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

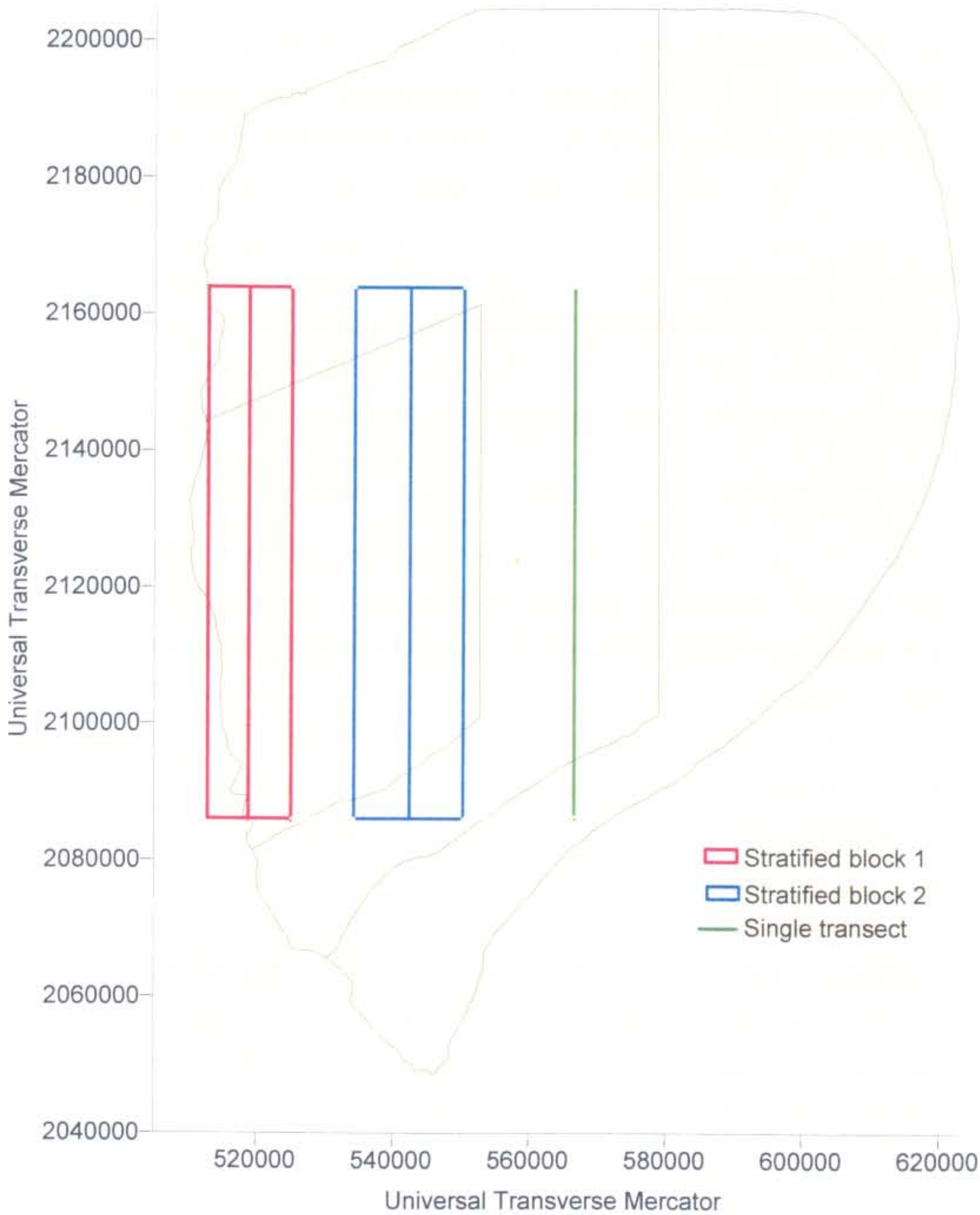

Figure 26: The transects, in three stratified blocks, flown across the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia in January 1997 to assess the proportional distribution of the subhabitats in the area.

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

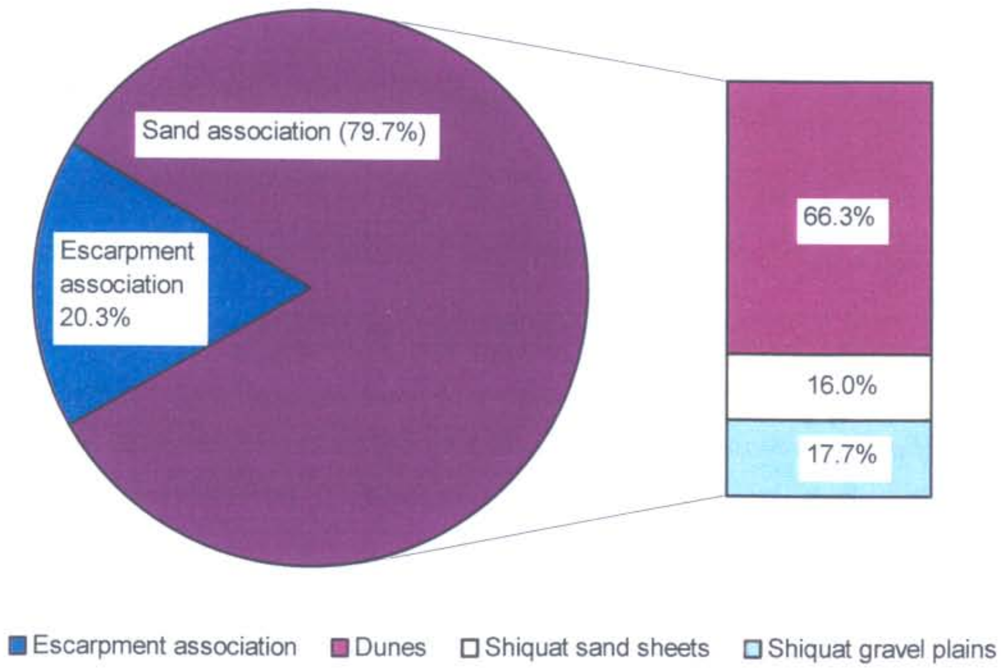

Figure 27: The proportional distribution in terms of surface area of the escarpment and sand associations with the subhabitats of the latter in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined through an aerial survey in January 1997.

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.

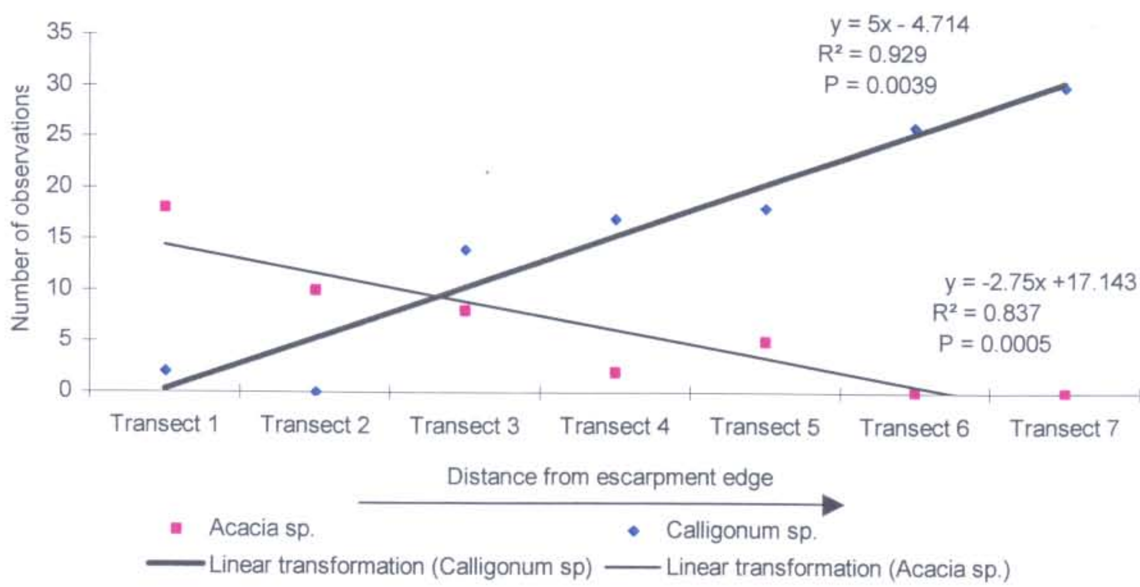

Figure 30: The relationship between the occurrence of *Acacia* and *Calligonum* trees and shrubs at increasing distances away from the escarpment edge on the western boundary of the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as determined through transects flown in a north-south 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

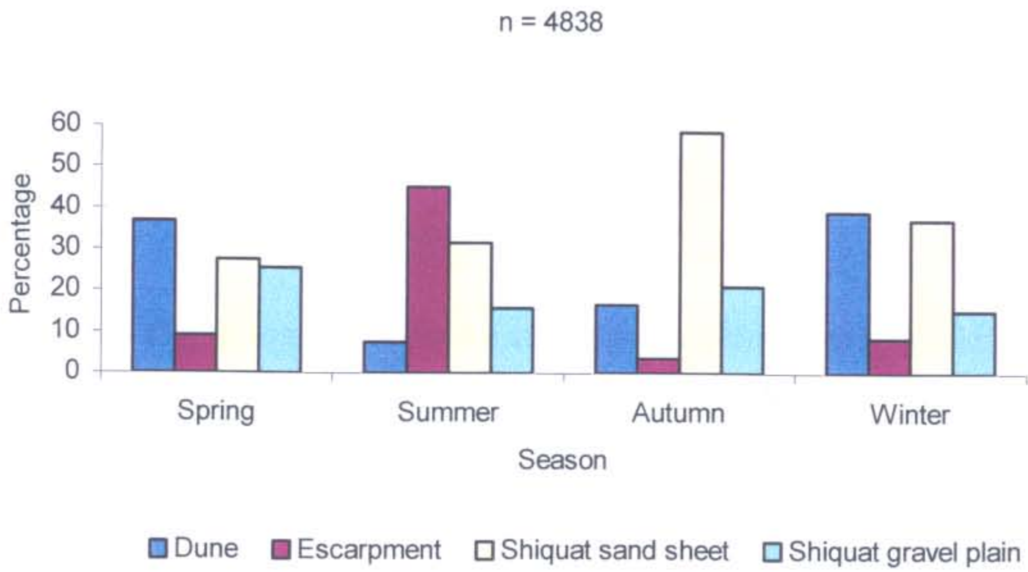

Figure 31: The frequency distribution of all the seasonal Arabian oryx observations in the different subhabitats in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, as observed from March 1995 to February 1997. The data are pooled across the years.

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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