determine the suitability of any particular area as a subhabitat for any given organism.

The reintroduction of animals as a conservation strategy has resulted in various unsuccessful projects. These projects often fail because the habitat requirements of the animals being released are not met in their area of release. This could be due to the deterioration of the habitat or it could be that an attempt is made to establish animals in an area where they have never occurred naturally due to unsuitable habitat. In the Limpopo province of South Africa one often finds that the gemsbok is released onto game ranches. This introduction of the gemsbok into areas outside of its historical range and where the habitat is unsuitable has adverse effects on the introduced populations. These effects range from the death of a large proportion of the animals involved, to a marked decrease in the productivity of the surviving animals, when compared with similar animals living in areas with suitable habitat (Strauss, *pers. obs.*). Moreover, in the South African National Parks, for example, 83.3% of all ungulate introductions into areas not historically occupied by the particular ungulates were considered failures more than 20 years after the event (Novellie & Knight 1994). This indicates that the availability of the appropriate habitat is one of the most important considerations when establishing or re-establishing ungulates.

In the current investigation the habitat utilisation of the Arabian oryxes that were reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia was studied. The extent to which environmental factors influence the habitat utilisation of the oryx were also investigated. An understanding of the habitat requirements of the Arabian oryx, and of the manner in which the different components or subhabitats are used on a seasonal basis by these animals, is essential in the light of future reintroductions. This part of the study is also important at the local management level of the 'Uruq Bani Ma'arid Protected Area, as no management plan can be formulated for a conservation area without detailed information on the subhabitat preferences of the wildlife species inhabiting such an area (Penzhorn 1982).

It was attempted to answer the following principal questions in this part of the study:

- Are there any seasonal differences in the way that the reintroduced Arabian oryxes use their habitat in the 'Uruq Bani Ma'arid Protected Area?

- What are the main driving forces behind the manner in which the Arabian oryxes use their habitat on a seasonal basis?
- What are the main habitat requirements for the Arabian oryxes?

Methods

The distribution and description of the subhabitats

At the time of the study there was no detailed information available on the extent and distribution of the different subhabitats within the 'Uruq Bani Ma'arid Protected Area. By using the 4-seat Maule aircraft of the National Commission for Wildlife Conservation and Development, seven transects were flown across the 'Uruq Bani Ma'arid Protected Area between 18° 55' N, 45° 09' E and 19° 35' N, 45° 40' E at approximately 152 m (500 ft) above ground level, on 19 January 1997. The regularity with which the northeast southwest aligned dunes occur, posed a problem as the data recording points could either be on the dunes or just between the dunes for transect after transect. It was therefore decided to keep the interval between recording points as short as possible. Consequently it was decided to record the subhabitat with every minute reading on the aircraft's Global Positioning System (GPS). Each of the seven transects consisted of 41 recording points.

The escarpment association, on the western edge of the protected area, is the most complex of the two vegetation associations because the topography includes the gravel plains and the sand sheets on the escarpment plateau, the mobile dunes and the incised wadis. These topographical features were used to distinguish the different subhabitats. The escarpment association is also most rich in trees and shrubs. As one progresses from the westernmost boundary of the 'Uruq Bani Ma'arid Protected Area towards the east, the number of trees and shrubs decreases and the habitat becomes more uniform. For this reason, the surface area of the protected area was stratified for the surveys. Due to time constraints the transects were flown in different directions, starting from the southern-most point in the eastern-most transect (stratified block 3) and commencing in a zigzag pattern to the western-most transect in stratified block one (Figure 26).

Due to the relative complexity of the escarpment association, three transects were flown at 3-minute intervals in this area (hereafter referred to a stratified block one). In stratified block 2, directly east of stratified block 1, three transects were flown at 5-minute intervals. This was done because the distribution of especially the *Acacia* trees and shrubs continues into the initial stages of the *shiquats,* which fall inside this stratified block. In stratified block 3, which solely consists of undulating sand dunes, a single transect was flown. This transect was 10-minutes flying time to the east of the last transect in stratified block 2. Experience in the 'Uruq Bani Ma'arid Protected Area revealed that the most common tree or shrub types in the area are *Acacia tortilis*, *Acacia ehrenbergiana* and *Calligonum crinitum* ssp. *arabicum*. Therefore only the genera *Acacia* and *Calligonum* were noted during the survey. The degree of availability of the trees and shrubs was recorded in one of three subjective classes at every recording point. These classes were none, few and many. Since this part of the survey was mainly done to determine the extent of shade available to the Arabian oryx, no attempt was made to differentiate between trees and shrubs.

There are two different vegetation associations which can be distinguished in the 'Uruq Bani Ma'arid Protected Area (Chapter 2). These are the escarpment association and the sand association, which can each be divided into a number of subhabitats. In the present study vegetation surveys were done to describe the different subhabitats in the protected area. The step-point method (Mentis 1981) was used in each survey. Each survey consisted of 150 step-points, with the exception of two surveys that consisted of 100 step-points only, with the plant species indicated at each point being recorded. The percentage crown cover was also recorded at 20-step intervals along each transect.

Habitat use

It has long been known that there is a relationship between animals and their environment, as illustrated by the accounts of the early travellers on the Arabian Peninsula (Thesiger 1948). Studies on mammalian herbivores in relation to their environment were initially simply qualitative descriptions of habitat use (Lamprey 1963; Pienaar 1963). In its simplest form quantitative studies on habitat use express habitat utilisation in terms of the proportion of animals seen in each subhabitat (Scogings, Theron & Bothma 1990). The comparison of the observed subhabitat use with the expected subhabitat use, according to subhabitat availability, is an extension of these simple quantitative studies (Hirst 1975). More complex quantitative analyses of the relationship between herbivores and their habitat include various multivariate analysis techniques. Among those techniques used often are discriminant function analysis (Ferrar & Walker 1974), multiple regression (Hirst 1975; Ben-Shahar 1986), correspondence analysis (Beardall, Joubert & Retief 1984; Ben-Shahar 1986; Engelbrecht 1986; Vermaak 1996) and detrended correspondence analysis (Scogings, *et al.* 1990). More recently the categorical modelling of data have also been used to determine the relationships between herbivores and their habitat (Weaver 1995; Von Holdt 1999). Multivariate analyses are now more accessible due to the development of rapid, flexible computer programs (Scogings, *et al.* 1990).

Studies using multivariate analysis techniques do not require information on the amount of subhabitat available, a record of habitat variables* at each animal location is sufficient. Some of the drawbacks of the traditional multivariate analysis methods include the assumption of normally distributed data, which is seldom justified in ecological data. Another drawback of many of the multivariate techniques is that a linear relationship between variables is assumed. In ecological data the relationship between variables is usually more complex (Beardall, *et al.* 1984).

In this part of the study 4838 observations of individual oryx were used for the analysis of habitat use. The data were collected by category and summarised in contingency tables.* These data were then subjected to statistical analyses using the SAS® computer program (SAS/STAT® 1999). For the analysis of the habitat utilisation data, three different analysis techniques were considered, one of which gave meaningful results.

Correspondence analysis is theoretically equivalent to a number of techniques, including reciprocal averaging, which is used in ecological and botanical studies (Hill 1974). Correspondence analysis provides a graphical display of data arranged in a two-way table of rows and columns. The only assumption is that the data are non-negative. The analysis is used to obtain a simultaneous graphic display of the relationship between the objects (rows) and the variables (columns) of a matrix of non-negative numbers. The matrix is subjected to a double-standardisation process, which means that it is re-scaled both column-wise and row-wise after which the principle axes are extracted. These axes are chosen in such a way that inertia is maximised. This inertia is calculated as a squared distance measure and it is proportional to the χ^2 statistic for testing the hypotheses of independence between rows and columns and is in fact a measure of the deviation of the data from this hypothesis (Beardall, *et al.* 1984). Greenacre (1981) as well as Greenacre and Underhill (1982) give detailed descriptions of the technique. Correspondence analysis was, however, found to be an inappropriate technique for analysing the habitat utilisation data in the present study due to the large number of variables investigated, the size of the data set and the subsequent complexity of the graphical displays (Grimbeek, *pers. comm.*[2]).

Cluster analysis, through the use of PROC VARCLUS (SAS/STAT® 1999) was another potential analysis technique that was investigated. This is a type of oblique component analysis, which is related to multiple group factor analysis (Harman 1976). The VARCLUS procedure divides a set of numeric variables into either disjoint or hierarchical clusters. Associated with each cluster is a linear combination of the variables in the cluster, the centroid component. Centroid components are unweighted averages of either the standardised variables or the raw variables. The procedure stops when each cluster satisfies a user-specified criterion involving either the percentage of variation accounted for or the second eigenvalue of each cluster (SAS/STAT® 1999). This technique was discarded in the present study after some investigation as it was also considered to be unsuitable due to the complexity of the data and the difficulty in interpretation of the clusters.

The categorical data modeling procedure (PROC CATMOD) analyses data that can be presented by a multiway contingency table. The rows of this table correspond to populations (or samples) formed on the basis of one or more independent variables. The columns of the table correspond to observed responses formed on the basis of one or more dependent variables. The frequencies in the table are assumed to follow a product multinomial distribution. This corresponds to a sampling design in which a simple random sample is taken for each population. PROC CATMOD uses either of the following:

- Maximum likelihood estimation of parameters for log-linear models and the analysis of generalised logits
- Weighted least-squares estimation of parameters for a wide range of general linear models

Linear models are fitted to functions of response frequencies and PROC CATMOD can be used for a wide variety of categorical data analyses such as linear and log-linear modeling, logistic regression, repeated measurement analysis and analysis of variance. Many of these analyses are generalisations of continuous data analysis methods. In the traditional sense, for example, analysis of variance refers to the analysis of means and the partitioning of variation among the means into various sources. In PROC CATMOD, however, analysis of variance is used in a generalised sense to denote the analysis of response functions and the partitioning of variation among those functions into various sources. The response functions might be mean scores or marginal probabilities, cumulative logits or other functions that incorporate the essential information from the dependent variables (SAS/STAT® 1999).

The habitat utilisation data collected in the 'Uruq Bani Ma'arid Protected Area were subjected to the categorical modelling procedure. Within PROC CATMOD the data were subjected to analyses of variance (ANOVA) by using the weighted least-squares technique for parameter estimation. Each observation in the current study entailed 19 variables. The categories of some of these variables were changed before analysis so as to get rid of categories containing none or

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only a few observations. An attempt was made to have the same number of categories for each variable across all four seasons. This was achieved for the majority of variables (Appendix A). The variables with their revised categories were then submitted to the PROC CATMOD. The habitat (VV16), with its four subhabitat categories, was used as the response variable, while the herd size (VV3) was used as a weighting factor. Variables were then selected for inclusion into the seasonal models, through a "bottom upwards" sequence using PROC CATMOD. This entailed running PROC CATMOD with just herd size (VV3) as the weighting factor in the model, while all other variables were in the pool for possible inclusion into the second step of the model. From the subsequent results the most significant variable with the highest χ^2-value was selected and included in the model for the next step (Table 10). Based on the example in Table 10, both the weighting factor (VV3) and the percentage green material on the trees (VV8) were included in the next run of the model, while all the remaining variables stayed in the pool for possible inclusion in a following run.

In this way more and more significant variables, as well as interactions between variables already in the model, were added to the model for each particular season until no more significant variables or interactions could be found. If any particular variable already in the model became non-significant in later steps of the model, the particular variable was excluded in the steps following the first non-significant observation of that variable, unless that variable was part of a significant interaction also found in the model. The model building was therefore hierarchical (Grimbeek, *pers. comm.*). Interactions between different variables are indicated with the abbreviation, vs., the interaction between the general condition of the vegetation and the percentage green material in the trees is therefore abbreviated as (VV6 vs. VV7).

Once the model for each season was saturated with variables, which happened when none of the remaining variables in the pool were significant in terms of those already in the model, the process was terminated and repeated for the next season. The next step was to create contrast statements for all the variables, and their categories, which were incorporated into each of the seasonal models. In effect a contrast statement is a hypothesis on the seasonal habitat use of the oryxes. These hypotheses are created, in turn, for each category of each variable and played off against the various categories of the response variable or subhabitat. For example: the general condition of the vegetation (VV6) was included in the final model built for autumn and consists of two categories, notably "good" and "bad". The response variable (VV16) has four subhabitat categories, notably dunes, escarpment area, *shiquat* sand sheets and *shiquat* gravel plains. The first set of hypotheses tested would then be:

When the vegetation is in good condition is it more likely that the animals would be found in

Table 10: The output of the hierarchical "bottom-upwards" approach used in PROC CATMOD to select the variables to be included in the seasonal models for further analysis (the variable selected from this run, for inclusion in the summer model is indicated in yellow).

VARIABLE	DF	CHI SQUARE	PROBABILITY
General vegetation condition	3	130.94	<0.0001
Tree density	3	71.71	<0.0001
Green material on trees (%)	12	215.27	<0.0001
Shrub density	6	166.67	<0.0001
Green material on shrubs (%)	12	174.65	<0.0001
Green grass (%)	6	205.72	<0.0001
Phenology	6	88.00	<0.0001
Grass height (cm)	3	29.94	<0.0001
Crown cover (%)	3	77.05	<0.0001
Cloud cover (%)	12	20.29	0.0618
Activity	9	62.56	<0.0001
Time of day	6	40.38	<0.0001
Wind strength	6	42.42	<0.0001
Wind direction	12	36.28	0.0003
Ambient temperature	6	37.56	<0.0001
Gender	3	0.91	0.8233

- the dunes than in the *shiquat* gravel plains
- the escarpment areas than in the *shiquat* gravel plains
- the *shiquat* sand sheets than in the *shiquat* gravel plains?

This process would then be repeated for each of the other subhabitats by again posing the same question.

When the vegetation is in good condition is it more likely that the animals would be found in:

- the *shiquat* gravel plains than in the *shiquat* sand sheets
- the dunes than in the *shiquat* sand sheets
- the escarpment areas than in the *shiquat* sand sheets?

These hypotheses are tested by means of odds ratios*, each with its own probability. An example of a significant odds ratio would for example be that during autumn the Arabian oryxes are twice as likely (Odds ratio 2:1; $P = 0.021$) to be found in the dunes when the vegetation is in good condition than in the shiquat gravel plains, therefore proving the first of the hypotheses listed above to be correct.

Results and discussion

The distribution and description of the subhabitats

No observations were made at 5% of the recording points in the first stratified block because these points were below the western edge of the escarpment and therefore outside the protected area. The majority (51.2%) of the observations in stratified block 1 was made in the sand association, while the remaining 48.8% were made in the escarpment association. In the three transects flown in stratified block 2, 88 (71.5%) of all the records were in the dunes, while 17.0% and 11.4% were in the *shiquat* gravel plains and *shiquat* sand sheets respectively. In the most easterly block the one transect flown resulted in 41 recording points, all of which were recorded in the dune areas. The *shiquat* sand sheets with its scattered sand sheets are therefore replaced by the sand dunes to the east of the protected area, where most of the habitat becomes an undulating sand mass.

By combining the data from the three stratified blocks, it is evident that the subhabitats of the sand association are the most widespread in the protected area (Figure 27), constituting 79.7% of the total area. Within this association the dunes (66.3%) are the most abundant subhabitat followed by the *shiquat* gravel plains (17.7%) and the *shiquat* sand sheets (16.0%). The escarpment association forms only 20.3% of the protected area, with the wadis being the most

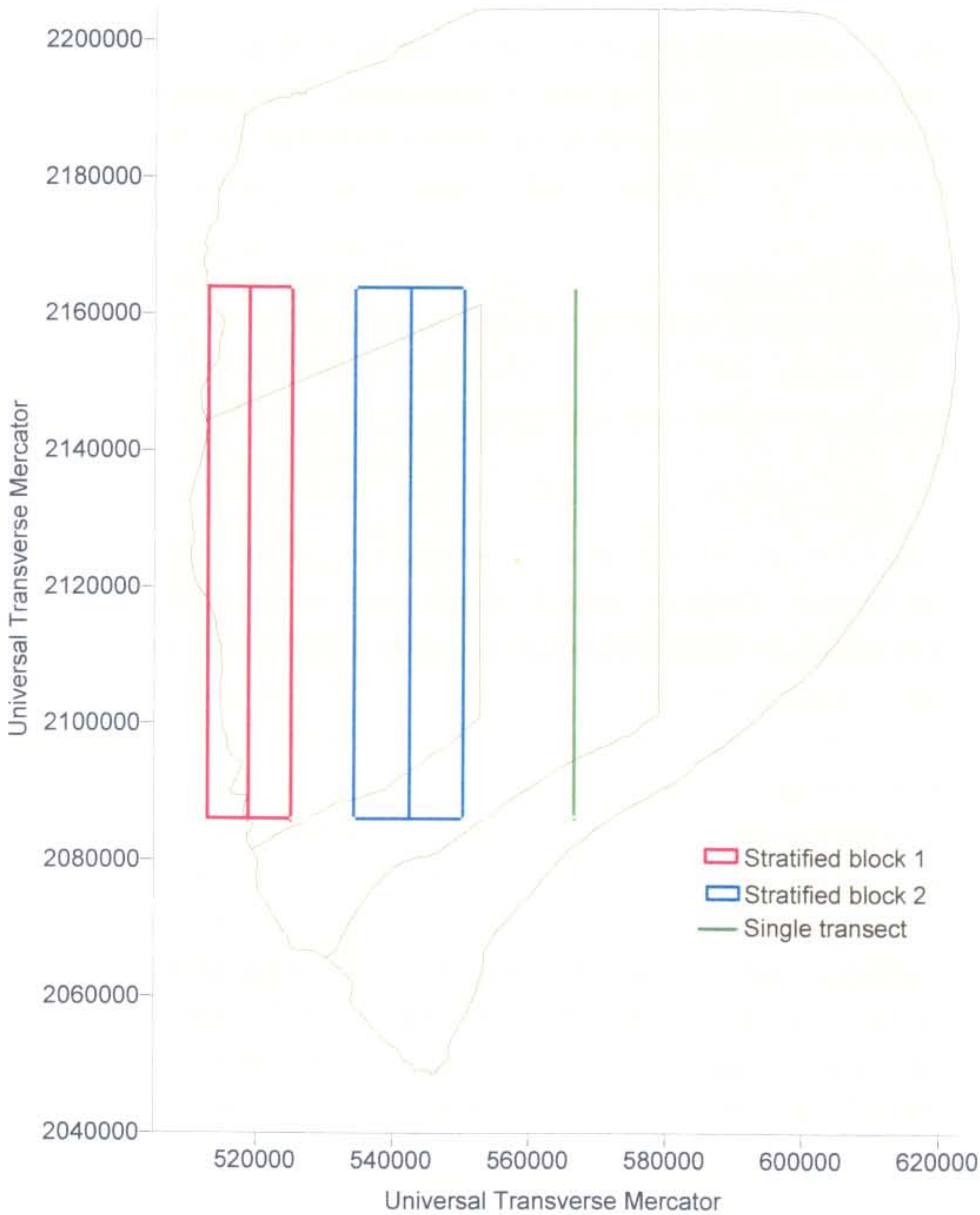

Figure 26: The transects, in three stratified blocks, flown across the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia in January 1997 to assess the proportional distribution of the subhabitats in the area.

abundant (45.6%) subhabitat in this association.

A total of 67 vegetation surveys was done in the 'Uruq Bani Ma'arid Protected Area. Of these, 16 surveys were done in the dunes, while 21 and 4 surveys were done in the *shiquat* sand sheets and the *shiquat* gravel plains respectively. Another 26 vegetation surveys were done in the escarpment zone. During these surveys a total of 55 plant species were recorded, 16 of which were not previously recorded in the protected area, bringing the total number of species known to occur in the area to 98 (Appendix B).

Based on the vegetation surveys, the largest diversity of plant species was recorded in the escarpment zone with 48 (87.3%) of the 55 plant species recorded during the surveys being found there. The escarpment association consists of the escarpment plateau with its sand sheets, gravel plains and the wadis (Figure 28). In the absence of sand the escarpment plateau is often devoid of any vegetation.

In areas where sand has accumulated, *Acacia* trees and especially shrubs are often found. Grass species found in these areas include *Panicum turgidum, Lasiurus scindicus, Stipagrostis foexiana, Aristida adscensionis* and *Dicanthium foveolatum*. Smaller shrubs that are often found in these areas include *Haloxylon salicornicum, Fagonia indica* and *Indigofera* spp. Near the heads of the wadis that are incised into the limestone plateau, *Acacia tortilis* trees and shrubs are common and perennial grasses such as *Dicanthium foveolatum, Stipagrostis plumosa* and *Stipagrostis foexiana* are found in these areas. Further down the wadis the *Acacia* trees are joined or replaced by *Leptadenia pyrotechnica*. Large tufted grasses such as *Panicum turgidum, Lasiurus scindicus* and *Pennisetum divisum* predominate, with shrubs such as *Haloxylon salicornicum* and *Crotalaria aegyptiaca*. Small perennial herbs include *Rhyncosia* spp. and *Heliotropium ramosissimum* (Dunham, Robertson & Wacher 1995). The percentage crown cover in the escarpment areas ranges widely from the bare escarpment gravel plains to the vegetation rich wadis. The percentage crown cover was, however, relatively high (6 to 20%) at the majority (61.5%) of recording points in the surveys.

The sand association consists of the dunes, the *shiquat* sand sheets and the *shiquat* gravel plains (Figure 29). The *shiquat* sand sheets and the dunes respectively contained 50.9% and 29.0% of the plant species recorded during the surveys. Only 9 (16.4%) of the recorded plant species were found in the *shiquat* gravel plains. The dunes are for the most part void of any vegetation. Shrubs found on the dunes are almost exclusively *Calligonum crinitum*, although *Haloxylon persicum* is locally abundant on one specific dune. Smaller shrubs

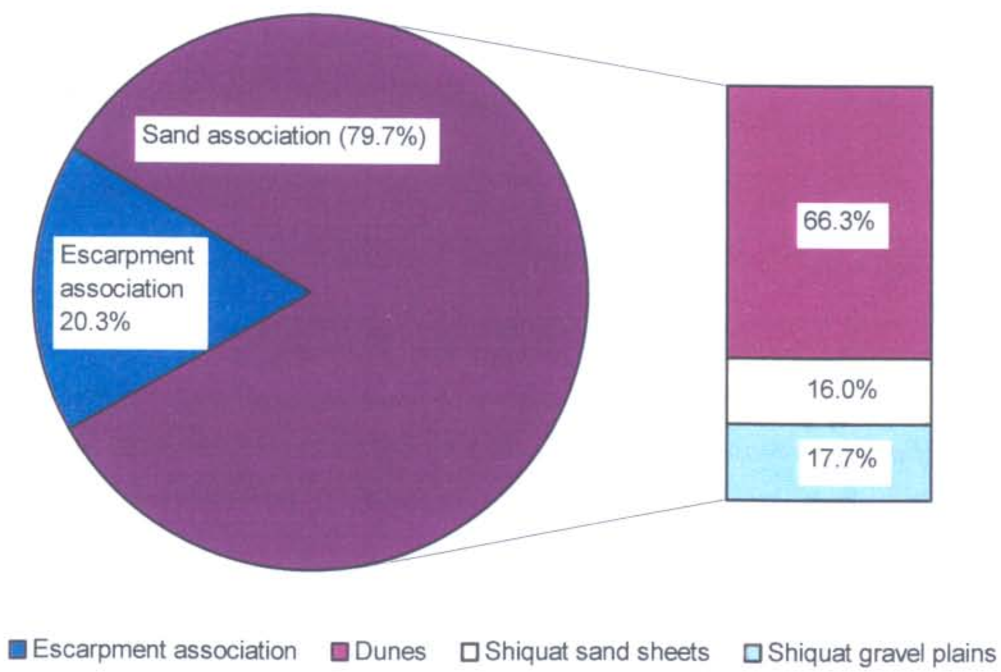

Figure 27: The proportional distribution in terms of surface area of the escarpment and sand associations with the subhabitats of the latter in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined through an aerial survey in January 1997.

include *Cornulaca arabica*, *Tribulus arabicus* and *Dipterygium glaucum*, while herbs such as *Heliotropium digynum* and *Moltkiopsis ciliata* are also found. Grass species in the dunes include *Stipagrostis plumosa*, *Stipagrostis drarii* and *Centropodia fragilis*, while the sedge *Cyperus conglomeratus* can be locally abundant. There is little variation in the percentage crown cover in the dunes. At all the recording points the percentage crown cover in the dunes was low (≤5%). *Acacia* trees and shrubs can be found in the *shiquat* sand sheets and the *shiquat* gravel plains, close to the escarpment association. As one moves deeper into the *shiquats* and further away from the escarpment association *Haloxylon salicornicum* shrubs replace the *Acacia tortilis* and *Acacia ehrenbergiana* trees and shrubs. Grasses on the *shiquat* sand sheets are mostly perennial and species such as *Panicum turgidum*, *Lasiurus scindicus* and *Stipagrostis plumosa* are frequently encountered. *Panicum turgidum* and *Stipagrostis plumosa* can also be found on the *shiquat* gravel plains, although less so than in the sand sheets.

As indicated before, the *Acacia* trees and shrubs predominate in the escarpment areas and the initial stages of the *shiquats*. As one moves further away from the escarpment edge in an easterly direction, the *Acacia* trees and shrubs decrease noticeably. A negative relationship exists between the distance from the escarpment edge and the occurrence of *Acacia* trees and shrubs (Figure 30). This relationship is significant ($P = 0.0039$). It does not, however, mean that there is no shade available in the form of shrubs further east into the *shiquats* of the 'Uruq Bani Ma'arid Protected Area. As the abundance of the *Acacia* trees and shrubs decreases with increasing distance away from the escarpment areas, the *Calligonum crinitum* subsp. *arabicum* shrub abundance increases with distance away from the escarpment. This relationship between the occurrence of the latter shrub and the distance away from the escarpment edge is also significant ($P = 0.0005$). It is not clear why the relationship between the frequency of occurrence and the distance away from the escarpment exists. It is possible that the water table is higher in the escarpment areas, and especially so in the wadis, due to the fact that water from the surrounding escarpment and even some *shiquat*s drain into these areas. This could explain why the *Acacias* species occur primarily on the escarpment areas, and why large trees are found in these areas and not in the other subhabitats.

Subhabitat use

Due to the vast amount of output generated by CATMOD (Appendix C), and for the sake of clarity, it was decided only to interpret those variables that were significant in two or more of the seasons (Table 11). A limited number of variables that were significant in only one

Figure 28: The escarpment association in the 'Uruq Bani Ma'arid Protected Area that consists of the plateau and the wadi subhabitats.

Figure 29: The sand association in the 'Uruq Bani Ma'arid Protected Area consists of the dune, the *shiquat* sand sheet and the *shiquat* gravel plain subhabitats.

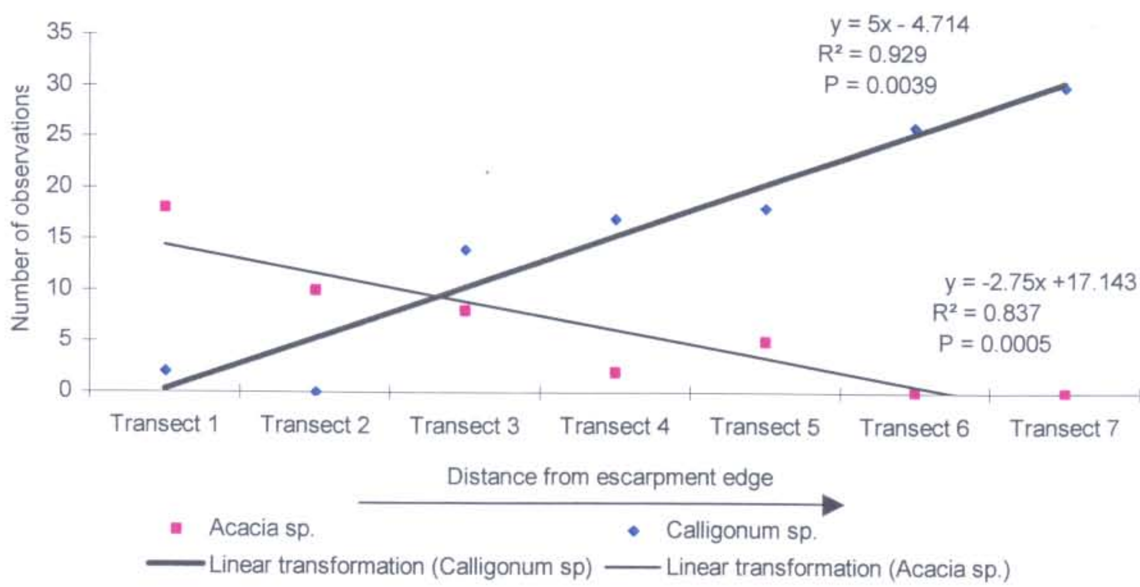

Figure 30: The relationship between the occurrence of *Acacia* and *Calligonum* trees and shrubs at increasing distances away from the escarpment edge on the western boundary of the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined through transects flown in a north-south pattern across the area. The values used do not refer to the number of individual plants but rather to the total number of observations per transect where the shrubs were recorded as present.

season were, however, also discussed if they were considered to be of particular importance during a particular season. When a single variable in a particular season was also found to be significant in interaction with another variable during the same season, the interaction is often discussed in the results, even when the particular interaction occurred in only one season. This is especially so when the interaction is considered to be ecologically more meaningful than the single variable. This practice is acceptable in interpreting CATMOD results as the significant variable(s) are still being dealt with, albeit in an interaction (Grimbeek, *pers. comm.*). An example of this is the percentage of green material in the trees (VV8), which as a single variable was significant in three seasons (Table 11). It is, however, only discussed as a significant single variable for autumn, and winter as VV8 was found in interaction during spring and summer. For the latter two seasons the interaction of the percentage green material in the trees and the percentage crown cover (VV8 vs. VV14) are presented.

The seasonal distribution of all the Arabian oryx observations, used for this part of the study, across the various subhabitats is shown in Figure 31. On a seasonal basis there is a definite shift in the extent of use of the various subhabitats. The escarpment areas seem, for example, particularly important to the Arabian oryxes during summer as 45.2% of all the observations during that season were made in these areas. During the other seasons, however, less than 10.0% of the seasonal observations of the animals were made in this area, illustrating the area's seasonal importance.

The final CATMOD models on which the odds ratios were calculated included 12 variables, including the weighting factor herd size (VV3), and 14 interactions between various variables (Table 11). The majority of the variables included in the final models were vegetation-based, such as the density of shrubs or the percentage green material in the grass layer, followed by such climatic variables as temperature and wind strength.

Notable subhabitat characteristics that were not included in the final models, and therefore were not of particular importance in the subhabitat use of the Arabian oryxes, included tree density (VV7), the percentage cloud cover (VV15) and the time of day (VV18). The absence of the tree density as one of the determining factors in subhabitat use is surprising, especially during summer. It is possibly indicative of Arabian oryx shade use behaviour. During the study period various observations were made of oryxes lying in the shade of large grass tussocks such as *Panicum turgidum*, indicating that the animals will use any form of shade that is available. It is also worth noting that the tree density was recategorised into only two categories for all seasons. These new categories represented conditions where the

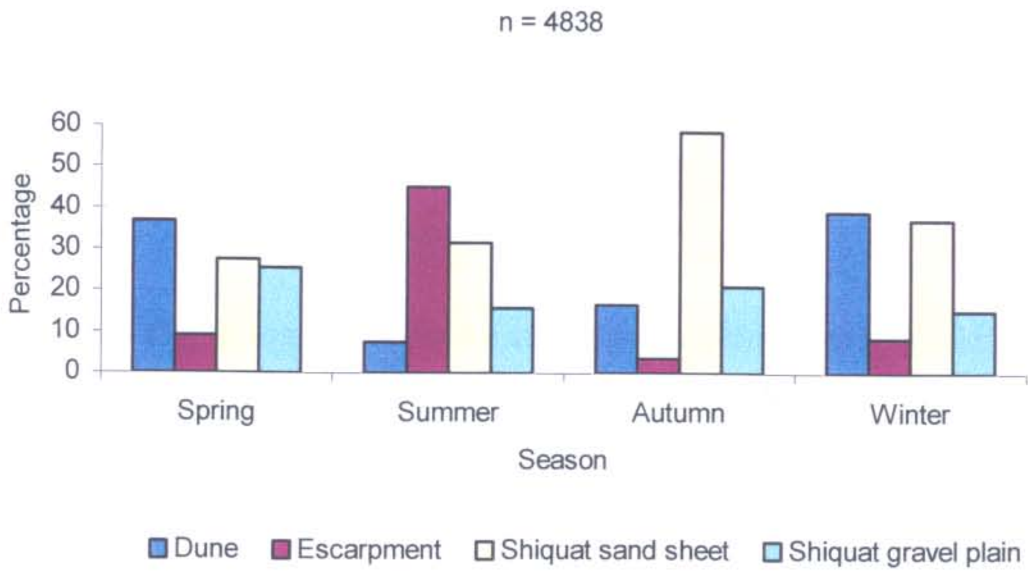

Figure 31: The frequency distribution of all the seasonal Arabian oryx observations in the different subhabitats in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed from March 1995 to February 1997. The data are pooled across the years.

trees were either present or absent. The first category of the tree density variable (VV7) represented the same condition as the first category of the next variable which deals with the percentage green material in the trees (VV8). These two variables are therefore confounded (Grimbeek, *pers. comm.*).

Gender (VV22) was another variable that was not included in the final models, indicating no significant differences in the way that the Arabian oryx males and females use their habitat in the 'Uruq Bani Ma'arid Protected Area. Even though no distinction was made between lactating and non-lactating females in the analysis, observations during the study period suggest that there is no difference in the subhabitats used by these females and the other oryxes. Since winter was the main calving season during the present study (Chapter 8) one would expect to see a difference in the subhabitat use patterns of male and female oryxes during this time, if such differences existed.

In other ungulates it has been found that the subhabitat used by the females differ from that used by the males during the time of calving and the period immediately following. This has been attributed to various reasons. For example, female moose selected their calving sites on the condition of the vegetation. In the areas that these females chose for calving the forage was of significantly higher quality than in randomly selected areas (Bowyer, van Ballenberghe, Kie & Maier 1999). Lactating females experience higher nutritional demands than non-lactating females and males (White & Luick 1984), therefore the selection of higher quality sites by parturient females.

Predation pressures also help shape the adaptations of ungulates for coping with the environment which they inhabit (Bowyer, Van Ballenberghe & Kie 1998; Bleich 1999; Kie 1999). In montane ungulates such as the mouflon *Ovis gmelini* Linnaeus, 1758, the lactating females often use so-called "escape terrain" because their lambs are vulnerable to predation, but the males and subadult females do not use these areas (Geist & Petocz 1977; Francisci, Focardi & Boitani 1985). The lactating mountain ungulate females therefore exhibit behaviour that seemingly is a trade-off between an anti-predator strategy and the use of high-quality forage (Bergerud, Butler & Miller 1984; Francisci, *et al.* 1985; Berger 1991). Although medium-sized carnivores such as the wolf *Canis lupus* Linnaeus, 1758 and the Arabian leopard do occur in the Arabian Peninsula, these animals are not found in the sandy deserts frequented by the oryx. Consequently the Arabian oryxes have evolved without being exposed to natural predators. It could therefore be due to this lack of natural predation that the Arabian oryx females do not show different patterns of subhabitat use, compared

Table 11: Results of the CATMOD procedure, with the subhabitat as dependent variable, to identify the individual variables and the interactions between various subhabitat variables of significance for further analysis in studying the subhabitat preferences of the Arabian oryxes. The study was done in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

VARIABLE	VARIABLE DESCRIPTION	SEASONAL SIGNIFICANCE			
		Spring	Summer	Autumn	Winter
VV3	Herd size	0.0008	<0.0001	<0.0001	0.0039
VV6	Vegetation condition			0.9165	0.0015
VV8	Percentage tree green	<0.0001	0.0506	<0.0001	<0.0001
VV9	Shrub density	<0.0001	<0.0001		0.0016
VV10	Percentage shrub green			0.0055	
VV11	Percentage grass green		<0.0001	0.0344	
VV12	Phenology	<0.0001		<0.0001	0.0012
VV13	Grass height	0.0018			
VV14	Percentage ground cover	0.1925	<0.0001	<0.0001	<0.0001
VV17	Activity	<0.0001		<0.0001	
VV19	Wind strength		0.7668		
VV21	Temperature			0.0143	0.0737
VV6 vs. VV12	Vegetation condition vs. Phenology			0.0008	
VV6 vs. VV14	Vegetation condition vs. Percentage ground cover			0.0010	
VV6 vs. VV17	Vegetation condition vs. Activity			0.0189	
VV6 vs. VV21	Vegetation condition vs. Temperature			0.0116	
VV8 vs. VV9	Percentage tree green vs. Shrub density				0.0016
VV8 vs. VV11	Percentage tree green vs. Percentage grass green		<0.0001		
VV8 vs. VV12	Percentage tree green vs. Phenology	0.0020			
VV8 vs. VV14	Percentage tree green vs. Percentage ground cover	0.0180	<0.0001		
VV8 vs. VV19	Percentage tree green vs. Wind strength		<0.0010		
VV9 vs. VV12	Shrub density vs. Phenology				0.0127
VV10 vs. VV17	Percentage shrub green vs. Activity			0.0072	
VV11 vs. VV14	Percentage grass green vs. Percentage ground cover		<0.0001		
VV12 vs. VV14	Phenology vs. Percentage ground cover	0.0002			
VV12 vs. VV21	Phenology vs. Temperature				0.0142

with the males, on a seasonal basis. There is no reason to believe that the Arabian oryx females do not experience the increased nutritional demand after parturition, as do other ungulate females. Another possible explanation as to why no different patterns of subhabitat use were detected for male and female oryxes could be that the study design was not sensitive enough to detect these differences, since that was not one the objectives of this particular study. Alternatively, it is quite possible that the females simply did not use their habitat any differently than the males. Because Arabian oryxes experience post-partum oestrus (Chapter 8), the parturient females were only rarely on their own. For example, during 1995 a mean number of 1.20 adult males relative to every female (n = 45) were seen with lactating females during the first month after the birth of the calf (Bothma & Strauss 1995), indicating that the females were rarely on their own following the birth of their calves.

Spring

The climatic variables were not important in influencing the way in which the Arabian oryxes used their habitat during spring, as indicated by the absence of these variables from the final model for this season. During spring the majority of the variables that were significant in determining the subhabitat use patterns of the Arabian oryxes were the interactions between various variables that describe the condition of the vegetation. The percentage green material in the grass layer (VV11) was, however, not a significant variable during this time of use.

The sand association that consists of the dunes, the *shiquat* sand sheets and the *shiquat* gravel plains was the association most used by the oryxes during spring. During such time 36.7% of all the Arabian oryx observations were made in the dunes, while 27.5% and 26.6% of the observations were made in the *shiquat* sand sheets and the *shiquat* gravel plains respectively. Less than 10.0% of all the Arabian oryx observations during the spring were made in the escarpment association.

Despite the low percentage of observations of animals in the escarpment areas, the oryxes were more likely to occur in this subhabitat under certain conditions. Shrub density (VV9) was for example an important variable in determining the habitat use of the Arabian oryxes during spring, especially in terms of the escarpment areas. At both low (1 to 5 plants per hectare) and medium (6 to 10 plants per hectare) shrub densities the animals were, for example, more likely to use the escarpment areas than either the dunes or the *shiquat* gravel plains. At medium shrub densities the oryxes were also twice as likely to be found in the *shiquat* sand sheets than in the dunes (P = 0.0483).

The oryxes were more likely to use the escarpment areas for feeding than either the dunes (Odds ratio = 3:1, P = 0.0051) or the *shiquat* gravel plains (Odds ratio = 2:1, P = 0.0409). In a similar fashion the animals were more likely to be seen walking in the escarpment areas than in either the dunes (Odds ratio = 4:1, P = 0.0004) or the *shiquat* sand sheets (Odds ratio = 3:1, P = 0.0101). Resting, whether standing up or lying down was also associated more with the escarpment areas than with the dunes. The significance of these variables in the escarpment areas cannot be explained at present. All indications are, however, that shrub density and therefore the availability of shade was not particularly important during this season, due to the indifference shown by the oryxes to the escarpment areas during the spring.

Of more significance seems to be the reasons why the oryxes used the dunes, the *shiquat* sand sheets and the *shiquat* gravel plains during the spring. Here, the condition of the vegetation as illustrated through the phenological state of the grass layer (VV12), the percentage crown cover (VV14) and the percentage green material in the trees (VV8) seems particularly important.

In the absence of trees, but in areas where the grass layer showed signs of fresh growth (VV8=0 vs VV12=2) the oryxes were three times more likely to use the dunes than the escarpment areas (P = <0.0001). Under similar conditions, there also was a greater chance of finding the oryxes in the dunes than in either the *shiquat* sand sheets (Odds ratio = 2:1, P = 0.0451) or the *shiquat* gravel plains (Odds ratio = 2:1, P = 0.0037). In addition, the oryxes were twice as likely to be found in either the *shiquat* sand sheets (P < 0.0001) or the *shiquat* gravel plains (P = 0.0031) than in the escarpment areas under such conditions. Both the *shiquat* sand sheets (Odds ratio = 2:1, P < 0.0001) and the *shiquat* gravel plains (Odds ratio = 2:1, P = 0.0031) were preferred to the escarpment areas when there were no trees present and the grass layer showed signs of fresh growth. The animals were also twice more likely to be found in the dunes than in the escarpment areas when there were no trees present and the grass layer mature and in flower (P < 0.0001). In the absence of both trees and grasses (VV8=0 vs VV12=4) the oryxes were more likely to occur in the dunes than in the escarpment areas (Odds ratio = 3:1, P = 0.0001), the *shiquat* sand sheets (Odds ratio = 4:1, P < 0.0001) or the *shiquat* gravel plains (Odds ratio = 3:1, P = 0.0010).

In general, the oryxes were more likely to be found in the *shiquat* sand sheets than in any other subhabitat when one considers the interaction of the percentage green material in the trees (VV8) and the phenology of the grass layer (VV12). The interaction between, for example, the trees being fully green and a sprouting grass layer (VV8=100 vs VV12=2) resulted in the oryxes being more likely to occur in the *shiquat* sand sheets than in any other subhabitat. The odds of the animals occurring in the *shiquat* sand sheets as opposed to the escarpment areas were significant (Odds ratio = 9:1, P = 0.0298). Not only did the sprouting grass layer attract the oryxes to the *shiquat* sand sheets, but the mature and flowering stands of the perennial grasses did so too. When the trees are 51 to 75% green and the grass layer mature and flowering, the *shiquat* sand sheets was the preferred subhabitat. The animals were more likely to be found in the *shiquat* sand sheets under such conditions than in the escarpment areas (Odds ratio = 5:1, P < 0.0001), the *shiquat* gravel plains (Odds ratio = 2:1, P = 0.0447) or the dunes (Odds ratio = 3:1, P < 0.0001). Because tree density (VV7) is confounded with the percentage green material in the trees (VV8) it is not clear whether the condition of the trees or simply the presence of trees were the important factor in these interactions. The microhabitat under the trees could influence the availability and the quality of grasses available in the *shiquat* sand sheets as opposed to the other subhabitats. Therefore it will also affect subhabitat use. For example, it is known that the *Acacia tortilis* trees in the Turkana district of Kenya can provide a suitable microclimate for herbaceous cover to flourish (Weltzin & Coughenour 1990). In a hot and dry environment, such as that in the 'Uruq Bani Ma'arid Protected Area, productivity is increased under the tree canopies due to the ameliorating influence of shade and increased soil fertility (Clary & Jameson 1981). It is also well-known that the cover provided by *Acacia tortilis* trees and shrubs is the preferred microhabitat of some of the more palatable grass species in southern Africa (Walker 1979).

Similar observations were, however, not made in the present study in the escarpment areas where trees and shrubs occur at higher densities than elsewhere. This is thought to be because the vegetation in the sand association seems to respond more rapidly to rainfall than do the escarpment areas. This view is supported by more recent observations during 2000 and 2001 (Robinson, *pers. comm.*[3]), which possibly also explains why the *shiquat* sand sheets were preferred to the dunes for feeding during spring (Odds ratio = 3:1, P = 0.0108).

During the spring of 1995 and 1996 the grass layer in the protected area was in good condition due to widespread rain in the area, with flowering specimens of *Stipagrostis plumosa* occurring in large stands on both the dunes and the *shiquat* sand sheets. Perennial grass species such as *Panicum turgidum* and to a lesser extent *Lasiuirus scindicus* also responded well to the rain and fresh growth was observed in most specimens. Mature and flowering stands of these species were also found, especially on the *shiquat* sand sheets.

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The grass species were, however, not the only attraction to the oryxes in the dunes, the *shiquat* sand sheets and the *shiquat* gravel plains. Many ephemeral species and large stands of especially the sedge *Cyperus conglomeratus* were also found in these areas during spring. According to Mandaville (1990) the above sedge can be abundant at times, and it is considered to be a useful grazing plant.

The condition of the vegetation and the importance of vegetation as a food source was the determining factor in the subhabitat use patterns of the Arabian oryxes during the spring. Elsewhere it has been indicated that the oryxes are mainly grazers, and that especially *Stipagrostis plumosa* forms a major part of the diet when it is available (Spalton 1993; 1995). In the present study it has also been suggested that *Cyperus conglomeratus* is an important component of the diet of the Arabian oryx during spring (Chapter 7).

In areas where the trees were absent and the percentage crown cover was low (VV8=0 vs. VV14=5) the sand association was preferred to the escarpment association. Under such circumstances, the animals were more likely to use the dunes than either the escarpment (Odds ratio = 3:1, P = <0.0001) or the *shiquat* sand sheets (Odds ratio = 2:1, P = 0.0006). In addition, the animals were twice as likely to be seen in either the *shiquat* sand sheets (P = 0.0142) or the *shiquat* gravel plains (P < 0.0001) than the escarpment areas in the absence of trees, and where the crown cover was low (VV8=0 vs. VV14=5). Where trees were absent and the percentage crown cover was high (VV8=0 vs. VV14=20) the chances of finding the oryxes on the dunes as opposed to the escarpment was two to one (P < 0.0001). In the presence of trees and where the crown cover was low the general trend was for the oryxes to be found in the escarpment areas, the *shiquat* sand sheets and the *shiquat* gravel plains as opposed to the dunes. For example, the chances of finding an oryx in the *shiquat* gravel plains was 13 times more likely than in the dunes (P < 0.0001) in areas where the trees were up to 50% green and the crown cover was low (VV8=50 vs. VV14=5). Similarly they were 35 times more likely for the oryxes to be in the escarpment areas as opposed to the dunes (P = 0.0140) when the trees were fully green and the percentage crown cover was low (VV8=100 vs. VV14=5). The escarpment area was preferred to all the other subhabitats when the trees were fully green and the percentage crown cover was high (VV8=100 vs. VV14=20).

Summer

During summer most (45.2%) of the observations of the Arabian oryxes were in the escarpment areas, while 31.6% were in the *shiquat* sand sheets. The *shiquat* gravel plains and the dunes were the subhabitats least used then, with 15.8% and 7.4% of the observations in these areas respectively then.

Neither the phenology of the grass layer (VV12) nor the animal activity (VV17) was a significant variable during summer. As in the spring, the climatic variables, with the exception of wind strength (VV19), were not important in determining subhabitat use. Tree density (VV7) was again not a significant variable, bearing in mind that this variable is confounded with the percentage green material in the trees (VV8), which was a significant variable in subhabitat use.

Shrub density (VV9) did, however, emerge as one of the important variables in determining the subhabitat use of the oryxes during the summer. In the presence of shrubs the oryxes were more likely to be found in the escarpment areas than in any of the other subhabitats, regardless of the shrub density. However, not all of these relationships were significant. At a medium shrub density (6 to 10 plants per hectare) the oryxes were six times more likely to be found in the escarpment areas than in the dunes ($P = 0.0237$).

It has been indicated earlier that the escarpment areas, and particularly the wadis which are incised into the escarpment, are the areas with the highest plant diversity within the 'Uruq Bani Ma'arid Protected Area. As one moves further east from the escarpment edge that occurs on the western boundary of the protected area, into the dunes the diversity of plant species decreases. It has also been shown that there is a negative relationship between the abundance of *Acacia* trees and shrubs and the distance moved away from the escarpment edge, while the density of *Calligonum* shrubs increases significantly with increasing distance away from the escarpment. Shade is therefore available in the dunes, and observations during the study period indicate that some of the animals do use the shade provided by the *Calligonum* shrubs in these areas. Nevertheless, the majority of the observations of the Arabian oryxes during summer were made in the escarpment association. This suggests that although shade is an important factor in the selection of the escarpment during the summer, there could also be additional factors of importance in this selection of subhabitat.

Acacia savannas in Africa and the Middle East support high numbers of large mammalian herbivores, and a considerable level of co-evolution has occurred between the herbivores and the *Acacia* plants (Coe & Coe 1987; Scholes & Walker 1993). For example, the shade of *Acacia* trees is essential for the water and energy conservation of several animal and plant species (Belsky, Mwonga, Amundson, Duxbury & Ali 1993; Milton & Dean 1995). In turn the *Acacia* trees and shrubs produce pods with a high protein content. When eaten by ungulates, the seeds are excreted in their faeces (Halevy 1974). This process not only facilitates the dispersal of seeds, but also increases germination because the digestion process scarifies the hard seed coating that ordinarily restricts germination (Miller & Coe 1993). Bothma (1980) has illustrated the importance of shade to the animals in the Kalahari system of southern Africa, and those results are also applicable here. In the Kalahari it was shown that the temperature of sand surface exposed to the sun increases to 70°C during summer. During the same time of year the sand temperature in the shade of a *Boscia albitrunca* tree was 20°C lower. At 30 cm above ground level the temperature in the shade of *Acacia* trees with well-defined, open trunks was up to 10°C lower than that measured at the same height above open sand. It is therefore suggested that the escarpment areas are the preferred subhabitat of the Arabian oryxes during summer at least in part because of the abundant shade available to the animals in these areas, but also because of the additional potential benefit in terms of protein from the seed pods of the *Acacia* trees and shrubs. Other factors are, however, also of potential importance in the oryxes selecting the escarpment areas during summer. These include the rockiness of these areas because it has, for example, been suggested that the thermal niche variation of the Kalahari sands exceeds that of the Sahara desert during summer. This wide thermal niche in the Kalahari has been attributed to the greater rockiness of the Sahara desert. It is known that rock absorbs less heat than sand during the day and retains the heat better at night, causing a narrower thermal niche than pure sand (Bothma unpublished). It is therefore possible that the daytime temperatures in the escarpment areas of the 'Uruq Bani Ma'arid Protected Area are lower than that on the open dunes, even in the absence of shade.

The interaction between the percentage of green material on the trees and the percentage crown cover (VV8 vs. VV14) was included in this model, as it was for spring. In areas where trees were absent and the crown cover low (VV8=0 vs. VV14=5) the oryxes preferred the dunes to the *shiquat* sand sheets (Odds ratio = 2:1, P = 0.0380). Under such conditions the oryxes were also more likely to be found in the escarpment areas than in either the *shiquat* sand sheets (Odds ratio = 3:1, P = 0.0003) or the gravel plains (Odds ratio = 2:1, P = 0.0386). In the absence of trees, but where the crown cover was high (VV8=0 vs. VV14=20) the oryxes preferred the escarpment areas to the dunes (Odds ratio = 4:1, P < 0.0001), the *shiquat* sand sheets (Odds ratio = 6:1, P < 0.0001) or the *shiquat* gravel plains (Odds ratio = 5:1, P < 0.0001). In the presence of trees, and at high levels of crown cover, the oryxes were more likely to be found in the *shiquat* sand sheets than in the other subhabitats. This was true regardless of the percentage of green material in the trees. Where the trees were, for example, 75% green and the percentage crown cover high (6 to 20%) the animals were twice as likely to occur in the *shiquat* sand sheets than in the escarpment areas (P = 0.0417).

The results indicate that in the summer the Arabian oryxes were indifferent to tree density in their choice of subhabitat use, possibly because of the relative abundance of shrubs in the escarpment areas. In addition, the animals also seem to be indifferent to the percentage green material in the trees, thereby ignoring this potential food source in the form of leaves, which will be particularly important to the oryxes during times of drought. The greater availability of potential food plants in the escarpment areas as indicated by the relatively high degree of crown cover, also attracts the oryxes to these areas during the summer. The greater species diversity in the escarpment areas, the higher availability of browse in terms of herbs and shrubs and the generally higher levels of crown cover means that the animals can minimise their movements in search of food, while also consuming a diet of higher protein content than that available in the grass layer of the other subhabitats during the summer. Similar observations have been made of the Dorcas gazelle *Gazella dorcas* (Linnaeus, 1758) in the Middle East (Baharav 1980), while diet changes during the dry season have been reported for various other ungulates (Chapter 7), including the springbok *Antidorcas marsupialis* (Zimmermann, 1780) in the Kgalagadi Transfrontier Park of southern Africa (Leistner 1967; Mills & Retief 1984). Even browsing ruminants like the kudu *Tragelaphus strepsiceros* (Pallas, 1766) are known to adjust their diet during the dry season when they consume plant species not eaten during the wet season (Owen-Smith 1994).

The interaction between the percentage green material in the grass layer and the percentage crown cover (VV11 vs. VV14) was also significant during summer. At low levels of grass greenness (1 to 25%) the oryxes were inclined to use the escarpment areas as opposed to the other subhabitats, if the level of crown cover was also low (≤5%) in the escarpment. For example, with low levels of grass greenness and a low percentage crown cover (VV11=25 vs. VV14=5) the oryxes were 241 times more likely to use the escarpment area than the *shiquat* sand sheets (P = <0.0001). At low levels of grass greenness and high levels of crown cover (VV11=25 vs. VV14=20) the escarpment area was still the preferred subhabitat of the oryxes. For example, these animals were 23 times more likely then to use the escarpment area than the dunes (P = 0.0151). The escarpment areas were therefore the preferred subhabitat during summer when the condition of the grass layer was poor (1 to 25% green) regardless of whether the percentage crown cover was low (≤5%) or high (6 to 20%). In areas where the grass was of medium quality, while the percentage crown cover was high (VV11=50 vs. VV14=20) the *shiquat* sand sheets was the preferred subhabitat.

Consequently it was more likely to find oryxes in the *shiquat* sand sheets under these conditions than in the escarpment area (Odds ratio = 27:1, P = 0.0001), the dunes (Odds ratio = 10:1, P = 0.0152) or the *shiquat* gravel plains (Odds ratio = 16:1, P = 0.0034). Elsewhere it has been suggested that Arabian oryxes consume more browse during the summer months to ensure sufficient intake of food with a protein level above that of subsistence level (Spalton 1995; Chapter 7). This would explain why the Arabian oryxes prefer the escarpment areas, at both low and high levels of crown cover when the grass layer is in a poor condition.

The Arabian oryx is primarily a grazer (Chapter 7) and will concentrate on the grass layer when the latter is in sufficient condition. This is illustrated by the fact that the *shiquat* sand sheets were the preferred subhabitat when the grass layer was of medium quality (26 to 50% green) and the crown cover high (6 to 20%). No work has been done to establish a possible relationship between the subjective assessment of the condition of the grass layer as used in this study and the actual crude protein content of the grass layer. The results from this study suggest, however, that the crude protein content of a grass layer of medium quality (26 to 50% green) is above the 5 to 6% crude protein subsistence level as suggested for the Arabian oryx by Spalton (1995). Therefore the oryxes once again concentrate on grazing, even when perennial herbs and shrubs are available due to the high levels of crown cover.

An additional variable, which is thought to be particularly important during the summer, is the occurrence of wind. When there was wind during the summer months the Arabian oryxes were more likely to be in the escarpment area than in the dunes, the *shiquat* sand sheets or the *shiquat* gravel plains, regardless of the strength of the wind. The odds of finding an oryx in the escarpment when a light wind (VV19=1) was blowing was significantly higher than for finding the animal on the dunes under similar conditions (Odds ratio = 4:1, P = 0.0073). Stanley-Price (1989) has indicated that the daily sea breeze that arrives in Jaaluni in Oman during summer lowers the air temperature by 10°C within a period of 10 minutes. Even though the wind in the 'Uruq Bani Ma'arid Protected Area does not carry cool, moist air from the coast, it is still suggested that the winds experienced in the escarpment areas there make the summer conditions more tolerable for the reintroduced Arabian oryxes.

However, the presence of wind during the summer does not always ameliorate the extreme climatic conditions. In Oman it has also been found that the combination of high temperatures and daily wind of high velocity could lead to desiccating conditions (Stanley-Price 1989). For example, during June 1984 the oryx in that country made use of the Jaaluni area where better shade and shelter from the desiccating wind occurred, amongst other things. No observations suggesting that the oryxes were seeking protection from the wind were, however, made during the present study.

Autumn

During autumn, 58.5% of all the observations of the Arabian oryxes were made in the *shiquat* sand sheets, with 21.1% and 16.7% of all the oryx observations being made in the *shiquat* gravel plains and the dunes respectively. The escarpment areas were the least used as only 3.7% of all the observations of the animals were made in these areas during the autumn. The density of the shrubs (VV9), and the interaction between the percentage green material on the trees and the percentage crown cover (VV8 vs. VV14) were not significant variables during the autumn. The variables describing the condition of the vegetation, such as the percentage green material in the trees (VV8) or the percentage green material in the grass layer (VV11) were the most important variables in determining the subhabitat use in the autumn. Additional variables, which were significant in determining subhabitat use during the autumn, included the ambient temperature and animal activity.

The Arabian oryxes preferred the *shiquat* sand sheets to the dunes (Odds ratio = 2:1, $P = 0.0239$), the *shiquat* gravel plains (Odds ratio = 2:1, $P = 0.0366$) and the escarpment (Odds ratio = 3:1, $P < 0.0001$) in areas where no trees were found (VV8=0). Even in the presence of trees, and regardless of the level of greenness of the trees the oryxes were more likely to be found in the *shiquat* sand sheets than in any of the other subhabitats. The fact that both activity and the percentage green material on the trees were included in the seasonal model could suggest that the trees are important in providing shade for the animals during the autumn when ambient temperatures are still relatively high. If this were the case, however, one would expect the interactions between the percentage green material in the trees and the activity of the oryxes (VV8 vs. VV17), or the activity and temperature (VV17 vs. VV21) to be significant variables in the seasonal model. Since this is not the case, it suggests that the animals were indifferent to the level of green material on the trees and consequently tree density, and that factors other than tree density or the percentage green material in the trees determined the oryx subhabitat use during the autumn.

The percentage crown cover (VV14) was a significant variable during the autumn. At low levels of crown cover (≤5%) the *shiquat* sand sheets were preferred to both the dunes (Odds ratio = 3:1, $P < 0.0001$) and the escarpment areas (Odds ratio = 3:1, $P < 0.0001$). Similarly the *shiquat* gravel plains were also preferred to both the dunes (Odds ratio = 2:1, P <

0.0001) and the escarpment areas (Odds ratio = 2:1, $P < 0.0001$) when the percentage crown cover was low (≤5%). At high levels of crown cover (6 to 20%) the *shiquat* sand sheets were preferred to all other subhabitats. Under such conditions it was three times more likely to find the oryxes in the *shiquat* sand sheets than in either the dunes ($P < 0.0001$) or the *shiquat* gravel plains ($P < 0.0001$). The animals were also four times more likely to be found in the *shiquat* sand sheets than in the escarpment areas ($P < 0.0001$) when the percentage crown cover was high (6 to 20%).

As during the summer months the percentage of green material in the grass layer (VV11) was a significant factor in determining the subhabitat use of the animals. Upon closer investigation, however, it seems that the Arabian oryxes preferred the *shiquat* sand sheets to all the other subhabitats, regardless of the level of green material in the grass layer. At low (1 to 25%), medium (26 to 50%) and high (51 to 75%) levels of green material in the grass layer, the animals were, for example, three times more likely to use the *shiquat* sand sheets than the escarpment area ($P < 0.0001$).

The general condition of the vegetation (VV6) was not significant in the final model on its own. During autumn it was, however, a significant variable in interaction with other variables such as phenology (VV6 vs. VV12) and animal activity (VV6 vs. VV17), amongst others. Even though these interactions were not significant in two or more seasons they are still discussed here because they are more informative than either the variables phenology (VV12) or activity (VV17) on their own. During the autumn, conditions existed where the general condition of the vegetation were mostly grey-brown in colour, with a tint of green (VV6=1), while in other areas the vegetation was mostly green with a shade of brown (VV6=2). The interaction of both these general vegetation condition scores with the phenology of the grass layer resulted in the *shiquat* sand sheets, and to a lesser extent the *shiquat* gravel plains, being used by the oryxes as opposed to the dunes and the escarpment area. When the general vegetation condition was mostly grey-brown in colour and the grass layer showed signs of fresh growth (VV6=1 vs. VV12=2) the animals were twice as likely to use the *shiquat* sand sheets than the dunes ($P < 0.0001$). The chances of finding the animals in the *shiquat* sand sheets were also significantly higher than in the *shiquat* gravel plains (Odds ratio = 2:1, $P = 0.0016$) or the escarpment area (Odds ratio = 3:1, $P < 0.0001$) under such conditions. When the general vegetation condition was mostly green with a shade of brown and the grass layer showed signs of fresh growth (VV6=2 vs. VV12=2) the *shiquat* sand sheets were also used significantly more often than the dunes, the escarpment area or the *shiquat* gravel plains. Under such conditions (VV6=2 vs. VV12=2) the animals were more often observed in the *shiquat* sand sheets than in the dunes (Odds ratio = 4:1, P <0.0001), the escarpment areas (Odds ratio = 4:1, P < 0.0001) or the *shiquat* gravel plains (Odds ratio = 2:1, P = 0.041).

The overall condition of the grass layer as represented by the percentage green material in the grass layer (VV11), is therefore not an important factor in determining the seasonal subhabitat use of the Arabian oryxes during the autumn. The phenology of the grass layer, however, seems to be an important factor in determining the subhabitat use of the oryxes during the autumn, whether it acts on its own or in interaction with other variables. This is especially so when the grass layer is showing signs of new growth. Throughout Eastern Saudi Arabia summer is the unfavourable season for plant growth, leading to dormancy or the evasion of drought through the production of seeds. Therefore the growth season of many desert plants begin in autumn or even winter, rather than in spring as in the more temperate regions (Mandaville 1990). Some of the perennial plants show active growth as early as September, well before the arrival of the first rains. The reasons for this are not quite clear but they could be associated with the shortening day length or moderating temperatures (Mandaville 1990). This will explain why the grass layer in the 'Uruq Bani Ma'arid Protected Area showed signs of fresh growth during this season, and before the first rains, regardless of the general condition score of the vegetation. It is therefore suggested here that the oryxes preferred the *shiquat* sand sheets to the other subhabitats during the autumn because of the fresh growth available on the grasses and other perennial plants.

The results from this study suggest that the *shiquat* sand sheets are the preferred subhabitat for feeding. The activity of the animals was only significant in interactions with the vegetation condition (VV6 vs. VV17) and the percentage green material on the shrubs (VV10 vs. VV17). Regardless of whether the general condition of the vegetation was mostly grey-brown (VV6=1 vs. VV17=1) or mostly green (VV6=2 vs. VV17=1) the *shiquat* sand sheets were the preferred subhabitat for feeding, and significantly so when compared with all the other subhabitats. For example, under conditions where the vegetation was mostly grey-brown in colour the oryxes were four times more likely to be engaged in feeding (VV6=1 vs. VV17=1) in the *shiquat* sand sheets than in the dunes (P < 0.0001) or the escarpment area (P < 0.0001). Under these conditions the oryxes were also more likely to engage in feeding in the *shiquat* sand sheets than in the *shiquat* gravel plains (Odds ratio = 3:1, P < 0.0001).

A similar trend was observed for the interaction between the percentage of green material in the shrubs and the activity of the animals (VV10 vs. VV17). The animals were observed feeding (VV17=1) in the *shiquat* sand sheets more frequently than in the dunes (Odds ratio = 5:1, P < 0.0001), the escarpment area (Odds ratio = 4:1, P < 0.0001) or the *shiquat* gravel plains (Odds ratio = 4:1, $P < 0.0001$) in the absence of any shrubs (VV10=0). The animals were also more likely to be engaged in feeding activities in the *shiquat* sand sheets than in the other subhabitats in the presence of shrubs, irrespective of the level of greenness of these shrubs. Despite the fact that shrub density was not included in the final model, it is suggested that the presence of shrubs in the *shiquat* sand sheets is important to the animals during the autumn. This may probably again be associated with the shade that the shrubs could provide to the animals during this time.

Winter

During the winter, the dunes and the *shiquat* sand sheets were used to a similar extent, with 39.1% and 37.2% of all the Arabian oryx observations being made in these areas respectively, while 15.2% of all the oryx observations were made in the *shiquat* gravel plains. As during spring and autumn, the escarpment area was again the area least used by the oryxes in the winter, with 8.5% of all the oryx observations being made in this area at that time.

During the winter, the percentage green material in the grass layer (VV11), the activity of the animals (VV17), and the interaction between the percentage green material in the trees and the percentage crown cover (VV8 vs. VV14) were not significant variables in the seasonal model. However, for the winter data the percentage green material in the trees (VV8) was recategorised into only two categories, namely no trees and trees that were mostly green (51 to 75%). Because of to this recategorisation, this variable (VV8) was completely confounded with that of tree density (VV7). This was apparent when no difference was found between the tree density and the percentage green material in the trees in the selection of variables for inclusion into the final seasonal models. In keeping with the other seasons, the percentage of green material in the trees (VV8) was included in the final model, while the variable tree density (VV7) was excluded.

During the winter months the oryxes are not subjected to heat stress, because of the relatively low temperatures experienced at that time. Consequently shade was not important to the animals then. Therefore the low frequency of observation of the animals in the escarpment areas. In the absence of trees it was least likely to see oryxes in the escarpment areas. It was, however, twice as likely to find the animals in the dunes ($P < 0.0001$), the *shiquat* sand sheets ($P < 0.0001$) or the *shiquat* gravel plains ($P = 0.0005$) than in the escarpment areas in the absence of trees. This is because the highest tree densities occur along the escarpment. Therefore the chances of finding the animals in areas without trees would be higher outside of the escarpment areas.

In the presence of trees, and where these trees were mostly green (51 to 75%), the dunes were the least favoured subhabitat. It was three times more likely to find the oryxes in the either escarpment areas (P = 0.0014) or the *shiquat* gravel plains (P = 0.0013) than in the dunes under such conditions. The oryxes were also more likely to be found in the *shiquat* sand sheets than in the dunes when the trees were up to 75% green (Odds ratio = 4:1, P < 0.0001).

In the absence of shrubs the Arabian oryxes were twice as likely to use the *shiquat* sand sheets than the dunes (P = 0.0338). The animals were also more likely to use the *shiquat* sand sheets than the dunes at shrub densities of 1 to 5 plants per hectare (Odds ratio = 2:1, P = 0.0126) and at densities of 6 to 10 plants per hectare (Odds ratio = 2:1, P = 0.0050). At low shrub densities (1 to 5 plants per hectare) it was twice as likely to find the oryxes on the dunes than in the escarpment areas (P = 0.0038) and three times as likely in either the *shiquat* sand sheets (P < 0.0001) or the *shiquat* gravel plains (P < 0.0001) than in the escarpment areas.

For the winter data the phenology of the grass layer was recategorised into only two classes. The first class represented areas where the grass showed signs of growth, from sprouting to being mature with flowers (VV12=1), while the second class represented areas where the grass was dormant to absent (VV12=4). Only the latter category (VV12=4) was significant in determining the subhabitat use patterns of the oryxes during the winter. The oryxes were therefore twice as likely to be found in the *shiquat* gravel plains than in either the dunes (P = 0.0113) or the escarpment areas (P = 0.0157) when the grass layer was dormant to absent. The oryxes were also more likely to be found in the *shiquat* sand sheets than in either the dunes (Odds ratio = 2:1, P < 0.0001) or the escarpment areas (Odds ratio = 2:1, P = 0.0001) under similar circumstances.

However, there were still areas where the grass layer showed signs of fresh growth, as illustrated by the interaction of the shrub density and the phenology of the grass (VV9 vs. VV12). In the presence of shrubs, at a low density (1 to 5 plants per hectare), the grass showed signs of fresh growth (VV9=1 vs. VV12=1). Wherever these conditions occurred, the animals preferred the *shiquat* sand sheets to both the dunes (Odds ratio = 2:1, P = 0.0137) and the escarpment areas (Odds ratio = 3:1, P < 0.0001). Similarly the oryxes preferred the *shiquat* gravel plains to the dunes (Odds ratio = 2:1, P = 0.0217) and the escarpment areas

(Odds ratio = 3:1; P < 0.0001) in areas with a low shrub density and where the grass layer was sprouting to mature (VV9=1 vs. VV12=1). The dunes were also preferred to the escarpment areas (Odds ratio = 2:1, P = 0.0160) under such conditions.

This interaction between shrub density and grass phenology during the winter is due to the environmental conditions during this time. In the present study 12 days of precipitation were recorded during the winter. This is all precipitation that occurred outside of spring during the entire study period. This precipitation was sometimes in the form of a thick mist, evident at first light and lasting for most of the morning (until ± 10:30). This mist was often associated with rain, although not necessarily so. At other times the precipitation was characterised by low clouds and soft rain (Strauss, *pers. obs.*). During these mists and the accompanying precipitation more water is available on and subsequently under an *Acacia* shrub, for example, than in areas devoid of shrubs, because of the large surface area of a shrub. It is therefore likely that the grass and other plant species that are found close to the shrubs would benefit from the extra water that collects from the shrubs on the sand. This explains the interaction between shrub density and a sprouting to mature grass layer during the winter. In the Jiddat al Harasis area of Oman the amount of water that can potentially reach plants growing underneath a tree or shrub was recently illustrated. On one such morning following a dense fog in the area an *Acacia tortilis* tree was shaken and the precipitation "rained" down. The amount of water falling from the tree was similar to that observed clinging and eventually falling from trees after a rain shower (Strauss, *pers. obs.*)

Under conditions of low crown cover (VV14=5) the animals preferred the *shiquat* gravel plains to the dunes (Odds ratio = 3:1, P < 0.0001), the escarpment areas (Odds ratio = 3:1, P = 0.0004) and the *shiquat* sand sheets (Odds ratio = 2:1, P = 0.0058). In contrast, the animals were more likely to occur in the *shiquat* sand sheets at high levels of crown cover (VV14=20) than in the dunes (Odds ratio = 3:1, P < 0.0001), the escarpment areas (Odds ratio = 3:1, P < 0.0001) or the *shiquat* gravel plains (Odds ratio = 4:1, P < 0.0001). It is not surprising that the oryxes prefer the *shiquat* sand sheets with its higher percentage crown cover during this time of the year. Earlier it has been indicated that many plants show their first signs of fresh growth during the autumn, and some into the winter even before the first rains. It has also been shown that vegetation in the sand associations responds sooner to precipitation than does the vegetation in the escarpment areas. By concentrating on the *shiquat* sand sheets in areas where the percentage crown cover is high, the animals therefore maximise opportunities to encounter grasses, forbs and shrubs that respond to the changing climatic conditions. In general, it is the forbs and dwarf shrubs that respond well to winter rains, and not the grasses, despite the observations in the present study. An example is the arid Karoo flora of South Africa, which shows episodic expansions into the Eastern Cape region of South Africa. This happens when the summer rainfall is low, while relatively high winter rainfall is recorded. The combination of relatively low summer and high levels of winter rainfall causes the karroid elements of the Karoo to expand at the expense of the more tropical floral elements (Robinson, *pers. comm.*)

Despite the above subhabitat and activity relationships, there seems to be no clear single driving force behind the subhabitat selection of the Arabian oryxes during the winter. Instead it seems that the majority of the significant differences in the subhabitat use patterns of the oryxes is characterised by the localised presence of certain subhabitat characteristics in a particular area, as opposed to the general absence of the same characteristics elsewhere.

Conclusions

The Arabian oryx shows different patterns of subhabitat use during the different seasons. The patterns in which the animals use their habitat are determined by different factors, depending on the season and the prevailing climatic conditions. During spring the rate of forage production in the dunes and the *shiquat* sand sheets and the phenological state of the vegetation in these areas are the primary factors influencing the selection of these subhabitats, as opposed to the others. Evidence shows that grasses respond well to spring rain, especially so in the sand association.

During the summer the vegetation structure and the availability of food are important to the animals. Here the structure of the subhabitat includes the availability of trees and, more importantly, of shrubs that can provide sufficient shade during the day. In addition, the percentage crown cover is important because energy and water preservation are the primary concerns of the animals during this time. The physical structure of the subhabitat itself is also important. In the escarpment areas the majority of observations of oryx use during the summer were in the wadis. These wadis are incised into the limestone plateau, creating an intricate network of valleys in the escarpment area. There is probably greater air flow, in the form of light breezes in these areas than in the other subhabitats, particularly around the 152 m high escarpment zone where there seems to be a constant movement of air.

During the autumn the oryxes expand their ranges and move out of the escarpment areas. This can be attributed to a variety of reasons, including temperature changes and the active growth shown by many plant forms in eastern Saudi Arabia during the autumn, following dormancy and seed production during the summer. It is not clear whether a possible decrease in the condition of the vegetation in the escarpment areas is important in the change of subhabitat use from summer into autumn.

The factors influencing the patterns of subhabitat use during winter are not as clearly defined as some of those identified during the other seasons. Precipitation during the winter, and the differences in micro-climatic conditions between various subhabitats due to subhabitat structure, seem to be important factors in determining subhabitat use during winter.

In summary, the way in which the Arabian oryxes use its habitat during spring, summer and autumn is driven by various environmental factors in conjunction with the structure of the subhabitat. During the winter, however, it seems as if the animals follow a more opportunistic approach in which they try and maximise their chances of encountering specific conditions. Some evidence does, however, suggest that during the winter the subhabitat use of the Arabian oryx is also driven actively by environmental conditions.

The habitat of the Arabian oryx can be described as an arid desert area without permanent surface water but where sufficient desert grasses, forbs and herbs are available as both a food source and to serve as cover for the newborn calves during their first month of life. Scattered shrubs and trees that provide sufficient shade to the oryxes during the hot summer months should also be available. According to the Bedouin people who are old enough to remember Arabian oryxes living in the Empty Quarter before, the animals used different parts of the area during the different seasons. During the summer months the animals concentrated on the western edge of the 'Rub al Khali, which is rich in vegetation and where shade is readily available (Al Murri, *pers. comm.*[4]). During the cooler months the animals moved eastwards and back into the sands to make use of the fresh plant growth on the dunes.

In conclusion it is suggested that the habitat in the 'Uruq Bani Ma'arid Protected Area did not undergo significant changes during the approximately 30-year period that the oryxes were absent from the area. In addition, the animals bred in captivity seemingly responded well to environmental cues, and on a broad scale made use of the area in a fashion similar to that remembered historically by the local Bedouin people.

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CHAPTER 7

FEEDING BEHAVIOUR

Introduction

The members of the genus *Oryx* are generally considered to be grazers. Gillet (1965) recorded that *Panicum turgidum* was an important food source for the scimitar-horned oryx, while Kingdon (1982) recorded that the diet of the Beisa oryx commonly included both *Aristida* and *Chrysopogon* spp. The fringe-eared oryx is predominantly a grazer, although it does take some browse too (Field 1975). The gemsbok is mainly a grazer (Eloff 1959; Leistner 1959; Skinner & Smithers 1990), with an alternative diet of ephemeral* plants (Dieckmann 1980).

The studies of Stewart (1963), Gillet (1988) and Asmodé (1990) on the Arabian oryx were an important reference base for the present study. The latter two studies were done on animals in captivity at the National Wildlife Research Centre at Taif in the Kingdom of Saudi Arabia, while Stewart (1963) did his study during Operation Oryx in the former Aden Protectorate (now southern Yemen). A more recent study by Spalton (1995) related the effects of rainfall on especially the nutritional quality of the food plants to the reproduction and mortality of the Arabian oryx. Anecdotal information on the feeding behaviour of the Arabian oryx in the wild was also collected by Carruthers (1935), Thesiger (1948; 1949), Talbot (1960), Loyd (1964), Raven, Nokes and Mac Neill (1965) and Shepherd (1965). These studies include lists of plants eaten, such as *Stipagrostis plumosa*, *Cyperus conglomeratus*, *Fagonia* spp. and *Tephrosia* spp. No long-term feeding studies covering all the seasons have been done to date on the Arabian oryx.

Analysis of Arabian oryx faeces which were collected during Operation Oryx in 1962 in the former Aden Protectorate revealed a high proportion of *Aristida plumosa* (currently *Stipagrostis plumosa*), as well as traces of *Lasiurus scindicus* in the diet of the animals (Stewart 1963). The same analysis also found that herbaceous plants form a small proportion of the diet. Herbaceous species which were identified as food items for the Arabian oryx during the above study include *Tephrosia apollinea*, *Tribulus pterocarpus, Tribulus alatus, Cassia senna* and *Monsonia glauca* (Stewart 1963).

Asmodé (1990) followed the feeding minutes approach of food plant preference and found that the Arabian oryx spends 65 % of its feeding time in eating grasses, with *Cynodon dactylon* and

Eragrostis papposa the two species that are consumed most often. These two species also have the highest protein content of all the grasses present at the National Wildlife Research Centre in Taif, Saudi Arabia (Gillet 1988, In: Asmodé 1990). At the same location it was found that the oryxes spent 28.9 % of their time in browsing, while 6.1 % was spent in feeding on herbs (Asmodé 1990). It was also found that 25 % of the Arabian oryxes dug for underground food plants while feeding. A similar behaviour has also been recorded for the fringe-eared oryx in Kenya (Root 1972), and the gemsbok in the Kalahari system of southern Africa (Williamson & Williamson 1988). The digging behaviour of an oryx has mainly been interpreted as a search for moisture-rich underground plant parts (Root 1972; Williamson 1987). In the case of the Arabian oryx, however, they dig for the moisture-rich parasitic growths which occur on the roots of *Haloxylon salicornicum* (Carruthers 1935; Stewart 1963). It has also been suggested that Arabian oryxes may eat underground plant parts to supplement their mineral intake (Asmodé 1990).

The use that animals make of their environment, but specifically the kinds of food that it consumes and the variety of subhabitats that it occupies, are central in the study of animal ecology (Johnson 1980). The aim of this part of the study was therefore to identify the plant species used as food items by the Arabian oryx, and to identify any selection for certain species. For the purposes of this study, selection of a plant species is defined as a degree of utilisation which is disproportionately high when compared with its availability in a given area (Johnson 1980). However, the data presented here are based on limited observations and should therefore be treated as provisional only.

Methods

Various techniques were used to determine the plant species composition of the diet of the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area. The Arabian oryxes released into the 'Uruq Bani Ma'arid Protected Area were kept in pre-release enclosures for approximately 5 weeks before their release into the open environment during the spring of 1995. During the time in captivity these animals were provided with alfalfa and hay as main food, and antelope pellets as supplementary food. Water was provided *ad libitum*. Within the first week of captivity the animals also ate the natural vegetation which grows on the escarpment sand sheets where the enclosures are situated.

After the release of the Arabian oryxes, these enclosures were closed to prevent any further grazing by the oryxes, gazelles, or any camels in the area. To determine the availability and the utilisation of the food plants in the enclosures, vegetation surveys were done in the enclosures, by using the step-point method (Mentis 1981). This resulted in a 768-point survey. In addition to recording the plant species present at every recording point, it was also noted whether any given plant was being utilised by the Arabian oryx or not.

In addition, two other techniques were used to determine the food plant availability and their utilisation by the Arabian oryxes in the open environment. The first of these was a technique, which was developed on site, because the relevant equipment necessary for following the direct observation method was not yet available at that time of the study. This technique involved following the tracks of oryxes in the sandy substrate to see what they fed on. It was therefore essential to locate a herd of Arabian oryx early in the morning while they were still feeding. A set of fresh tracks was then followed and all the plants encountered along a particular set of tracks were inspected for any signs of utilisation by the oryxes. All the plants that were being fed upon by the oryxes were then circled with a line that was drawn on the ground. For this technique it was estimated that an Arabian oryx could reach plants up to 0.5 m away on either side of its tracks, while moving in a certain direction. Therefore, all the plants within 0.5 m on either side of a particular set of tracks were considered to be available to a particular oryx, and were therefore also recorded. This approach was repeated for one to five sets of tracks in any given survey for a given herd.

The above technique was used in the sand association, which consist of the dune, *shiquat* sand sheet and *shiquat* gravel plain subhabitats. It yielded a total survey distance of 406 m in the dunes and 3 371 m in the *shiquat* sand sheets. The disadvantages of this technique are that it is labour intensive, while being limited in use to areas covered in sand or soft gravel where the oryx tracks are visible and relatively easy to follow. The technique is also intrusive, and often results in unequal sampling distances because of disturbance to the animals being followed.

The third technique used was the direct observation of feeding oryxes with the aid of a telescope. This technique is widely used in studies of herbivore diet composition studies (Holechek, Vavra & Pieper 1982). A major advantage of this technique is that it is relatively unintrusive. Therefore, it leads to limited disturbance of newly released animals. Furthermore, it is relatively cheap and simple and does not require elaborate laboratory work (Cornelis, Casaer & Hermy 1999). The major disadvantages of the technique are the difficulty of identifying plants over a distance and quantifying the volume and number of plants eaten (Free, Hansen & Sims 1970; Holechek *et al.* 1982). Despite these disadvantages this technique was selected for use in the present study due to the sparse vegetation which facilitates identification of the plant species consumed by the oryxes.

Quantitative information can, however, be obtained by using either the feeding minutes approach as used here or the bite-count approach (Holechek *et al.* 1982). In the feeding minutes approach the time spent by an Arabian oryx while grazing on each plant species is quantified. It is also assumed to be proportional to the abundance of the species in the diet (Bjugstad, Crawford & Neal 1970 In: Holocheck *et al.* 1982). However, annual plants may be under-represented in the results obtained with this technique, because of their small size and difficult identification (Strauss *pers. obs.*).

Direct observation of the feeding oryxes in the present study started in June 1996 and continued until February 1997. During summer the feeding oryxes were studied in the escarpment areas and the sand association of the study area for a total of 384 minutes, with actual feeding data being collected for 13.8 % (53.1 minutes) of this time. The surveys continued in autumn and winter during which the oryxes were studied for 135 and 160 minutes respectively. However, during the latter two seasons, the feeding studies were only done in the sand association. Actual feeding data were collected for 50.4 % (68 minutes) and 27.7 % (44.3 minutes) of the total observation time for autumn and winter respectively.

In each period of observation an animal of known age and sex class was observed until it moved out of range, at which time another suitable animal was selected for observation. A suitable animal was one that was feeding close enough to the observer to make identification of the food plants being eaten relatively easy. With the aid of the telescope all the plants which were eaten could be identified. The feeding data were then quantified by recording the duration of each feeding bout on a particular plant species. A distinction was made between grazing and browsing. An oryx was considered to be grazing when it was feeding on the grass species in the area. Vegetation other than grasses was considered to be browse, a category that includes annual herbs, shrubs, trees and the fruit or seeds associated with these plants. After the animals had left the area, the feeding site was scrutinised at close range in an attempt to identify any small food plants, which could not be identified through the telescope.

A vegetation survey using a 150-point step-point method (Mentis 1981) was also done in the area where the animals had fed recently, to determine the availability of the different plant species in that area. The plant species were recorded at every second step.

Results and discussion

Independence from free water, or the lack of a requirement to drink water, represents the greatest challenge facing the evolution of mammals. Its achievement signifies the highest level of specialisation (Spinage 1986). The members of the genus *Oryx* are renowned for their ability to survive in areas where permanent water is lacking (Carruthers 1935; Talbot 1960; Loyd 1964; Taylor 1968; Saiz 1975; Jungius 1982; Green 1986; Harrison & Bates 1991). Carruthers (1935) was probably one of the first westerners travelling in the Arabian Peninsula to realise that although the Arabian oryx does not have to drink water it does need moisture in some form or other. Consequently the animals will select plants that can provide them with the necessary moisture to survive in their harsh environment. The need for moisture in order to survive in harsh climates has also been proven empirically by Giddings (1990) for the gemsbok.

During the study period, 84 plant species from 32 families were recorded in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The reintroduced Arabian oryxes used 33 of these plant species from 17 different families as food plants from February 1995 to February 1997 (Table 12).

Feeding studies inside the pre-release enclosures

The results of the step-point method of plant analysis (Mentis 1981) inside the pre-release enclosures indicated the presence of 16 different plant species. Only seven of these were, however, utilised by the enclosed oryxes. Grasses formed 98.4 % of all the plants utilised as food plants by these oryxes. *Panicum turgidum* was the most common grass species present (Table 13), with 48.7 % of all the available specimens being utilised by the oryxes. This grass species also formed 37.5 % of all the plants being used as food items by the oryxes. *Stipagrostis plumosa* was also abundant inside the enclosures and 90.7 % of all the specimens in the enclosures were used as food plants by the oryxes. This grass species was the most abundant plant in the diet of the oryxes in the pre-release enclosures where it formed 53.1% of all the plants used as food. All of the *Stipagrostis ciliata* plants and 62.1 % of all the *Lasiurus scindicus* plants present there were also used as food plants by the enclosed oryxes.

Inside the pre-release enclosures, 381 grazing plants and 331 browsing plants, including seedlings, were recorded. The Arabian oryx, however, used 66.7 % of all the grazing plants recorded as food items, and only 1.2 % of all such browsing plants. It is hypothesised here that the availability of water, alfalfa, hay and supplementary food in the form of antelope pellets to the oryxes throughout their time in the enclosures influenced their choice of food plants. The more succulent browsing plants in the area were therefore not utilised much by the oryxes as

Table 12: The plant species and parts used as food items by the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia in both the pre-release enclosures and the wild after release from March 1995 to February 1997.

FAMILY	SPECIES	PLANT PARTS
Boraginaceae	*Heliotropium digynum*	Leaves and stems
	Moltkiopsis ciliata	Leaves
Capparaceae	*Dipterygium glaucum*	Leaves and stems
Caryophyllaceae	*Polycarpaea repens*	Entire plant
Compositae	*Scorzonera tortuosissima*	Entire plant
Cruciferae	*Farsetia burtonae*	Entire plant
	Farsetia stylosa	Entire plant
Cucurbitaceae	*Citrullus colocynthis*	Fruit
Cyperaceae	*Cyperus conglomeratus*	Entire plant
Geraniaceae	*Monsonia nivea*	Entire plant
Hyacinthaceae	*Dipcadi erythraeum*	Entire plant
Leguminosae	*Acacia tortilis*	Leaves and pods
	Acacia ehrenbergiana	Leaves and pods
	Crotalaria aegyptiaca	Leaves
	Tephrosia purpurea	Leaves
Neuradaceae	*Neurada procumbens*	Entire plant
Nyctaginaceae	*Boerhavia elegans*	Entire plant
Poaceae	*Aristida adscensionis*	Leaves, stems and infloresence
	Centropodia fragilis	Leaves, stems and infloresence
	Centropodia forskalii	Leaves, stems and infloresence
	Dicanthium foveolatum	Leaves, stems and infloresence
	Lasiurus scindicus	Leaves, stems and infloresence
	Panicum turgidum	Leaves, stems and infloresence
	Stipagrostis ciliata	Leaves, stems and infloresence
	Stipagrostis drarii	Leaves, stems and infloresence
	Stipagrostis foexiana	Leaves, stems and infloresence
	Stipagrostis plumosa	Leaves, stems and infloresence
Polygalaceae	*Polygala irregularis*	Entire plant
Polygonaceae	*Calligonum crinitum*	Leaves and stems
Rubiaceae	*Kohautia caespitosa*	Entire plant
Zygophyllaceae	*Fagonia indica*	Leaves and stems
	Tribulus pentrandus	Leaves, stems and flowers
	Tribulus arabicus	Leaves, stems and flowers

Table 13: The utilisation of plant species by the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia in the pre-release enclosures for 5 weeks before their release during March 1995.

PLANT	PLANTS AVAILABLE		PLANTS EATEN		PERCENTAGE OF AVAILABLE PLANTS BEING EATEN
	Total number	%	Total number	%	
Grasses:					
Panicum turgidum	199	27.9	97	37.5	48.7
Lasiurus scindicus	29	4.1	18	7.0	62.1
Stipagrostis ciliata	2	0.3	2	0.8	100.0
Stipagrostis plumosa	151	21.2	137	53.1	90.7
Subtotal	381	53.5	254	98.4	66.7
Browse:					
Polycarpaea repens	35	4.9	1	0.4	2.9
Dipcadi erythraeum	16	2.2	2	0.8	12.5
Heliotropium ramosissimum	16	2.2	0	-	-
Aerva javanica	2	0.3	0	-	-
Fagonia indica	25	3.6	0	-	-
Scorzonera tortuosissima	18	2.6	0	-	-
Rhazya stricta	4	0.6	0	-	-
Acacia oerfota	1	0.1	0	-	-
Kohautia caespitosa	15	2.1	1	0.4	6.7
Senna italica	1	0.1	0	-	-
Indigophera spinosa	2	0.3	0	-	-
Citrullus colocynthis	5	0.7	0	-	-
Seedlings	191	26.8	0	-	-
Subtotal	331	46.5	4	1.6	1.2
Total	712	100.0	258	100.0	36.2

especially water was available at all times. This hypothesis is supported by the increase in the number of available browse plants used by the oryxes as food items after their release into the open environment, when all provision of supplementary food and water ceased. By following the tracks of a group of oryx it was found that these animals used 35.0 % of all the available browsing plants. Direct observation of the feeding oryxes in the wild in the present study also confirms this use pattern, with the oryxes spending 29.0 % of their feeding time in browsing.

Diet composition based on following tracks

After the release of the oryxes, an attempt was made to identify the plant species utilised by them in the wild and to quantify the amounts available by following the tracks of a feeding herd. Such surveys were done in the sand association of the dunes and on the sand sheets in the *shiquats*. In the survey on the dunes, nine plant species were within reach of the oryxes whose tracks were being followed. Of these, only five species were utilised by the oryx. A total of 60 (11.6 %) of the individual plants which were available to a feeding Arabian oryx were unidentified. The majority of these were seedlings.

Only five plants (4.0 %) which were eaten by the Arabian oryx on the dunes could not be identified positively. Of those identified *Cyperus conglomeratus* formed 21.4 % of the plants available and was used most frequently (56.5 %) of all the plants eaten (Table 14). The most abundant plant species in the dunes was the grass *Stipagrostis plumosa* that represented 50.2% of the plants available to the oryxes, and which formed 30.6 % of all the plants eaten by the oryxes in the dunes. The other plants used as food items by the oryxes in the dunes were *Moltkiopsis ciliata, Heliotropium digynum* and *Panicum turgidum*. These species, however, each formed less than 5.0% of the total number of plants eaten by the oryxes.

The same technique was used in five different surveys on the *shiquat* sand sheets, where 15 different plant species were recorded (Table 15), of which 10 were the maximum number of species available to any particular oryx at any given time. *Panicum turgidum, Stipagrostis plumosa* and *Lasiurus scindicus* were the only grass species found on the *shiquat* sand sheets during the surveys to determine the diet composition of the oryx. These species formed 33.3% of all the plants available to the feeding oryxes, and 77.9 % of all the plants eaten. Relative to its abundance in the area, *Lasiurus scindicus* was the grass species, preferred on the *shiquat* sand sheets. Of the 131 available plants, 85 (64.9 %) were eaten by the oryxes (Table 15). These plants form 29.8 % of all the plants eaten in the *shiquat* sand sheets. *Panicum turgidum* formed 43.5 % of the total number of plants eaten, and 31.0 % of the available plants of this species was used as food by the oryxes. The oryxes rarely fed on the smaller plant species such as *Dipcadi erythraeum* and *Fagonia indica*. The fact that plant species such as *Monsonia nivea* and *Polygala irregularis* and seedlings were rarely recorded as food plants of the oryxes may possibly be due to the way in which these animals feed. An oryx will usually pull small plants out of the sand entirely, whereafter the entire plant is consumed, leaving no signs of feeding behind. Therefore any seedlings and other small plant species fed on would not be recorded in a subsequent survey, making the apparent lack of feeding on these plants a false conclusion. A similar problem was encountered with the direct observation of feeding oryxes. In the latter technique the seedlings and plant species of similar size were grouped under the unidentified class of plants utilised by the oryxes. The combination of the small size of these plants and the fact that the muzzle of an oryx would be on the ground while feeding made it virtually impossible to positively identify seedlings and other small species as being food items of the Arabian oryx.

Direct observation of feeding oryxes in the escarpment association during the summer

Results of direct observation of feeding by the Arabian oryxes are only available for the summer, autumn and winter. These data are based on a total of 40 740 seconds (679 minutes) of observation time during which actual feeding data were collected for 9 919 seconds (165 minutes) or 24.3 % of the total observation time. No data could be collected during the spring of 1995 because the required telescope was not available at that time. No such feeding data were collected during the spring of 1996 either because further oryx releases took place during this time. Because of the pressure to closely monitor the newly released oryxes then, additional time had to be spent in trying to locate and keep up with the oryxes. Consequently, the feeding studies on the Arabian oryxes during spring had to be sacrificed for a greater cause which was considered to be more vital to the survival of these oryxes.

The reason why actual feeding data on the Arabian oryxes were collected for only 24.3 % of the total observation time was mainly because of the distribution of the vegetation in the area (Stewart 1963) and the long distances that an oryx has to cover during a feeding bout to obtain enough moisture and energy for its daily requirements.

During the summer the Arabian oryxes frequented the escarpment areas on the western side of the 'Uruq Bani Ma'arid Protected Area (Chapter 6). This area consists of gravel plains, sand sheets and wadis incised in the limestone plateau. Feeding studies by direct observation were therefore done in these areas.

Table 14: The utilisation of plant species by the reintroduced Arabian oryxes on the dunes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined by following the tracks of the animals over a distance of 406 m during the spring of 1995.

PLANT	PLANTS AVAILABLE		PLANTS EATEN		PERCENTAGE OF AVAILABLE PLANTS BEING EATEN
	Number	%	Number	%	
Grasses:					
Panicum turgidum	17	3.3	2	1.6	11.7
Stipagrostis plumosa	260	50.4	38	30.6	14.6
Subtotal	277	53.7	40	32.2	14.4
Browse:					
Cyperus conglomeratus	111	21.5	70	56.5	63.1
Heliotropium digynum	13	2.5	5	4.0	38.5
Moltkiopsis ciliata	9	1.4	4	3.3	44.4
Dipterygium glaucum	12	2.3	0	-	-
Tribulus arabicus	11	2.1	0	-	-
Polycarpaea repens	1	0.2	0	-	-
Farsetia burtonae	24	4.7	0	-	-
Unidentified	60	11.6	5	4.0	8.3
Subtotal	241	46.3	84	67.8	67.7
Total	518	100.0	124	100.0	23.9

Table 15: The utilisation of plant species by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The data are pooled from five feeding surveys on the *shiquat* sand sheets as determined by following the tracks of the animals over a distance of 3371 m during the spring of 1995.

PLANTS	PLANTS AVAILABLE		PLANTS EATEN		PERCENTAGE OF AVAILABLE PLANTS BEING EATEN
	Number	%	Number	%	
Grasses:					
Panicum turgidum	400	10.9	124	43.5	31.0
Stipagrostis plumosa	689	18.8	13	4.5	1.9
Lasiurus scindicus	131	3.6	85	29.8	64.9
Subtotal	1220	33.3	222	77.8	18.2
Browse:					
Tribulus arabicus	266	7.3	23	8.1	8.6
Cyperus conglomeratus	63	1.7	36	12.6	57.1
Dipcadi erythraeum	22	0.6	3	1.1	13.6
Dipterygium glaucum	3	0.1	0	-	-
Heliotropium salicornicum	6	0.2	0	-	-
Fagonia indica	665	18.2	1	0.4	0.2
Tephrosia purpurea	20	0.5	0	-	-
Heliotropium digynum	2	0.1	0	-	-
Farsetia stylosa	50	1.4	0	-	-
Citrullus colocynthis	4	0.1	0	-	-
Polygala irregularis	675	18.5	0	-	-
Monsonea nivea	435	11.9	0	-	-
Seedlings	125	3.4	0	-	-
Unidentified	101	2.8	0	-	-
Subtotal	2437	66.7	63	22.2	2.6
Total	3657	100.0	285	100.0	7.8

In the wadis, six plant species were used as food by the oryxes. These included the grasses *Stipagrostis plumosa*, *Aristida adscensionis* and *Panicum turgidum* (Table 16) which combined were used for only 7.3 % of the total feeding time of the oryxes in these areas. In the wadis the oryxes spent 63.4 % of their time in browsing, while a further 29.3 % of the feeding time was being spent on eating unidentified plants. The prostrate herb *Citrullus colocynthis* was utilised by the oryxes for 40.5 % of their feeding time in the wadis, while 20.0 % of the feeding time in such areas was spent on eating the annual herb *Neurada procumbens*. The perennial herb *Polycarpaea repens* was fed on for 2.9 % of the time.

During the assessment of the availability of the food plants in the wadi areas, only two plant species used by the oryxes as food were recorded. These were the annual herbs *Neurada procumbens* that formed 43.0 %, and the grass *Stipagrostis plumosa* that formed 14.0 % respectively of all the plants recorded as present. Although *Citrullus colocynthis* was the plant that was most often utilised by the oryxes, it was not recorded in the surveys done to record presence and abundance. It is possible that the fruits of *Citrullus colocynthis* may serve as a source of moisture for the oryxes during the hot summer months (bin Harbi 1962, In: Stewart 1963) because these fruits contain much moisture (Green 1986). While in captivity in Arabia during 1962, it has also been noted that the Arabian oryx consume the fruits of this herb (Stewart 1963). Even the wild ass *Equus hemionus* Pallas, 1775, the porcupine *Hystrix africaeaustralis* Peters, 1852 and the ostrich are known to eat the pulp of the fruits of *Citrullus colocynthis* (Doughty 1888, In: Harrison & Bates 1991; Green 1986) in the Arabian Peninsula. Similar observations have been made in the Kalahari system of southern Africa where the fruit of another member of this genus, *Citrullus lanatus*, is eaten for its moisture content by the gemsbok and the blue wildebeest during the dry season (Shortridge 1934; Skinner & Smithers 1990; Knight 1991).

In contrast to the 63.4 % of the feeding time in the wadis being spent in browsing, the total browsing time in the escarpment area was only 8.5 % during the summer. Although based on limited data, browsing seems to be an important feeding strategy for the oryxes in the wadi areas during the summer. An increase in the consumption of browse during the summer months has also been observed in other members of the genus *Oryx*. These include the gemsbok in both the Hester Malan Nature Reserve (Dieckmann 1980) and the Kgalagadi Transfrontier Park of Southern Africa (Knight 1991), and the fringe-eared oryx in Kenya (Field 1975). In the Middle East similar observations have been made for Dorcas gazelle (Baharav 1980; 1982; Newby 1984) and in North America the elk *Cervus elaphus* Linnaeus, 1758 has shown similar changes in feeding strategy (Hobbs, Baker, Ellis & Swift 1979). In India it has been found that both the blackbuck *Antilope cervicapra* (Linnaeus, 1758), which is a grazer, and the chinkara or Dorcas gazelle, which is a browser used the pods of the *Prosopis cineraria* tree during summer. Based on faecal analysis it was found that the blackbuck consumed significantly more *Prosopis cineraria* pods during the summer than did the chinkara (Goyal, Bohra, Ghosh & Prakash 1988). Such changes in the diet of ungulates are not uncommon. It has been suggested that an optimally foraging ungulate should become less selective as the food availability declines and become increasingly opportunistic in its diet choice. This tendency should also increase during periods of prolonged drought (Owen-Smith 1982; Van der Walt, Retief, Le Riche, Mills & De Graaff 1984).

Changes in the dietary composition of ungulates have been related to the nutritional quality of the food available to such animals. It has been suggested, for example, that the gemsbok in the Kgalagadi Transfrontier Park increases the amount of browse in its diet during the hot, dry season to ensure a diet with a protein content higher than 6 % (Knight 1991). A similar suggestion has also been made for the Arabian oryxes in Oman (Spalton 1995). If the protein level of the food of an oryx drops to below this level, the food becomes uneconomical to digest in terms of energy production and gains, and the rate of nitrogen excretion exceeds that of intake (Owen-Smith 1982).

The seasonal changes in the feeding strategy of the Arabian oryx is by no means absolute, and it will continue to graze the grass species in a given area because some of the plants will continue to have protein levels above a subsistence level (Spalton 1995). The consumption of browse by the Arabian oryx can play a vital role in maintaining a high quality of diet. Just like the gemsbok (Knight 1991), the Arabian oryx is probably limited in the quantity of browse that it can consume because of the digestion-retarding secondary chemical compounds that are common in many dicotyledonous plants (Cooper & Owen-Smith 1985). The morphological restrictions of the rumen in handling excessive amounts of highly fermentative food (Hofmann 1989), probably limit the quantity of browse that an Arabian oryx can consume further.

In addition there probably is a close link between the seasonal utilisation of the subhabitats and the food plants used by the Arabian oryx. In the 'Uruq Bani Ma'arid Protected Area the wadis are relatively rich in vegetation which includes trees and shrubs that can provide the animals with sufficient shade during the summer. The oryxes can therefore minimise their movements when in search of food because of the relatively large diversity of plant species and its abundance in this subhabitat, while remaining close to plants that can supply sufficient shade. Similar observations have been made on the Dorcas gazelle in the Middle East. During the dry season these gazelles move into the wadis where they concentrate their feeding on the succulent parts of browse plants such as the *Acacia* species, despite the relative scarcity of these plant parts. This is done more to optimise their moisture intake than their energy intake (Baharav & Rosenweig 1985). The *Acacia* subhabitat is presumably preferred because the animals are protected from direct solar radiation under the tree canopy. They can therefore minimise their movements while searching for food and cover, while maximising their energy efficiency in the process (Baharav 1980).

Lasiurus scindicus, *Stipagrostis plumosa*, *Dicanthium foveolatum* and *Panicum turgidum* were the only grasses which were fed upon by the oryxes in the escarpment area sand sheets during the summer. These species represented 93.9 % of the total feeding time observed in the escarpment area sand sheets, while the remaining 6.1 % of the total feeding time was spent on plants that could not be identified. *Lasiurus scindicus* and *Stipagrostis plumosa* were the most abundant grass species found in the area and each formed 16.0 % of the available plants in the area. *Lasiurus scindicus* was also used in 66.1 % of the total feeding time of the oryxes in the escarpment area sand sheets, while *Stipagrostis plumosa* was used in 26.4 % of such time. *Dicanthium foveolatum* and *Panicum turgidum* were used in 1.0 % and 0.4 % of the total feeding time respectively. *Dicanthium foveolatum* represented 6.0 % of the available plants in the area, while *Panicum turgidum* was not recorded in the vegetation surveys.

On the escarpment gravel plains, the grasses *Lasiurus scindicus, Stipagrostis plumosa* and *Dicanthium foveolatum* were used in 73.6 % of the total time spent on feeding by the oryxes. Of this time, 60.5 % was spent on *Stipagrostis plumosa,* which only formed 25.0 % of the available plants found in the area. Unidentified plants were used in 26.4 % of the total feeding time spent by the oryxes while they were on the escarpment gravel plains. No browsing was recorded for the Arabian oryx in either the escarpment sand sheets or the escarpment gravel plains during the summer.

Direct observation of feeding oryxes in the sand association during the summer

In the sand association six plant species were identified as food for the Arabian oryxes in the *shiquat* sand sheets, and three more in the dunes (Table 17). The majority (48.1 %) of the total feeding time on the dunes was spent on the grass *Centropodia fragilis*, while the sedge *Cyperus conglomeratus* was eaten for 46.2 % of the feeding time. The remaining 5.7 % of the time spent feeding in the dunes was devoted to the perennial shrublet *Moltkiopsis ciliata.* However, this plant was not recorded in the step-point vegetation surveys, being relatively rare. *Cyperus* *conglomeratus* was the most abundant plant species in the dunes, representing 60.0 % of all the plants recorded. The grass *Centropodia fragilis* formed 20.0 % of all the plants found in the dunes.

In the *shiquat* sand sheets, *Lasiurus scindicus* was most often eaten, being the focus of 31.1 % of the total feeding time. *Stipagrostis plumosa* was used for 15.2 % of such time. Neither *Lasiurus scindicus* nor *Citrullus colocynthis* was recorded in the vegetation surveys to record plant abundance in the *shiquat* sand sheets. *Citrullus colocynthis* was used for 10.6 % of the feeding time in the *shiquat* sand sheets. *Tephrosia purpurea* and *Crotalaria aegyptiaca* were also known important browse species in these areas.

Direct observation of feeding oryxes in the sand association during the autumn

During the autumn the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area spent most of their time in the sand association (Chapter 6). Feeding studies done in the sand dunes identified 10 plant species as food plants for these oryxes (Table 18) during this time. On the sand dunes *Centropodia fragilis* was the most abundant plant species, forming 40.0 % of the plants available to the oryxes. *Centropodia fragilis* was also utilised most often, with 56.1 % of the total feeding time being spent on this grass species. The grasses *Lasiurus scindicus* and *Stipagrostis drarii* were not recorded in the vegetation surveys done to record presence and abundance. The latter two species were only used for 0.5 % and 8.2 % of the total feeding time by the oryxes respectively. *Tribulus arabicus* was the browse species that was used most often by the oryxes in the dunes where it formed 20.1 % of the feeding time. This species represented 7.0 % of the available plants in the area.

Direct observation of feeding oryx during the winter

During the winter direct observation of feeding oryxes continued in the sand associations as the oryxes then mostly occupied these areas (Chapter 6). *Centropodia fragilis* and *Stipagrostis drarii* were the only grass species recorded as being used as food plants by the feeding oryxes in the sand dunes during this time (Table 19). *Centropodia fragilis* was used most often, being used for 58.7 % of the total feeding time there. This grass species also formed 15.0 % of the total number of plants recorded in the area. By contrast, the grass *Stipagrostis drarii* was most abundant in the area, being 30.0 % of all the plants available to the feeding oryxes. However, the oryxes only spent 16.6 % of their feeding time on this species. The perennial herb *Tribulus arabicus* was the browse plant that was used most often, being used for 12.0 % of the total feeding time of the

Table 16: The utilisation of plant species by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The data are pooled for all the surveys in the escarpment association as determined by direct observation for a total feeding time of 1536 seconds during the summer of 1996.

SUBHABITAT	PLANT	TIME USED IN SECONDS	PERCENTAGE OF TOTAL FEEDING TIME	ABUNDANCE AS PERCENTAGE OF ALL PLANTS RECORDED
Wadi	**Grasses:**			
	Stipagrostis plumosa	10	4.8	14
	Aristida adscensionis	3	1.5	-
	Panicum turgidum	2	1.0	-
	Browse:			
	Citrullus colocynthis	83	40.5	-
	Neurada procumbens	41	20.0	43
	Polycarpaea repens	6	2.9	-
	Unidentified	60	29.3	-
	Subtotal	205	100.0	57
Escarpment sand sheet	**Grasses:**			
	Lasiurus scindicus	682	66.1	16
	Stipagrostis plumosa	272	26.4	16
	Dicanthium foveolatum	11	1.0	6
	Panicum turgidum	4	0.4	-
	Unidentified	63	6.1	-
	Subtotal	1032	100.0	38
Escarpment gravel plain	**Grasses:**			
	Lasiurus scindicus	37	12.4	8
	Stipagrostis plumosa	181	60.5	25
	Dicanthium foveolatum	2	0.7	13
	Unidentified	79	26.4	-
	Subtotal	299	100.0	46
Total		1536	-	-

Table 17: The utilisation of plant species by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The data are pooled for all the surveys in the sand association as determined through direct observation for a total feeding time of 1650 seconds during the summer of 1996.

SUBHABITAT	PLANT	TIME USED IN SECONDS	PERCENTAGE OF TOTAL FEEDING TIME	ABUNDANCE AS PERCENTAGE OF ALL PLANTS RECORDED
Dune	**Grasses:**			
	Centropodia fragilis	278	48.1	20
	Browse:			
	Cyperus conglomeratus	267	46.2	60
	Moltkiopsis ciliata	33	5.7	-
	Sub total	578	100	80
Shiquat sand sheet	**Grasses:**			
	Lasiurus scindicus	333	31.1	-
	Stipagrostis plumosa	163	15.2	36
	Browse:			
	Citrullus colocynthis	114	10.6	-
	Tephrosia purpurea	140	13	20
	Crotalaria aegyptiaca	125	11.7	6
	Polygala irregularis	2	0.2	9
	Unidentified	195	18.2	-
	Sub total	1072	100	71
Total		1650	-	-

Table 18: The utilisation of plant species by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The data are pooled for all the surveys in the dunes as determined by direct observation for a total feeding time of 4077 seconds during the autumn of 1996.

PLANT	TIME USED IN SECONDS	PERCENTAGE OF TOTAL FEEDING TIME	ABUNDANCE AS PERCENTAGE OF ALL PLANTS RECORDED
Grasses:			
Lasiurus scindicus	20	0.5	-
Stipagrostis plumosa	330	8.1	-
Panicum turgidum	295	7.2	7
Centropodia fragilis	2289	56.1	40
Browse:			
Tribulus arabicus	819	20.1	7
Moltkiopsis ciliata	30	0.8	-
Cyperus conglomeratus	33	0.8	7
Calligonum crinitum	54	1.3	-
Heliotropium digynum	78	2.0	13
Tephrosia purpurea	42	1.0	-
Unidentified	87	2.1	-
Total	4077	100.0	74

Table 19: The utilisation of plant species by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia. The data are pooled for all the surveys in the dunes as determined by direct observation for a total feeding time of 2656 seconds during the winter of 1996.

PLANT	TIME USED IN SECONDS	PERCENTAGE OF TOTAL FEEDING TIME	ABUNDANCE AS PERCENTAGE OF ALL PLANTS RECORDED
Grasses:			
Centropodia fragilis	1561	58.7	15
Stipagrostis plumosa	440	16.6	30
Browse:			
Cyperus conglomeratus	76	2.9	7
Tribulus arabicus	320	12.0	19
Unidentified	259	9.8	-
Total	2656	100.0	-

oryxes. This species formed 19.0 % of the plants available to the feeding oryxes in this area.

In the present study the family Poaceae represented 30.3 % of the plant species used as food plants by the Arabian oryxes. This confirms the grazer status of the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area. *Stipagrostis plumosa, Centropodia fragilis, Panicum turgidum, Lasiurus scindicus* and *Stipagrostis drarii* proved to be abundant food plants to the oryxes during all the seasons. These grasses are all perennial and formed 53.0 % of all the plants that were eaten in the pre-release enclosures and 64.0 % of such plants identified from following the tracks of different herds of feeding oryx. Direct observation of the feeding oryxes showed that perennial grasses formed 70.0% of their total feeding time. This is in agreement with Gillet (1988) who found that the Arabian oryx prefers perennial grasses as a food source, because these grasses have fresh shoots which are available to the feeding animals for most of the year.

Stipagrostis plumosa is an important food plant of the Arabian oryx. While the animals were enclosed in the pre-release enclosures, this grass formed 98.4 % of all the known plants utilised by them. Direct observation showed that this grass was used for 37.0 % of their grazing time by these animals in the open environment. The large difference between these two figures is probably because of the greater variety of plants available to the oryx in the open environment when compared with that available inside the pre-release enclosures. Historically, *Stipagrostis plumosa* is known to be an important source of food for the Arabian oryx. According to Carruthers (1935) the oryxes of the now extinct northern population in the Great Nafud desert of Saudi Arabia "fed chiefly on a tall yellow grass called 'nussi' (*Stipagrostis plumosa*)" and that "succulent grasses such as 'nussi' and 'sabat' (*Aristida* spp.) are doubtless their favourite food." *Stipagrostis plumosa* is also recognised as an important food plant to the oryxes in the Jiddat-al-Harasis of Oman, especially after rain when the Arabian oryx will feed almost exclusively on the flowering heads of this grass (Stanley-Price 1989; Tear 1992; Spalton 1995). It is known that *Stipagrostis plumosa* is hygroscopic (Stanley-Price 1989) and therefore rich in moisture.

The abundance of *Stipagrostis plumosa* in the diet of the Arabian oryx is no doubt related to its hygroscopic quality. In the Jiddat-al-Harasis area of Oman it was found that samples of this grass that were collected early in the morning contained at least 5.0 % more moisture than samples from the same plants during the late afternoon. No condensed water was found on the plants sampled, confirming the hygroscopic nature of this grass species (Stanley-Price 1989). Based on the hygroscopic nature of this grass it can be expected that the oryxes would primarily feed on it during the mornings to maximise their intake of moisture.

In the present study browse formed 30.0% of the feeding time of the oryxes. This corresponds well with the 29.0 % of browsing observed by Asmodé (1990) for the Arabian oryx. It is, however, surprising that the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area makes so little use of the *Acacia* species as food plants. According to Gillet (1988) *Acacia ehrenbergiana* and *Acacia tortilis,* which both occur in the 'Uruq Bani Ma'arid Protected Area, are high in nutritional value. At the National Wildlife Research Centre in Taif, Saudi Arabia, it was found that these plants contain 18.2 % digestible crude protein and 9.6 % water. Thorns do, however, limit the extent to which the Arabian oryx will use these plants. The oryxes will probably only use these plants when fresh growth is available and before lignification of the new growth takes place (Gillet 1988). It is possible that the condition of the vegetation in the 'Uruq Bani Ma'arid Protected Area was of such quality at the time of this study that it was not necessary for the Arabian oryx to utilise the *Acacia* species to its full extent as a food source. In Oman, the first observations of an oryx browsing selectively on a *Prosopis cineraria* tree during the dry season were made between 1987 to 89, approximately 5 years after their reintroduction there (Tear 1992).

Digging behaviour when feeding has been observed during the feeding studies on the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area. It was, however, mostly seen when the oryxes were feeding on annual or small perennial plants. The impression gained was that the animals cleared these food plants from the sand that may have accumulated over the plant parts. Gillet (1988) observed that feeding Arabian oryxes at the National Wildlife Research Centre in Taif, Saudi Arabia excavate the weak roots of *Tragus racemosus* by a strong front hoof kick, whereafter the plant is picked up with the lips. In the present study a single observation has been made of an Arabian oryx which dug deep into the sand, with its front hooves, and then completely consumed an unidentified tuber in the escarpment association. Similar observations on the digging behaviour of the Arabian oryx have been made by other authors (Carruthers 1935; Asmodé 1990; Harrison & Bates 1991), as well as on other members of the genus *Oryx* (Root 1972; Williamson 1987; Williamson & Williamson 1988).

This digging behaviour of the Arabian oryx has always been associated with a search for moisture-rich plant parts that occur under the sand surface. Utilising this untapped source of moisture when the vegetation is dry enables the Arabian oryx to enter and stay in areas where other ungulates cannot survive (Asmodé 1990). No digging behaviour were initially observed in the Arabian oryx reintroduced into the Jiddat-al-Harasis area of Oman (Stanley-Price 1989). In later years, however, such observations have been made in Oman and they have been ascribed to the reintroduced Arabian oryxes learning, with time, how to make use of this potential source of water and food in their native habitat (Tear, Mosley & Ables 1997).

Conclusions

Based on the results obtained in the present study it seems that the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area is primarily a grazer, although it will browse on herbs and woody plant species at times. These results support those of Carruthers (1935), Talbot (1960), Stewart (1963), Gillet (1988), Asmodé (1990) and Spalton (1995) on the Arabian oryx. It furthermore suggests that although the Arabian oryx may be a grazer mainly, its feeding strategy may vary within the same season depending on the prevailing climatic conditions and the subhabitat used.

The Arabian oryx is well adapted to its arid environment. In the present study both the captive-bred animals and those from the Mahazat as Sayd Protected Area showed a variety of feeding and behavioural strategies which enabled them to survive in the deserts of Arabia before their extinction in the wild. The fact that the Arabian oryxes were not supplied with any water after release into the open environment and their subsequent performance in the area suggest that their minimum water requirements were met by the moisture obtained from their food. Work elsewhere suggests, however, that learning is a likely component of the foraging strategy of reintroduced animals (Lieberman, Rodriguez, Paez & Wiley 1993; Tear 1994; 1995). Therefore it is likely that some feeding strategies that were not observed during the study period could become commonplace in the future, especially when more severe climatic conditions are experienced.

In the present study various techniques were used to determine the diet composition of the reintroduced animals. Different techniques are, however, biased in different ways (Cornelis, Casaer & Hermy 1999). Future work on feeding should therefore concentrate on using a standardised technique between seasons. During the feeding studies on the Arabian oryx by direct observation, plants that were being fed on by these animals were not recorded in the vegetation surveys to determine presence and abundance. This could indicate that the step-point method (Mentis 1981) is not the best-suited technique for vegetation surveys in a sparsely vegetated area such as the 'Uruq Bani Ma'arid Protected Area. Circular sampling plots around a central stake in the ground would possibly be better suited for determining presence and abundance of plant species.

CHAPTER 8

POPULATION DYNAMICS

Introduction

The survival ability of a species in a given area mainly depends on the ability of its members to maintain sufficient rates of nutrient intake. This, in turn, is reflected in the survival, growth and reproductive rates of the population (Knight 1991). Population dynamics therefore reflect the physiological and reproductive reaction of members of a population to various intrinsic or extrinsic factors. Extrinsic factors influencing the dynamics of a population are those factors that are not directly linked to the members of a population but which could influence the performance of such a population. Extrinsic factors include climate, primary productivity and the effects of disease or predators, amongst others. Intrinsic or density-dependent factors, also known as self-regulatory factors, are linked directly to a given population. These factors include the growth, age and sex composition, social organisation and the behaviour of a population (Bothma 1996). Both the extrinsic and intrinsic factors regulate the dynamics of a population but they operate effectively at different population densities (Caughley & Krebs 1983).

The aim of the reintroduction of the Arabian oryx into the 'Uruq Bani Ma'arid Protected Area was to establish a viable, self-sustainable population (Chapter 10). The reintroduction of ungulates involves understanding and the application of the significance of factors such as the ideal age for reintroducing individuals, ideal sex ratios, season for release, and more (IUCN 2000). In addition, it has been shown that population persistence is more likely when the number of founders is large, the rate of increase is high and the effect of competition is low (Griffith, Scott, Carpenter & Reed 1989; Stanley-Price 1989; Bothma 1996).

Mammals in general have two mortality phases. These are the high initial mortalities among young animals, which is followed by a phase in which further mortalities are low at first before increasing again (Bothma 1996). In many reintroductions large proportions of founder animals die shortly after release (Stanley-Price 1989). This suggests that the reintroduced animals are once again subject to the aboriginal, environmental factors which previously regulated their numbers. Analysis of the causes of mortality would reveal underlying patterns, which could be overcome through management action. In addition it gives a clearer understanding of the nature of the problems faced by the reintroduced population during establishment (Stanley-Price 1989).

The purposes of this part of the study were to report the basic facts on the reproductive performance of the reintroduced Arabian oryx population during the first 2 years after release, and to relate these facts to the age and sex class composition of the reintroduced population. This in turn will enable an evaluation of this particular reintroduction against the ideal circumstances as described by Stanley-Price (1989). The data and results presented here will also be used in a following chapter where a population viability assessment, through demographic modeling, will be done.

Methods

Data on the natality and mortality of the Arabian oryxes were collected in conjunction with data on the spatial distribution of the animals. Data collected included all the observations of mating behaviour, including activities such as circling* ("*paarungskreisen*") and goose-stepping* ("*laufschlag*") as described by Walther (1958) for captive oryx, and flehmen* as described by Schneider (1931). The identities of the animals involved and the dates of all such observations were noted.

Fecundity schedule

An age specific fecundity schedule was calculated for all the females and all the births to those females living in the 'Uruq Bani Ma'arid Protected Area during the study period. The fecundity rate of a particular age class was the product of all the females entering that age class and all the births to those females while in that age class. For example, during the study period 28 females entered the >2 to 3 year old age class, 16 of which produced calves. The age-specific fecundity rate for the >2 to 3 year old female Arabian oryxes therefore was 0.57 (16/28 = 0.57).

Seasonality of calving

The calving distribution is presented graphically by means of a frequency histogram. The calving distribution was tested for randomness on a seasonal basis only because sample sizes were too small for analysis on a monthly basis. The Chi-square analysis technique was used and the null-hypothesis tested for was that there is an equal chance of calving occurring during any season. The test was performed at the 95% confidence interval ($P<0.05$).

The date of conception was calculated by offsetting the date of calving by 9 months (Stanley-Price 1989). The time of conception was analysed for correlation with temperature by means of a linear regression and Pearson's correlation coefficient. The correlation between the length of daylight and the time of conception could not be analysed because no data on the daylength could be obtained from the Meteorological and Environmental Protection Agency (MEPA) in Riyadh, Saudi Arabia.

Mortality schedule

Data on the mortality of the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area were collected whenever an animal was known to have died. Because of the intensive monitoring of the oryxes in the area, every reintroduced Arabian oryx that died was located. The cause of death was determined through the analysis of organ samples collected from dead animals. The rate of organ autolysis is, however, influenced by climatic conditions. Therefore in the 'Uruq Bani Ma'arid Protected Area the high ambient temperatures which accelerate the onset of autolysis*, make it imperative that all organ samples be collected from a dead animal within 4 hours after death (Ostrowski *pers. comm.*[5]).

Autopsies were performed on the animals if they were located within a reasonable time after death. All organ samples were stored in a 10% formalin concentration in a refrigerator until such time as the samples could be sent to a veterinary laboratory. The samples were either sent to the Veterinary Faculty at the University of Utrecht in the Netherlands or to *Laboratoire D'anatamo-Pathaologie* at the Veterinary Faculty of Maisons-Alfort in France.

An age-specific mortality schedule was calculated for the Arabian oryxes in the protected area during the study period. The mortality rate in the different yearly age classes was based on the number of animals entering that specific age class and the number that died while in that age class. For example, during the study period 53 Arabian oryxes entered the >2 to 3 year old age class, four of which died before entering the next age class. The age-specific mortality rate for the >2 to 3 year old age class therefore was 0.075 (4/53 = 0.075).

Survival rate

The survival rate of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area was calculated over the 2-year study period. The finite rate of survival of a population can be estimated with a sample of radio-tracked animals for a given period (White & Garrot 1990). The number of animals still alive at the end of the selected period (n_1) divided by the number of animals alive at the start of that period (n_0) gives an estimate of survival within the population.

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Therefore,

$$\hat{S} = n_1 / n_0$$

with the variance of √ being estimated by:

$$Var(\hat{S}) = \hat{S}(1 - \hat{S}) / n_0$$

because n_1 is a binomially distributed value (White & Garrot 1990). The 95% confidence interval for the variance ($\hat{S}$) is calculated as $\hat{S} \pm z_\alpha \sqrt{Var(\hat{S})}$, where z_α is the z-statistic for an appropriate probability level. For the calculated intervals to be correct the observations must be independent, since these procedures were developed from the binomial distribution (White & Garrot 1990). This means that the survival of one animal cannot be dependent upon the survival of another. Because of this assumption in the calculation of the survival rate the calves were not included in these calculations.

Population growth rate

The growth rate of a population changes continually in proportion to its varying size and structure and due to variation in the environmental resources (Bothma 1996). The growth rate in a population at any given time is known as the exponential growth rate (r).

Exponential growth implies that the growth rate of the population either increases or decreases with time as opposed to a constant growth rate (Bothma 1996). It is therefore practical to assign a value to the exponential growth rate of a population. The values assigned to the exponential growth rate can either be negative or positive. A benefit of these growth rate values is that the value zero (0) means that there is no growth in the population. Consequently a positive value of *r* means that the population is growing, while a negative value indicates that the population is declining. Another advantage of the exponential formulation of the growth rate is the ability to convert easily between time units (Caughley 1977; Bothma 1996).

The simplest way to calculate the exponential growth rate (r) from consecutive population counts is with the equation:

$\log_e(N_t) = \log_e(N_0) + r(t)$, where:

$\log_e(N_t)$ = the population size after time interval t

$\log_e(N_0)$ = the population size at the beginning of the time interval t

r = the exponential growth rate

The exponential growth rate (r) of the reintroduced Arabian oryx population was calculated separately for the period from March to December 1995 and from January 1996 to February 1997. As these two time periods differ in length the exponential growth rate is expressed as the exponential growth per month to facilitate comparison. Animals released over a 3-month period were considered to be from one release in this analysis. For example, in calculating the exponential growth rate for the period from March to December 1995, N_0 was taken as 31, or the 31 animals that were released during that year. In doing so, the calculated growth rate of the population only reflects the births and deaths recorded in the population during that time and not during any further releases.

Results and discussion

Natality

The Arabian oryx females fell into two groups, notably those that arrived in the protected area without having calved previously (n=35) and those that arrived after producing their first calf elsewhere (n=2). All of the females reintroduced into the 'Uruq Bani Ma'arid Protected Area reached sexual maturity during the study period. Both of the females that arrived after giving birth elsewhere produced calves within the protected area, while 26 (74.3%) of the females that had never calved before reintroduction calved at least once during the study period. During the study period 39 calvings, including five abortions were recorded.

The age at first calving ranged from 581 to 1121 days (Table 20), with a mean of 894.1 days ± 1 SD of 156 days. This agrees with what is known for oryx in captivity (Vié 1996) and for wild born oryx in Oman (Spalton 1992). The minimum age at first breeding in the captive population at the National Wildlife Research Centre in Taif, Saudi Arabia was 645 days (Vié 1996) indicating that females can become sexually mature and conceive at approximately 13 months of age. It should be noted that the minimum age at first breeding of 581 days, as observed in the present study is thought to have been an abortion as no calf was found even though it was obvious that the female had calved. The youngest female to produce and successfully raise a calf in the present study was 723 days (23.8 months) old.

During the study period 11 females produced their second calves in the protected area. The ages of these females ranged from 1021 to 1278 days with a mean of 1163.0 ± 79.5 days. The calving interval between the first and the second calf ranged from 265 to 359 days, with a mean calving interval of 306.1 ± 36.0 days. In addition, two females produced their third calves at a mean age of 1773.0 ± 56.6 days. The mean calving interval between the second and third calves was 283.5 ± 19.1 days. The calving interval for all females combined ranged from 265 to 359 days, with a mean calving interval of 297.3 ± 33.5 days.

Post-partum ovulation* is common in ungulates and has been recorded in various members of the Hippotraginae, including the addax (Densmore & Kraemer 1986), roan antelope (Joubert 1976), gemsbok (Dieckmann 1980), and the scimitar-horned oryx (Gill & Cave-Brown 1988). Post-partum ovulation was also observed in the captive Arabian oryx females at the National Wildlife Research Centre at Taif, Saudi Arabia. Based on an endocrinological study it was found to occur 18 days after parturition in captive female Arabian oryxes (Sempéré, Ancrenaz, Delhomme, Greth & Blanvillain 1996). At the same facility the mean length of the ovulation cycle in the Arabian oryx female was calculated as 22 ± 3.6 days (Vié 1996). By using a mean gestation period of 264 days (Stanley-Price 1989) it was calculated that 54.4%, 27.3% and 18.2% respectively of the conceptions of the second and third Arabian oryx calves in the present study occurred within 30, 60 and more than 90 days post-partum. This indicates that in the present study the majority of the conceptions in the multiparous females occurred during the post-partum oestrus* period.

Fecundity

From March 1995 to February 1997 there were 39 births to 28 females. The fecundity schedule was therefore calculated for 39 births and all the oryx females in the wild. In five instances a female calved twice in the same age class (3 to 4 years old). Calving twice in the same age class is not surprising, given the aseasonal nature of breeding and early post-partum* conception in the Arabian oryxes (Spalton 1995). In Oman the data on the Arabian oryxes there suggested that calving twice in the same age class led to a subsequent delay in the following conception because the probability of calving in the next age class decreased. This observed delay in the following conception is a consequence of the greater nutritional demands of two consecutive births, and perhaps the inability to regain sufficient physical condition for early conception (Spalton 1995).

The fecundity schedule is illustrated in Figure 32 and the data for the schedule appear in Table 21. The fecundity of the female oryxes differed for the different age classes. The fecundity among females between 1 and 2 years old was only 9.0%, with one of 11 females in that age class giving birth. Even though the Arabian oryx females can breed at the age of 20 months (Spalton 1995), the mean age at first breeding in the present study was 29.4 ± 5.1 months, indicating a low fecundity rate at the age of first breeding. An increase in fecundity was observed with an increase in age. Maximum fecundity was observed in females between 4 and 5 years old. It should be noted that the sample size in the >4 to 5 year old age class was small with a calf produced by each of the two females aged between 4 and 5 years old. Due to the limited age distribution of the reintroduced population there were no females older than 5 years during the study period.

During the 2-year study period 69.6% of the oryx females that gave birth successfully did so before the age of 30 months. This is similar to the 70.0% observed for captive females at the National Wildlife Research Centre (Vié 1996). The fecundity schedule in large mammals follows a characteristic pattern (Eberhardt 1985) which starts with low fecundity rates in the age class in which it is first possible to breed (Spalton 1995). This low phase is followed by an increase in fecundity, which in turn is followed by a period where the fecundity rates remain relatively constant (Williamson 1991; Spalton 1995) before decreasing again (Clutton-Brock 1984; Green 1990). The fecundity schedule observed during the present study is similar to that described for the Arabian oryx in Oman (Spalton 1995) and also conforms well to the general pattern which is characteristic for large mammals.

Variation in the food supply is correlated with climatic variables such as rainfall and the population size increases and decreases in response to increasing and decreasing food availability in the habitat (Pellew 1983). Apart from food quantity, a definite link exists between the nutritional quality of the food plants and reproduction in mammals (Bronson 1985). Knight (1991), for example, related the number of gemsbok calves born in the Kalahari system to the rainfall that occurred in the previous summer, while Novellie (1986) found a correlation between the percentage of bontebok *Damaliscus dorcas dorcas* (Pallas, 1767) calves born in South Africa and the rainfall during the preceding 12-month period. Similarly, the breeding success of scimitar-horned oryx in the African Sahel was also linked to rainfall (Morrow, Wildt & Monfort 1999). It is interesting to note that although the number of breeding age Arabian oryx females in the 'Uruq Bani Ma'arid Protected Area increased linearly from 1995 to 2000, the proportion of such females with calves did not. The proportion of breeding age females with calves at heel increased from 62.5% during 1995 to 73.5% during 1996, before reaching a peak of 97.2% during 1997 (Wacher unpublished). This increase in the proportion of breeding age females with calves is linked directly with the widespread rain that occurred in the protected area during both 1995 and 1996. The effect that drought has on the productivity of the oryx females in the study area were also witnessed between September 1999 and June 2000 when only 13.7% of 51 identifiable (reintroduced) females had calves at heel (Strauss unpublished).

It is expected that the fecundity of the female oryxes in the 'Uruq Bani Ma'arid Protected Area will increase as the females become older, if the extrinsic factors such as environmental conditions allow it to happen. In Oman it was found that the primary factor that influences fecundity was the condition of the grazing resource, and that the probability of an oryx being fecund in any year decreased following low levels of crude protein in the diet in the preceding year (Spalton 1995). In the same study it was found that female Arabian oryxes reach constant high reproductive rates from the age of 6 years, and that maximum reproductive potential was recorded in the 11 to 12 year (n=6) and 12 to 13 year (n=4) age classes.

Seasonality of calving

The Arabian oryx females produce calves throughout the year, with calves being born during all the months except April and July in the present study (Figure 33). There is, however a clear peak during December, when 31.6% of all the births during the study was recorded. There were too few births during the present study to test for randomness of distribution during the different months. On a seasonal basis, however, it was found that 63.2% of all the births occurred during the winter (December to February), and that the uneven distribution on a seasonal basis was significant ($\chi^2 = 30.814$, d.f. = 3, $P < 0.05$). Neither the distribution of the calvings nor of the conceptions was therefore randomly distributed on a seasonal basis. The Arabian oryxes reintroduced into Oman also produced calves throughout the year (Stanley-Price 1989; Spalton 1995) and a peak was observed from December to February for desert-born females, while no peak in calving could be distinguished for the reintroduced females (Spalton 1995). As could be expected due to the year-round favourable conditions and the occurrence of a post-partum oestrus, the Arabian oryxes in captivity produced calves throughout the year with no clear peak (Vié 1996).

As indicated previously, it was impossible to test the effect of daylength on Arabian oryx conception rates. It is, however, suspected that the effect of daylength will not be particularly important in influencing conception in the Arabian oryx in the Arabian Peninsula. In the temperate regions, photoperiod is a common environmental cue to time breeding events in seasonally reproductive species. In arid habitats, however, it is generally accepted that variations in temperature, rainfall and consequently food availability serve as the cues for regulating reproduction (Morrow *et al.* 1999). In Oman it was suggested that conceiving during the long-day months might have adaptive values for the Arabian oryx, as the females will then calve during the cooler months. Such a conception and consequently calving pattern would reduce the exposure of the calves to heat stress, while benefiting the water economies of the females through a reduced demand on lactation (Stanley-Price 1989). Spalton (1995), however, concluded that photoperiod was not involved in stimulating conception amongst the desert-born

Table 20: The age in days at first calving and the calving interval in days for individual Arabian oryx females reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

FEMALE NUMBER	AGE AT BIRTH OF FIRST CALF	CALVING INTERVAL	
		First to Second calf	Second to Third calf
1	914	286	-
7	980	274	-
9	921	357	-
12	-	-	270
14	-	-	297
15	900	308	-
17	854	265	-
18	817	281	-
20	899	306	-
21	1211	-	-
22	723	-	-
23	796	359	-
24	830	-	-
25	790	-	-
26	862	267	-
32	805	-	-
33	744	-	-
46	581	-	-
47	1209	-	-
49	934	-	-
54	1211	-	-
56	1023	-	-
64	929	-	-
65	873	-	-
66	871	-	-
73	1186	-	-
78	771	-	-
81	702	-	-
Mean	894.1	306.1	283.5

oryx in Oman. Instead it was shown that dietary crude protein in the grazing resource served as a link between rainfall and conception. The nutritional condition of the food plants at the time of conception, and not at parturition, therefore seems to be the driving force behind the timing of reproduction in the desert-born Arabian oryx females in Oman (Spalton 1995). No pattern in conception could, however, be distinguished for the reintroduced female oryxes in Oman (Spalton 1995) and conception in these females was not obviously influenced by nutritional factors.

There is a weak negative correlation ($r = -0.066$, d.f. = 10, $P > 0.05$) between conception in Arabian oryx females and the monthly ambient temperature, as illustrated in Figure 34. This suggests that ambient temperature may have little effect on the breeding patterns of a female Arabian oryx. A similar observation has been made in Oman, where no link between ambient temperature and the observed breeding pattern could be distinguished. The fact that calving during the summer months has been mostly avoided in Oman, has been attributed to the chance timing of the rainfall and the resultant nutritional conditions of the grazing resource in the area (Spalton 1995). The same is true for the present study, where the majority of conceptions took place during the spring.

Although no analysis of nutritional quality of the food plants of the Arabian oryxes has been done in the present study, the results correspond well with that obtained by Spalton (1995) for desert-born oryx females. Recent observations in the 'Uruq Bani Ma'arid Protected Area, where widespread rain has not fallen since 1997, indicates that the majority of oryx females are not conceiving and that few calves are being born (Strauss *pers. obs.*). A female in a good physical condition is more likely to conceive than one in a poor physical condition. This has also been found in the bontebok in South Africa (Novellie 1986). In domestic sheep it has been shown that the ovulation rate is affected by nutrition, with higher ovulation rates being associated with higher nutritional condition (Gordon 1983). These findings are in contrast to most of the seasonal breeding African ungulates where rainfall does not act on conception but where food quality at the time of parturition influences the timing of the births (Owen-Smith 1990). It can therefore be concluded that the Arabian oryx is an opportunistic breeder and that the females will conceive as soon as conditions allow it to do so. In general the opportunistic or aseasonal breeders occur in arid areas where the rainfall is unpredictable (Skinner & van Jaarsveld 1987). The populations of such animals can therefore crash in unfavourable conditions, but opportunistic breeding will allow an early recovery (Spalton 1995).

Mortality

Table 21: The age-specific fecundity schedule for 39 births that were recorded for the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

AGE CLASS IN YEARS	NUMBER OF FEMALES (A)	NUMBER OF OFFSPRING (B)	FECUNDITY (B/A)
0-1	12	0	-
>1-2	11	1	0.09
>2-3	28	16	0.57
>3-4	21	20	0.95
>4-5	2	2	1.00
Mean	-	-	0.65

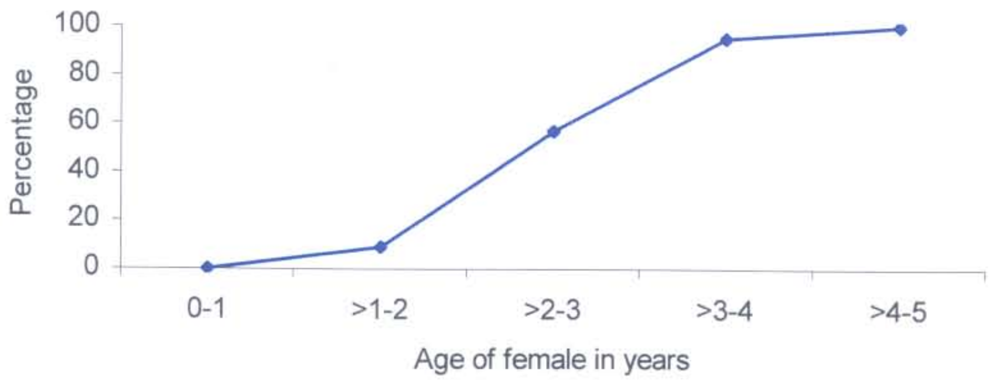

Figure 32: The percentage age-specific fecundity rate for 28 Arabian oryx females in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

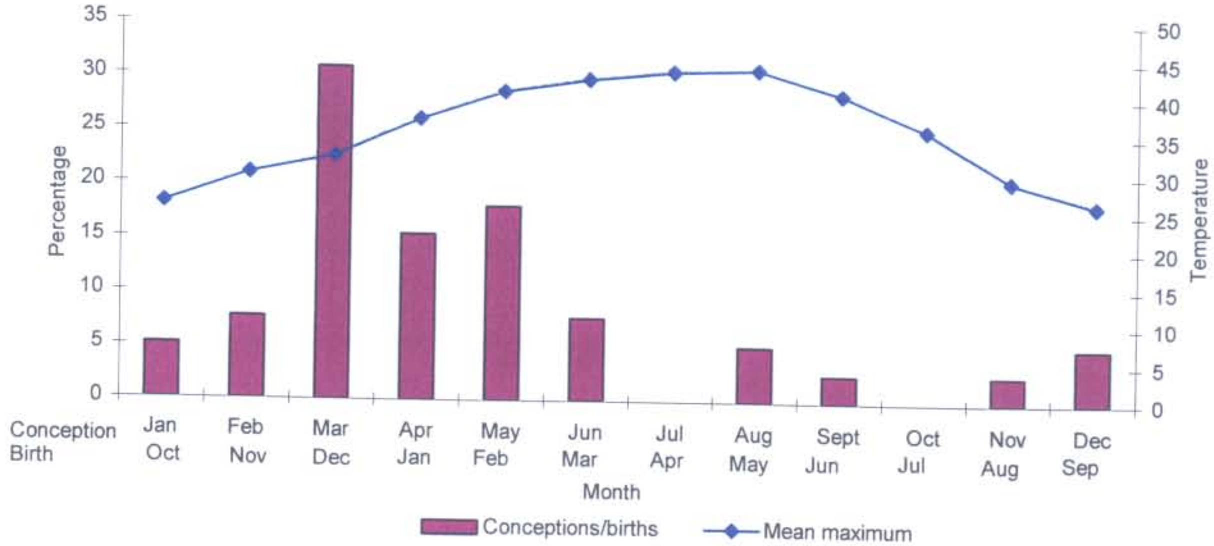

Figure 33: The monthly distribution of 39 Arabian oryx conceptions and births, and the mean maximum monthly temperature (°C) recorded in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

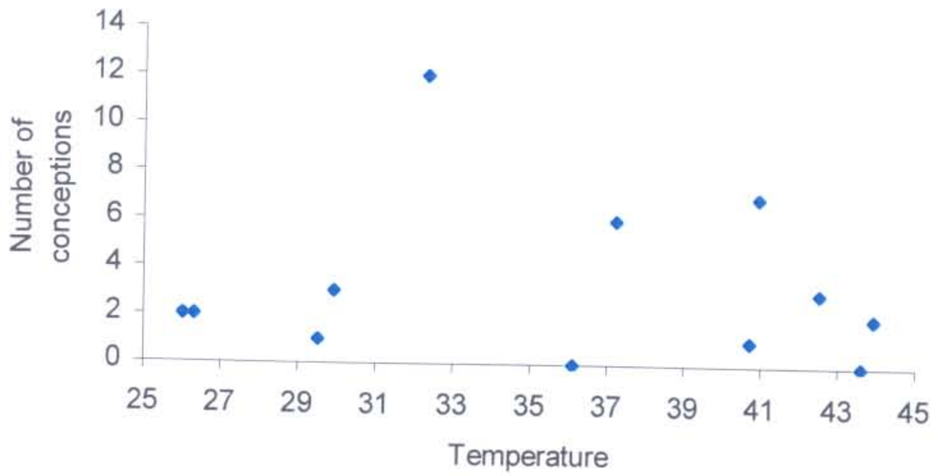

Figure 34: A scatter diagram indicating the relationship between 39 Arabian oryx conceptions and the mean maximum ambient temperature (°C) as observed in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997 (Pearson's correlation coefficient r = -0.006, d.f. = 10, P › 0.05).

From March 1995 to May 1996, a total of 66 Arabian oryxes were reintroduced into the study area. At the end of the study period, 60 of these reintroduced Arabian oryxes were still alive. The survival rate ($\hat{S}$) of the population from the official release in March 1995 to the end of February 1997 was 0.91 (91%), with a variance (Var $\hat{S}$) of 0.001 (1%). The 95% confidence interval, where $\alpha = 0.05$ and $z_\alpha = 1.96$ was 0.84 to 0.98 (84 to 98%). The deaths recorded for calves less than 1 year old represented 45.5% of all recorded mortalities. The mortality schedule, indicating age-specific mortality rates, is illustrated graphically in Figure 35, and the data that were used to calculate the mortality rates are presented in Table 22.

The mortality rate expressed as a percentage represents the proportion of all animals that entered a given age class and died before entering the next age class. The highest mortality rate (11.0%) was recorded for the juveniles (0 to 1 years old), while a 2.0% mortality rate was recorded for the yearlings (>1 to 2 years old). During the study period the mortality among the >2 to 3 year olds reached 8.0%, and included the only adult female to die during the study period. No deaths were recorded in animals more than 4 years old. In Oman the highest mortality rate was recorded for animals more than 13 years, while 17.0% of juveniles born in the area (n=178) died in that age class (Spalton 1995).

Loudon (1985) reported a 20.0% neonatal mortality rate for an expanding captive population of Arabian oryxes. Reduced juvenile survival has been associated with an increase in animal density and consequently an increase in competition for food (Skogland 1985). For example, in the state of Montana in the United States of America, the neonatal and summer fawn mortality rates of the white-tailed deer *Odocoileus virgianus dacotensis* (Zimmermann, 1780) ranged between 10.0 and 48.0% over a 5-year study period. In that study a positive linear relationship was found between the summer fawn mortality and the density of adult females (Dusek, Mackie, Herriges & Compton 1989). There are no data to suggest that the juvenile mortality in the 'Uruq Bani Ma'arid Protected Area was density-dependent. This agrees with the study of Spalton (1995) in Oman and, as in that study, it is because of the simultaneous increase in the number of animals in the area and the range used by them. Spalton (1995) did, however, relate juvenile survival to the condition of the grazing resource and found that survival in juveniles decreased at times of absolute food shortage. Conditions of food shortage have not yet been experienced in the 'Uruq Bani Ma'arid Protected Area.

The U-shaped mortality pattern as described by Caughley (1966) is characterised by high neonatal mortality, lower mortality during the middle age classes and an increase in mortality as senescence is approached (Eberhardt 1985). This mortality pattern, which is characteristic of most mammals, was not observed in the present study (Figure 35). This may be due to the

Table 22: The age-specific mortality rates for reintroduced and wild born Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

AGE CLASS IN YEARS	NUMBER OF ANIMALS	NUMBER OF DEATHS	MORTALITY RATE
0-1	45	5	0.11
>1-2	49	1	0.02
>2-3	53	4	0.08
>3-4	26	1	0.04
>4-5	4	0	0.00
>5-6	2	0	0.00
>6-7	1	0	0.00
>7-8	1	0	0.00

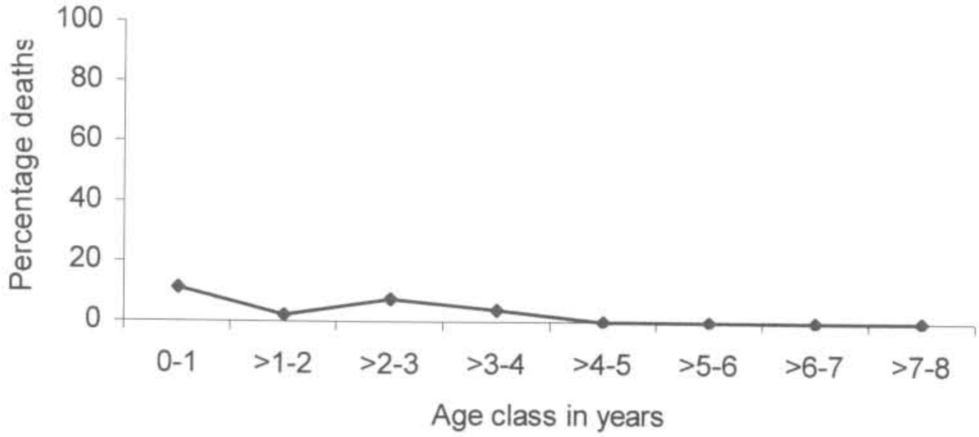

Figure 35: The mortality schedule for 11 deaths in the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

limited age distribution of the reintroduced animals.

Perinatal mortality

The perinatal mortality, which is the sum of the neonatal mortality up to 10 days after birth, reached 12.8% (n = 5) during the present study. It is suspected that the dead calves were either stillborn or aborted as none of them was ever seen alive (Table 23). Perinatal mortality reached its highest levels in females calving for the first time and 80.0% of all instances of such mortality were recorded in primiparous females with 15.4% of all primiparous females losing their calves during the study period. The mean age of the primiparous females that lost their calves was 28.7 ± 9.4 months. This mean age was not significantly different ($t = 0.812$, $df = 24$, $P > 0.05$) from that of primiparous females whose calves survived the first 10 days after birth. The perinatal mortality figures recorded in the present study are relatively low when compared to those recorded in other wild ungulate populations. In Oman, perinatal mortality reached 21.0% in the reintroduced Arabian oryx population (Stanley-Price 1989). During 1998, 19.0% (n = 42) of the Arabian oryx calves born in the Mahazat As Sayd Protected Area in the Kingdom of Saudi Arabia were found dead before reaching 10 days of age. It is suspected, however, that as much as 55.0% of the calves born in the above mentioned protected area may have died before reaching the age of 10 days during 1998 (Ostrowski, *pers. comm.*).

The perinatal mortality figures for the captive Arabian oryx herds at the National Zoological Gardens in Pretoria, South Africa and at its breeding facility in Lichtenburg in the North West Province are approximately 9.0% and 13.0% respectively (Schoeman unpublished[6]). In captivity, perinatal mortality in scimitar-horned oryx under free-ranging conditions reached 13.3% (n = 15), and 29.0% for all artiodactyls at the Whipsnade Park in the United Kingdom (Kirkwood, Gaskin & Markham 1987). Gogan and Barrett (1987) reported perinatal mortality rates of 85.7% (n=21) in an expanding population of tule elk *Cervus elaphus namodes* that was reintroduced to California. The perinatal mortality rate for the Arabian oryx observed in the present study therefore compares favourably with that observed in oryxes in other areas and for other animals.

Causes of mortality

The mortality rate of the reintroduced oryxes reached 9.0% during the study period, as six animals of varying age, including one adult female died during this time (Table 23). Injuries incurred during dominance disputes between adult male oryxes caused the deaths of three

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(60.0%) of the adult males that died. The mean age of the adult male oryxes that died due to fighting was 35.8 ±3.5 months. Deaths due to fighting are not common in ungulates. It has, however, been reported for the Arabian oryxes in Jordan's fenced Shaumari Reserve (Abu Jafer & Hays Shahin 1989), the fenced Mahazat As Sayd Protected Area in Saudi Arabia (Greth & Schwede 1993) and in the unfenced Jiddat al Harrasis area of Oman (Spalton 1995). According to Spalton (1995) competition between Arabian oryx males is most intense between the ages of 5 and 8 years old, a time when 71.4% of the mortalities in male oryxes in that age category (n=7) result from fighting.

Autopsies were performed and organ samples were collected from one of the dead Arabian oryx males and from the female that died. The other four animals were not located soon enough after death to allow the collection of such samples. Analysis of the organ samples collected from the male oryx showed a congestion of the lungs and an acute oedema* in the lungs. Neither of the sets of organ samples collected showed any signs of infectious disease. A survey in the area, however, indicated that there are infectious diseases in the livestock in and around the area (Sandoka 1996). The female oryx that died had a 2.5-month old calf at the time of her death. Blood samples were collected from this calf to test for possible antigens that would have been passed to the calf from the mother if the mother had had an infectious disease. It was found that the calf presented a high positive serological titre to pasteurellosis *Pasteurella multocida* Type A (Ostrowski *pers. comm.*). It has, however, been suggested that the high *Pasteurella* titres encountered in the blood of this calf could be a reflection of its mother having been vaccinated rather than the calf being infected. Maternal antibodies only disappear from a juvenile's circulation at 3 months of age (Flamand, *pers. comm.*[7]).

Population growth rate

During 1995, the Arabian oryx population was established in the 'Uruq Bani Ma'arid Protected Area through three releases which took place during March, April and June of that year (Figure 36). In addition five calves were born, while two reintroduced animals died during the same period. The exponential growth rate for the period March to December 1995 was 0.092 (9.2%). During 1996 a further 35 oryxes were released while 29 calves were born. A further four oryxes died during this time. For the period January 1996 to February 1997 the exponential growth rate (r) was 0.309 (30.9%).

It is generally accepted that most wildlife populations display a similar growth curve form when

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Table 23: The causes of death of Arabian oryxes of different ages (months) in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

ANIMAL NUMBER	SEX	AGE	CAUSE OF DEATH
10	Male	25.0	Unknown, the animal was found approximately 1 week after death
24	Female	29.8	Unknown, an autopsy was inconclusive. *Pasteurella* titres were found in the female's 2.5-month old calf
19	Male	39.1	Physical injuries, an autopsy revealed congested lungs and acute oedema. No signs of disease
61	Male	16.8	Cause of death unknown. Died approximately 261 km from its release site
5	Male	32.2	Physical injuries
6	Male	36.0	Physical injuries
-	Unknown	0.0	The first calf of Female 46 who was 19.1 months old. The calf was never located
-	Unknown	0.0	The first calf of Female 21 who was 39.8 months old. The calf was partly scavenged when found
-	Unknown	0.0	The first calf of Female 81 who was 23.1 months old. The calf was never located
-	Unknown	0.0	The second calf of Female 26 who was 37.1 months old. The calf was never located

the number of animals in relation to time elapsed is presented graphically. The growth of an animal population follows a clearly defined pattern over time, and generally follows an S-shaped curve (Figure 37)(Caughley 1977; Odum 1983; Bothma 1996). In the initial establishment phase the births and deaths are about equal and the population increases slowly. After the initial slow establishment phase follows a period of exponential growth where the natural resources of the environment (extrinsic factors) are unlimited for a given species. As the exponential growth of the population continues, deficiencies of one form or another starts to influence the birth and survival rates of the population (Bothma 1996), while the effect of the intrinsic or density-dependent factors also becomes important in regulating the population. It is commonly accepted that population size is regulated by extrinsic factors such as food availability (Sinclair 1977; Fryxell 1987). This leads to a decrease in population growth and ultimately to a fluctuating equilibrium where the natural births and deaths balance each other (Bothma 1996).

During the first 9-month period (March to December 1995) after the official release, the births outnumbered the deaths by a factor of 2.5. The growth rate of 9.2% is higher than what one would expect from the establishment phase of a population where the number of births usually are only slightly higher than the observed deaths (Bothma 1996). The exponential growth rate (r) increased more than three-fold for the period January 1996 to February 1997 and the births outnumbered the deaths by a factor of 7.25. This increase in growth rate is due to a combination of factors. These factors are the increase in the founder population in the 'Uruq Bani Ma'arid Protected Area during 1996, when the number of breeding age females was increased by 425% from 8 to 34, as well as the good climatic conditions which resulted in an ample food supply of sufficient quality. This in turn resulted in the majority of the animals, and especially the females, being in excellent physical condition, which is ideal for conception.

During the period January 1996 to February 1997 the Arabian oryxes entered the exponential growth phase. This growth phase is characterised by unlimited resources (Bothma 1996) and the absence of density-dependent factors that could regulate the population growth. If the observed exponential growth rate (r = 30.9%) had remained constant, the oryx population would have increased to 200 animals within the next 3 years. Due to the good environmental conditions and the fact that the protected area is unfenced, intrinsic factors should still not have been prominent in regulating population growth in the 'Uruq Bani Ma'arid Protected Area. The primary factor in regulating the population growth in this area would be environmental, while density-dependent factors will always be secondary in that effect.

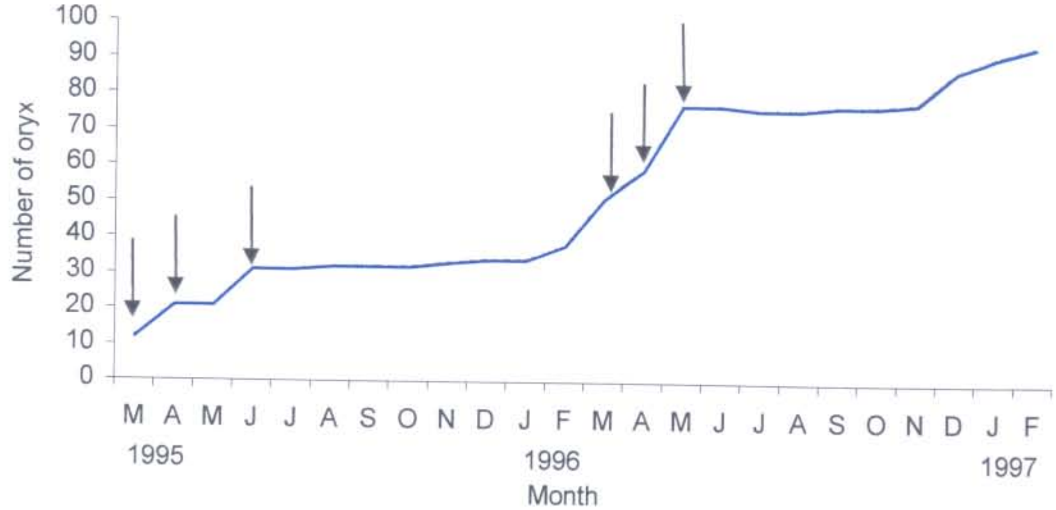


Figure 36: The actual growth of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Arrows indicate the six months of release.

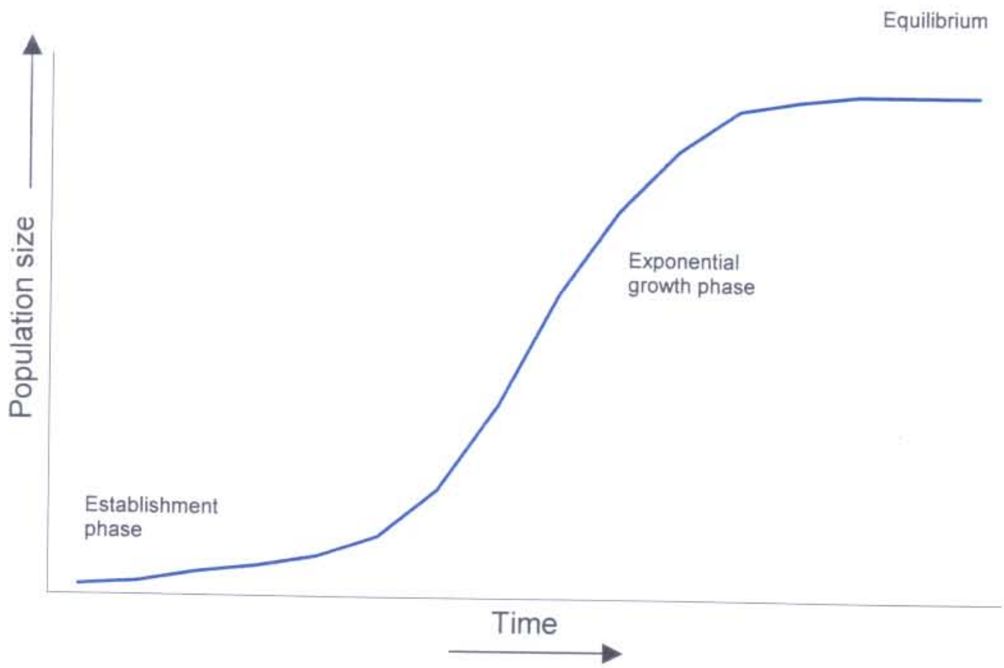


Figure 37: The characteristic growth phases of animal populations (Bothma 1996).

Conclusions

Shortly after the release of the first group of Arabian oryxes into the 'Uruq Bani Ma'arid Protected Area, widespread rain fell in the area. Because of the good environmental conditions, the condition of the vegetation, and the resulting physical condition of the female oryxes, calves were born during both years of the study. For the period 1996 to 1997, 75% of the females of breeding age had calves at heel. During surveys conducted in 2000, only 13.7% of identifiable breeding age females had calves, confirming the fact that food quality is the driving force behind the productivity of the Arabian oryxes in the Arabian Peninsula.

Releasing older females of higher fecundity instead of mainly primiparous females, might have increased the productivity of the reintroduced oryx population. Since no signs of infectious diseases were found in the organ samples collected from some of the dead animals, it is not quite clear why 12.8% of the new calves died during or shortly after birth, unless one attributes it to the inexperience of the females. The fact that the majority of the multiparous females conceived during the post-partum oestrus period not only confirms the good environmental conditions, but it also attests to the fact that the limited age structure of the reintroduced population did not noticeably impinge on the productivity of the population.

Ultimately the successful reintroduction of a species partly depends on a clear understanding of the possible effects that both the extrinsic and intrinsic factors can have on the dynamics of the reintroduced population, as well as the levels at which these factors operate. Based on the results from this study it is suggested that the reintroduced Arabian oryx population is regulated by extrinsic factors such as environmental conditions. Due to the unfenced nature of the 'Uruq Bani Ma'arid Protected Area and the ranging behaviour of the species it also suggested that intrinsic factors will always be secondary in regulating the dynamics of this population.

CHAPTER 9

ACTIVITY

Introduction

Quantitative data on the activity patterns of various antelopes have become readily available over time as a result of a large number of studies of antelope behaviour. These data all indicate that a diurnal activity regime is characteristic of all antelopes, but that variations caused by external and internal factors are superimposed on the general regime (Jarman & Jarman 1973).

Studies on the activity of animals can contribute to understanding the ecological limitations imposed on whole populations of a species, and more particularly upon individuals of certain reproductive categories within the population (Jarman & Jarman 1973). Furthermore, for reintroduced animals it is important to know how they interact with their environment so that populations can be managed effectively (Williamson, Tatwany, Rietkerk, Delima & Lindsay 1991). By quantifying the activity patterns shown during different seasons it is also possible to describe the relationship that exists between the animals and their environment. Such information on the ability of the animals to adapt to fluctuating conditions provide a scientific basis for practical decisions on various matters, including the suitability of a given habitat for the translocation of certain species of wildlife (Norton 1981).

According to Jarman and Jarman (1973), social behaviour can be divided into two components. The first one deals with behaviour in response to external factors, which in turn are attributes of the environment such as food availability and dispersion. The second deals with behaviour imposed from within the population by differences between the reaction of individual members to each other. It is generally accepted that this second category of behaviour is largely manifested in the organisation of the population (Jarman & Jarman 1973).

Each individual animal allocates its time optimally in relation to its specific metabolic and energy requirements. Comparing the time activity budgets between the different seasons and different years can help to explain any adjustments which are made by animals to variations in their environment (Giroux & Bédard 1990).

The purpose of this part of the study of the Arabian oryx therefore was to investigate and quantify the daily activities of the reintroduced animals by apportioning their daytime 12-hour activity cycles into mutually exclusive categories over a period of one year. This provides important background information for a wider behavioural and ecological study of the reintroduced Arabian oryx of the study area.

Methods

Altmann (1974) discusses seven different methods of sampling for observational studies of social behaviour in detail. Each of these techniques has different recommended uses, and each one differs in its suitability for providing unbiased data of various kinds. In activity studies the behaviour of an animal may either be regarded as events or states. The difference is that events are instantaneous while states have appreciable duration (Altmann 1974).

The most widely used method for quantifying the daytime activity of ungulates was first described for Zebu cattle *Bos taurus* (Linnaeus, 1758) in East Africa (Harker, Rollinson, Taylor, Gourlay & Nunn 1954). This technique has subsequently been used by both Richards (1966) and Smith (1968) who studied caged golden hamsters *Mesocricetus auratus* (Waterhouse, 1839) and squirrels *Tamiasciurus* spp. (Trouessart, 1880) respectively. Studies on the defassa waterbuck *Kobus ellipsiprymnus defassa* (Ogilby, 1833), warthog *Phacochoerus aethiopicus* (Pallas, 1766), Hartmann zebra *Equus zebra hartmannae* Linnaeus, 1758 and elephants *Loxodonta africana* (Blumenbach, 1797) followed (Spinage 1968; Clough & Hassam 1970; Joubert 1972; Wyatt & Eltringham 1974). Lewis (1977) also used the technique in comparing the activity patterns of eland *Taurotragus oryx* (Pallas, 1766), oryx, buffalo *Syncerus caffer* (Sparrmann, 1779) and zebu cattle. More recently the activity patterns of moose in western Alaska (Gillingham & Klein 1992) and reintroduced giraffe *Giraffa camelopardalis* (Linnaeus, 1758) in the Kgalagadi Transfrontier Park (Kruger 1994) of Southern Africa have been studied using this technique.

The technique involves classifying the behaviour of the animals into a number of specific and easily recognisable activities. According to this technique an individual's current activity is recorded at preselected time intervals (Altmann 1974). This results in a sample of states but not of events. When the behaviour of all the visible group members is sampled within a short space of time the observations approach being a simultaneous sample of all the individuals in the group. This form of instantaneous sampling is referred to as scan sampling (Altmann 1974). Such sampling has been used throughout the present study.

An important consideration in using the scan sampling technique is that an attempt should be made to scan each individual in the group for the same period of time. This type of analysis is therefore best suited to studies in which aspects of social behaviour can be lumped into a few easily distinguishable categories (Altmann 1974). The technique readily provides data appropriate to estimating the percentage of time spent on the various activities that are recognised; and on behavioural synchrony within the herd.

In the present study, an Arabian oryx group was located during the afternoon preceding the day of the study. On the day of the study, the last known position of the herd on the previous day was then used to re-locate the animals rapidly. The diurnal activity of the group was then studied. The activity of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area was sampled over a period of 14.6 days during 1995. During this time 10 560 scans comprising 176 hours of observation were made. An attempt was also made to study the nocturnal activities of the oryxes. Even during full moon, however, it was found that a specific oryx could not be identified positively by using the tag numbers alone. It was therefore also too difficult to identify an individual oryx on any other night, when the moon was in a different and darker phase. Analysis then was therefore impossible.

Diurnal activity was recorded for mixed herds of Arabian oryxes between 06:00 and 18:00 on 14 days during 1995, with a single activity study done between 06:00 and 14:00 on another day. These activity studies were distributed across all the seasons. The standard scanning procedure requires one scan of the herd at 5-minute intervals, being repeated 12 times during each hour. Since all the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area were individually identifiable, only the identification number of each individual and the activity observed at the time of scanning were noted.

The activities recorded included feeding, ruminating, walking, standing in the sun, standing in the shade, lying down in the sun, lying down in the shade, ruminating while standing, ruminating while lying down, running away, and social interactions. Because of the inherent time restraints when scanning different animals with the selected technique, an animal's activity was recorded as walking only if the animal was actually seen moving without feeding during a scan period. Following Dieckmann (1980), ruminating was identified by the lateral jaw movement of an oryx while standing and/or lying down. When the head of an oryx was obscured behind other animals or vegetation, it was noted that rumination could not be determined. This means that all the values given on rumination here are minimum values because some of the oryxes could have been ruminating while their heads were obscured.

Social interactions are usually subdivided into courtship and dominance behaviour. Courtship behaviour as studied here included flehmen, circling, goose-stepping and mating. Dominance behaviour included dominant and submissive behaviour through means of posturing, as well as fighting, shrub-horning and squat-defecating.

Meteorological data were collected at 2-hourly intervals during the activity studies, and consisted of the following variables: ambient temperature recorded in the shade of the vehicle, wind direction as determined by compass bearing, and wind strength determined subjectively either as no wind, mild wind, strong wind or very strong wind. Cloud cover and visibility were also recorded.

Following Norton (1981) and Kruger (1994), the results are presented as percentage frequencies of each activity for every half-hour period through the daylight hours. The time allocated to the different activities was calculated by converting the percentage of observations for that half-hour period to minutes by using a factor of 0.3. When an animal, for example, spent 80% of its time during a specific half-hour in feeding, then the actual time spent on feeding would be 80 x 0.3 = 24 minutes.

Because no activity data are available for subadult male Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area during the spring, the diurnal activity data were analysed for two different periods. Firstly, comparisons were made between adult males, adult females and subadult females for the spring. Secondly, the behaviour of all the age and sex classes, including the subadult males, was compared for the summer, autumn and winter.

Multi-factor analysis of variance was used to determine whether any significant differences existed in the observed activity patterns between the age and sex classes, and season. One-way analysis of variance was used to determine if any significant differences existed in the observed activity patterns between seasons, within the different age and sex classes. To determine statistically whether there was a relationship between increasing ambient temperature and the percentage of oryx that was found to be resting in the shade, a linear regression equation based on the method of least squares (Zar 1974) was applied. The confidence level was set at 95% ($\alpha = 0.05$) in all the statistical analysis procedures.

Results and discussion

The distribution of the daily behavioural activities of the Arabian oryx during the four seasons in the 'Uruq Bani Ma'arid Protected appear in Table 24 and Figures 38 to 41. These results show the following:

Feeding

Feeding was the most time consuming activity of the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area during all the seasons, except the winter. Peak feeding times (51.7% of all observations) was usually in the early morning from sunrise to approximately 10:00. After 10:00 the oryx only fed occasionally (14.0% of all observations). Feeding resumed after 14:00 and continued until the end of observations at sunset. During the latter period, 34.3% of all the observations made on the oryxes were of feeding animals.

During spring it was found that there was no significant difference (P = 0.8269) in the time spent in feeding by the different age and sex classes. Multi-factor analysis of variance revealed that age and sex class on its own was not a significant (P = 0.0833) factor in determining the amount of time spent in feeding (Table 25) during the remaining three seasons. Season, however, was a significant (P = 0.0000) factor. Similarly, the relationship between the age and sex class and season was significant (P = 0.0008) during summer, autumn and winter. This indicates that the seasonal patterns of feeding behaviour differed between the different age and sex classes. For example, the adult females spent more time in feeding during the winter than did the subadult females, while the opposite was true during the summer and autumn. This seasonal change in the time spent in feeding by these two age classes is due to the different nutritional demands experienced by the adult and subadult females due to their different reproductive statuses (Lewis 1977; Norton 1981). Elsewhere it has been shown that births in the present study peak during winter (Chapter 8). It is also known that the energetic costs of lactation to female mammals are responsible for a major increase in their energetic requirements (Hanwell & Peaker 1977).

Therefore the adult females should spend more time in feeding during the winter than the subadult females. The same is probably true during the summer and autumn, but high ambient temperatures and the need for preserving water and energy are additional factors that influence behaviour during these seasons. Consequently it is more important for the

Table 24: The proportional distribution of the different daily activities shown by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the different seasons of 1995. Data were collected during one day per month and resulted in 10 560 scans comprising 176 hours of observation.

SEASON	AGE AND SEX CLASS	ACTIVITY											
		Feeding		Walking		Resting		Ruminating		Social		Other	
		Minutes	%	Minutes	%	Minutes	%	Minutes	%	Minutes	%	Minutes	%
SPRING	Adult male	238	33.1	104	14.4	206	28.6	125	17.4	25	3.5	22	3.0
	Adult female	268	37.2	97	13.5	210	29.2	114	15.8	4	0.5	27	3.8
	Sub adult female	265	36.8	72	10	257	35.7	89	12.4	10	1.4	27	3.8
SUMMER	Adult male	131	18.2	120	16.7	400	55.6	48	6.7	13	1.8	8	1.1
	Adult female	131	18.2	123	17.1	393	54.6	49	6.8	2	0.3	22	3.1
	Sub adult male	179	24.9	162	22.5	243	33.8	54	7.5	13	1.8	69	9.6
	Sub adult female	155	21.5	157	21.8	306	42.5	44	6.1	2	0.3	56	7.8
AUTUMN	Adult male	236	32.7	154	21.4	246	34.2	32	4.4	14	1.9	38	5.3
	Adult female	255	35.4	150	20.8	231	32.1	9	1.3	1	0.1	74	10.3
	Sub adult male	203	28.2	193	26.8	261	36.3	13	1.8	9	1.3	41	5.7
	Sub adult female	271	37.6	154	21.4	239	33.2	12	1.7	5	0.7	39	5.4
WINTER	Adult male	180	27.3	243	36.8	189	28.6	10	1.5	32	4.8	6	0.9
	Adult female	197	29.8	247	37.4	201	30.5	3	0.5	7	1.1	5	0.8
	Sub adult male	177	26.8	282	42.7	161	24.4	5	0.8	25	3.8	10	1.5
	Sub adult female	191	28.9	242	36.7	189	28.6	15	2.3	15	2.3	8	1.2

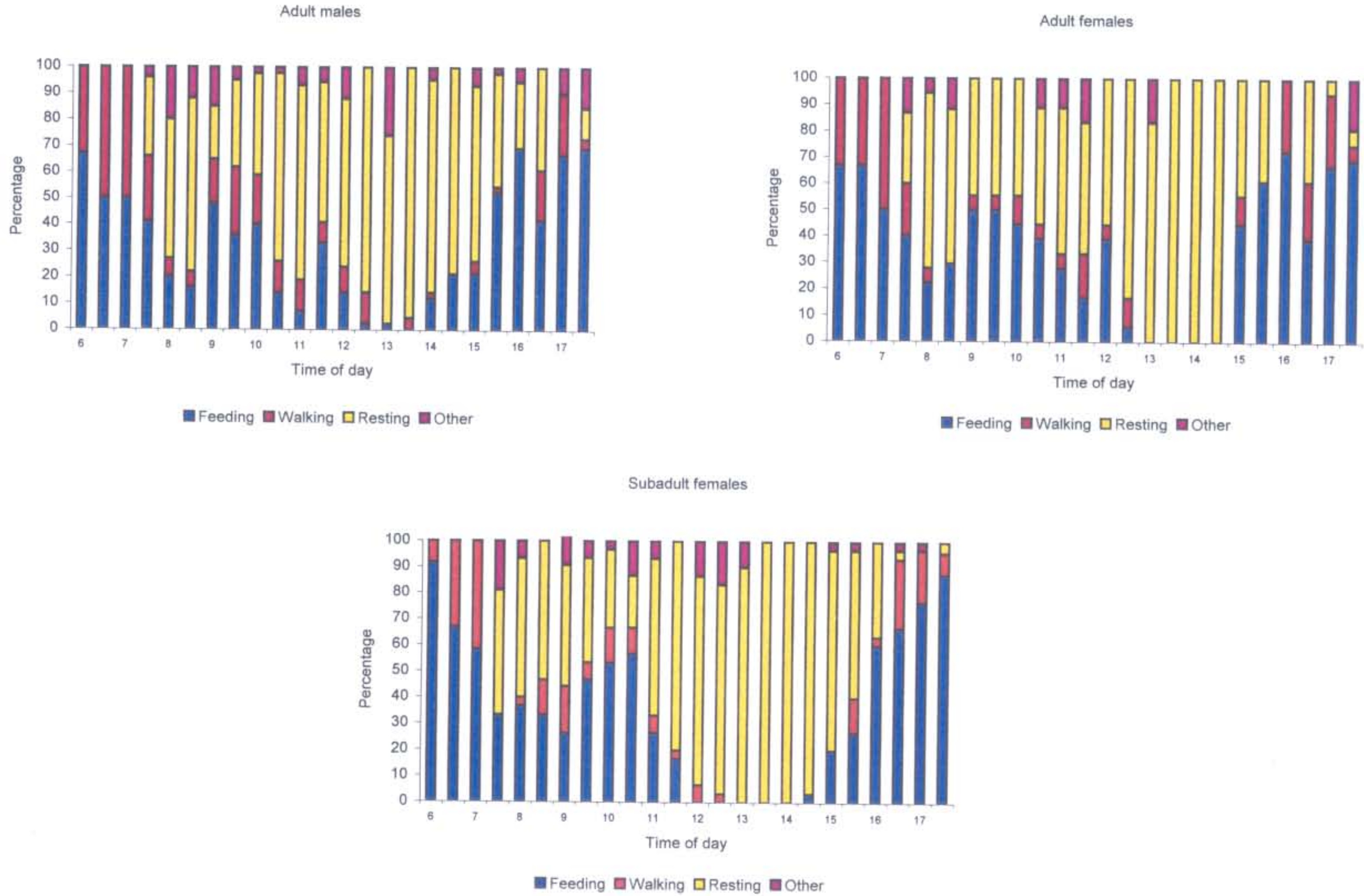


Figure 38: The frequency distribution of some of the diurnal activities of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed during the spring of 1995.

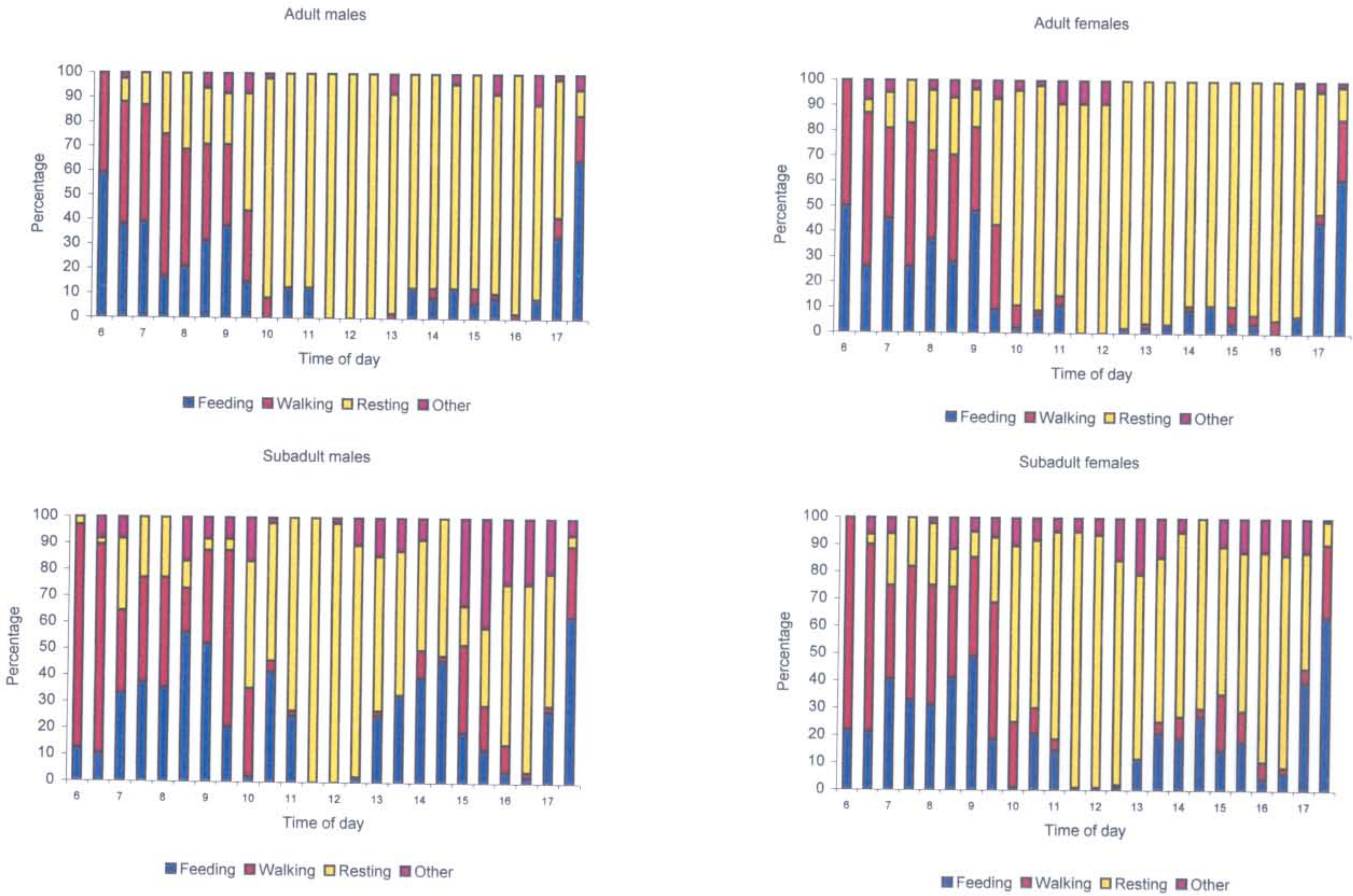


Figure 39: The frequency distribution of some of the diurnal activities of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed during the summer of 1995.

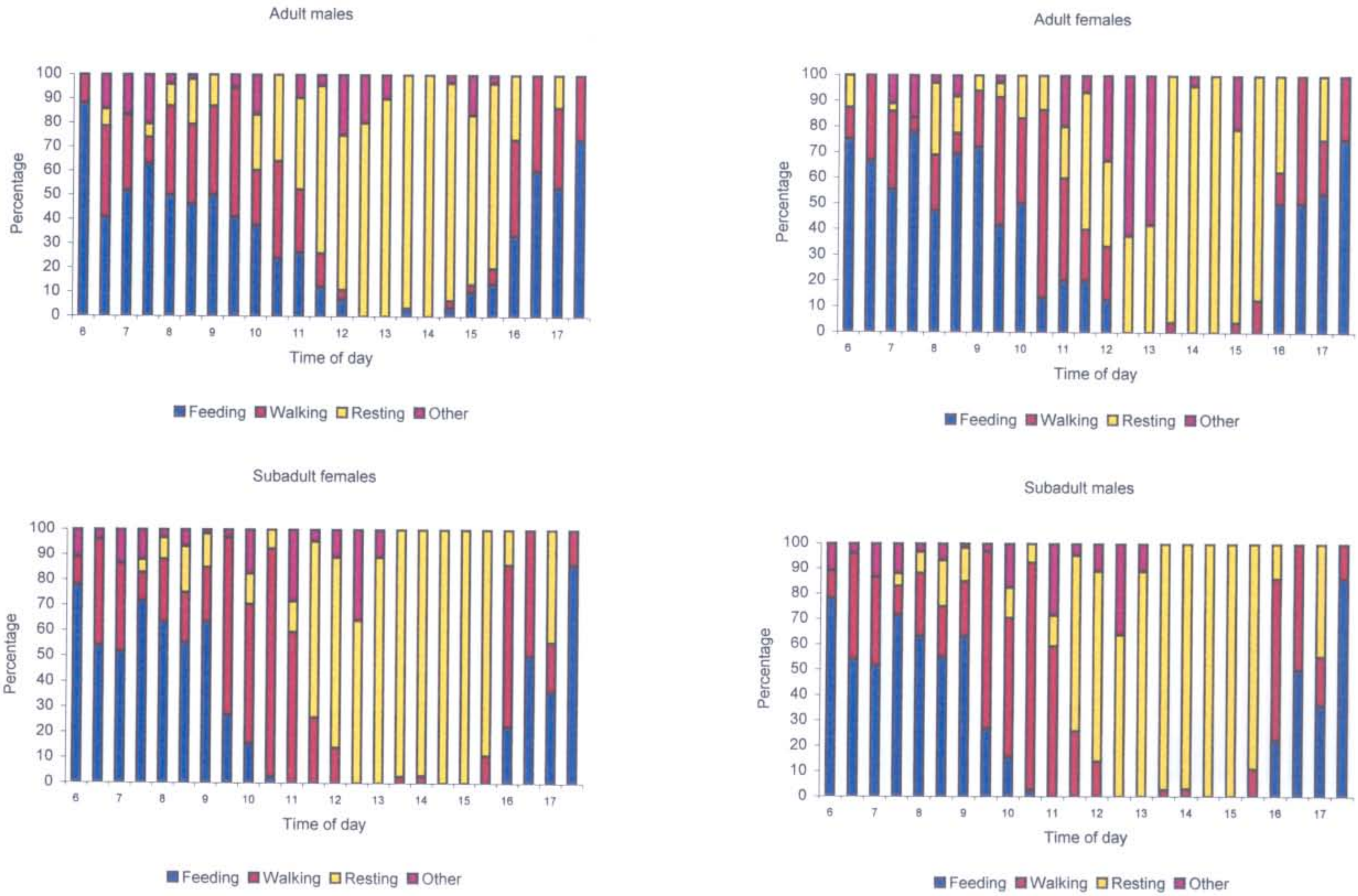


Figure 40: The frequency distribution of some of the diurnal activities of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed during the autumn of 1995.

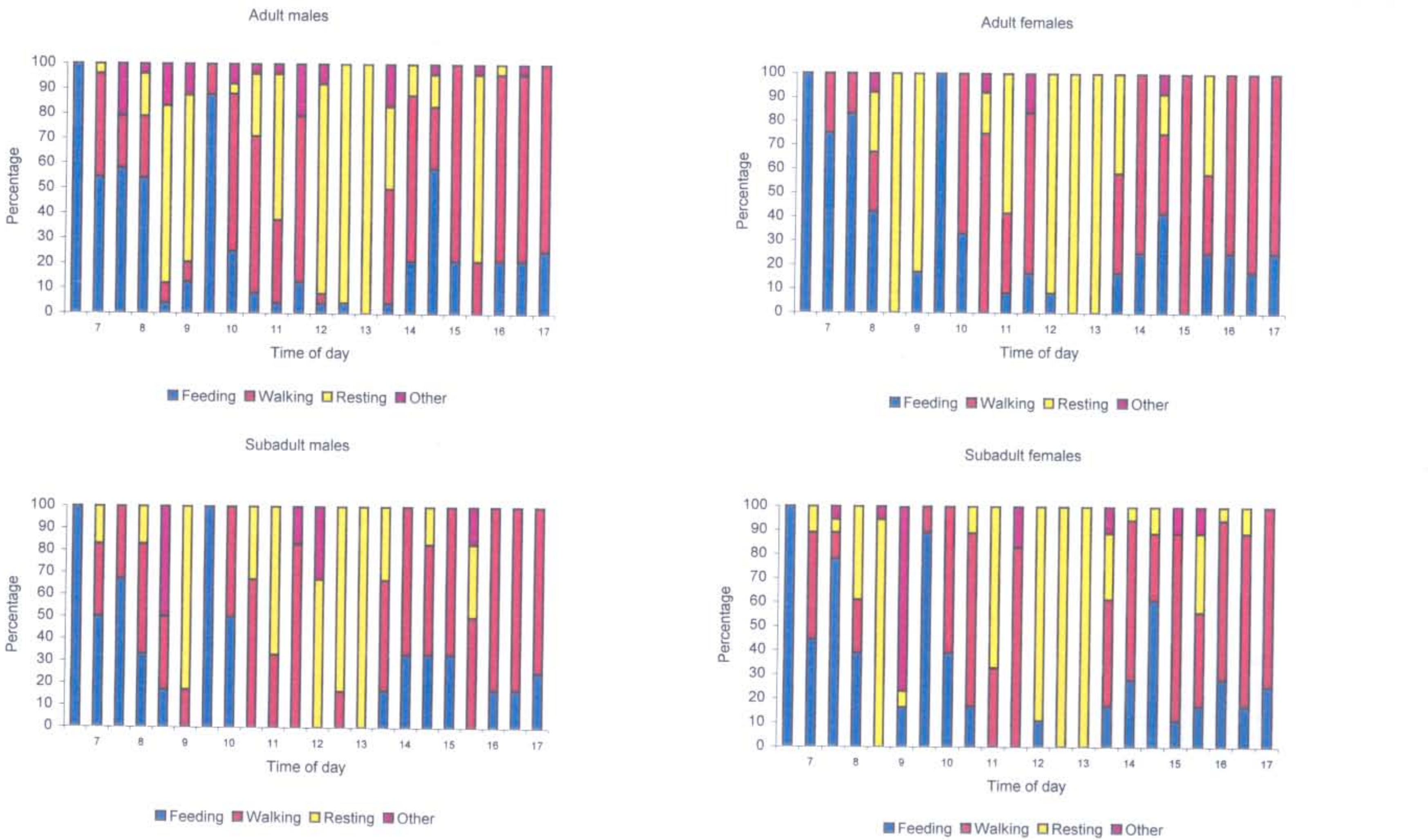


Figure 41: The frequency distribution of some of the diurnal activities of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed during the winter of 1995.

adult females to limit their activities during the daylight hours than it is for the subadult females or any other age and sex class to do so.

Comparatively, the Arabian oryx spends most time in feeding during the spring while the least time is spent in this activity during the summer. Significant differences exist in the actual time spent in feeding by the Arabian oryx when spring is compared with summer ($P = 0.0000$) and winter ($P = 0.0244$). Significant differences ($P = 0.0003$) also exist in the actual time spent feeding by the oryxes during summer and autumn. It is thought that the proportion of time spent on feeding in the early mornings before sunrise and the early evenings after sunset is higher during the summer than during spring, autumn and winter. During summer the oryxes therefore spend less actual feeding time during the daytime than in any of the other seasons, despite the difference between summer and winter not being statistically significant ($P = 0.1453$).

The benefits of an increase in feeding activity before and after sunset during summer, would be twofold. Firstly, it would promote the preservation of both energy and water. Secondly, it could potentially increase the amount of moisture obtained by the Arabian oryxes because the dry grass absorbs moisture from the desert air during the night, even on nights when there is no dew (Taylor 1968; 1969). This accumulation of moisture is explained by the drop in nighttime temperature, the accompanying increase in the relative humidity of the desert air and the fact that certain desert plants are known to be able to absorb moisture from the air.

Owen-Smith (in Norton 1981) suggested that most antelopes follow a feeding pattern where considerably less time is spent in feeding during the night than in the day, due to predator vulnerability during the night. However, in the harsh environment occupied by the Arabian oryx, pressure from predators is low due to the fewer predator species and lower prey densities found in these areas (Stanley-Price 1989). In addition the environment is so harsh that the need for moisture-rich food would probably outweigh the possible risk of predation when feeding during the night.

Although grazing occurs during all the hours of the day, the clear interaction found here between the time of day and season of feeding ($P = 0.0000$) indicates that the time of day influences the distribution of feeding activities of the oryxes between seasons. It has already been shown that there is a clear shift in the mean seasonal locations (Chapter 5) and consequently in the preferred subhabitat used by the reintroduced oryxes on a seasonal basis (Chapter 6). These changes, which are at least in part due to climatic conditions,

Table 25: A multi-factor analysis of variance test on the time spent feeding by the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the summer, autumn and winter of 1995. Significant factors are shaded in yellow.

FACTOR	D.F.	F-RATIO	P - VALUE
Age and sex class	3	2.27	0.0833
Time of day	23	59.97	0.0000
Season	2	60.37	0.0000
Age and sex class X Time of day	69	1.17	0.2160
Age and sex class X Season	6	4.10	0.0008
Time of day X Season	46	27.56	0.0000

undoubtedly influence the activity cycles and therefore the feeding behaviour of the reintroduced animals. For example, during the spring or winter the animals are found to graze for long periods of the day, while in the summer it is not uncommon to find the animals shading under trees or shrubs at 07:30. The lack of interaction (P = 0.2160) between the age and sex classes and the time of feeding shows that the feeding patterns of the different age and sex classes are synchronised throughout the day over all the seasons. It is, however, known that outside the rut yearling and subadult animals in many ruminant species typically spend less time in feeding than the adults of the same species (Bunnell & Gillingham 1985). Therefore, age does have some influence on the feeding patterns of some ruminants.

Although the differences are not significant (P = 0.7404) an Arabian oryx female spends more time in feeding during the daylight hours than does a male in the 'Uruq Bani Ma'arid Protected Area. Similar observations have been made on gemsbok in the Hester Malan Nature Reserve of South Africa (Dieckmann 1980) and for klipspringer *Oreotragus oreotragus* (Zimmermann, 1783) in South Africa (Norton 1983). In the klipspringer study the foraging time of the females was 39.0% higher than that of the males. In East Africa, Lewis (1977) found that lactating oryx and eland females spent 8.0% and 5.0% more time in feeding respectively than did the males. The reasons for all these differences in feeding times between females and males are all because gestation and lactation cause the females to have higher nutritional demands than the males.

Walking

Movement towards shade is linked with feeding in the sense that an individual oryx will feed while moving to its desired place of resting. When the prevalent climatic conditions, and subsequently the distribution of the feeding plants in the study area, are taken into consideration, walking should form a large portion of the daily activities of an oryx. It was therefore not unexpected to find that the walking activities did indeed peak in the same period as the feeding ones.

No significant differences (P = 0.4775) were found between the time spent walking by the different age and sex classes during spring. The multi-factor analysis of variance showed that age and sex class is not a significant (P = 0.5060) factor in determining the time spent on walking. This indicates that all the adult oryxes but especially the males do not show any preference for or attempt to keep other oryxes away from certain feeding areas (Chapter 2). However, season proved to be an important factor, indicating significant (P = 0.0000) differences in the amount of time spent in walking by the oryxes during different seasons. There was no relationship, in terms of walking, between season and age and sex class (P = 0.9980), which indicates that the behaviour of the different age and sex classes was similar for all seasons.

Comparatively, the Arabian oryx spends the least amount of time on walking during the spring, while most time was spent on this activity during the winter. Significant differences in walking intensity occur between the spring and autumn (P = 0.0028) and the spring and winter (P = 0.0002). The differences in walking intensity between the autumn and winter (P = 0.0009) and between the summer and winter (P = 0.0001) were also significant. The fact that the Arabian oryx walks less during the spring than in any of the other three seasons is probably because vegetation of higher quality is more readily available in the spring than in any of the other seasons. In terms of vegetation quality and quantity the opposite is true for the winter, which explains why the oryxes then spend so much time walking as they search for food.

The different intensity of walking in the summer as opposed to the winter is probably the result of different combinations of environmental conditions during these two seasons. The high summer ambient temperatures will make the oryxes less active then, and the low quality of the vegetation during the winter will force them to move greater distances in search of adequate food. It is well-known that the distribution, abundance and the quality of food can influence the activity patterns of ungulates in the Northern Hemisphere (Renecker & Hudson 1989). Consequently such a result is to be expected.

The higher search rate for food in the winter also explains why feeding was not the most time consuming activity then when compared with the other seasons. Hudson (1985) states that large herbivores have high total forage requirements and that these requirements may be most difficult to meet under extreme winter conditions. Consequently, the Arabian oryx can be expected to spend more time on walking during the season of low food abundance. The animals spent less time in walking during the autumn than the winter because of the fresh growth that is available on the perennial plants during the autumn, even before the first rains (Chapter 6). The availability of food of sufficient quality therefore does not require the animal to roam widely.

Resting without ruminating

The typical relationship between the different resting activities of the Arabian oryx is illustrated in Figure 42. Although these activities occur throughout the day from as early as 07:00, resting peaks from the late morning (10:00) until approximately mid-day (14:00), a period when 56.0% of all the resting observations in this study were made.

During the spring the subadult females spend significantly (P = 0.0142) more time in resting in the shade than the adult females. During the remaining three seasons multi-factor analysis of variance tests showed that both age and sex class (P = 0.0443) and season (P = 0.0000) were significant factors in influencing the time spent in resting in the shade by the oryxes. In addition, the interaction between age and sex class and season was also significant (P = 0.0289).

The only significant (P = 0.0309) difference in time spent in resting by the various age and sex classes was between the adult and subadult males. A significant difference (P = 0.0289) was found in the frequency of resting between the age and sex class and the season involved. This also indicates that the nature of this interaction between the adult and subadult males changes over the seasons. During the summer, for example, an adult male Arabian oryx spends significantly (P = 0.0011) more time in resting in the shade than a subadult male. This is due to the social organisation of the reintroduced animals. It has often been observed that an adult male will stand up from where it was lying in the shade and walk across to another tree or shrub where another animal is lying. If this adult male is dominant to the animal that it is approaching, the latter will get up and move away, allowing the adult male to take over the vacated shade. Often the displaced animal will first stand in the sun or feed before looking for another place to lie down; often also in the sun. Shade use therefore is a form of competitive behaviour. No significant differences were found in the total times which adult and subadult male Arabian oryxes spend resting in the shade during the autumn (P = 0.7329) or the winter (P = 0.3225).

Comparatively speaking, the different age and sex classes of Arabian oryx spend most time in resting in the shade during the hot summer months, and least during the winter (Table 26). Significantly (P = 0.0000) more time was spent resting in the shade by the oryxes during the summer than the winter. In the summer the oryxes spend 44.3% of their time in resting in the shade but in the winter it occupies <1.0% of their time. There are also significant differences in the time spent resting in the shade by all the oryxes between the summer and autumn (P = 0.0004) as well as the autumn and winter (P = 0.0000). These differences are attributed to the changing environmental conditions and specifically in the decreasing ambient temperatures from the summer through autumn to the winter.

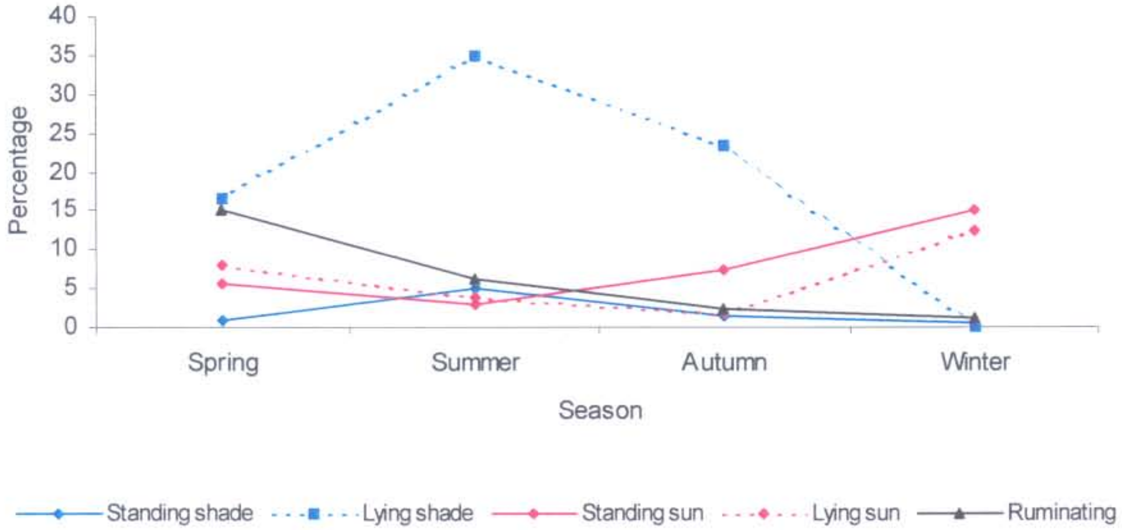


Figure 42: The percentage of time spent in various resting activities by the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the different seasons of 1995.

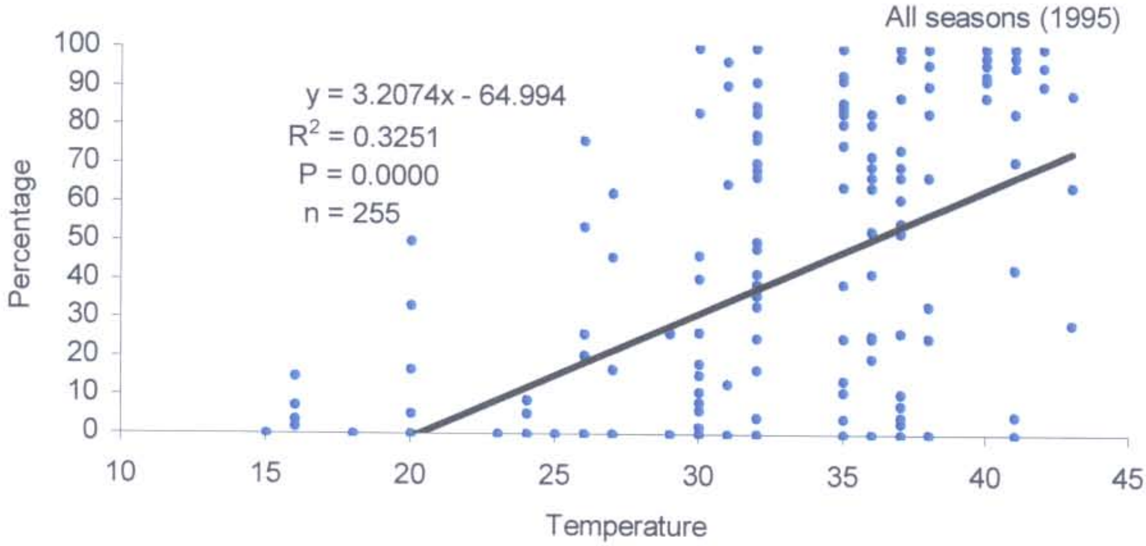
Table 26: The time spent resting by the reintroduced Arabian oryxes during the day in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined through instantaneous scans of different herds during 1995.

SEASON	AGE AND SEX	RESTING IN THE SHADE						RESTING IN THE SUN					
		Standing		Lying		Ruminating		Standing		Lying		Ruminating	
		Minutes	%	Minutes	%	Minutes	%	Minutes	%	Minutes	%	Minutes	%
SPRING	Adult male	8.4	0.3	76.7	3.6	77.3	3.6	47.5	2.2	74.2	3.4	46.6	2.2
	Adult female	5.0	0.2	85.1	3.9	28.4	1.3	52.8	2.4	70.3	3.3	86.3	4.0
	Subadult male	-	-	-	-	-	-	-	-	-	-	-	-
	Subadult female	10.9	0.5	194.6	9.0	65.2	3.0	21.8	1.0	29.7	1.4	24.4	1.1
	Subtotal	24.3	1.0	356.4	16.5	170.9	7.9	122.1	5.6	174.2	8.1	157.3	7.3
SUMMER	Adult male	37.3	1.3	327.6	11.4	42.4	1.5	19.4	0.7	16.1	0.6	6.3	0.2
	Adult female	46.4	1.6	318.1	11.0	41.8	1.5	11.4	0.4	17.3	0.6	7.1	0.2
	Subadult male	25.1	0.9	143.0	5.0	23.2	0.8	32.3	1.1	43.3	1.5	30.7	1.1
	Subadult female	32.1	1.1	216.6	7.5	22.6	0.8	23.5	0.8	33.4	1.2	7.3	0.3
	Subtotal	140.9	4.9	1005.3	34.9	130.0	4.6	86.6	3.0	110.1	3.9	51.4	1.8
AUTUMN	Adult male	23.8	0.8	171.2	5.9	26.6	0.9	44.0	1.5	7.3	0.3	5.0	0.2
	Adult female	3.0	0.1	158.2	5.5	2.2	0.1	48.9	1.7	21.2	0.7	7.0	0.2
	Subadult male	4.5	0.2	179.9	6.2	10.8	0.4	63.0	2.2	13.8	0.5	2.2	0.1
	Subadult female	14.2	0.5	163.2	5.7	11.6	0.4	54.0	1.9	8.0	0.3	0.0	0.0
	Subtotal	45.5	1.6	672.5	23.3	51.2	1.8	209.9	7.3	50.3	1.8	14.2	0.5
WINTER	Adult male	15.0	0.6	0.0	0.0	0.0	0.0	92.5	3.5	81.3	3.1	10.0	0.4
	Adult female	0.0	0.0	0.0	0.0	0.0	0.0	97.7	3.7	102.6	3.9	2.3	0.1
	Subadult male	0.0	0.0	0.0	0.0	0.0	0.0	100.6	3.8	60.0	2.3	5.0	0.2
	Subadult female	0.0	0.0	0.0	0.0	0.0	0.0	108.5	4.1	80.1	3.0	15.0	0.6
	Subtotal	15.0	0.6	0.0	0.0	0.0	0.0	399.3	15.1	324.0	12.3	32.3	1.3
Total		225.7	-	2034.2	-	352.1	-	817.9	-	658.6	-	255.2	-

In the spring the actual time spent in resting in the sun by the subadult females was significantly less than that by the adult males ($P = 0.0164$). Season was a significant ($P = 0.0000$) factor in determining the amount of time spent resting in the sun by the Arabian oryxes. Neither age and sex class ($P = 0.7225$) nor the interaction between age and sex class and season ($P = 0.8138$) were found to be significant factors in determining the amount of time spent resting in the sun by the Arabian oryxes. During the winter the oryxes spend significantly more time in resting in the sun than during both the summer ($P = 0.0007$) and the autumn ($P = 0.0000$). This is the result of different prevailing climatic conditions during these seasons.

Of all the observation time spent on all of the age and sex classes of the Arabian oryxes during the summer, 52.9% was on resting activities as compared with 29.2% for the winter. The relationship between increasing ambient temperature and the proportion of animals resting in the shade was highly significant ($P = 0.0000$) for the entire monitoring period (Figure 43). This is so despite the fact that only 32.5% of the variance in the percentage animals resting in the shade were explained by the variance in the ambient temperature ($R^2 = 0.325$). During the summer of 1995 the relationship between increasing ambient temperature and the proportion of the oryxes resting was also found to be significant ($P = 0.0000$). During this time 44.2% of the variance in the percentage animals resting in the shade could be explained by the variance in the ambient temperature ($R^2 = 0.4415$). These results show that there is a direct relationship between an increase in the ambient temperature and the degree of resting in the shade by the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area during all the seasons, but especially so during the summer.

The variation in the time spent by an Arabian oryx in resting in either the shade or the sun during the different seasons appears to be related to solar radiation and therefore to ambient temperature. The advantages in resting in the shade during the summer months are obvious in that the animals are sheltered from direct exposure to the sun. The difference in the ambient temperature in the sun as opposed to that in the shade is severe, as indicated earlier (Chapter 6). In the present study it has often been observed that an oryx will scrape in the sand before lying down in the shade of a tree or shrub. This is done to remove the upper, warm layer of the sand so as to get to the lower, unexposed and consequently cooler sand before lying down. This would again help in keeping the body temperature low during the summer. During the summer when the ambient temperature can reach levels in excess of 45 °C in the shade an Arabian oryx probably builds up a heat load during the day that dissipates at night, as does the Beisa oryx and the gemsbok. The Beisa oryx adapts to a waterless environment by making use of adaptive heterothermy* (Taylor 1968; 1969). This



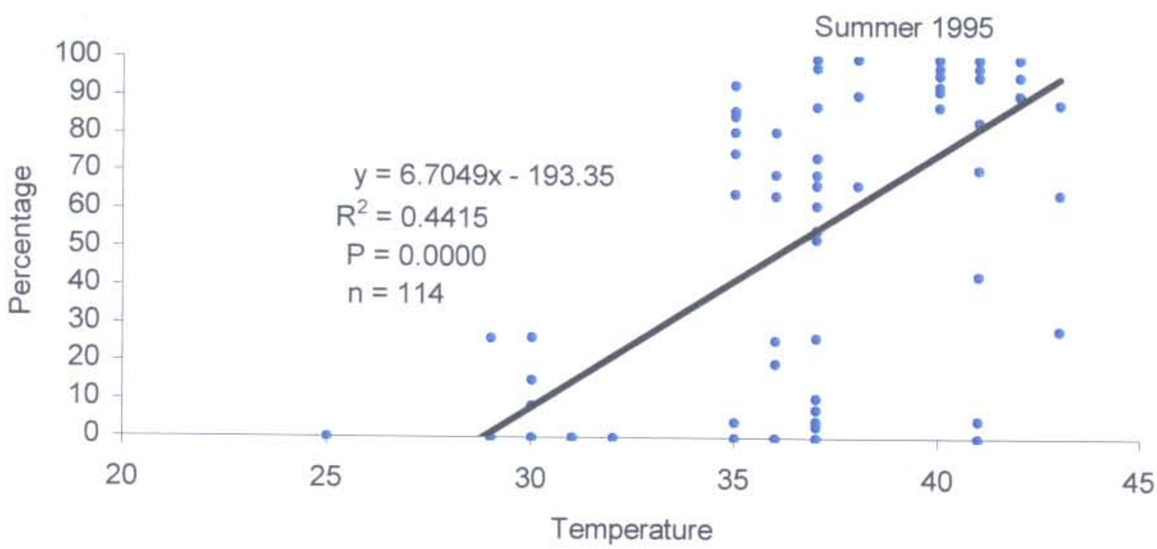


Figure 43: The relationship between increasing ambient temperature (°C) and the proportion of time spent by the reintroduced Arabian oryxes resting in the shade during each 30-minute period of the day as observed from 06:00 to 18:00 at different times in 1995 in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia.

means that the oryx has an endothermic* ability to allow its body temperature to fluctuate in response to environmental stresses (Grenot 1992). This is done by accommodating extreme body temperatures, and by decreasing the amount of metabolic heat produced. It is known that the Beisa oryx can increase its body temperature to a level in excess of 45 °C for as long as 8 hours (Taylor 1968).

Such hyperthermia*, has also been observed in gazelles. It enables these animals to prevent the loss of large amounts of water even under severe heat loads. This is accomplished by reducing the amount of heat gained, creating a smaller difference in temperature between the animal and its environment. It saves water and energy through a reduced need for evaporative cooling (Wilson 1989). This ability is considered to be the critical factor in the survival of these animals in desert conditions (Taylor 1968). It is also known that the Beisa oryx does not sweat when its body temperature increases above 41 °C. Instead these animals pant like a mammal carnivore to lose an excess of heat. During the high ambient temperatures of the summer, the brain of an oryx, which is more sensitive to high temperatures than the rest of the body, is therefore kept cooler than the rest of the body by a countercurrent cooling system in the cavernous sinuses. Cool venous blood from the nasal passages drains into these sinuses, reducing the temperature of the arterial blood on its way to the brain (Taylor 1969).

Resting and ruminating

Ruminating takes place while an animal is standing up, lying down or walking around (Innis 1958; Dagg & Foster 1976). During the present study, ruminating was recorded only when an Arabian oryx was standing or lying down because it was not possible to distinguish whether an animal was chewing freshly plucked food or was ruminating while walking.

During the spring no significant differences (P = 0.5891) exist in the actual time spent on ruminating by the different age and sex classes. During the other three seasons, season was found to be a significant (P = 0.0000) factor in determining the amount of time spent by the oryxes in ruminating, while neither the age and sex class (P = 0.7253) nor the interaction between the age and sex class and season (P = 0.8618) were significant factors.

The Arabian oryx spends most time in ruminating during the summer, and the least in doing so during the winter. The difference between the actual time spent ruminating by all the oryxes in the summer and winter was significant (P = 0.0000). Significantly more time (P = 0.0002) was also spent on ruminating by all the oryxes in the summer than in the autumn.

Elsewhere it has been indicated that the Arabian oryx changes its diet during the hot summer months, as does other grazers (Chapter 7). The amount of time spent in ruminating during the summer is possibly linked to the high fibre diet consumed by the animals during such time. During the autumn, however, many of the perennial plants in the 'Uruq Bani Ma'arid Protected Area show signs of fresh growth, even before the first rains (Chapter 6). The animals are therefore able to feed on succulent, fresh, sprouting vegetation that probably requires less rumination. Dieckmann (1980) found that the gemsbok in the Hester Malan Nature Reserve, South Africa, spends the least amount of time on ruminating during the late winter (July and August). This was attributed to the diet of the gemsbok, which mostly consists of ephemerals* during this time. These plants are succulent and require little rumination. The low levels of rumination during the winter in the present study are probably partly due to the increased walking activity in search for food.

Social activity

During the spring, the adult male Arabian oryxes were socially the most active of the three age and sex classes observed. In comparison, significantly more time was spent on social activities by the adult males than the adult (P = 0.0050) and the subadult females (P = 0.0432). Of all the social activities observed during the spring, 71.0% involved the adult males and 23.8% the subadult females. Adult females were involved in 5.2% of all the social activities observed during spring. Of all the social activities recorded for all ages of female Arabian oryxes, 83.0% were in response to courtship behaviour displayed by an adult male. Spalton (1995) showed that the condition of the vegetation and the subsequent physical condition of the females are the determining factors in the reproductive cycle of the Arabian oryx. The high rate of social activity observed in the adult males during spring is thought to be due to the fact that these animals had been in the wild for a short time only. As the animals came from more than one release group there was considerable interaction between the males in an attempt to establish a dominance hierarchy. Also important during this time was the fact that many females came into oestrus during the spring because of the good environmental conditions that existed then.

Multi-factor analysis of variance showed that significant differences exist in the time being spent on social activities by the oryxes in the summer, autumn and winter (P = 0.0137). There are also significant differences (P = 0.0184) in the time being spent on social activities by the different age and sex classes. The interaction between the age and sex classes and season relevant to social activities was not significant (P = 0.9598), however. On a seasonal basis all the Arabian oryxes spend significantly more time on social activities during the winter than during either the summer (P = 0.0312) or the autumn (P = 0.0267). Significantly different times (P = 0.0002) were also spent on social activities by adult males compared with adult females. Adult male Arabian oryxes also spend significantly more time (P = 0.0103) on social activities than do the subadult females. The generally reduced activity levels during the hot months can explain the lower frequency of social interactions that was found in the summer. The differences found between the times spent on social activities by all oryxes in the winter when compared with the autumn cannot yet be explained.

The fact that there is no significant difference in the time (P = 0.5827) spent on social activities by adult and subadult male Arabian oryxes during the summer, autumn and winter, indicates that the majority of social interactions observed during these seasons were between these two age and sex classes. During these seasons, the male Arabian oryxes were involved in 83 social interactions, 65.0% of which were associated with enforcing the dominance hierarchy amongst the male Arabian oryx. The remaining 35.0% was associated with sexual behaviour.

Activity synchrony within herds

The Arabian oryx in the 'Uruq Bani Ma'arid Protected Area is synchronised in its behaviour and an entire herd will change from one activity to another within a relatively short time.

Following Berry (1980) this is illustrated here by relating the active to the inactive periods, and expressing the one as a proportion of the other (Figure 44). From these data, two clear periods of activity are shown, which are interspersed with a major period of inactivity. The rapid change from activity to inactivity demonstrates the high degree of activity synchrony within the herds. This synchrony is to a large extent thought to be due to contagious activities as has already been reported by Dieckmann (1980) for the gemsbok. Most of these activities involve feeding and lying down. A large portion of the herd usually follows the lead of an individual. Once that individual animal starts to display a particular type of activity they all follow. These contagious activities are not observed in all ungulates and are at least in part related to the climatic conditions that the animals are subjected to. For example, in western Alaska it was found that the activities of moose were not highly synchronised, and synchronised activity patterns were not observed at sunrise and sunset. These results led to the suggestion that the moose in western Alaska does not have to maintain a specific diel rhythm during the winter (Gillingham & Klein 1992). Moose are, however, heat-intolerant (Renecker & Hudson 1986) and show higher levels of activity synchrony under warm conditions.

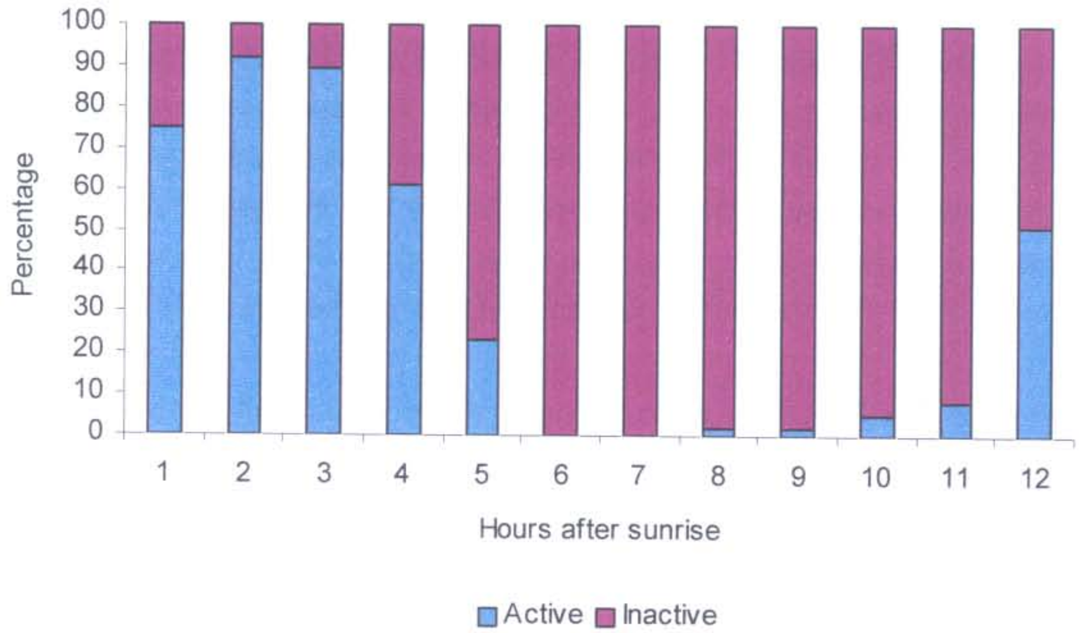


Figure 44: The proportion of time spent being active or inactive by the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia as measured for 12 observations per hour for 12 hours during 1995.

Conclusions

The basic activity pattern of the Arabian oryx follows the typical pattern of diurnal ungulates, with feeding peaks in the early morning and late afternoon. This pattern is the same for all the seasons, despite the fact that more time is spent in feeding at night and in the early morning before sunrise during the summer. This activity pattern is similar to that described by Jarman & Jarman (1973) for the impala *Aepyceros melampus* (Lichtenstein 1812), Walther (1973) for the Thomson's gazelle, Petit *et al.* (1987) for captive Arabian oryx, Launay & Launay (1991) for sand gazelle and Kruger (1994) for giraffe. The daily activity of the Arabian oryx furthermore conforms to a polyphasic activity pattern as described in the Beisa oryx by Walther (1978). Activity peaks occur early in the mornings and late in the afternoons, and are associated with feeding behaviour.

The activity pattern of the Arabian oryx is driven by two main factors. They are the seasonal climatic conditions and the quality of the vegetation. Fresh growth in the perennial plants, and new growth of the annual plants are most likely after the spring rains, although some fresh growth also occurs in the autumn. Therefore spring and autumn are the seasons during which the Arabian oryx spends more time in feeding than in walking in search of food. By contrast, most time is spent on walking during the winter in an attempt to obtain enough forage of sufficient quality to sustain an individual during this lean period. The lowest level of activity in the Arabian oryx occurs in the hot summer months when the animals spend most of their day in resting. The increase in the percentage of individuals found resting as the ambient temperature increases, supports the suggestion that climatic conditions play an important role in determining the activities of the Arabian oryx. Reduced levels of activity in daytime in the summer are an important energy- and water-saving strategy that results in a decrease in the metabolic heat produced by the Arabian oryx.

In the 'Uruq Bani Ma'arid Protected Area, the grazing activity of the Arabian oryx occupies 29.2% of the total time, while 41.1% of such time is spent in resting, including rumination. The fact that the Arabian oryx spends more time resting and ruminating than in feeding suggests that the quantity and quality of the available vegetation was not a limiting factor to the number of Arabian oryx in the area during the study period.

CHAPTER 10

POPULATION VIABILITY ANALYSIS

Introduction

The primary causes of species decline are often obvious and deterministic, and include over-harvesting, conversion of the natural habitat which renders it lost to the particular species, pollution, local and global climate changes, exotic competitors, and predators among others. Although the primary causes of species decline are often easy to understand they are also much more difficult to reverse (Miller & Lacy 1999). An example of this is the recent near-demise of the free-living Arabian oryx population in Oman. Because of severe poaching, that population, which once numbered in excess of 400 animals in 1996, is no longer considered viable unless it is boosted by additional releases (Spalton, Lawrence & Brend 1999).

According to Caughley (1994) there are two different paradigms operating within conservation biology. These are the small population paradigm, which deals with the risk of extinction inherent in small numbers, and the declining population paradigm which is concerned with the processes by which populations are driven to extinction by agents external to them. The small population paradigm deals mostly with the population genetic and population dynamics problems faced by a population which is at risk of extinction due to its small size (Caughley 1994). The declining population paradigm focuses mainly on ways of detecting, diagnosing and halting a predicted or an actual population decline. In the declining population paradigm the problem is seen as a population that is in trouble due to something external that has changed. Consequently the size of the population is of no great relevance (Caughley 1994). All the effort is then aimed at determining why the population is declining and how the trend can be reversed. Both these approaches have much in common (Hedrick, Lacy, Allendorf & Soulé 1996), as they both focus on the fate of a given species. Although these two paradigms have been reconciled recently (Hedrick *et al.* 1996) and a broader understanding of the factors influencing endangerment and extinction*, through an inclusive approach to population viability analysis has been advised, they still form the basis for approaches to assessing extinction risk (Mace & Hudson 1999).

Population viability is the anticipation through data modelling of the likelihood that a population will persist for some arbitrarily chosen time into the future (Shaffer 1981; 1987). A concept that is closely related to population viability is minimum viable population analysis.

This type of analysis gives an estimate of the minimum number of organisms of a particular species that constitutes a viable population (Boyce 1992). Population viability analysis embraces the minimum viable population concept, without attempting to estimate the absolute minimum population necessary to keep the species viable (Soulé 1987). The viable population concept was formalised by Shaffer (1981) who presented four stochastic factors that affect population viability. These factors are demographic stochasticity, genetic stochasticity, environmental stochasticity and catastrophe. It has been stressed that the factors causing species extinction are interrelated and dynamic (Shaffer 1981; Gilpin & Soulé 1986). Subsequently Gilpin and Soulé (1986) suggested an integrated viability analysis for assessing the persistence of a species, which deals with demographic and genetic factors, while also introducing the concept that persistence expectations are probabilities.

Population viability analysis has been a popular modelling tool in conservation ever since its development (Ludwig 1999). It offers the prospect that sophisticated mathematical tools can be used to provide quantitative estimates of important quantities relating to threatened populations, such as the expected time to extinction or the probability of a population surviving for the next 100 years. There is, however, substantial disagreement in the literature regarding the usefulness of population viability analysis in conservation (Boyce 1992; Ludwig 1999). A concern often raised is the impression that population viability analysis provides exact results (Beissinger & Westphal 1998; Reed, Murphy & Brussard 1998). This has led to the suggestion that the results from the population viability models should be used in a relative fashion by comparing outcomes among model alternatives (Ralls & Taylor 1997; Beissinger & Westphal 1998). This has, for example, been done for the African elephant *Loxodonta africana* (Blumenbach, 1797) in Kenya (Armbruster & Lande 1993), African wild dogs *Lycaon pictus* (Temminck, 1820) in the Selous Game Reserve (Vucetich & Creel 1999), the lower keys marsh rabbit *Sylvilagus palustris hefneri* (Bachman, 1837) of Florida (Forys & Humphrey 1999) and a warthog population in the Andries Vosloo Kudu Reserve, South Africa (Somers 1997).

In the present study the computer prgram VORTEX (Miller & Lacy 1999) was used to model the future of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area. The Conservation Breeding Specialist Group of the IUCN (Miller 1995; In: Brook, Cannon, Lacy Mirande & Frankham 1999) has used this particular program extensively in population viability analysis on a number of species, including the Cape mountain zebra *Equus zebra zebra* (Novellie, Miller & Lloyd 1996). VORTEX has also been used in modelling the Arabian oryx population in Oman (Spalton 1995) and a roan antelope population in Kenya (Magin &

Kock 1997). In addition the populations of blue crane *Anthropoides paradiseus*, wattled crane *Bugeranus carunculatus* and the grey crowned crane *Balearica regulorum* in the Mpumalanga province of South Africa have also been modelled with this program (Morrison 1998). VORTEX is considered to be the simulation program most widely used in population viability analysis (Caughley 1994).

The aim of this part of the study was therefore to assess the performance of the reintroduced Arabian oryx population over the short (10-year) and the medium (100- year) term and to answer the following principal questions:

- Could the population growth rate of the reintroduced Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area have been increased through a stable age distribution?
- Which sex ratio would give the optimal growth rate for the reintroduced Arabian oryx population?
- What effect would catastrophes have on the medium term (100-year) survival of the reintroduced Arabian oryx population?
- What likely effect would the additional release of oryxes have on the population growth rate and the persistence of the reintroduced population?
- What would the likely effect on the reintroduced population be if oryxes were removed from the population in an uncontrolled manner such as through poaching?
- On which population parameters should management actions concentrate to ensure the survival of the reintroduced Arabian oryx population over the medium term?

Methods

VORTEX is based on a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. In addition to environmental stochasticity, VORTEX can also model the effect of catastrophic events. Population dynamics are modelled by VORTEX, as discrete, sequential events that occur according to probabilities that are random variables, following user-defined distributions (Lacy 1993). A population is simulated over a specified time interval by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism. These events include mate selection, mortality, increment of age by one year, migration among populations, removals, supplementation, and the truncation to the ecological capacity, if necessary. The simulation is then iterated a number of times, as specified by the user, and produces a distribution of outcomes that the actual population might experience under similar conditions in the wild.

Basic model

The basic model was run over a 10-year period with 1000 iterations. The data used were those that were collected from March 1995 to February 1997. The assumptions made and the vital rates used in the basic model were as follows:

- Inbreeding depression was incorporated into the calculations by using the default values in VORTEX for the number of lethal alleles (3.14) and the percentage (50.0%) of the genetic load that is due to lethal alleles.
- Catastrophes were not included in the basic model.
- The mating system is polygynous and all the adult male oryxes (older than 4 years) were considered to be in the breeding pool.
- The age at first breeding for a female oryx, i.e. the age when the first calf is born, was taken as 3 years and the maximum age of reproduction was estimated to be 15 years.
- The ratio of males to females at the time of birth was taken to be 50.0%. Equal numbers of males and females were therefore born.
- Reproduction was density-independent.
- It was assumed that 80.0% of the breeding age females, with an estimated standard deviation of 15.0%, could breed during any year of the basic model. The maximum number of young that a female could produce within a time cycle of a year was two, and 21.0% of female oryxes produced twice within such a time. The remaining 79.0% of female oryxes that produced calves did so only once within a given year.
- The Arabian oryx population at the time of modelling was the 66 oryxes released into the 'Uruq Bani Ma'arid Protected Area from March 1995 to February 1997 (Table 27).
- The ecological capacity of the 'Uruq Bani Ma'arid Protected Area was estimated to be 400 Arabian oryxes, with a standard deviation of 80 animals (20.0%). This is an estimated figure, based on knowledge of the core protected area and the critical summer range as identified by Wacher (1997) as well as the low primary productivity in the area. A population of 400 oryxes in the 2500 km^2 core area of the 'Uruq Bani Ma'arid Protected Area translates to a density of 0.16 oryx per kilometre squared. This density estimate is approximately midway between the observed minimum and maximum oryx densities of 0.1 and 0.4 oryx per kilometre squared as observed in Oman (Tear 1992). No trend in the ecological capacity was modelled.

- The oryx population in the basic model was not supplemented and no harvesting took place.

Corrected basic model

The variables and assumptions used in this more realistic model is the same as those used in the basic model, unless otherwise specified. Due to the more realistic mortality figures the corrected basic model was used as the basis for all the subsequent models investigated through VORTEX. More realistic mortality figures, mimicking the characteristic u-shaped mortality curve in ungulates (Chapter 8) have been estimated. The new mortality figures (Table 27) are based on those observed in the present study and reported elsewhere (Stanley-Price 1989; Spalton 1995).

The corrected basic model was then used to model the reintroduced population over a 10-year period, for comparison with the basic model. The corrected basic model was also used for all the models over the 100-year period. Catastrophes were included in the latter models but not in the former.

Catastrophes

The catastrophes that were included in the corrected basic model and run over a 100-year period were all related to environmental conditions. Due to the variability of the annual rainfall in the southern parts of the Kingdom of Saudi Arabia (Mandaville 1990) four different drought scenarios of differing intensities, were modelled. Each of these scenarios influenced the productivity of the female oryxes and the survival rates of each of the age and sex classes recognised. A year of normal rainfall as used in this part of the study represents a year during which rain fell somewhere within the protected area, and which would result in fresh grazing being available to the animals. The drought scenarios modelled were:

- A year of normal rainfall followed by a year of no rainfall: Here the severity factor for reproduction was set at 0.75, while that for survival for all the age classes was set at 0.85. If, for example, 80.0% of the breeding age females reproduce within a year of normal conditions in this scenario, only 60.0% (80 x 0.75 = 60) of the breeding age females would reproduce during a year without rainfall. The severity factor for survival influences the survival of the different age and sex classes in a similar way. The probability of such a catastrophe occurring was estimated at 20.0%.

Table 27: The age and sex distribution of the starting population of Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, and their respective mortality rates (± 1SD) as observed from March 1995 to February 1997, and the more realistic age and sex class-specific mortality rates (± 1SD) as used in the corrected basic model.

AGE CLASS	ORYX NUMBER		MORTALITY RATE							
			BASIC MODEL				CORRECTED BASIC MODEL			
	Males	Females	Males	SD	Females	SD	Males	SD	Females	SD
0-1	2	4	5.5	5.0	5.5	5.0	20.0	20.0	20.0	20.0
>1-2	19	25	4.8	5.0	0.0	5.0	5.0	5.0	5.5	5.0
>2-3	5	7	22.0	5.0	2.9	5.0	5.0	5.0	5.0	5.0
>3-4	2	1	11.0	5.0	0.0	5.0	10.0	5.0	5.0	5.0
>4-5	0	0	0.0	5.0	0.0	5.0	10.0	10.0	5.0	5.0
>5-6	1	0	0.0	5.0	0.0	5.0	10.0	10.0	5.0	5.0
Total	29	37	-	-	-	-	-	-	-	-

- A year of normal rainfall followed by two consecutive years of no rainfall: Here the severity factor for reproduction was set at 0.50, while that for survival of the different age and sex classes was set at 0.75. The probability of a catastrophe of this nature occurring was estimated at 10%.
- A year of normal rainfall followed by three consecutive years of no rainfall: In this case the severity factors for reproduction and survival of the different age and sex classes were set at 0.20 and 0.75 respectively. The probability of the occurrence of this catastrophe was set at 10.0%.
- A year of normal rainfall followed by five consecutive years of no rainfall: Here the severity factors for reproduction and survival were set at 0.00 and 0.50 respectively. There was an estimated 10.0% probability of a catastrophe of this nature occurring. This catastrophe was included in all the VORTEX models, which were then run over a period of 100 years, with the exception of the corrected basic model where no possibility of a catastrophe was included.

The effect of management decisions on population growth

The main reason for this part of the analysis was to determine which management options would ensure the highest population growth rate under conditions similar to that observed during the present study. In addition, the extent to which the population and its persistence would be affected by various actions, including management, was investigated. To do so the following manipulations were done.

- The age distribution of the oryxes was changed from the actual observed age distribution to a stable age distribution. For this purpose only the size of the initial starting population was specified, whereafter VORTEX distributed those 66 animals according to the stable age distribution calculated from the life table as created by VORTEX.
- The actual sex ratio of the reintroduced population was changed to determine what ratio of adult female to male oryxes would be best for maximum population growth when reintroducing Arabian oryx. The number of breeding age females per male oryx that were modelled was 1, 2, 3, 5 and 10.
- The likely effect that additional releases would have on the reintroduced population was modelled through the additional release of oryxes during years three, four and five after the initial reintroduction. The total number of oryx released during such time was 55 at a ratio of 1.1 females per male (animals 2 years old and more).

- The effect that increasing mortality rates in the various age and sex classes would have on the population growth rate and the medium-term survival of the Arabian oryx population was investigated through sensitivity analyses.

Results and discussion

Basic model

Using the vital rates as recorded from March 1995 to February 1997 as well as the previously specified assumptions, VORTEX yielded a mean projected Arabian oryx population of 363.81 ± 65.37 (±1SD) animals after 10 years (Figure 45). The mean projected population growth rate ($r = 0.218$; ± 0.115) before truncation due to reaching the specified ecological capacity in the simulation model was lower than that observed during the study period ($r = 0.354$; Chapter 8). The final observed heterozygosity of the simulated populations were 0.994 ± 0.004. The probability of persistence over the modelling period was 1.00. This means that the model predicts certain survival over the 10-year modelling period.

Despite the vital rates used, the projected mean population growth rate as modelled here, was lower than that observed during the study period (Chapter 8). This is attributed to the stochastic nature of the modelling process and the differences in calculating the growth rates. The mean population growth rate as calculated in the basic model is, however, too optimistic, even though it is lower than that observed during the study period. The study period was characterised by above normal rainfall resulting in exceptionally favourable environmental conditions. Consequently the data on the vital rates collected during this time clearly cannot be taken as representative of normal long-term conditions.

Corrected basic model

In the corrected basic model the Arabian oryx population still showed positive growth ($r = 0.175 \pm 0.151$), but it increased slower than in the basic model (Figure 45). This is due to the more realistic mortality rates that were used in the corrected basic model. Over the 10 years that this population was modelled, the projected population increased from 66 oryxes at the time of release to 313 ± 66.97. The probability of persistence was still 1.00 after the end of the 10-year modelling period. The projected size of the final population is slightly lower than that of the basic model. This is of no particular importance and it is attributed to the stochastic nature of the models. In the population models used by Tear (1994) both ecological capacity and environmental variation were incorporated. The starting population of 89 oryxes in that model increased to a projected mean size of approximately 200 animals after a 10-year modelling period (Spalton 1995). The main reason for the differences in the final population sizes after 10 years in this study and in the models used by Tear (1994) is that different methods of analyses were used. This is also clear from the models used on the Arabian oryx in Oman where the VORTEX and RAMAS/age programs (Ferson, Rholf, Ginzburg, Jacques & Akcakaya 1990 In: Spalton 1995) were used. Due to the differences among the various packages, Brook *et al.* (1999) who used several packages in analysing whooping crane *Grus americana* viability, cautioned against interpreting the projections of a model that is based on a single population viability package only.

The projected population estimates that were derived from both the basic and the corrected basic models in the present study were substantially lower after 10 years than those projected for the reintroduced oryx in Oman (Spalton 1995). In that study VORTEX yielded a projected mean population size of 960 ± 378 oryxes after a 10-year modelling period. The starting population in those models consisted of 124 oryxes, with a ratio of two breeding age females per male. The differences in the mean projected population sizes as modelled in Oman and in the present study can be attributed to three factors in addition to the stochastic nature of the models. The first is the fact that Spalton (1995) used the median age of 2 years as the age of first breeding for the female oryxes in the models of that study. This was done based on the suggestion by Lacy (1993) that the median age at first breeding and not the earliest observed age of first breeding should be used in the VORTEX models. In the present study the median age at first breeding was 2.4 years. This figure is, however, based on actual data that were collected during a period of exceptional environmental conditions. Therefore it is not considered to be representative of more realistic environmental conditions. Consequently a more conservative age at first breeding of 3 years old was used for female oryxes in the present VORTEX modelling. Secondly, lower mortality rates were used in the Spalton (1995) models than in the present study. The higher mortality rates used in the present study were based on the harsher environmental conditions that the oryxes in the present study are subjected to, when compared to the population in Oman. Therefore it was decided to err on the conservative side, by underestimating rather than overestimating the projected population size. Thirdly, there were differences in the size and sex ratio of the starting populations in the two studies. In Oman the starting population was more than double that in the present study, and the sex ratio of two females per male (Spalton 1995) was more conducive to population increase than the approximately parity in the sex ratio in the present study.

Even though some of the vital rates in the corrected basic model of the present study were adjusted downwards to incorporate probable years of lower rainfall, no trends in the ecological capacity were modelled, neither were any catastrophes included. The projected results of the corrected basic model over a 10-year period should therefore still be treated with caution, especially so because a single population viability analysis program was used in the analysis. Nevertheless, the models show that the population will most likely increase continuously if environmental conditions remain similar to that observed during the study period, until ecological capacity is reached, and in the absence of any catastrophes.

Catastrophes

The projected effect that different catastrophes may have on the projected oryx populations is presented in Table 28. The simulation of drought conditions in the present study indicated that even in the worst case scenario (5 years of drought, no breeding, and a 50.0% survival rate) did the modelled populations show positive growth ($r = 0.069 \pm 0.319$) over the medium term. Under such conditions a starting population of 66 oryxes reached a mean projected population size of 220.35 ± 129.07 after a 100-year modelling period. Furthermore, the models indicate that the oryx population would more than likely survive periods of up to 5 years without rain, given that these periods of catastrophe follow years of normal rainfall. After a 5-year drought the probability of extinction was 10.0%. During such a drought it is likely that no calves would be born, because of the decreasing nutritional value of the food plants, and consequently the decreasing physical condition of the breeding age females (Spalton 1995).

It is, however, more likely that more than one of the possible catastrophes would be encountered by an oryx population during a 100-year period. Of the four catastrophe combinations modelled, all but one resulted in excessively high probabilities of extinction during the modelling period. The worst case scenario where all the catastrophes are encountered during the modelling period resulted in a negative, mean projected population growth rate and a mean projected final population size of 45.92 ± 59.62 oryxes. The probability of persistence during the 100-year modelling period was 8.6%.

Mace and Lande (1991) indicated that populations with probabilities of extinction of 10.0% or more should be considered as vulnerable. Saltz (1996), however, suggested an even more conservative value of 1.0% or more, if factors other than demographic stochasticity (such as environmental stochasticity) are considered. Although these theoretical values might seem conservative, especially if applied across the board to all species, it would probably be wise

Table 28: The projected effect of different catastrophes of different intensity when acting individually or in combination on Arabian oryx populations modelled with VORTEX for a projected period of 100 years.

CATASTROPHE	SEVERITY FACTOR EFFECT ON		FREQUENCY	MEAN FINAL POPULATION	SD	MEAN FINAL HETEROZYGOSITY	SD	MEAN POPULATION GROWTH RATE	SD	SURVIVAL PROBABILITY
	Breeding	Survival								
Individual effects										
No catastrophe	No effect	No effect	-	343.06	59.99	0.951	0.016	0.164	0.142	0.998
One dry year	0.75	0.85	20	324.12	65.34	0.946	0.018	0.123	0.166	0.999
Two dry years	0.50	0.75	10	324.82	71.22	0.946	0.018	0.126	0.186	0.997
Three dry years	0.20	0.75	10	319.70	73.25	0.946	0.017	0.120	0.202	1.000
Five dry years	0.00	0.50	10	220.35	129.07	0.895	0.082	0.069	0.319	0.941
Combined effects										
One, 2 and 3 dry years	-	-	-	212.73	108.78	0.895	0.083	0.037	0.248	0.916
Two and 5 dry years	-	-	-	170.22	118.98	0.865	0.117	0.031	0.340	0.745
Three and 5 dry years	-	-	-	122.64	128.95	0.871	0.108	0.027	0.343	0.724
All catastrophes	-	-	-	45.92	59.65	0.780	0.195	-0.049	0.372	0.087

Note: The individual severity factors stay the same when various catastrophes are combined within a 100-year modelling period.

to consider the Arabian oryx population that was reintroduced into the 'Uruq Bani Ma'arid Protected Area as vulnerable, because relatively little is still known about the species in this variable environment. It is also too early to consider the reintroduction of the Arabian oryxes into the 'Uruq Bani Ma'arid Protected Area an unqualified success.

Management options

There are many facets to consider in the management of animals that are to be reintroduced. These include the background and age of the individual founders and the composition of the groups to be released. In many cases the chances of survival of a reintroduced population can be enhanced by management methods such as reproductive manipulation (Stanley-Price 1989). The criteria used for the selection of the founder population for the reintroduction in the present study have been discussed elsewhere (Chapter 3). In this section the effect that different group compositions in terms of the ratio of adult females per male will have on the population growth rates are investigated, as well as the effect that additional releases will have on these rates.

At the age of first breeding of a male and female Arabian oryx, the mean projected population growth rates in all the modelled populations were higher than that of a population with a stable age and sex composition, irrespective of the ratio of females to males (Table 29). This is because VORTEX automatically assigns a proportion of the starting population to most of the recognised age and sex classes when a population with a stable age structure is modelled. Inevitably VORTEX considers some of the animals as being below breeding age. The disadvantage of releasing a population with a stable age and sex structure is that there is a reproductive delay because a proportion of the animals still has to reach breeding age (Stanley-Price 1989). The release of a population with a stable age and sex structure does have advantages in that there is a set social structure at the time of release, which could reduce both inter- and intraspecific conflict, thereby enhancing the survival of the reintroduced animals, such as with the reintroduction of elephants into the Pilanesberg National Park in the North West Province of South Africa. At the time of that reintroduction no technique existed to translocate adult male elephants, while the translocation of subadult animals and adult females posed no problem. Due to the resulting unnatural social system that the subadult males found themselves in, various problems occurred, including interspecific aggression with white rhinoceroses *Ceratotherium simum* (Burchell, 1817) which led to the death of at least one white rhinoceros (Slotow, van Dyk, Poole, Page & Klocke 2000). Subsequently a recommendation was made only to move entire family groups

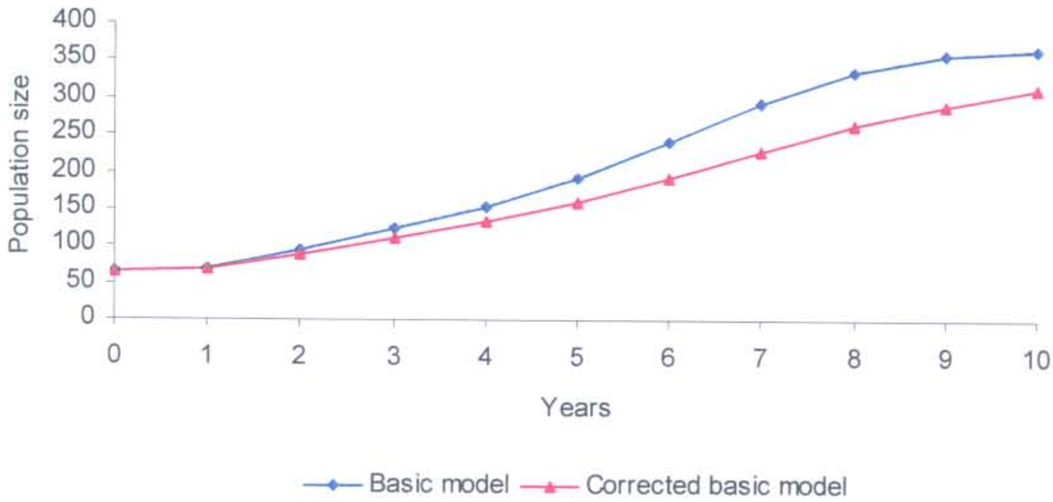


Figure 45: The comparative projected mean growth curves of modelled Arabian oryx populations. The vital rates in the basic (blue) and the corrected basic (red) models were the same, with the exception of more realistic mortality figures being used in the latter model.

Table 29: The mean projected population growth rates (r) for Arabian oryx populations with different ratios of breeding age females per male at the time of release, as modelled over a 10-year period.

FEMALES PER MALE	MEAN POPULATION SIZE AT YEAR					MEAN GROWTH RATE	SD
	2	4	6	8	10		
1	107.60	149.36	211.68	278.41	324.07	0.184	0.153
2	123.57	182.86	258.56	317.26	338.24	0.209	0.162
3	132.57	199.59	277.28	326.78	342.39	0.222	0.168
5	142.06	213.64	292.13	336.25	348.09	0.232	0.175
10	150.19	228.49	301.42	339.48	349.34	0.238	0.182
Stable age	93.69	132.71	186.69	249.18	300.57	0.167	0.145

of elephant, including adult males. No such problems have occurred since. These problems experienced are not surprising because release groups mimicking the natural social structures are considered as the single most critical factor in attempting to ensure successful reintroductions in animals that are not asocial (Stanley-Price 1989).

The highest mean projected population growth rate (r = 0.238 ± 0.182) was attained in a modelled population when the sex ratio was 10 breeding age females per male. A ratio of five breeding age females to a single breeding age male yielded a similar projected mean growth rate (r = 0.232 ± 0.175) after 10 years. The latter growth rate resulted in a projected mean population of 255.02 ± 61.71 after a 5-year period, which is comparable to the mean population size of 270.02 ± 64.58 after the same number of years when the sex ratio used was 10 breeding age females per male (Figure 46). Elsewhere it has been shown that the size of the reintroduced population is critical to successful reintroduction and that the more rapid the population grows the higher the probability of the reintroduction will be of being a success (Dixon, Mace, Newby & Olney 1991). The rate of increase of a population largely depends on the breeding biology of the species in question, notably the age at first breeding and the calving interval. Therefore animals such as the Arabian oryx are more likely to be reintroduced successfully than for example the orang-utan *Pan troglodytes* (Blumenbach, 1775). This is so because the Arabian oryx first breeds at a relatively young age, and at short intervals thereafter, while the orang-utan starts to breed late in life and has long breeding intervals (Stanley-Price 1989).

When the modelled Arabian oryx population was augmented with an additional release of 55 animals over a 3-year period, it increased from 66 to a projected mean population size of 343.84 ± 60.74 over a 10-year period (Figure 47). During the years of supplementation the projected mean population growth rate (r) was 0.439 ± 0.151. During the rest of the years the projected mean population growth rate was 0.158 ± 0.145. Across the entire 10-year modelling period, the mean projected growth rate was 0.215 ± 0.184, before growth ceases when the ecological capacity would be exceeded. The high standard deviation in the mean projected growth rate across the modelling period is indicative of the differences which will occur in the growth rates during years of supplementation as opposed to those years without additional releases.

In these models the additional releases had a positive effect on the reintroduced population in that the initial establishment phase of the population was short. Within 2 years after the initial release, the modelled Arabian oryx populations were already in the exponential growth

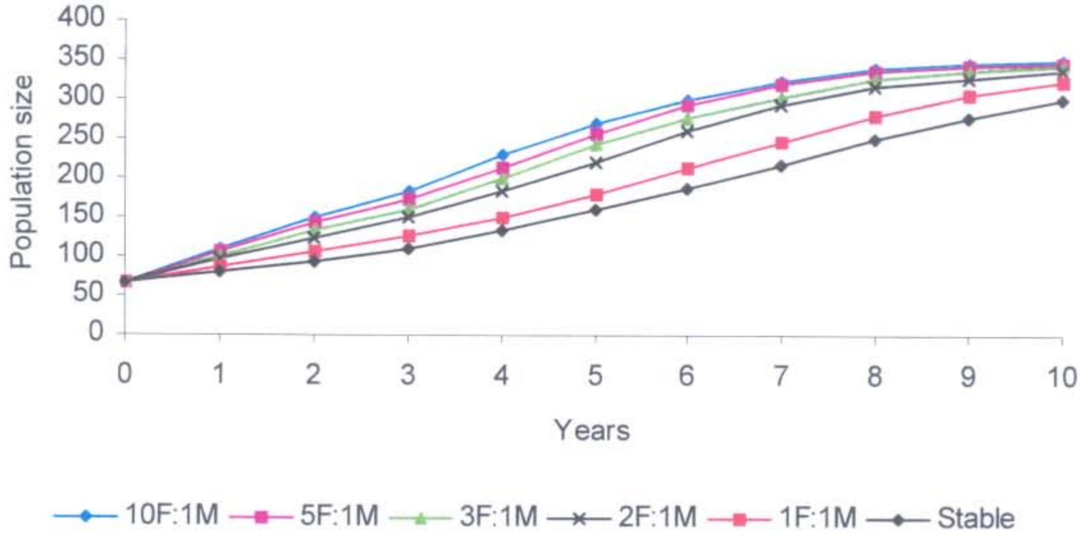


Figure 46: The comparative growth curves of Arabian oryx populations with different ratios of breeding age females per male, as modelled over a 10-year period, indicating the mean projected annual population size after 1000 iterations.

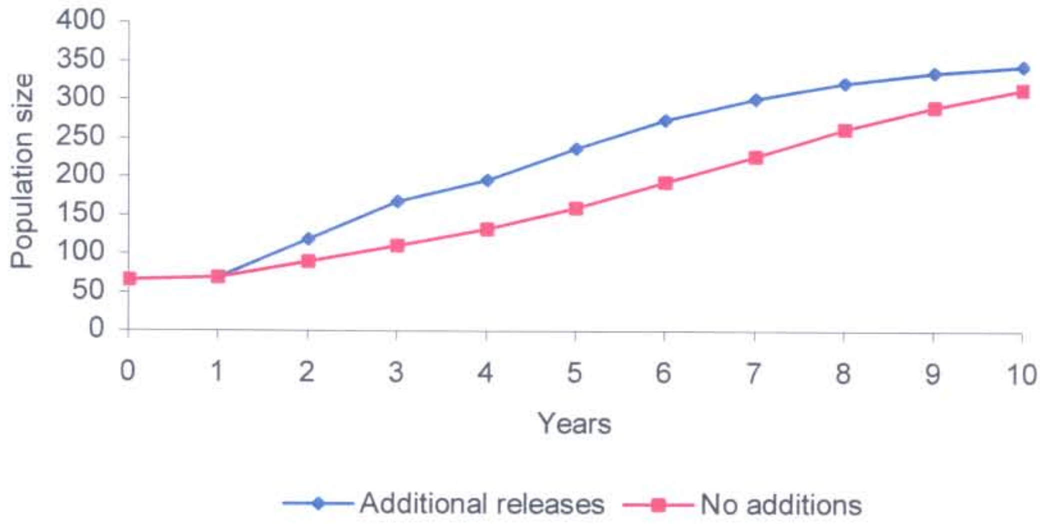


Figure 47: The comparative population growth curves of Arabian oryx populations with (blue) and without (red) the additional release of 55 animals during the third, fourth and fifth years of a simulation before ecological capacity is reached.

phase. In the exponential growth phase the resources available to the population are unlimited and population growth occurs unhindered (Bothma 1996). This exponential growth is not due to a sudden increase in productivity, however, because the ratio of calves to adult females was virtually the same in all the models whether using additional releases (65.0% calving rate) or not (64.3% calving rate). Rather, the modelled populations entered the exponential growth phase because of an increase in the number of breeding age females, which was a direct result of the additional releases. This increase in the number of females of breeding age, combined with the favourable environmental conditions in the models, led to more females conceiving and giving birth successfully. Not only did the modelled populations with additional releases grow more rapidly, but they also reached greater population sizes and mean projected population sizes. Based on the models used in this part of the study and the assumptions associated with these models the additional release of 55 oryxes over a 2-year period was beneficial to the reintroduced Arabian oryx population because it accelerated the population growth.

The additional release of oryxes into the population over the medium term (100 years) was not modelled because the corrected basic model indicated that the population growth rate levels off and becomes asymptotic after about 10 years into the model, when the ecological capacity is reached. The additional release of animals into a population close to its ecological capacity will, therefore have little positive effect on the population, because it cannot significantly increase its population size without a concomitant increase in the ecological capacity of the area. Whether it would have any negative effects is not clear. It is, for example, known that the additional release of adult male mountain gazelles into the wadi systems of the 'Uruq Bani Ma'arid Protected Area disrupted the established social hierarchy among the males (Wacher, *pers. comm.*[8]). This in turn could result in increasing competition between these males, increasing adult male mortality rates and finally lowering lamb production. Elsewhere such disruptions of the social structure have also been observed while it has also been noted that additional releases could introduce pathogens to populations (Cunningham 1996).

It is likely that future additional releases of Arabian oryxes into the protected area will have a significant effect on the population growth when these releases take place at the end of catastrophic droughts, provided that the resident population is not yet at or close to the ecological capacity of the area. This will allow the number of breeding age animals once

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again to be increased, which in turn could result in increased population growth provided that the environmental conditions allow it to happen.

The effect of increasing mortality on population persistence

The projected effect that an increase in the mortality rates of adult male and female Arabian oryxes would have on the size of a population over the medium term is illustrated graphically in Figure 48. An increase of 5.0% in the mortality rate of adults resulted in a mean projected population size of 186.02 ± 120.50 animals after 100 years of simulation. The mean maximum population size that would be reached after such time is 201.21 ± 119.02, or approximately half the estimated ecological capacity of the area. The mean projected population growth rate during this modelling period is r = 0.038 ± 0.320. As could be expected, increases of 10.0% and 15.0% in the adult mortality rates resulted in even lower projected population growth rates and mean population sizes after a 100-year period. In the worst case scenario where adult mortality was increased by 15.0%, the modelled populations experienced a projected mean negative growth rate (r = -0.22 ± 0.323). Subsequently the mean population size after 100 years of modelling would be 103.65 ± 103.19 animals. Such increases in the mortality rates of adult male and female Arabian oryxes will result in 71.1% of all the modelled populations becoming extinct within 100 years (Figure 49). The first extinction will occur after a mean of 51.55 ± 24.45 years since the original release.

The modelled populations were relatively insensitive to an increase in the mortality rate of the juvenile male oryxes only. In the worst case scenario where the juvenile mortality rate of the males was set at 60.0%, the modelled populations still reached a projected mean population size of 233.77 ± 121.20 animals after 100 years. During that time the projected mean population growth rate was r = 0.067 ± 0.318 and the probability of persistence was 0.899 (Figure 50). This indicates that 89.9% of the modelled populations will survive the modelling period, despite the fact that 60.0% of the juvenile males did not survive. At the end of the modelling period the final projected heterozygosity was 0.879 ± 0.089. In contrast, the modelled populations were sensitive to an increase in the mortality rate of the juvenile females. In this instance the worst case scenario resulted in a projected negative population growth rate (r = -0.019 ± 0.302) over a period of 100 years, with a final mean projected population size of 78.65 ± 88.86 oryxes. The majority (65.2%) of the modelled populations will become extinct during the modelling period (Figure 50) and the final projected heterozygosity of the modelled populations was 0.836 ± 0.165. However, such a skewed juvenile mortality rate, where the juvenile female oryxes disappear from the population at a much higher rate than the juvenile males, seems unlikely to occur under normal circumstances. It does, nevertheless, illustrate the sensitivity of the populations to increasing mortality rates in the juvenile females.

A simultaneous increase in the mortality rates of juvenile male and female oryxes through disease, drought or predation would also affect the reintroduced population adversely (Figure 51). An increase in the mortality rate of juvenile Arabian oryxes to 50.0%, for example, will decrease the probability of oryx populations persisting over a period of 100 years to 0.60, indicating that 40.0% of all the populations are likely to face extinction within that time frame. Such levels of mortality among the juveniles are not considered to be unrealistic. Mace (*pers. comm.* In: Magin & Kock 1997) suggested that the mortality rate of juvenile roan antelope could reach levels of up to 60.0% due to predation, because the young of these animals hide during the first few weeks after birth. Fryxell (1987) reported mortality rates of up to 50.0% in the white-eared kob *Kobus kob leucotis* (Erxleben, 1777) calves, while Somers (1997) used a 55.0% first year mortality rate in modelling a warthog population. According to Beudels, Durant & Harwood (1992) a decrease in the calf mortality of the roan antelope within the national parks of Burundi could result in substantial annual population growth, thereby reducing the probability of extinction of these small and isolated populations. In cheetah populations it was, however, found that increased cub survival plays a minor part in increasing population growth or population persistence (Crooks, Sanjayan & Doak 1998). That study revealed that the protection of adult cheetahs was more important in maintaining viable populations than a decrease in cub mortality due to predation, for example. That is partly attributed to the breeding biology of the cheetah where females have relatively large litters and where such litters can be produced rapidly after the loss of a previous litter.

Currently predation is not likely to cause high mortality rates in the Arabian oryx within the 'Uruq Bani Ma'arid Protected Area. This is due to the absence of predators larger than the red fox *Vulpes vulpes* (Linnaeus, 1758) in the area as revealed by trapping (Seddon & van Heesnik, *pers. comm.*[9]) and a lack of any signs that suggests otherwise (Strauss, *pers. obs.*). Cognisance should, however, be taken of the potentially devastating effect that a lack

[9] Dr. P. Seddon & Dr. Y. van Heesnik, National Wildlife Research Centre, P. O. Box 1086, Taif, Kingdom of Saudi Arabia.

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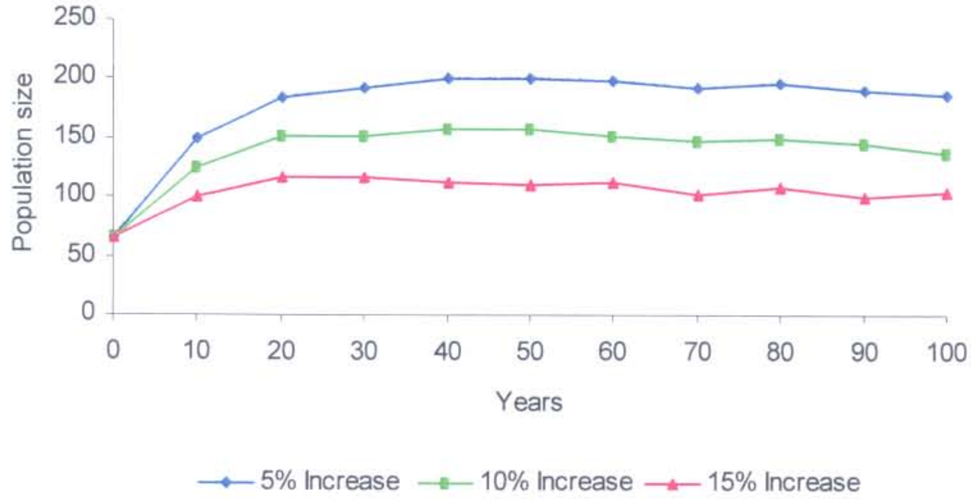


Figure 48: The comparative effect that an increasing mortality rate in adults will have on the growth of the modelled Arabian oryx populations over a period of 100 years.

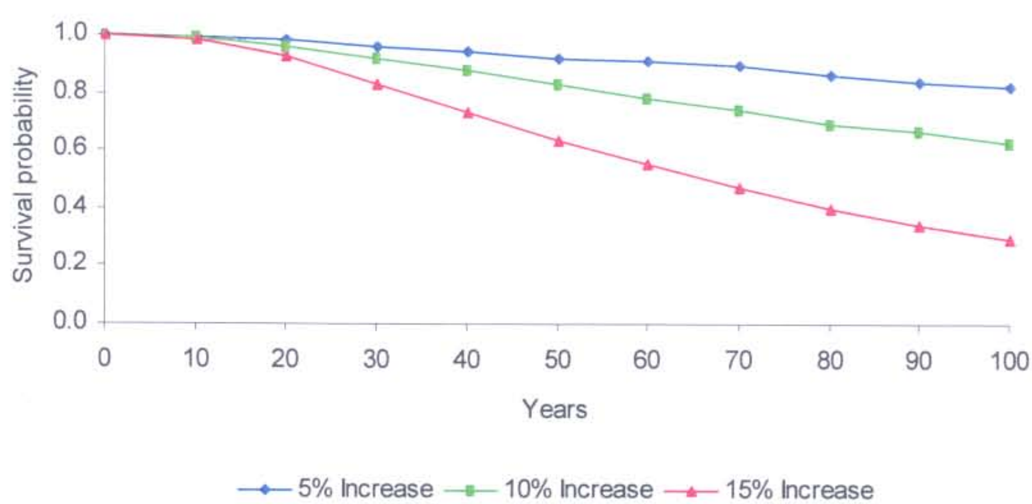
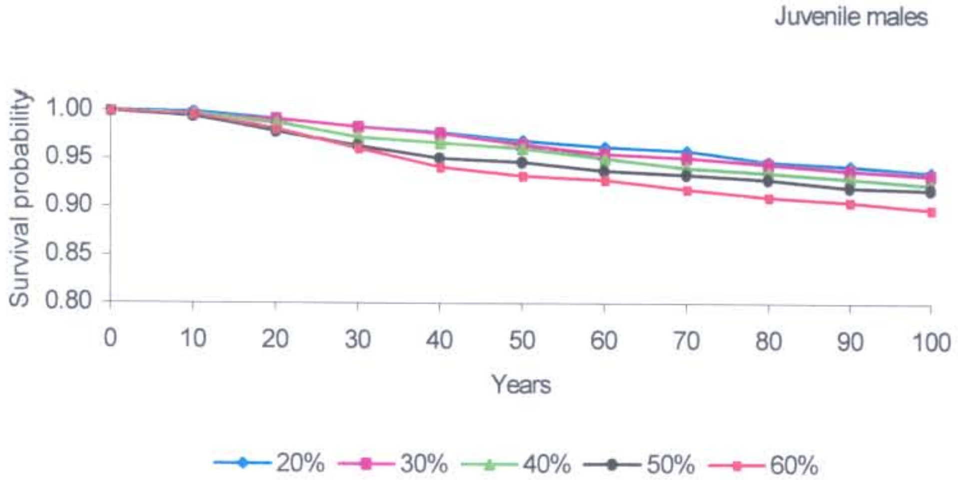


Figure 49: The effect of increasing mortality rates in adults on the survival probabilities of the modelled Arabian oryx populations over a period of 100 years.



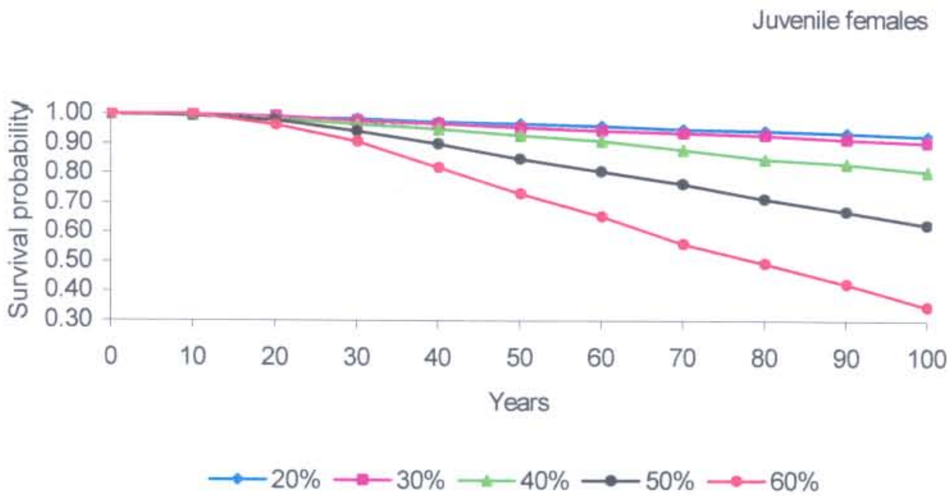


Figure 50: The effect of increasing mortality rates in juvenile males and juvenile females on the survival probability of modelled Arabian oryx populations during the medium term (100 years) when the mortality rates of the adult males and females are kept constant.

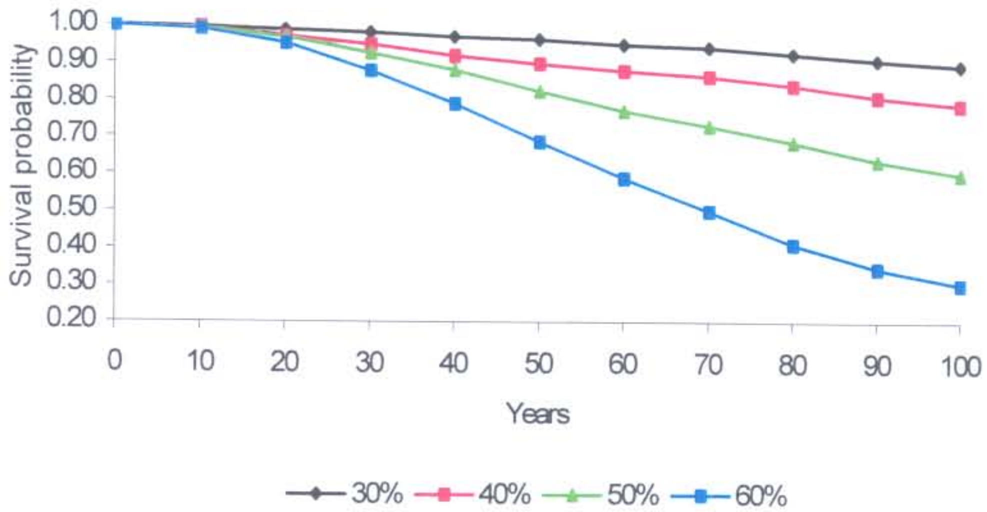


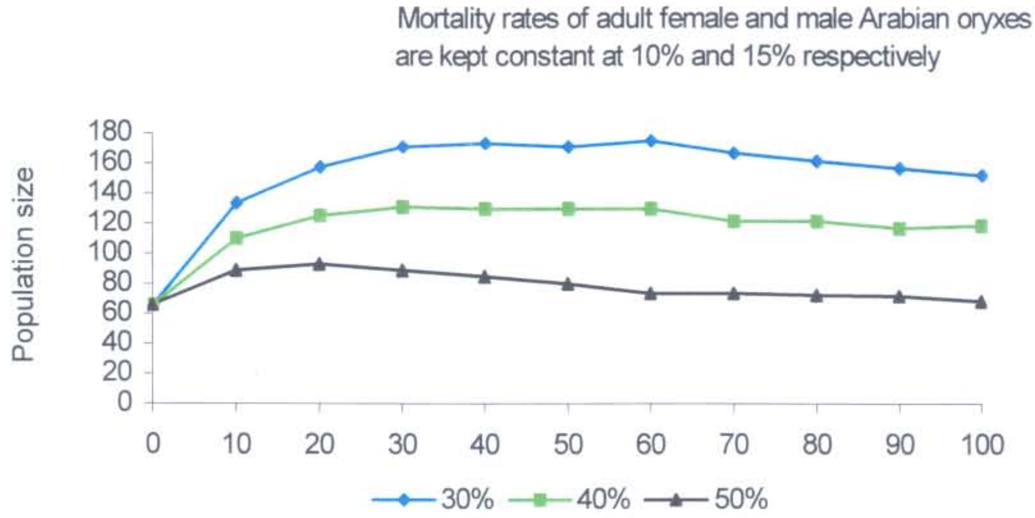
Figure 51: Sensitivity analyses indicating the survival probabilities of the modelled Arabian oryx populations over a period of 100 years, at increasing rates of mortality in juveniles and constant rates in the adults.

of female recruitment could have on the population, due to the potential decrease in the number of females reaching breeding age. It is known that mainly female oryxes have been targeted in the live-capture of oryx in Oman. The devastating effect that that has had on the resident population has been well-documented (Spalton, *et al.* 1999).

It is likely that the mortality rates of various age and sex classes would increase simultaneously in the event of large-scale poaching. With a simultaneous increase in the mortality rates of more than one age group, the effect on the population parameters over 100 years is amplified. Various scenarios regarding the mortality rates of juvenile, adult male and adult female oryxes were modelled in an attempt to simulate this. The results are illustrated graphically in Figures 52 and 53. A medium level of poaching was simulated by setting the mortality rate of the juveniles at 30.0% and that of the adult females and males at 10.0% and 15.0% respectively. This resulted in a mean projected population growth rate of $r = 0.020 \pm 0.315$ after a 100-year modelling period. This means that the projected population will increase from the initial 66 oryxes to a mean of 152.07 ± 118.04 during the modelling period. In 1000 simulation over 100 years, 772 (72.2%) of the modelled populations will survive. The final projected heterozygosity of the modelled populations was 0.860 ± 0.124.

A further increase in either the mortality rate of the juveniles, the adult males or the adult females will cause negative, mean projected population growth rates over the modelling period. For example, a juvenile mortality rate of 40.0% in addition to mortality rates of 10.0% and 15.0% respectively in adult females and males resulted in a mean projected population size of 118.93 ± 106.40, from a mean projected population growth rate of $r = -0.004 \pm 0.312$ over the 100-year modelling period. The survival probability of populations with such mortality rates is 0.51. Such an increase in the mortality rates furthermore will result in a decrease in the final projected heterozygosity to 0.839 ± 0.137 in the modelled populations.

These results show that relatively small simultaneous increases in the mortality rates of the different age and sex classes, due to poaching for example, could have a devastating effect on the future survival of the Arabian oryx population. Apart from environmental catastrophes, poaching is probably the biggest potential threat to the reintroduced Arabian oryx population. Poaching has also been found to be major threat in other antelope populations. In Kenya, for example, the poaching of roan antelope between 1985 and 1990 reduced the population from approximately 110 individuals to between 30 and 35 animals, representing an increase of 10.0% in the mortality rate of the adults over the estimated 5.0% natural mortality rate in



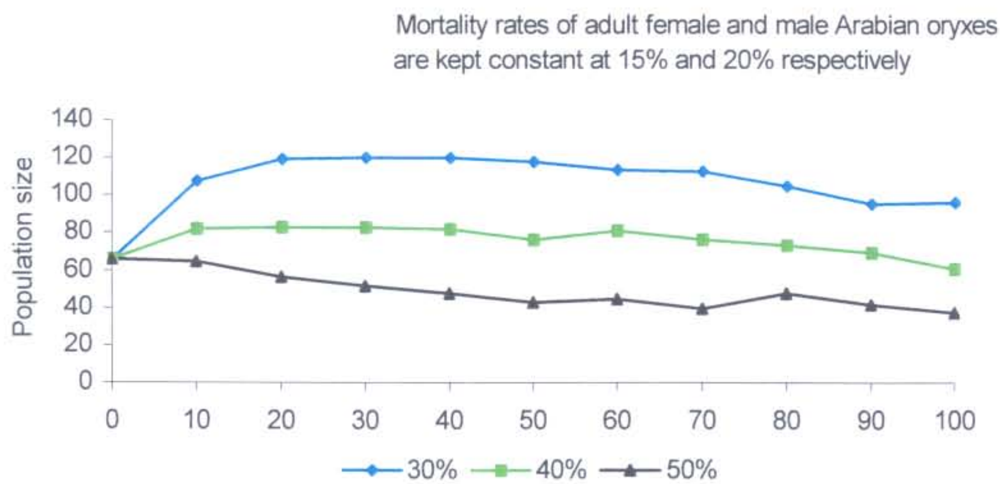
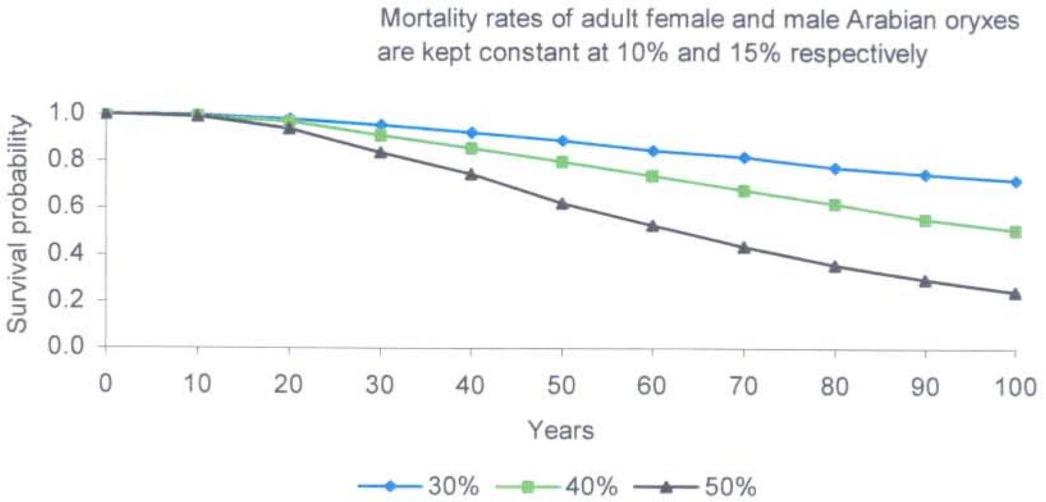


Figure 52: Sensitivity analyses showing the comparative projected population growth curves of the modelled Arabian oryx populations with increasing mortality rates of juveniles at different rates of mortality in the adult males and females.



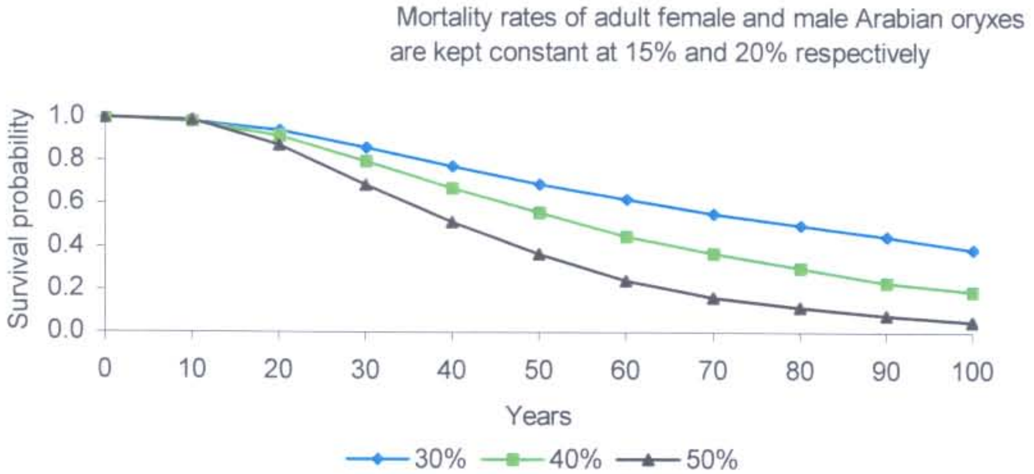


Figure 53: Sensitivity analyses showing the survival probabilities of the modelled Arabian oryx populations over a period of 100 years with increasing mortality rates in the juveniles at different rates of mortality in the adult female and male oryxes.

adult roan antelope (Magin & Kock 1997). Similarly the Arabian oryx population in Oman decreased from an excess of 400 individuals in October 1996 to 138 individuals in September 1998 because of poaching (Spalton *et al.* 1999). This represents a 65.5% decrease in the size of the Arabian oryx population over a 2-year period.

The results of the models in this part of the study also indicate that the survival of especially the female oryxes is of particular importance to the persistence of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area. The importance of adult survival for population growth is well documented for many moderately to long-lived species (Casswell 1989; Emlen & Pikitch 1989; Lande 1991; Doak, Kareiva & Klepetka 1994; Heppell, Walters & Crowder 1994). Tear (1994) suggested that management action in Oman should be focused on maintaining survivorship of young oryx. Therefore, supplementary food and water should be supplied to herds where young animals can be found during periods of drought. Since droughts develop over time it would seem, however, that a monitoring program focussing on the well being of especially the breeding age females could be particularly useful in determining and predicting the effect of the drought on the population. As is the case with the brown bear *Ursus arctos* (Linnaeus, 1758) in Spain (Wiegand, Naves, Stephan & Fernandez 1998) the survival of females should be the principal management target in the 'Uruq Bani Ma'arid Protected Area because the females are critical to the recovery of the population. Similar conclusions were reached in studies of grizzly bears *Ursus arctos horribilis* in Yellowstone National Park (Knight & Eberhardt 1985).

Recent work done on the Arabian oryx in the Mahazat as Sayd Protected Area in the Kingdom of Saudi Arabia has suggested that the Allee effect influenced population growth in that area (Treydte, Williams, Bedin, Ostrowski, Seddon, Marshall, Waite & Ismail 2001). The Allee effect is characterised by the inability of the social structure of small populations to function once the size of the population decreases to below a certain level. This results in decreased productivity because the animals are unable to find mates once the population density decreases below a certain level. This, in turn, leads to an even smaller population, worsening the problem (Primack 1998). Although VORTEX caters for the analysis of the Allee effect in the population models, this option was not included in any of the models in the present study. Monitoring during the present study indicated that 62.0% of the breeding age females conceived and delivered calves during 1995. During the same year 25.0% of the breeding age females, or 40.0% of those females that calved, conceived in captivity at either the National Wildlife Research Centre or in the protected area enclosures before release. During 1996, however, 73.5% of the breeding age females in the protected area produced calves, while 97% of such females gave birth during 1997 (Chapter 8). These results strongly suggest that the Allee effect did not influence the birth rate in the 'Uruq Bani Ma'arid Protected Area.

Conclusions

The prediction models presented in this study indicate that under the observed environmental conditions and subject to the specified assumptions within the models, the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area is secure over the short term, but could become vulnerable over the medium term.

Release groups with stable age distributions showed lower projected population growth rates and consequently lower final population sizes than all the other release groups where varying ratios of female to male oryxes were modelled. A ratio of 10 adult females per male showed the highest projected population growth rates. A ratio of five adult females per male is, however, more ideal because of the high attrition rate among the adult males when compared to the females. The latter ratio will result in population growth rates that are similar to a ratio of 10 adult females per male.

The Arabian oryx populations that were modelled here showed that catastrophes such as a 5-year drought period will affect the reintroduced population, but it will not be enough to drive the population to extinction. Various combinations of catastrophe, however, will mostly prove to be fatal for the modelled populations. Because of the effect that such catastrophes could have on the population, the oryx females, especially the adult females, should be the focus of management activities during periods of drought. This has been confirmed through sensitivity analyses. While the projected populations seem to tolerate increasing mortality rates in the males, they are sensitive to increasing mortality rates in the females. The additional release of animals has the potential to impact positively on the population already established, provided that the population has not yet reached the ecological capacity for the habitat.

This chapter has focussed on some of the direct causes of population decline which could eventually lead to the extinction of the Arabian oryx population that was reintroduced into the 'Uruq Bani Ma'arid Protected Area. The causes of endangerment and possible extinction are manifold (Primack 1998), however, and include direct causes such as those modelled here, others such as habitat destruction, or even less direct pathways to extinction. Less direct pathways, which could also influence persistence time, include the mechanisms by which females choose their mates and the effect that those mechanisms have on the effective population size (Blumstein 1998). Bearing this in mind there are many factors that could potentially influence the future survival of the reintroduced Arabian oryx in the 'Uruq Bani Ma'arid Protected Area. It is therefore imperative that the population be monitored continuously, that the data collected are analysed continuously and that those hypotheses that are formulated from the data are tested in the field.

CHAPTER 11

MANAGEMENT RECOMMENDATIONS

Introduction

Some conservation agencies operate on the premise that population persistence can be ensured with the protection of a piece of the natural habitat of an animal population (Belovsky, Bissonette, Dueser, Edwards, Luecke, Ritchie, Slade & Wagner 1994). However, the conservation of biodiversity, or any part of it, usually requires judicious wildlife management. Desert ecosystems, however, normally require less intense management than the more mesic and species rich areas (Bothma & Strauss 1995).

The management of wildlife in the past has been explained on the basis of two concepts, namely conservation and preservation (Thomson 1992). The basic difference between conservation and preservation management is based on whether the animal species being dealt with are considered as endangered by the International Union for Conservation of Nature and Natural Resources (IUCN). If a species is not considered as endangered, then conservation management, which is based on the sustainable utilisation of natural resources, is aimed at. When a species is considered as endangered, however, preservation management, which is aimed at the protection of the endangered species, is followed. Preservation management forms the basis of the Arabian oryx management programme in the 'Uruq Bani Ma'arid Protected Area. Elsewhere a management plan and specific management objectives have been formulated for the 'Uruq Bani Ma'arid Protected Area (Bothma & Strauss 1996). The aim of this section is therefore to concentrate on the future management of the Arabian oryx population, while also giving some guidelines for future reintroductions. Criteria for the periodic assessment of the reintroduced population and possible future populations are also given.

Management objectives

Well-defined management objectives are essential for any wildlife management plan (Mentis & Collinson 1979; Bothma 1996). The objective of the reintroduction of the Arabian oryx into the 'Uruq Bani Ma'arid Protected Area was simply to re-establish a free-ranging, self-sustainable population. From this follows the primary management objective for the Arabian oryx population in the area. It is:

- To maintain a free-ranging, self-sustainable Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area

Management recommendations

The captive management of the animals chosen for reintroduction can contribute significantly to the rate of population growth after release, the heterozygosity of the reintroduced population, and ultimately to the success of the reintroduction. The sand gazelles which were reintroduced into the 'Uruq Bani Ma'arid Protected Area during 1995 and 1996 were, for example, carefully managed in captivity to maximise their initial contribution to the reintroduction process. In captivity before release into the wild the female gazelles all had the opportunity to conceive from selected males. These potentially pregnant females were then released into the protected area with males other than those that impregnated them while in the enclosures in captivity (Wacher *pers. comm.*). Soon after release a large proportion of these females produced young, thereby increasing the size of the population considerably (Strauss, *pers. obs.*). A similar approach could be followed with future reintroductions or the release of additional oryxes to augment existing populations.

The escarpment areas and especially the wadis are seasonally of great importance to the reintroduced Arabian oryxes (Chapter 5, 6). It is essential to recognise the value of these areas. Consequently the disturbance and utilisation of these areas inside and outside the core protected area should be limited. This is especially so due to the fact that the complete interaction between the animals and the *Acacia* stands in these areas are not fully understood yet.

Competition for food among the Arabian oryxes of the 'Uruq Bani Ma'arid Protected Area is likely to be high during both the summer, when the animals are concentrated in the escarpment areas, and the winter when the animals travel long distances to get sufficient food. Consequently, it is advisable to control the livestock numbers in the area because large concentrations of livestock can have a serious effect on the amount and quality of forage available to all wildlife in the protected area. Moreover such food is already a limited resource there. If the livestock situation in the 'Uruq Bani Ma'arid Protected Area is not monitored closely then the limited food resource might become a limiting factor for the survival of the Arabian oryx in the area.

The condition of the grazing resource determines the performance of the animals, including the breeding potential of the females (Spalton 1995; Strauss, *pers. obs.*). During periods of prolonged drought, however, both the quantity and the quality of the vegetation in the area decrease, which in turn lead to decreasing productivity in the oryx population. However, since the 'Uruq Bani Ma'arid Protected Area is unfenced, the animals are able to make use of the best areas in a vast desert system (Strauss, Al-Khaldi & Ghamidi 2000). Therefore interference with the reintroduced population should be kept to a minimum unless the well-being of the population is at risk (Bothma & Strauss 1995). As indicated earlier, special attention should be given to the adult female oryxes during periods of prolonged drought because they are the key to the recovery of the population. As a consequence it has been suggested that active action should be taken when 50% of the adult female oryxes are considered to be in a poor physical condition (Wacher In: Strauss *et al.* 2000).

None of the management recommendations are attainable without the long-term monitoring of the reintroduced Arabian oryx population. Long-term monitoring of reintroduced animals is considered essential for any reintroduction project (Stanley-Price 1989; Tear 1992; Bothma & Strauss 1995). The long-term monitoring of a reintroduced population is also important so as to evaluate the progress made by the reintroduced animals. Therefore, some criteria have been proposed for the periodic evaluation of reintroduction programmes (Ostermann, Deforge & Edge 2001). These criteria involve both the captive and the reintroduced populations. They are:

- The survival and the recruitment rates in the demographically and genetically managed captive population must be high
- Both the survival and the recruitment rates of the captive-bred animals released into the wild must be within the normal range of values for that or similar species
- The reintroduced population must have a positive population growth rate
- One or more viable wild populations must have been established as a result of the reintroduction

While the above criteria are useful for periodically evaluating the reintroduction process, and the state of both the captive and the reintroduced populations, they do not assess whether a reintroduction has been successful or not. Sarrazin and Barbault (1996) have pointed out the need for additional criteria to establish whether a reintroduction has been successful. These authors list three criteria that a population has to meet before becoming self-sustaining. They are:

- The successful breeding of the first wild-born individual (Kleiman, Beck, Dietz & Dietz 1991)

- A recruitment rate that is higher than the mortality of the adults over a 3-year period (Cade & Temple 1995)
- Reaching the minimum viable population size (Beck, Rapaport, Stanley-Price & Wilson 1994)

It is recommended here that the Arabian oryx population that was reintroduced into the 'Uruq Bani Ma'arid Protected Area be monitored on an annual basis and that the proposed criteria for evaluating and finally assessing the success of the reintroduction be used to determine the relative performance of the population.

The additional release of animals into the population in the 'Uruq Bani Ma'arid Protected Area is a potentially powerful management tool. However, the additional release of animals into this area, and the likely effects of such releases should be considered carefully. Additional releases of oryx are only justified if they can make a positive contribution to the reintroduced population. According to Saltz (1998) such positive contributions to a reintroduced population include:

- Increasing the population size, and therefore reducing the susceptibility of the population to demographic and environmental stochasticity
- Increasing the geographical range
- Increasing the genetic base of the population

As suggested earlier (Chapter 10) the relative contribution of additional releases will, however, decrease as the population increases towards ecological capacity and as the range of the population expands. Recent indications are that the National Commission for Wildlife Conservation and Development (NCWCD) is striving towards a minimum oryx population of 500 within the 'Uruq Bani Ma'arid Protected Area. The origin of this figure of 500 oryx is most likely linked to the minimum viable population concept. The latter is thought to be no fewer than 500 animals (Beck, *et. al.* 1994). Maintaining a minimum population of 500 oryxes in the present area, however, is unrealistic because it is doubtful that the ecological capacity of the currently protected area can maintain such a number, even during years of widespread rainfall. As predicted for the oryx population in Oman (Spalton 1995), the population in 'Uruq Bani Ma'arid is likely to grow continuously during several favourable years, during which time the animals will continue to expand their range and many animals will leave the protected area. Because it is impossible to manage the oryx population over the whole of the 'Rub al Khali, it is also these animals that are most likely to die when adverse environmental conditions set in and the oryx population declines. Consequently, all the management efforts on the Arabian oryx should be concentrated within the core protected area. This area contains habitat that is in better condition than elsewhere, while it also contains the all important summer escarpment plateau and its incised wadi subhabitat of the oryxes. In addition, it might also be necessary in the future to increase the size of the escarpment area that is currently under protection, to ensure enough suitable summer subhabitat for an increasing Arabian oryx population.

The future survival of the Arabian oryx in Saudi Arabia does not, however, depend on the number of oryxes released only into the 'Uruq Bani Ma'arid Protected Area. It is strongly advised that further reintroductions of the Arabian oryx be made into other protected areas with suitable habitat within the country. With time and proper planning this could result in the development of a natural Arabian oryx meta-population within Saudi Arabia.

Alternatively the Arabian oryx populations in the Mahazat As Sayd and the 'Uruq Bani Ma'arid Protected Areas, and those captive animals at the National Wildlife Research Centre in Taif, could be considered as subpopulations of a single meta-population within the country and be managed accordingly. Elsewhere it has been shown that the survival probability of the existing oryx populations in the 'Uruq Bani Ma'arid and Mahazat as Sayd Protected Areas and that of another proposed reintroduced oryx population, will be enhanced by such a meta-population management approach (Strauss in press).

An Arabian oryx meta-population in the Kingdom of Saudi Arabia would increase the chances of survival of the species, because it is difficult to anticipate that many subpopulations would go extinct simultaneously (Ripa & Lundberg 2000). Various authors have also indicated that some level of contact between different populations enhances the survival prospects of those populations (Beudels, Durant & Harwood 1992; Vucetich & Creel 1999). In addition it has been suggested that multiple, independent Arabian oryx populations would be necessary to ensure the persistence of the oryx in the wild on an evolutionary time scale and that multi-national co-operation would be necessary for spatially structured populations to exist (Tear 1994).

To improve the growth rate of the future reintroduced populations, it is essential to release the correct ratio of breeding age females to males. Based on the population viability analysis which was conducted as part of this study, it is suggested that a ratio of five breeding age females per male be considered for future reintroductions. Also, the release of females older than 4 years of age could potentially increase the population growth rate of a new population, because these females have higher fecundity rates than primiparous ones.

Future research perspectives

The aim of this section is to briefly outline possible future work associated with the current study that could be done in the 'Uruq Bani Ma'arid Protected Area. Several more detailed studies on, or associated with, the way in which the oryxes use their habitat could be done in the future because they would enhance the understanding of this desert ecosystem. These include:

- The interesting interaction of the oryxes especially with their summer habitat, the escarpment areas and the associated wadis. An in-depth study of the feeding patterns of the oryxes in the escarpment area and the interaction between these animals and the *Acacia* stands would greatly enhance the current knowledge on ungulate survival in hyper-arid environments.
- The present study suggested a change in the feeding resources used by the Arabian oryxes, varying from grazing to browsing on a seasonal basis. The ecological separation of the oryxes, sand gazelles and especially the mountain gazelles, which favour the escarpment areas, could also be done because they all compete for the same food sources in the escarpment areas during summer. Among other things this would indicate whether oryx and sand gazelle numbers are a potentially limiting factor to the mountain gazelle population in the area.

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APPENDIX A

Data set variable definition as used for analysis using the CATMOD procedure to determine the seasonal habitat use of the reintroduced Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, from March 1995 to February 1997.

VARIABLE	VARIABLE DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF VARIABLE CATEGORIES	CATEGORY AND / OR ABBREVIATION USED
VV6	General vegetation condition	Recorded	3	1. Overall grey-brown with tint of green 2. Green in colour with shade of brown 3. Fully green
		Recategorised for all seasons	2	1. Mostly brown in colour 2. Mostly green in colour
VV7	Tree density	Recorded	4	1. No trees (0) 2. <5 trees per hectare (5) 3. 6-15 trees per hectare (6-15) 4. >5 trees per hectare (>15)
		Recategorised for all seasons	2	1. No trees (0) 2. Trees present (1)
VV8	Green material on trees (%)	Recorded	5	1. No trees (0) 2. 1 to 25% green (25) 3. 26 to 50% green (50) 4. 51 to 75% green (75) 5. 76 to 100% green (100)
		Recategorised for spring and autumn	4	1. No trees (0) 2. 1 to 50% green (50) 3. 51 to 75% green (75) 4. 76 to 100% green (100)

VARIABLE	VARIABLE DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF VARIABLE CATEGORIES	CATEGORY AND / OR ABBREVIATION USED
VV8	Green material on trees (%)	Recategorised for winter	2	1. No trees (0) 2. 51 to 75% green (75)
VV9	Shrub density	Recorded	4	1. No shrubs (0) 2. <5 shrubs per hectare (<5) 3. 6 to 15 shrubs per hectare (6-15) 4. >15 shrubs per hectare (>15)
		Recategorised for all seasons	3	1. No shrubs (0) 2. <5 shrubs per hectare (1-5) 3. >5 shrubs per hectare (>5)
VV10	Green material on shrubs (%)	Recorded	5	1. No shrubs (0) 2. 1 to 25% green (25) 3. 26 to 50% green (50) 4. 51 to 75% green (75) 5. 76 to 100% green (100)
		Recategorised for spring	3	1. No shrubs (0) 2. 1 to 75% green (75) 3. 76 to 100% green (100)
		Recategorised for autumn	3	1. No shrubs (0) 2. 1 to 50% green (50) 3. 51-75% green (75)
		Recategorised for winter	2	1. No shrubs (0) 2. 1 to 75% green (75)

VARIABLE	VARIABLE DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF VARIABLE CATEGORIES	CATEGORY AND / OR ABBREVIATION USED
VV11	Grass green (%)	Recorded	4	1. 1 to 25% green (25) 2. 26 to 50% green (50) 3. 51 to 75% green (75)
		Recategorised for all seasons	3	1. 1 to 25% green (25) 2. 26 to 50% green (50) 3. 51 to 75% green (75)
VV12	Phenology of the grass layer	Recorded	5	1. No grass (0) 2. Sprouting (1) 3. Intermediate without flowers (2) 4. Mature with flowers (3) 5. Dormant (4)
		Recategorised for spring, summer and autumn	3	1. Sprouting to intermediate; no flowers (2) 2. Mature with flowers (3) 3. Dormant to absent (4)
		Recategorised for winter	2	1. Sprouting to mature with flowers (2) 2. Dormant to absent (4)
VV13	Grass height (cm)	Recorded	4	1. No grass (0) 2. 1 to 25cm tall (25) 3. 26 to 50cm tall (50) 4. 51 to 75cm tall (75)
		Recategorised for all seasons	2	1. 1 to 25cm tall (25) 2. >25cm tall (50)

VARIABLE	DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF VARIABLE CATEGORIES	CATEGORY AND / OR ABBREVIATION USED
VV14	Crown cover (%)	Recorded	4	1. No cover (0) 2. 1 to 5% cover (5) 3. 6 to 20% cover (20) 4 >20% cover (50)
		Recatogorised for all seasons	2	1. <5% cover (5) 2. >5% cover (20)
VV15	Cloud cover (%)	Recorded	5	1. No clouds (0) 2. 1 to 25% cloud cover (25) 3. 26 to 50% cloud cover (50) 4. 51 to 75% cloud cover (75) 5. 76 to 100% cloud cover (100)
		Recatogorised for autumn	2	1. No clouds (0) 2. Cloud cover (25)
VV16	Habitat type	Recorded	7	1. Dunes (1) 2. *Shiquat* sand sheets (21) 3. *Shiquat* gravel plains (22) 4. Pan at foot of dunes (23) 5. Wadi (3) 6. Escarpment sand sheets (41) 7. Escarpment gravel plains (42)
		Recatogorised for all seasons	4	1. Dunes (1) 2. *Shiquat* sand sheets (21) 3. *Shiquat* gravel plains (22) 4. Escarpment (3)

VARIABLE	VARIABLE DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF VARIABLE CATEGORIES	CATEGORY AND / OR ABBREVIATION USED
VV17	Activity	Recorded	7	1. Feeding (1) 2. Walking (2) 3. Resting standing - in shade (31) 4. Resting standing - in sun (32) 5. Resting lying - in shade (41) 6. Resting lying - in sun (42) 7. Running away (5)
		Recatogorised for all seasons	4	1. Feeding (1) 2. Walking (2) 3. Resting standing (31) 4. Resting lying (41)
VV18	Time of day	Recorded	-	1. Actual time of day
		Recategorised for all seasons	3	1. Up to 09:59 (1) 2. 10:00 to 15:00 (2) 3. After 15:00 (3)
VV19	Wind strength	Recorded	4	1. No wind (0) 2. Light wind (1) 3. Medium wind (2) 4. Strong wind (3)
		Recatogorised for all seasons	3	1. No wind (0) 2. Light wind (1) 3. Medium to strong wind (2)

VARIABLE	DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
VV20	Wind direction	Recorded	17	1. No wind (0) 2. Northern wind (1) 3. Southern wind (2) 4. Eastern wind (3) 5. Western wind (4) 6. North eastern wind (5) 7. North western wind (6) 8. South eastern wind (7) 9. South western wind (8) 10. North north-eastern wind (9) 11. East north-eastern wind (10) 12. East south-eastern wind (11) 13. South south-eastern wind (12) 14. West south-western wind (13) 15. South south-western wind (14) 16. North north-western wind (15) 17. West north-western wind (16)
		Recategorised for all seasons	5	1. No wind (0) 2. Northern wind (1) 3. Southern wind (2) 4. Eastern wind (3) 5. Western wind (4)
VV21	Ambient temperature (°C)	Recorded	-	1. Actual temperature was recorded
		Recategorised for spring, summer and autumn	3	1. Low (<30°) 2. Medium (30 to 35°C) 3. High (>35°C)

VARIABLE	DESCRIPTION	RECORDED AS / RECATEGORISED FOR	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND / OR ABBREVIATION USED
VV21	Ambient temperature (°C)	Recategorised for winter	2	1. Low (<20°C) 2. Medium (>20°C)
VV22	Gender	Recorded as	2	1. Male 2. Female

APPENDIX B

Taxonomic list of the plants found in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia during the study period from March 1995 to February 1997. Classification follows that of Collenette (1985). An asterisk (*) denotes plant species found in the course of this study that have not been recorded previously in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia.

ACANTHACEAE

Blepharis ciliaris (L.) B. L. Burtt

AIZOACEAE

Limeum arabicum Friedrich

Limeum obovatum Vicary (= *Limeum humile*)

AMARANTHACEAE

Aerva javanica (Burm. f.) Schultes

APOCYNACEAE

Rhazya stricta Decne.

ASCLEPIADACEAE

Glossonema varians (Stocks) Benth. ex. Hook. f.

Leptadenia pyrotechnica (Forssk.) Decne.

Pergularia tomentosa L.

BORAGINACEAE

Arnebia hispidissima (Lehm.) DC.

Gastrocotyle hispida (Forssk.) Bunge

Heliotropium digynum (Forssk.) C. Chr.

Heliotropium ramosissimum (Lehm.) Sieb. ex A. DC.

Heliotropium rariflorum Stocks

Moltkiopsis ciliata (Forssk.) I. M. Johnst.

Trichodesma africanum (L.) R. Br. *

BURSERACEAE

Commiphora myrrha (Nees) Engl.

CAPPARACEAE

Capparis sinaica Veill. (=*Capparis cartilaginea* Decne.)

Cleome amblyocarpa Baratte & Murb.

Cleome brachycarpa Vahl ex DC. *

Cleome rupicola Vicary

Dipterygium glaucum Decne.

Maerua crassifolia Forssk.

CARYOPHYLLACEAE

Polycarpaea repens (Forssk.) Asch. et Schweinf.

CHENOPODIACEAE

Cornulaca monocantha Delile (= *Cornulaca arabica*)

Halothamnus bottae Jaub. et Spach

Haloxylon persicum Bunge

Haloxylon salicornicum (Moq.) Bunge ex Boiss.

Salsola spinescens Moq.

COMPOSITAE

Atractylis carduus (Forssk.) C. Chr.

Centaurea pseudosinaica Czerep.

Iphiona scabra DC.

Launaea mucronata (Forssk.) Muschl.

Pulicaria glutinosa Jaub. & Spach

Pulicaria incisa (Lam.) DC.

Pulicaria crispa (Forssk.) Oliver

Scorzonera tortuosissima Boiss.

CONVOLVULACEAE

Convolvulus asyrensis Kotschy (= *Convolvulus* sp aff. *cephalopodus*)

Convolvulus glomeratus Choisy

Convolvulus prostratus Forssk. (= *Convolvulus deserti* Hochst. ex Steud. s. l.)

Seddera sp.

CRUCIFERAE

Eremobium aegyptiacum (Sprengel) Asch. et Schweinf. ex Boiss.

Farsetia burtoniae Oliver

Farsetia longisiliqua Decne.
Farsetia stylosa R. Br.
Morettia parviflora Boiss.

CUCURBITACEAE
Citrullus colocynthis (L.) Schrad.

CYNOMORIACEAE
Cynomorium coccineum L.

CYPERACEAE
Cyperus aucheri Jaub. et Spach (= *Cyperus conglomeratus* Rottb. agg. according to Mandaville (1990))

EPHEDRACEAE
Ephedra foliata Boiss. ex C.A. Mey.

EUPHORBIACEAE
Chrozophora tinctoria (L.) Raf.
Euphorbia granulata Forssk.

GERANIACEAE
Monsonia nivea (Decne.) Webb

HYACINTHACEAE
Dipcadi unicolor (Stocks) Baker

LABIATAE
Leucas inflata Benth. *
Salvia aegyptiaca L.

LEGUMINOSAE
Acacia ehrenbergiana Hayne
Acacia hamulosa Benth.
Acacia oerfota (Forssk.) Schweinf.
Acacia tortilis (Forssk.) Hayne
Astragalus fatmensis Hochst. ex Choiv.

Crotalaria aegyptiaca Benth. *
Crotalaria sp. aff. *leptocarpa* Balf. f.
Indigofera argentea Burm. f.
Indigofera spinosa Forssk.
Psoralea plicata Delile
Rhyncosia schimperi Boiss.
Senna holosericea (Fresen) Greuter
Senna italica Mill.
Tephrosia purpurea (L.) Pers.
Tephrosia quartiniana Greuter & Burdet

MENISPERMACEAE
Cocculus pendulus (J. R. & G. Forst.) Diels

MORINGACEAE
Moringa peregrina (Forssk.) Fiori

NEURADACEAE
Neurada procumbens L.

NYCTAGINACEAE
Boerhavia elegans Choisy *

OROBANCHACEAE
Cistanche phelypaea L. Cout.

POACEAE
Aristida adscensionis L. *
Centropodia fragilis (Guinet & Sauvage) Pope
Centropodia forskalii (Vahl) Pope
Dicanthium foveolatum (Del.) Roberty
Lasiurus scindicus Henr.
Panicum turgidum Forssk.
Stipagrostis ciliata (Desf.) de Wint.
Stipagrostis drarii (Tackh.) de Wint.
Stipagrostis foexiana (Maire & Wilczek) de Wint.
Stripagrostis plumosa (L.) Munro ex T. Anders

Stipa capensis Thunb.

Cenchrus ciliaris L.

Pennisetum divisum (Gmel.) Henr.

Chrysopogon plumulosus Hochst. *

Echinocloa spp. *

Enneapogon desvauxii P. Beauv. *

Tragus recemosus (L.) All. *

POLYGALACEAE

Polygala irregularis

POLYGONACEAE

Calligonum crinitum ssp. *arabicum* (Sosk.) Sosk.

RESEDACEAE

Reseda muricata Presl

Ochradenus baccatus Del.

RHAMNACEAE

Ziziphus spina-christi (L.) Willd.

RUBIACEAE

Kohautia caespitosa Schnitzl.

RUTACEAE

Haplophyllum tuberculatum (Forssk.) A. Juss.

SOLANACEAE

Lycium shawii Roem. et Schult.

ZYGOPHYLLACEAE

Tribulus arabicus Hosni. s. l.

Tribulus pentandrus Forssk. agg.

Fagonia indica Burm. f.

Zygophyllum simplex L. *

Seetzania lanata (Willd.) Bullock *

APPENDIX C

The final output of the PROC CATMOD as done to determine the seasonal habitat use of the reintroduced Arabian oryx into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, from March 1995 to February 1997, indicating all the significant variables.

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
SPRING							
Green material on trees (%)	VV8=0	Dune	Escarpment	3:1	<0.0001	2.11	4.08
		Dune	*Shiquat* sand sheet	2:1	0.0017	1.2	2.21
		Dune	*Shiquat* gravel plain	2:1	0.0007	1.25	2.34
		Shiquat sand sheet	Escarpment	2:1	0.0012	1.26	2.58
		Shiquat gravel plain	Escarpment	2:1	0.0035	1.19	2.47
	VV8=50	Escarpment	Dune	6:1	0.0140	1.41	21.33
		Shiquat sand sheet	Dune	4:1	0.0318	1.12	12.96
		Shiquat gravel plain	Dune	4:1	0.0495	1.00	13.48
	VV8=75	Escarpment	Dune	3:1	0.0044	1.34	4.85
		Shiquat sand sheet	Dune	3:1	0.0019	1.47	5.51
	VV8=100	Escarpment	Dune	48:1	0.0004	5.54	416.00
		Escarpment	*Shiquat* sand sheet	7:1	0.0407	1.09	49.78
		Escarpment	*Shiquat* gravel plain	15:1	0.0127	1.79	130.50
Shrub density	VV9=0	Escarpment	Dune	5:1	0.0008	1.92	12.17
		Shiquat sand sheet	Dune	4:1	0.0044	1.51	9.23
		Shiquat gravel plain	Dune	4:1	0.0044	1.55	10.72
	VV9=1	Escarpment	Dune	3:1	0.0210	1.17	6.65
		Escarpment	*Shiquat* gravel plain	2:1	0.0411	1.04	5.71
	VV9=2	Escarpment	Dune	4:1	0.0004	1.92	9.91
		Escarpment	*Shiquat* gravel plain	3:1	0.0111	1.27	6.43
		Shiquat sand sheet	Dune	2:1	0.0483	1.01	5.20
Phenology	VV12=2	*Shiquat* sand sheet	Dune	2:1	0.0144	1.17	3.98
		Shiquat sand sheet	Escarpment	3:1	0.0002	1.73	5.95

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS Lower	Upper
Phenology	VV12=3	*Shiquat* sand sheet	Dune	3:1	0.0002	1.57	4.31
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.71	4.40
		Shiquat gravel plain	Escarpment	2:1	0.0319	1.05	3.01
	VV12=4	Escarpment	Dune	92:1	0.0001	9.42	903.30
		Escarpment	*Shiquat* sand sheet	31:1	0.0011	3.95	236.50
		Escarpment	*Shiquat* gravel plain	26:1	0.0043	2.80	249.80
Grass height (cm)	VV13=25	Escarpment	Dune	3:1	0.0087	1.33	7.01
	VV13=50	Escarpment	Dune	5:1	0.0003	2.09	11.76
		Escarpment	*Shiquat* gravel plain	3:1	0.0340	1.07	5.86
		Shiquat sand sheet	Dune	4:1	0.0029	1.55	8.48
Crown cover (%)	VV14=5	Escarpment	Dune	4:1	0.0046	1.54	10.65
		Shiquat sand sheet	Dune	3:1	0.0106	1.33	8.48
		Shiquat gravel plain	Dune	3:1	0.0311	1.11	8.54
	VV14=20	Escarpment	Dune	4:1	0.0054	1.48	9.43
		Escarpment	*Shiquat* gravel plain	3:1	0.0173	1.22	7.87
Activity	VV17=1	Escarpment	Dune	3:1	0.0051	1.44	8.01
		Escarpment	*Shiquat* gravel plain	2:1	0.0409	1.04	5.55
		Shiquat sand sheet	Dune	3:1	0.0180	1.19	6.45
	VV17=2	Escarpment	Dune	4:1	0.0004	1.95	10.17
		Escarpment	*Shiquat* sand sheet	3:1	0.0101	1.27	5.74
	VV17=31	Escarpment	Dune	4:1	0.0045	1.52	9.63
		Shiquat sand sheet	Dune	3:1	0.0477	1.01	6.26
	VV17=41	Escarpment	Dune	4:1	0.0028	1.60	9.76
		Shiquat sand sheet	Dune	4:1	0.0028	1.58	9.06
Green material on trees (%) vs. Phenology	VV8=0 vs. VV12=2	Dune	Escarpment	3:1	<0.0001	2.18	4.76
		Dune	*Shiquat* sand sheet	2:1	0.0451	1.01	2.04
		Dune	*Shiquat* gravel plain	2:1	0.0037	1.19	2.47
		Shiquat sand sheet	Escarpment	2:1	<0.0001	1.50	3.36
		Shiquat gravel plain	Escarpment	2:1	0.0031	1.24	2.85

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Green material on trees (%) vs. Phenology	VV8=0 vs. VV12=3	Dune	Escarpment	2:1	<0.0001	1.51	3.36
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.89	3.97
		Shiquat gravel plain	Escarpment	2:1	0.0001	1.47	3.27
	VV8=0 vs. VV12=4	Dune	Escarpment	3:1	0.0001	1.83	6.66
		Dune	*Shiquat* sand sheet	4:1	<0.0001	1.93	6.91
		Dune	*Shiquat* gravel plain	3:1	0.0010	1.52	5.30
	VV8=50 vs. VV12=2	*Shiquat* sand sheet	Escarpment	5:1	0.0160	1.32	15.35
	VV8=50 vs. VV12=3	*Shiquat* sand sheet	Dune	4:1	0.0081	1.42	10.52
		Shiquat sand sheet	Escarpment	3:1	0.0389	1.06	7.87
		Shiquat gravel plain	Dune	3:1	0.0281	1.13	9.20
	VV8=50 vs. VV12=4	Escarpment	Dune	164:1	0.0034	5.40	5002.50
		Escarpment	*Shiquat* sand sheet	39:1	0.0184	1.85	808.00
	VV8=75 vs. VV12=2	*Shiquat* sand sheet	Dune	2:1	0.0213	1.13	4.67
		Shiquat gravel plain	Dune	3:1	0.0002	1.78	6.65
	VV8=75 vs. VV12=3	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.79	4.65
		Shiquat sand sheet	Escarpment	5:1	<0.0001	2.78	7.71
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0447	1.01	2.58
		Shiquat gravel plain	Dune	2:1	0.0240	1.08	2.96
		Shiquat gravel plain	Escarpment	3:1	0.0001	1.67	4.93
	VV8=75 vs. VV12=4	Escarpment	Dune	14:1	0.0023	2.57	77.72
		Escarpment	*Shiquat* sand sheet	10:1	0.0073	1.88	56.75
	VV8=100 vs. VV12=2	*Shiquat* sand sheet	Escarpment	9:1	0.0298	1.24	60.26
	VV8=100 vs. VV12=4	Escarpment	Dune	109118:1	<0.0001	334.70	3.56E7
		Escarpment	*Shiquat* sand sheet	5305:1	0.0012	29.39	9.58E5
		Escarpment	*Shiquat* gravel plain	3902:1	0.0049	12.23	1.25E6
Green material on trees (%) vs. Crown cover(%)	VV8=0 vs. VV14=5	Dune	Escarpment	3:1	<0.0001	2.13	4.50
		Dune	*Shiquat* sand sheet	2:1	0.0006	1.31	2.64
		Shiquat sand sheet	Escarpment	2:1	0.0142	1.11	2.51
		Shiquat gravel plain	Escarpment	2:1	<0.0001	1.53	3.39

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS Lower	Upper
Green material on trees(%) vs. Crown cover(%)	VV8=0 vs. VV14=20	Dune	Escarpment	3:1	<0.0001	1.73	4.50
		Dune	*Shiquat* gravel plain	2:1	0.0011	1.36	3.42
		Shiquat sand sheet	Escarpment	2:1	0.0143	1.14	3.34
	VV8=50 vs.VV14=5	Escarpment	Dune	8:1	0.0055	1.84	33.84
		Shiquat gravel plain	Dune	13:1	<0.0001	3.61	45.87
		Shiquat gravel plain	*Shiquat* sand sheet	3:1	0.0437	1.04	11.73
	VV8=75 vs. VV14=5	Escarpment	Dune	3:1	0.0036	1.44	6.39
		Shiquat sand sheet	Dune	4:1	0.0002	2.02	9.93
		Shiquat gravel plain	Dune	3:1	0.0037	1.49	7.80
	VV8=100 vs. VV14=5	Escarpment	Dune	35:1	0.0140	2.05	593.10
		Shiquat sand sheet	Dune	14:1	0.0332	1.23	163.00
	VV8=100 vs. VV14=20	Escarpment	Dune	66:1	0.0003	6.76	645.50
		Escarpment	*Shiquat* sand sheet	22:1	0.0048	2.56	189.20
		Escarpment	*Shiquat* gravel plain	19:1	0.0115	1.93	179.10
Phenology vs. Crown cover(%)	VV12=2 vs. VV14=5	Dune	Escarpment	9:1	0.0077	1.79	45.63
		Shiquat sand sheet	Escarpment	21:1	<0.0001	5.07	85.28
		Shiquat gravel plain	Escarpment	7:1	0.0157	1.44	34.30
	VV12=2 vs. VV14=20	Escarpment	Dune	4:1	0.0012	1.74	9.49
	VV12=3 vs. VV14=5	Dune	Escarpment	7:1	0.0001	2.61	20.19
		Shiquat sand sheet	Escarpment	9:1	<0.0001	3.64	22.66
		Shiquat gravel plain	Escarpment	7:1	0.0001	2.61	19.78
	VV12=3 vs. VV14=20	Escarpment	Dune	7:1	0.0064	1.70	25.33
		Shiquat sand sheet	Dune	5:1	0.0118	1.45	20.17
	VV12=4 vs. VV14=5	Escarpment	Dune	20:1	<0.0001	4.73	82.97
		Escarpment	*Shiquat* sand sheet	6:1	0.0110	1.49	21.83
		Escarpment	*Shiquat* gravel plain	9:1	0.0028	2.10	35.86
	VV12=4 vs. VV14=20	Escarpment	Dune	430:1	0.0004	15.36	12020.60
		Escarpment	*Shiquat* sand sheet	163:1	0.0008	8.28	3229.90
		Escarpment	*Shiquat* gravel plain	80:1	0.0093	2.95	2196.40
SUMMER							
Green material on trees(%)	VV8=0	Dune	*Shiquat* sand sheet	2:1	0.0457	1.01	2.95
		Escarpment	*Shiquat* sand sheet	5:1	<0.0001	2.72	7.69
		Escarpment	*Shiquat* gravel plain	3:1	<0.0001	1.77	5.41

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Green material on trees(%)	VV8=0	Escarpment	Dune	3:1	0.0002	1.59	4.41
Shrub density	VV9=2	Escarpment	Dune	6:1	0.0237	1.28	31.08
Grass green (%)	VV11=25	Escarpment	Dune	42:1	0.0045	3.19	563.00
		Escarpment	*Shiquat* sand sheet	90:1	0.0004	7.37	1103.40
		Escarpment	*Shiquat* gravel plain	16:1	0.0323	1.26	207.30
Wind strength	VV19=1	Escarpment	Dune	4:1	0.0073	1.46	11.49
Green material on trees(%) vs. Grass green(%)	VV8=0 vs. VV11=25	Escarpment	Dune	5:1	<0.0001	2.50	11.22
		Escarpment	*Shiquat* sand sheet	7:1	<0.0001	3.17	13.75
		Escarpment	*Shiquat* gravel plain	5:1	<0.0001	2.54	11.23
	VV8=0 vs. VV11=50	Dune	*Shiquat* sand sheet	4:1	0.0006	1.80	8.62
		Escarpment	*Shiquat* sand sheet	6:1	<0.0001	2.91	14.18
		Escarpment	*Shiquat* gravel plain	3:1	0.0069	1.35	6.48
	VV8=0 vs. VV11=75	Escarpment	Dune	2:1	0.0225	1.11	4.16
		Escarpment	*Shiquat* sand sheet	2:1	0.0130	1.19	4.29
	VV8=50 vs. VV11=25	Escarpment	Dune	3:1	0.0200	1.18	6.75
		Escarpment	*Shiquat* sand sheet	3:1	0.0405	1.04	6.11
		Escarpment	*Shiquat* gravel plain	4:1	0.0016	1.73	10.36
	VV8=50 vs. VV11=75	*Shiquat* sand sheet	Escarpment	11:1	0.0132	1.63	67.70
	VV8=100 vs. VV11=25	Escarpment	Dune	156636:1	0.0254	4.35	5.64E9
		Escarpment	*Shiquat* sand sheet	3476303	0.0036	139.10	8.69E10
	VV8=100 vs. VV11=50	*Shiquat* sand sheet	Escarpment	49574	0.0020	53.00	4.64E7
Green material on trees(%) vs. Crown cover(%)	VV8=0 vs. VV14=5	Dune	*Shiquat* sand sheet	2:1	0.0380	1.03	3.79
		Escarpment	*Shiquat* sand sheet	3:1	0.0003	1.71	6.14
		Escarpment	*Shiquat* gravel plain	2:1	0.0386	1.04	3.83
	VV8=0 vs. VV14=20	Escarpment	Dune	4:1	<0.0001	2.28	8.10
		Escarpment	*Shiquat* sand sheet	6:1	<0.0001	3.47	12.05
		Escarpment	*Shiquat* gravel plain	5:1	<0.0001	2.51	9.19
	VV8=50 vs. VV14=20	*Shiquat* sand sheet	Dune	3:1	0.0406	1.05	11.58
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	0.0191	1.27	14.01
	VV8=75 vs. VV14=5	*Shiquat* gravel plain	*Shiquat* sand sheet	4:1	0.0152	1.29	10.58
	VV8=75 vs. VV14=20	*Shiquat* sand sheet	Dune	3:1	0.0104	1.29	6.77
		Shiquat sand sheet	Escarpment	2:1	0.0417	1.03	5.77
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	0.0006	1.91	10.60
Green material on trees(%) vs. Wind strength	VV8=0 vs. VV19=1	Escarpment	Dune	3:1	<0.0001	2.13	4.98
		Shiquat gravel plain	Dune	2:1	0.0009	1.37	3.41

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Green material on rees(%) vs. Wind strength	VV8=0 vs. VV19=1	Escarpment	*Shiquat* sand sheet	5:1	<0.0001	2.99	7.07
		Shiquat gravel plain	*Shiquat* sand sheet	3:1	<0.0001	1.93	4.82
		Escarpment	*Shiquat* gravel plain	2:1	0.0441	1.01	2.25
	VV8=0 vs. VV19=2	Escarpment	Dune	4:1	0.0024	1.58	8.44
		Dune	*Shiquat* sand sheet	4:1	0.0022	1.69	10.68
		Escarpment	*Shiquat* sand sheet	15:1	<0.0001	6.09	34.41
		Escarpment	*Shiquat* gravel plain	8:1	<0.0001	3.00	20.77
	VV8=75 vs. VV19=0	*Shiquat* sand sheet	*Shiquat* gravel plain	7:1	0.0418	1.08	52.05
	VV8=75 vs. VV19=1	Escarpment	Dune	3:1	0.0003	1.76	6.59
		Shiquat sand sheet	Dune	2:1	0.0350	1.05	3.98
		Shiquat gravel plain	Dune	3:1	0.0034	1.41	5.59
	VV8=75 vs. VV19=2	*Shiquat* gravel plain	*Shiquat* sand sheet	4:1	0.0121	1.36	12.15
Grass green(%) vs. Crown cover(%)	VV11=25 vs. VV14=5	Escarpment	Dune	78:1	0.0018	5.10	1206.60
		Escarpment	*Shiquat* sand sheet	241:1	<0.0001	17.16	3378.20
		Escarpment	*Shiquat* gravel plain	19:1	0.0319	1.29	276.40
	VV11=25 vs. VV14=20	Escarpment	Dune	23:1	0.0151	1.83	286.40
		Escarpment	*Shiquat* sand sheet	34:1	0.0048	2.92	391.10
		Escarpment	*Shiquat* gravel plain	14:1	0.0389	1.14	168.50
	VV11=50 vs. VV14=20	*Shiquat* sand sheet	Dune	10:1	0.0152	1.57	68.88
		Shiquat sand sheet	Escarpment	27:1	0.0001	5.12	142.50
		Shiquat sand sheet	*Shiquat* gravel plain	16:1	0.0034	2.50	103.00
AUTUMN							
Vegetation condition	VV6=1	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.79	4.28
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.00	4.98
		Shiquat gravel plain	Escarpment	2:1	0.0413	1.02	2.74
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0031	1.24	2.87
	VV6=2	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.23	4.50
		Shiquat gravel plain	Dune	2:1	0.0480	1.00	2.20
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.11	4.49
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	<0.0001	1.47	3.09
Green material on trees(%)	VV8=0	*Shiquat* sand sheet	Dune	2:1	0.0239	1.04	1.83
		Dune	Escarpment	2:1	<0.0001	1.74	3.35
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.47	4.52

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Green material on trees(%)	VV8=0	*Shiquat* gravel plain	Escarpment	2:1	<0.0001	1.79	3.43
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0366	1.02	1.78
	VV8=50	*Shiquat* sand sheet	Dune	3:1	0.0008	1.50	4.67
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.38	7.64
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0011	1.45	4.45
	VV8=75	*Shiquat* sand sheet	Dune	4:1	<0.0001	3.12	6.26
		Shiquat gravel plain	Dune	2:1	<0.0001	1.60	3.46
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.30	4.78
		Shiquat gravel plain	Escarpment	2:1	0.0056	1.18	2.64
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0003	1.33	2.65
	VV8=100	Escarpment	Dune	2:1	0.0247	1.12	5.10
		Shiquat sand sheet	Dune	5:1	<0.0001	2.48	9.13
		Shiquat sand sheet	Escarpment	2:1	0.0307	1.07	3.73
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0050	1.32	4.81
Green material on shrubs(%)	VV10=0	*Shiquat* sand sheet	Dune	2:1	0.0001	1.51	3.62
		Shiquat sand sheet	Escarpment	2:1	0.0002	1.52	3.85
	VV10=50	*Shiquat* sand sheet	Dune	5:1	<0.0001	3.31	7.73
		Shiquat sand sheet	Escarpment	5:1	<0.0001	2.97	7.12
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.83	4.19
	VV10=75	*Shiquat* sand sheet	Dune	2:1	<0.0001	1.59	3.04
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.94	3.80
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	<0.0001	1.40	2.66
Grass green(%)	VV11=25	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.31	4.82
		Shiquat gravel plain	Dune	2:1	0.0005	1.37	3.12
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.00	4.37
		Shiquat gravel plain	Escarpment	2:1	0.0061	1.19	2.83
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0120	1.11	2.33
	VV11=50	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.30	4.69
		Shiquat gravel plain	Dune	2:1	0.0095	1.13	2.48
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.22	4.69
		Shiquat gravel plain	Escarpment	2:1	0.0150	1.10	2.47
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0002	1.38	2.78
	VV11=75	*Shiquat* sand sheet	Dune	2:1	<0.0001	1.61	3.51
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.10	4.79
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.74	3.79

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Phenology	VV12=2	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.40	4.14
		Shiquat gravel plain	Dune	2:1	0.0112	1.10	2.05
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.62	4.56
		Shiquat gravel plain	Escarpment	2:1	0.0022	1.20	2.26
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	<0.0001	1.61	2.75
	VV12=3	*Shiquat* sand sheet	Dune	6:1	<0.0001	3.49	9.09
		Shiquat gravel plain	Dune	3:1	0.0002	1.59	4.56
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.52	6.79
		Shiquat gravel plain	Escarpment	2:1	0.0142	1.15	3.40
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0015	1.32	3.31
	VV12=4	*Shiquat* sand sheet	Escarpment	2:1	0.0025	1.30	3.44
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0112	1.15	2.94
Crown cover(%)	VV14=5	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.99	3.85
		Shiquat gravel plain	Dune	2:1	<0.0001	1.48	3.05
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.92	3.82
		Shiquat gravel plain	Escarpment	2:1	0.0001	1.43	3.01
	VV14=20	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.29	4.38
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.56	5.03
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	2.23	4.26
Activity	VV17=1	*Shiquat* sand sheet	Dune	5:1	<0.0001	3.48	6.54
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.62	5.03
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	<0.0001	2.69	5.06
	VV17=2	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.67	3.88
		Shiquat gravel plain	Dune	2:1	0.0029	1.26	3.12
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.71	4.12
		Shiquat gravel plain	Escarpment	2:1	0.0022	1.30	3.31
	VV17=31	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.81	4.63
		Shiquat gravel plain	Dune	2:1	0.0012	1.39	3.82
		Shiquat sand sheet	Escarpment	3:1	0.0001	1.58	4.09
		Shiquat gravel plain	Escarpment	2:1	0.0063	1.22	3.37
	VV17=41	*Shiquat* sand sheet	Dune	2:1	0.0028	1.31	3.67
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.20	6.72
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0002	1.60	4.66
Temperature (°C)	VV21=1	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.16	5.02
		Shiquat gravel plain	Dune	2:1	0.0002	1.51	3.75

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Temperature (°C)	VV21=1	*Shiquat* sand sheet	Escarpment	3:1	<0.0001	2.13	5.14
		Shiquat gravel plain	Escarpment	2:1	0.0003	1.49	3.83
	VV21=2	*Shiquat* sand sheet	Dune	3:1	<0.0001	2.12	3.96
		Shiquat gravel plain	Dune	2:1	0.0469	1.00	2.02
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.19	4.20
		Shiquat gravel plain	Escarpment	2:1	0.0279	1.04	2.13
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	<0.0001	1.49	2.77
	VV21=3	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.82	4.08
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.97	4.60
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.90	4.33
Vegetation condition vs. Phenology	VV6=1 vs. VV12=2	*Shiquat* sand sheet	Dune	2:1	<0.0001	1.58	3.63
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.00	4.85
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0016	1.29	2.95
	VV6=1 vs. VV12=3	*Shiquat* sand sheet	Dune	4:1	0.0026	1.56	8.22
		Shiquat gravel plain	Dune	3:1	0.0314	1.09	6.49
		Shiquat sand sheet	Escarpment	4:1	0.0042	1.49	8.46
		Shiquat gravel plain	Escarpment	3:1	0.0405	1.04	6.69
	VV6=1 vs. VV12=4	*Shiquat* sand sheet	Dune	2:1	0.0001	1.55	3.95
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.72	4.70
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.60	4.11
	VV6=2 vs. VV12=2	*Shiquat* sand sheet	Dune	4:1	<0.0001	3.04	5.71
		Shiquat gravel plain	Dune	2:1	0.0007	1.29	2.61
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.77	5.30
		Shiquat gravel plain	Escarpment	2:1	0.0041	1.18	2.42
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	<0.0001	1.67	3.08
	VV6=2 vs. VV12=3	Escarpment	Dune	2:1	0.0159	1.12	3.03
		Shiquat sand sheet	Dune	9:1	<0.0001	5.88	13.35
		Shiquat gravel plain	Dune	3:1	<0.0001	1.68	4.42
		Shiquat sand sheet	Escarpment	5:1	<0.0001	3.17	7.30
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	2.17	4.89
Vegetation condition vs. Crown cover(%)	VV6=1 vs. VV14=5	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.70	4.49
		Shiquat gravel plain	Dune	3:1	0.0001	1.63	4.49
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.75	4.84
		Shiquat gravel plain	Escarpment	3:1	0.0001	1.68	4.82
	VV6=1 vs. VV14=20	*Shiquat* sand sheet	Dune	3:1	<0.0001	1.74	4.41

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Vegetation condition vs. Crown cover(%)	VV6=1 vs. VV14=20	*Shiquat* sand sheet	Escarpment	3:1	<0.0001	2.10	5.57
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	2.20	5.50
	VV6=2 vs. VV14=5	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.91	4.04
		Shiquat gravel plain	Dunes	2:1	0.0165	1.10	2.53
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.68	3.76
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0107	1.13	2.47
	VV6=2 vs. VV14=20	*Shiquat* sand sheet	Dunes	4:1	<0.0001	2.43	5.39
		Shiquat sand sheet	Escarpment	4;1	<0.0001	2.44	5.81
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.79	4.17
Vegetation condition vs. Activity	VV6=1 vs. VV17=1	*Shiquat* sand sheet	Dunes	4:1	<0.0001	1.74	6.72
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.91	4.84
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	2.25	5.38
	VV6=1 vs. VV17=2	*Shiquat* sand sheet	Dunes	2:1	0.0042	1.33	4.54
		Shiquat gravel plain	Dunes	2:1	0.0098	1.22	4.22
		Shiquat sand sheet	Escarpment	2:1	0.0150	1.17	4.19
		Shiquat gravel plain	Escarpment	2:1	0.0295	1.07	3.89
	VV6=1 vs. VV17=31	*Shiquat* sand sheet	Dunes	4:1	<0.0001	2.27	7.11
		Shiquat gravel plain	Dunes	3:1	0.0010	1.50	5.04
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.06	6.62
		Shiquat gravel plain	Escarpment	3:1	0.0031	1.37	4.67
	VV6=1 vs. VV17=41	Dune	Escarpment	3:1	0.0187	1.19	6.95
		Shiquat sand sheet	Escarpment	4:1	0.0012	1.73	9.24
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0380	1.05	5.06
	VV6=2 vs. VV17=1	*Shiquat* sand sheet	Dunes	5:1	<0.0001	3.62	7.78
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.86	6.54
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	<0.0001	2.61	5.87
	VV6=2 vs. VV17=2	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.63	4.26
		Shiquat gravel plain	Dunes	2:1	0.0390	1.03	2.94
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.90	5.36
		Shiquat gravel plain	Escarpment	2:1	0.0091	1.20	3.69
	VV6=2 vs. VV17=31	*Shiquat* sand sheet	Dunes	2:1	0.0209	1.12	3.89
	VV6=2 vs. VV17=41	*Shiquat* sand sheet	Dunes	3:1	<0.0001	2.02	5.95
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.05	6.67
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.82	5.80
Vegetation condition vs. Temperature (°C)	VV6=1 vs. VV21=1	*Shiquat* sand sheet	Dunes	3:1	0.0014	1.46	4.87

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Vegetation condition vs. Temperature (°C)	VV6=1 vs. VV21=1	*Shiquat* sand sheet	Escarpment	4:1	<0.0001	2.10	7.47
		Shiquat gravel plain	Escarpment	2:1	0.0075	1.27	4.70
	VV6=1 vs. VV21=2	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.73	4.16
		Shiquat gravel plain	Dunes	2:1	0.0138	1.13	2.83
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.96	4.90
		Shiquat gravel plain	Escarpment	2:1	0.0033	1.27	3.33
	VV6=1 vs. VV21=3	*Shiquat* sand sheet	Dunes	3:1	0.0011	1.54	5.68
		Shiquat sand sheet	Escarpment	3:1	0.0068	1.30	5.06
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0029	1.41	5.35
	VV6=2 vs. VV21=1	*Shiquat* sand sheet	Dunes	4:1	<0.0001	2.37	6.95
		Shiquat gravel plain	Dunes	3:1	<0.0001	1.91	6.18
		Shiquat sand sheet	Escarpment	3:1	0.0004	1.57	4.88
		Shiquat gravel plain	Escarpment	2:1	0.0067	1.27	4.33
	VV6=2 vs. VV21=2	*Shiquat* sand sheet	Dunes	3:1	<0.0001	2.17	4.51
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.01	4.40
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.86	4.05
	VV6=2 vs. VV21=3	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.63	3.88
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.21	5.64
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.89	4.73
Green material on shrubs(%) vs. Activity	VV10=0 vs. VV17=1	*Shiquat* sand sheet	Dunes	5:1	<0.0001	3.48	7.95
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.41	5.65
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	<0.0001	2.88	6.57
	VV10=0 vs. VV17=2	*Shiquat* sand sheet	Dunes	3:1	<0.0013	1.47	4.94
		Shiquat gravel plain	Dunes	4:1	<0.0001	2.02	6.44
		Shiquat sand sheet	Escarpment	2:1	0.0145	1.17	4.11
		Shiquat gravel plain	Escarpment	3:1	0.0005	1.61	5.34
	VV10=0 vs. VV17=31	*Shiquat* gravel plain	Dunes	3:1	0.0111	1.26	5.98
	VV10=0 vs. VV17=41	*Shiquat* sand sheet	Escarpment	3:1	0.0098	1.35	8.92
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0274	1.12	7.28
	VV10=50 vs. VV17=1	*Shiquat* sand sheet	Dunes	7:1	<0.0001	4.28	12.66
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.22	6.65
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	<0.0001	2.56	7.24
	VV10=50 vs. VV17=2	*Shiquat* sand sheet	Dunes	4:1	0.0002	1.89	8.06
		Shiquat sand sheet	Escarpment	4:1	0.0004	1.84	8.38
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0193	1.15	4.63

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS Lower	CONFIDENCE LIMITS Upper
Green material on shrubs(%) vs. Activity	VV10=50 vs. VV17=31	*Shiquat* sand sheet	Dunes	7:1	<0.0001	3.26	16.55
		Shiquat gravel plain	Dunes	4:1	0.0087	1.39	9.61
		Shiquat sand sheet	Escarpment	6:1	<0.0001	2.46	12.53
		Shiquat gravel plain	Escarpment	3:1	0.0398	1.05	7.26
	VV10=50 vs. VV17=41	*Shiquat* sand sheet	Dunes	3:1	0.0315	1.11	8.67
		Shiquat sand sheet	Escarpment	5:1	0.0016	1.88	15.25
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	0.0347	1.08	7.99
	VV0=75 vs. VV17=1	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.97	3.98
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.33	4.88
		Shiquat sand sheet	*Shiquat* gravel plain	3:1	<0.0001	1.89	3.82
	VV10=75 vs. VV17=2	*Shiquat* sand sheet	Escarpment	2:1	0.0030	1.30	3.66
		Shiquat gravel plain	Escarpment	2:1	0.0323	1.05	3.05
	VV10=75 vs. VV17=31	*Shiquat* sand sheet	Dunes	2:1	0.0006	1.38	3.31
		Shiquat sand sheet	Escarpment	2:1	0.0001	1.54	3.80
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0122	1.13	2.69
	VV10=75 vs. VV17=41	*Shiquat* sand sheet	Dunes	2:1	0.0003	1.52	4.03
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.79	5.18
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0007	1.46	4.05
WINTER							
Vegetation condition	VV6=1	*Shiquat* gravel plain	Dunes	2:1	0.0474	1.00	1.97
	VV6=2	*Shiquat* sand sheet	Dunes	3:1	0.0002	1.61	4.45
		Shiquat sand sheet	Escarpment	3:1	0.0002	1.62	4.78
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0240	1.08	3.10
Green material on trees(%)	VV8=0	Dune	Escarpment	2:1	<0.0001	1.73	3.48
		Shiquat sand sheet	Escarpment	2:1	<0.0001	1.58	3.15
		Shiquat gravel plain	Escarpment	2:1	0.0005	1.32	2.67
	VV8=75	Escarpment	Dunes	3:1	0.0014	1.43	4.39
		Shiquat sand sheet	Dunes	4:1	<0.0001	2.25	6.93
		Shiquat gravel plain	Dunes	3:1	0.0013	1.47	4.91
Shrub density	VV9=0	*Shiquat* sand sheet	Dunes	2:1	0.0338	1.06	4.32
	VV9=1	*Shiquat* sand sheet	Dunes	2:1	0.0126	1.11	2.46
		Dunes	Escarpment	2:1	0.0038	1.24	3.06
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.11	4.92

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Shrub density	VV9=1	*Shiquat* gravel plain	Escarpment	3:1	<0.0001	1.69	3.99
	VV9=2	*Shiquat* sand sheet	Dunes	2:1	0.0050	1.22	3.04
Phenology	VV12=4	*Shiquat* sand sheet	Dunes	2:1	<0.0001	1.57	3.75
		Shiquat gravel plain	Dunes	2:1	0.0113	1.14	2.85
		Shiquat sand sheet	Escarpment	2:1	0.0001	1.53	3.72
		Shiquat gravel plain	Escarpment	2:1	0.0157	1.11	2.83
Crown cover(%)	VV14=5	*Shiquat* gravel plain	Dunes	3:1	<0.0001	1.66	4.56
		Shiquat gravel plain	Escarpment	3:1	0.0004	1.52	4.25
		Shiquat gravel plain	*Shiquat* sand sheet	2:1	0.0058	1.23	3.35
	VV14=20	*Shiquat* sand sheet	Dunes	3:1	<0.0001	1.90	3.69
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.03	3.90
		Shiquat sand sheet	*Shiquat* gravel plain	4:1	<0.0001	2.52	4.99
Temperature (°C)	VV21=1	*Shiquat* sand sheet	Dunes	2:1	<0.0001	1.55	3.55
		Shiquat sand sheet	Escarpment	2:1	0.0002	1.45	3.39
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0391	1.02	2.33
	VV21=2	*Shiquat* sand sheet	Dunes	2:1	0.0385	1.02	2.30
		Shiquat sand sheet	Escarpment	2:1	0.0272	1.05	2.39
Green material on trees(%) vs. Shrub density	VV8=0 vs. VV9=0	*Shiquat* sand sheet	Dunes	2:1	0.0226	1.06	2.26
		Dunes	Escarpment	2:1	0.0006	1.37	3.18
		Shiquat sand sheet	Escarpment	3:1	<0.0001	2.14	4.92
		Shiquat gravel plain	Escarpment	2:1	0.0005	1.39	3.27
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0309	1.04	2.22
	VV8=0 vs. VV9=1	Dunes	Escarpment	3:1	<0.0001	2.33	5.13
		Shiquat sand sheet	Escarpment	2:1	<0.0001	1.59	3.52
		Shiquat gravel plain	Escarpment	2:1	0.0013	1.30	2.92
		Dunes	*Shiquat* sand sheet	2:1	0.0367	1.02	2.08
		Dunes	*Shiquat* gravel plain	2:1	0.0019	1.24	2.55
	VV8=0 vs. VV9=2	Dunes	Escarpment	2:1	0.0138	1.16	3.61
	VV8=75 vs. VV9=0	Escarpment	Dunes	5:1	0.0057	1.64	18.06
	VV8=75 vs. VV9=1	*Shiquat* sand sheet	Dunes	4:1	<0.0001	2.25	7.10
		Shiquat gravel plain	Dunes	3:1	0.0002	1.73	5.76
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.43	7.94
		Shiquat gravel plain	Escarpment	3:1	<0.0001	1.86	6.43
	VV8=75 vs. VV9=2	Escarpment	Dunes	3:1	0.0005	1.66	6.08
		Shiquat sand sheet	Dunes	5:1	<0.0001	2.81	9.72

VARIABLE	CATEGORY	HABITAT A	HABITAT B	A:B	P-VALUE	CONFIDENCE LIMITS	
						Lower	Upper
Green material on trees (%) vs. Shrub density	VV8=75 vs. VV9=0	*Shiquat* gravel plain	Dunes	3:1	0.0041	1.36	5.02
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0189	1.12	3.57
Shrub densiy vs. Phenology	VV9=0 vs. VV12=4	*Shiquat* sand sheet	Dunes	3:1	0.0027	1.51	7.06
		Shiquat gravel plain	Dunes	2:1	0.0329	1.08	5.77
	VV9=1 vs. VV12=1	*Shiquat* sand sheet	Dunes	2:1	0.0137	1.11	2.44
		Shiquat gravel plain	Dunes	2:1	0.0217	1.07	2.39
		Dunes	Escarpment	2:1	0.0160	1.11	2.74
		Shiquat sand sheet	Escarpment	3:1	<0.0001	1.88	4.35
		Shiquat gravel plain	Escarpment	3:1	<0.0001	1.82	4.27
	VV9=1 vs. VV12=4	*Shiquat* sand sheet	Dunes	2:1	0.0448	1.01	2.75
		Dunes	Escarpment	2:1	0.0069	1.24	3.83
		Shiquat sand sheet	Escarpment	4:1	<0.0001	2.08	6.36
		Shiquat gravel plain	Escarpment	2:1	0.0030	1.35	4.32
	VV9=2 vs. VV12=4	*Shiquat* sand sheet	Dunes	3:1	0.0064	1.31	5.29
		Shiquat gravel plain	Dunes	2:1	0.0312	1.07	4.26
Phenology vs. Temperature (°C)	VV12=1 vs. VV21=1	*Shiquat* sand sheet	Dunes	2:1	0.0001	1.53	3.77
		Shiquat sand sheet	Escarpment	2:1	0.0024	1.29	3.26
		Shiquat sand sheet	*Shiquat* gravel plain	2:1	0.0142	1.12	2.79
	VV12=4 vs. VV21=1	*Shiquat* sand sheet	Dunes	2:1	0.0032	1.32	3.97
		Shiquat sand sheet	Escarpment	2:1	0.0034	1.34	4.31
	VV12=4 vs. VV21=2	*Shiquat* sand sheet	Dunes	3:1	0.0001	1.59	4.18
		Shiquat gravel plain	Dunes	2:1	0.0093	1.18	3.15
		Shiquat sand sheet	Escarpment	2:1	0.0006	1.44	3.89
		Shiquat gravel plain	Escarpment	2:1	0.0269	1.07	2.93

APPENDIX D

Glossary of terms

The following terms are used in this study. An asterisk (*) denotes terms that are explained within this glossary.

Asymptotic: In the present study this term refers to the situation in the range calculations where a further addition of observations of any particular animal results in a minimal increase in the size of the range used by that animal.

Auto-correlation: A statistical measure of the strength of association between pairs of values of a time series as a function of the time interval that separates them (Lincoln, Boxshall & Clark 1998).

Bio-geographical regions (or realms): The major divisions of the terrestrial environment characterised by their overall flora and fauna (Lawrence 1995).

Cambrian: The geological period lasting from approximately 590 to 505 million years ago and during which many phyla of multi-cellular animals first arose (Lawrence 1995).

Circling ("Paarungskreisen"): In the present study this refers to the situation observed when a male and female stand side by side facing in different directions; the male subsequently attempts to move in behind the female in order to get into a position where the female can be mounted. The female prevents this by maintaining the side by side position, and consequently the animals move round in a circle. It is often observed when a female reaches oestrus *.

Contingency table: A table consisting of data in two or more rows and columns in which the observations or individuals are classified according to two variables *. The relationship between the variables can be measured using tests of independence, such as the chi-squared test (Lincoln *et. al.* 1998).

Cretaceous period: The last period of the Mesozoic Era from approximately 140 to 170 million years ago, during which time chalk was being laid down and occurring after the Jurassic and before the Tertiary* Periods (Lawrence 1995).

Endangered: in the proposed IUCN Criteria for threatened species, a taxon is considered as endangered when it is known to be at a very high risk of extinction* in the wild in the near future (Lincoln, *et al.* 1998).

Endothermic ability: The ability to maintain a body temperature that varies only within narrow limits, by means of internal mechanisms such as the dilation or expansion of blood vessels (Allaby 1991).

Eocene: An early era of the Tertiary* Period, between the Paleocene* and the Oligocene*, lasting from approximately 55 million to 40 million years ago (Lawrence 1995).

Ephemeral: A plant that completes its life cycle within a brief period (Lawrence 1995).

Evapo-transpiration: The loss of water from the soil by evaporation from the surface and by transpiration from the plants growing in it (Lawrence 1995).

Extinction: In the present study the term refers to the situation where a taxon disappears from the wild, even though some specimens could still be alive in captivity.

Flehmen: A behaviour of probable sexual significance which is exhibited by felids, ungulates and some other mammals when examining a scent mark (usually of urine). Having sniffed at the scent mark or urine the animal performing flehmen lifts its head with its mouth partly open and the upper lip drawn backwards (Lawrence 1995).

Goose-stepping ("Laufenschlag"): In the present study this refers to the lifting of and the subsequent downwards "kick" of the front hoof of a male oryx between the back legs of a female oryx. Often observed when a female is in oestrus.*

Hyperthermia: An increase in body temperature above normal levels, which is used by some animals that live in hot climates as a water conservation strategy (Lawrence 1995).

Lacustrine: Pertaining to lakes or ponds (Lawrence 1995; Lincoln *et al.* 1998)

Lag gravels: Gravels associated with and deposited through the movement of water.

Least squares method: In statistics this is a technique of curve-fitting and of estimating the parameters of the corresponding equation. It involves choosing the parameters to minimise the sum of the squared differences between the observed values and their respective expected values (Lincoln, *et al.* 1998)

Minimum area convex polygon: A polygon with all the internal angles smaller than 180°. It is called a minimum polygon because it is the smallest area convex polygon that contains all locational points (Worton 1987). It is used to describe range sizes of animals visually.

Miocene: A geological era of the Tertiary* Period between the Oligocene* and the Pliocene* lasting from approximately 25 million to 5 million years ago (Lawrence 1995).

Model: A simplified description of a system, which is used as an aid to understanding the system. Mathematical models are constructed from numerical values given to the components of the system and the relationships among components (Allaby 1988).

Odds ratio: The odds ratio represents the probability of a success compared with the probability of a failure. For example, if an event is five times more likely to occur than not to occur, the odds are five to one that it will occur (Freund & Simon 1991).

Oedema: The swelling of body tissues because of an accumulation of tissue fluids (Lawrence 1995). It is often associated with an injury.

Oestrus: The period of maximum sexual receptivity, or heat, in female mammals. It is usually also the time of release of the ova (Lincoln, *et al.* 1998)

Oligocene: A geological era in the Tertiary* between the Eocene* and the Miocene* lasting from approximately 38 to 25 million years ago (Lawrence 1995).

Ovulation: The shedding of an ovum or ova from the ovary (Lawrence 1995).

Paleocene: The earliest era of the Tertiary* period, before the Eocene* and lasting from approximately 65 to 55 million years ago (Lawrence 1995).

Phenology: The recording and the study of periodic biological events, such as flowering, breeding and migration in relation to climatic and other environmental factors (Lawrence 1995).

Physiognomic: The characteristic features or appearance of a plant community or vegetation (Lincoln, *et al.* 1998)

Physiographic regions: Pertaining to the geographical features of the surface of the Earth (Lincoln, *et al.* 1998)

Pliocene: The geological epoch that followed the Miocene* and preceded the Pleistocene, lasting from around 5 million years to 2 million years ago (Lawrence 1995).

Polyphasic activity pattern: In the present study this refers to an activity pattern characterised by more than one period of activity.

Population: Social aggregations of the same animal species occupying a particular space at a particular time. A group of individuals sharing some common features and living in a defined area that is considered without regard to the interrelationships among them (Allaby 1988).

Post-partum: Occurring after parturition (Lincoln, *et al.* 1998). The condition experienced post-partum is only associated with the female that gave birth.

Precambrian: The time before the Cambrian *. It is generally considered as the era lasting from the earliest formation of rocks until approximately 590 million years ago, and it is divided into two eons, the Proterozoic and the earlier Archaean Eons. The Precambrian saw the origin of life, the evolution of living cells and the evolution of the eucaryotic cell. The first multi-cellular animals arose towards the end of this era (Lawrence 1995).

Reintroduction: The intentional movement of an organism into a part of its native range from which it has disappeared or become extirpated in historic times as a result of human activities or natural catastrophes (IUCN 1987).

Tertiary Period: A geological period lasting from approximately 65 million years to 2 million years ago (Lawrence 1995).

Transect: In the present study this term refers to a line used for sampling. There are two examples in the present study. The first are the lines walked for sampling the presence or absence of plant species in the different habitat types; the second are the straight lines flown to assess the proportional distribution of the various habitat types and the distribution of plants that could provide shade to the oryx.

Translocation: The movement of living organisms from one area to end in their free release in another area. Three main classes of translocation can be distinguished. They are: introduction, reintroduction* and restocking (IUCN, 1987).

Variable: Any symbol or term to which a number of different numerical values may be assigned (Lincoln *et al.* 1998).

Wadi: The Arabic term referring to a watercourse or riverbed.