# 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 comglomeratus* | 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.