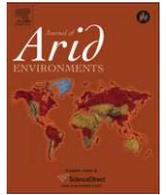


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Effects of an exceptional drought on daily activity patterns, reproductive behaviour, and reproductive success of reintroduced Arabian oryx (*Oryx leucoryx*)

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ABSTRACT

Activity patterns, social behaviour, and reproductive success of Arabian oryx were monitored in a reintroduced population in Mahazat as-Sayd Protected Area, Saudi Arabia. During the first year of the study, precipitation was 38% lower than the long-term average, whereas rainfall in the following year resulted in precipitation that was 92.8% of the long-term average. These dramatically different rainfall conditions corresponded with distinct patterns in various environmental parameters (air and soil temperature, humidity, wind speed, solar radiation, air pressure). Daily activity patterns, the frequency of social behaviours, and foraging activity were significantly reduced during the drought period. The frequency of reproductive behaviour was significantly related to daytime, air temperature and radiation, with a pronounced reduction of reproductive activities during the drought. Monthly rates of conceptions were considerably lower during the drought. Our results substantiate the idea that extended dry periods affect the population development of Oryx, but also raise questions about habitat suitability and carrying capacity. Future management of Arabian oryx should consider extreme climatic events as factors influencing various aspects of the ecology and behaviour of this species. This aspect may become even more important in the face of climate change, including a future increase of extreme climatic events.

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1. Introduction

Captive breeding and repatriation programmes are widely used to restock wild populations (Ryder, 1986, 1987). A famous example of the reintroduction of an ungulate species that has gone extinct in the wild is the Arabian oryx (*Oryx leucoryx*). Historically, the species was found throughout the Arabian Peninsula, but was eradicated entirely in 1972 by over-hunting and poaching (Henderson, 1974). Prior to extirpation, several captive breeding programmes were initiated with the intention to re-establish the Oryx in its native habitats (Stanley Price, 1989; Talbot, 1960). The first reintroduction back into the wild was initiated in 1982 into the Arabian Oryx Sanctuary on the Jiddat al-Harasis, a 25,000 km² reserve in central Oman (Spalton et al., 1999). In Saudi Arabia, the Saudi Wildlife Commission (SWC) has engaged in an ambitious reintroduction programme with the purpose to re-establish the Arabian oryx also in the Kingdom.

In March 1990, a founder population of 17 Oryx was released into Mahazat as-Sayd Protected Area, a 2244 km² fenced reserve in west-central Saudi Arabia (Ostrowski et al., 1998). With a few subsequent additions (55 animals) from the captive world herd (Mésochina et al., 2003; Seddon et al., 2003), and from natural births (Seddon and Ismail, 2000), the population increased steadily, until in August 2002 it reached an estimated size of 160–200 individuals in Mahazat as-Sayd (Mésochina et al., 2003). Currently, the Arabian oryx population in the protected area consists of about 320 animals and appears to be viable and self-sustaining (Cunningham, 2008; Strauss, 2008). Still, such small populations are inevitably more prone to local extinction due to random (stochastic) effects or extreme climatic events (Burkey, 1989; Lande et al., 2003; Shaffer, 1981).

Placing wild animals in enclosed protected areas introduces a variety of new management issues, especially during times of drought and stress. Between 2006 and the end of 2008 the study area in Mahazat as-Sayd received below-average rainfall with only localized spring showers during April 2008 (locally 1–15 mm precipitation; Cunningham, 2009a). This period of drought resulted in high mortalities of Oryx in the reserve, with virtually no offspring being born (Islam et al., 2007, 2010).

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Studies addressing the ecology of reintroduced Arabian oryx in Saudi Arabia are still scant, and more information is needed to provide conservation managers with substantial data helping to handle severe droughts and animal mass die-offs, since the occurrence of such catastrophic die-offs may greatly reduce the long-term viability of the population (Young, 1994). Most reported cases of large mammal die-offs are thought to be attributable to food scarcity rather than, for example, disease outbreaks, particularly in herbivores (Young, 1994). For herbivores such as ungulates, availability of sufficient food is typically directly related to precipitation or the availability of ground water. Arabian oryx are independent of surface water and obtain the required water from their food and from oxidative water (Ostrowski et al., 2002; Taylor, 1968, 1972). Reduced precipitation, however, often comes with a set of other climatic parameters that may, in turn, affect various aspects of the animals' ecology and behaviour. Under reduced precipitation and poor food availability and quality, behavioural patterns such as feeding activity (time devoted to searching food) and social activities will most likely be affected. A corresponding reduction of mating activity, for example, will lead to reduced reproduction and, therefore, has the potential to aggravate the negative effects of mass die-off. Fluctuating climatic conditions may, therefore, result in similarly pronounced fluctuations in population size, and may lead to an increased risk of extinction (Treydte et al., 2001).

In this study we tested whether climatic conditions alter the daily activity patterns of a large desert-dwelling herbivore, the Arabian oryx (*O. leucoryx*), while comparing drought and non-drought periods. Based on reports from other ungulates inhabiting savannah (Lewis, 1975) or desert habitats (Taylor, 1968, 1972), we predicted that daily foraging patterns would be positively related to air humidity, but negatively to increasing ambient temperature. We predicted increased food searching effort along with reduced social activity during the catastrophic drought event in 2006 (for similar results from the ungulate community in Mana Pools National Park, Zimbabwe see Dunham, 1994), while reproductive behaviour should be reduced (Coulson et al., 2000; Leuthold, 1977). Finally, we demonstrate that reduced reproductive behaviour directly translates into fewer offspring being conceived/born during the period of drought. We discuss how reduced reproduction in conjunction with mass mortalities during periods of drought, and increased reproduction in conjunction with limited movement opportunities during wet periods, will lead to large fluctuation in population size and inevitably lead to an increased extinction risk (Treydte et al., 2001).

2. Material and methods

2.1. Study area

The Mahazat as-Sayd Protected Area is located in west-central Saudi Arabia and consists of a gently undulating sand and gravel plain at about 900 m altitude comprising dwarf-scrubland dominated by *Acacia tortilis* trees, other *Acacia* spp. as well as *Maerua crassifolia* trees (Fischer et al., 1998). Perennial grasses, such as *Panicum turgidum*, *Lasiurus scindicus* and *Octochloa compressa*, which are important Oryx forage species (Ostrowski et al., 2002), are abundant on sandy areas and in valley depressions. Net primary production in Mahazat as-Sayd is low and rainfall is unpredictable and patchily distributed (Treydte et al., 2001). Mean temperature ranges from 17 °C in winter to 34 °C in summer, but maximum temperatures in summer often exceed 45 °C (Ostrowski and Williams, 2006; Treydte et al., 2001). Mahazat as-Sayd is completely fenced (2244 km²) and was gazetted in 1988 as a reintroduction site for Arabian oryx, Houbara bustards (*Chlamydotis undulata macqueenii*) and the Arabian sand gazelle (*Gazella subgutturosa marica*) (Child and Grainger, 1990). Predators were

originally eradicated from the reserve, but recent observations report on the presence of Arabian wolf (*Canis lupus*) in Mahazat as-Sayd (Cunningham and Wronski, 2010).

Our study was carried out between 1st February 2008 and 31st May 2009. Data collection was conducted during two phases: the first (14th February 2008 until 28th October 2008) was within the time of drought, while the second (6th November 2008 until 26th May 2009) was during distinctly moister weather conditions. The onset of rain was on the 3rd November 2008, and a total rainfall of 65.7 mm was measured during that month (Islam et al., 2010). Prior to the rainfall in November 2008 an extended dry period (drought) was observed, with no or very little rain between 2006 and the end of 2008 (during April 2008 locally 1–15 mm; Cunningham, 2009a). Our definition of drought is based on an average of 8 mm total precipitation between 2006 and November 2008, compared to an annual mean of approximately 7 mm between 1991 and 2005, in conjunction with unusually high temperatures (Islam et al., 2010). The mean maximum temperature (\pm SD) between 2006 and 2008 was 36.33 ± 1.15 °C, while average values for the period between 1991 and 2005 were 33.60 ± 3.03 °C.

2.2. Data collection

Oryx groups were encountered arbitrarily throughout the study area, including all major habitat types described for the reserve (Gillet and Launay, 1990). Oryx in the study area were not individually distinguishable, and repeated sampling of individuals could, therefore, not be avoided. Also, recordings were carried out irrespective of sex or age (with the understanding that reproductive behaviour involved two individuals of the opposite sex), but juveniles were excluded from the behavioural scans. We carried out 32 sampling sessions during the dry period, including a total of 164 sighted animals and 25 sampling sessions in the wet period, including a total of 227 animal sightings. We applied scan-sampling in combination with instantaneous or fixed-interval-time-point-sampling (Altmann, 1974; Martin and Bateson, 1993), taking data points every 15 min from all individuals within the focal group. In total 1515 records (scans) were taken during the drought period, and 1121 records during the non-drought period.

Sampling sessions were conducted during daytime, each lasting between 6 and 12 h. Observations usually started around 06:00 a.m. or midday and ended at 12:00 a.m. or 18:00 p.m., respectively. At each sampling point the activity of all animals in the group was recorded and assigned to one of the following behavioural categories: feeding, moving, social behaviours (i.e., reproductive behaviour, agonistic behaviour, and marking), lying, standing or anti-predator behaviour. Activity recordings were conducted from a vehicle at distances of 100–300 m using either 9×40 mm binoculars or a $25\text{--}40 \times 75$ mm spotting scope. We simultaneously recorded climatic data (air and soil temperature, relative humidity, wind speed, sun radiation and air pressure) in Mahazat as-Sayd Protected Area using HOBO H8 climate data loggers (Onset Computer Corporation, Massachusetts, USA).

Whenever calves were encountered during and after the study period, their age was estimated. Birth events could not be monitored but the putative date of conception was estimated by subtracting the estimated age of a calf as well as the gestation period of oryx (255 ± 1.5 days; Sempéré et al., 1996) from the day of sighting.

The period of drought we considered here could be regarded as not being the usual reproductive period for the studied Oryx population. Reproduction in ungulates is typically timed to ensure that parturition occurs at a favourable time of the year to maximise offspring survival (Apio et al., 2009; Baharav, 1983; Skinner and van Jaarsveld, 1987). Species that inhabit arid areas with unpredictable environmental conditions, however, display more opportunistic

breeding patterns, with calves born over a more extended time period than ungulates from mesic or tropical environments (Skinner and van Jaarsveld, 1987; Skinner and Louw, 1996; Vie, 1996). Indeed, births of Arabian oryx calves are described to occur throughout the year with no distinct reproductive season (Vie, 1996). Both sampling periods included in this study (drought and non-drought), therefore, covered the potential “normal” reproductive period.

Conception events were related to the number of females present in the protected area and expressed as rates, i.e., the number of conceptions/(number of females \times number of months during the drought and non-drought period, respectively). Female Oryx numbers in Mahazat as-Sayd (drought: 209 females, non-drought: 214 females) were obtained from bi-annual aerial or ground surveys (Cunningham, 2008; Islam et al., unpublished data). Since male and female Oryx could not be distinguished from the aircraft, total estimates were divided by two, assuming that 50% of the population are females.

2.3. Data analysis

Data from each scan were expressed as a percentage for the entire group. Data from different scans for the same group were naturally not independent; also, we could not decide with certainty whether a group encountered on one day was observed again on a subsequent day. To minimize potentially confounding effects of non-independence of the data and to avoid possible pseudoreplication, we used a conservative approach of averaging data from all scans (from all groups encountered) for each daily 15 min interval (e.g., 05:45 a.m., 06:00 a.m. etc.) for the two sampling periods separately. This resulted in 100 sampling points being used in the regression analyses (50 for the drought and non-drought period each). For data analysis we first combined several behaviours as “activity” (feeding, moving, reproductive behaviour, agonistic interactions, marking and standing alert) and phases of inactivity (lying, standing). Moreover, some of the above-mentioned behaviours occurred frequently enough to allow for a meaningful statistical analysis; hence, feeding, reproductive, agonistic and marking behaviour were also analysed separately.

We subjected the behavioural data (i.e., percentages of the total time budget) to arcsine (square root)-transformation and all climate data to natural log-transformation to approximate normal distributions and used transformed data for all statistical tests. Overall activity, feeding activity, as well as social behaviours (i.e., reproductive, agonistic and marking behaviour) were used as dependent (response) variables for step-wise backwards multiple regressions. Predictor (independent) variables [continuous variables: air and soil temperature, wind speed, radiation, air pressure, humidity as well as daytime, and the binary factor sampling period (drought or non-drought)] were excluded if $P > 0.10$. It is worth mentioning at this point that several predictor variables (i.e., climatic data) were certainly interrelated, but unlike analyses of variance (ANOVA), multiple regressions are robust to interrelated predictor variables.

As conceptions were too infrequent to be analysed in a multiple regression, rates of conceptions were compared between drought and non-drought periods using Chi square test.

3. Results

3.1. Drought effects

An effect of the sampling period (drought vs non-drought) was uncovered for overall activity, feeding, and reproductive behaviour (Table 1). Both overall activity and feeding behaviour were reduced

during the drought (Fig. 1A, B). A particularly dramatic decline was observed in the case of reproductive behaviour, and Oryx during the drought exhibited only 23.7% of the reproductive behaviour shown during the non-drought period (Fig. 1C).

Reconstructions of conceptions revealed 33 conceptions between November 2008 and May 2009 (i.e., within the time of non-drought), while only 10 conceptions were reconstructed for the period of drought (between February 2008 and October 2008). A Chi square test revealed significant differences in rates of conceptions ($\chi^2 = 8.78$, $df = 1$, $P < 0.01$; Fig. 1D).

3.2. Diurnal effects

Daytime had a significant effect on all variables considered (Fig. 2). Overall activity was lowest during midday, but increased towards the late afternoon when air temperature was still high (maximum air temperature around 16:00 h). On the other hand, resting was highest during midday hours and decreased towards the afternoon. Peaks in feeding and searching for food (i.e., moving) were observed in the early morning and in the late afternoon. These activities corresponded with increased anti-predator behaviour that was not observed while the animals were resting during the hot daytime. Reproductive behaviour and other social activities were most common throughout the morning and in the late afternoon. This general pattern was observed during both, the drought period as well as during the non-drought period (Fig. 2A, B).

3.3. Further climatic effects

Several other abiotic factors had an influence on the measured dependent variables (Table 1). We calculated Spearman rank correlation coefficients (r_s) to illustrate the directions of those effects. The same trends reported below were uncovered when

Table 1

Results from step-wise backwards multiple regressions using (a) overall activity ($R^2 = 0.89$, all excluded variables: $P \geq 0.52$), (b) feeding ($R^2 = 0.85$, excluded variables: $P \geq 0.23$), (c) reproductive behaviour ($R^2 = 0.50$, excluded variables: $P \geq 0.69$), (d) agonistic behaviour ($R^2 = 0.36$, excluded variables: $P \geq 0.24$), and (e) marking behaviour ($R^2 = 0.14$, excluded variables: $P \geq 0.35$) as dependent variables [arcsine (square root)-transformed percentages]. Factors were excluded if $P > 0.10$.

	B	SE	t	P
<i>(a) Overall activity</i>				
Drought vs non-drought	-0.62	0.15	-4.24	<0.0001
Daytime	1.70	0.46	-1.93	<0.0001
Wind speed	-0.09	0.05	-0.21	0.057
Radiation	-0.00	0.00	-22.24	<0.0001
Air pressure	0.18	0.03	5.76	<0.0001
<i>(b) Feeding</i>				
Drought vs non-drought	-0.19	0.07	-2.83	0.006
Daytime	0.83	0.24	3.50	0.001
Soil temperature	-0.02	0.01	-3.36	0.001
Radiation	-0.03	0.01	-2.08	<0.0001
<i>(c) Reproductive behaviour</i>				
Drought vs non-drought	-0.26	0.09	-2.96	0.004
Daytime	1.42	0.31	4.51	<0.0001
Air temperature	-0.05	0.01	-4.14	<0.0001
Radiation	0.00	0.00	3.90	<0.0001
<i>(d) Agonistic behaviour</i>				
Daytime	0.19	0.04	4.45	<0.0001
Humidity	0.01	0.00	7.29	<0.0001
<i>(e) Marking behaviour</i>				
Daytime	0.07	0.03	2.14	0.040
Air pressure	0.01	0.00	3.90	<0.0001

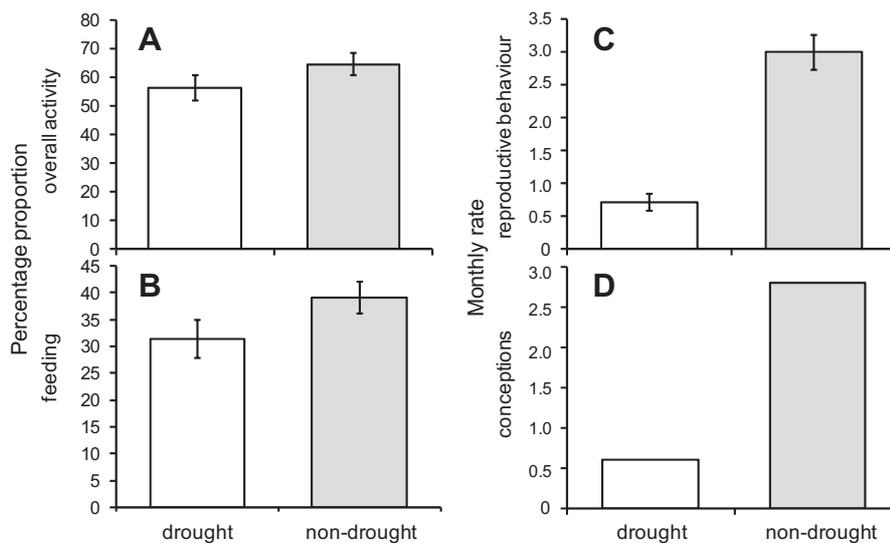


Fig. 1. Statistically significant effects of drought uncovered by multiple regression analyses on (A) overall activity, (B) feeding, and (C) reproductive behaviour in Arabian oryx in Mahazat as-Sayd Protected Area (for test results see Table 1). Data are percentages of total time budgets. (D) Also monthly rates of reproductive behaviour and conceptions (monthly rates per numbers of females) were found to differ between drought and non-drought periods (see main text). Error bars in A–C represent standard errors (SE).

analysing data from the drought and non-drought periods separately (results not shown).

Overall activity increased with decreasing wind speed ($r_s = -0.28$, $P = 0.0054$, $N = 100$), and with decreasing sun radiation ($r_s = -0.92$, $P < 0.0001$). Even though air pressure had an effect in the main model (Table 1), no significant effect was detected when testing for a correlation between overall activity and air pressure ($r_s = +0.14$, $P = 0.165$). Feeding behaviour was negatively correlated with soil temperature ($r_s = -0.33$, $P < 0.0001$) and sun radiation ($r_s = -0.90$, $P < 0.0001$).

Reproductive behaviour decreased with increasing air temperature ($r_s = -0.28$, $P = 0.0060$). Even though an effect of sun radiation was detected in the main model (Table 1), no significant correlation was detected when testing for correlations between frequencies of reproductive behaviour and sun radiation ($r_s = -0.10$, $P = 0.32$). Finally, agonistic behaviour was positively correlated with humidity ($r_s = +0.40$, $P < 0.0001$), and marking behaviour increased with increasing air pressure ($r_s = +0.32$, $P = 0.0016$).

4. Discussion

The focus of our study was on drought effects, and we detected a profound influence of the drought on the behaviour of Arabian oryx, in particular on their reproductive activities. We are aware of the fact that our present study covers only 16 months, and more (long-term) data on this topic will need to be collected in the future. Reduced reproductive behaviour was found to directly translate into fewer conceptions, i.e., we found evidence for reduced reproductive success during the drought period. As all behaviours considered here showed pronounced variation in relation to various diurnal (and other) climatic factors, we start our discussion by acknowledging those effects (Section 4.1) before discussing drought effects and their management implications.

4.1. Fluctuating environmental conditions and the behaviour of Arabian oryx

We predicted that daily foraging (and general activity) patterns would be positively related to humidity, but negatively to

increasing ambient temperatures. For both parameters no such correlation was detected; still, foraging activity was negatively related to soil temperature and sun radiation. Sun radiation has a strong impact on the body temperature of desert-dwelling mammals (Cain et al., 2006; Hetem et al., in press), and therefore, has a more direct impact on their behaviour than ambient air temperature.

Physiological and behavioural adaptations help Arabian oryx to resolve the problem of being exposed to direct sun radiation and overheating (Cain et al., 2006; Finch and Western, 1977; Hetem et al., in press; Ostrowski et al., 2006; Stanley Price, 1989; Seddon and Ismail, 2000; Taylor, 1972). Our results are in congruence with those of Seddon and Ismail (2000), showing that Oryx are less active on warmer days (when they increase lying and standing in shaded areas) at the expense of time allocated to feeding. Contrary to our findings, Seddon and Ismail (2000) found an inverse relationship between ambient (air) temperature and feeding, while in our study soil temperature was negatively correlated with feeding. This apparent discrepancy, however, may easily be explained by the fact that soil temperature was not included in Seddon and Ismail's (2002) analysis.

4.2. Drought effects

We predicted increased food searching effort (determined herein as 'moving') along with reduced social activity during the catastrophic drought event in 2007/2008 (compare Cunningham, 2009a and Dunham, 1994). Overall activity was decreased during the drought, but this effect was driven, at least in part, by the reduction of foraging activity (Fig. 1A, B). When we consider the behavioural category 'moving' alone, Oryx indeed spent more time moving (on average 23.2% of the daily time budget) during the drought than during the moister period (20.6%). Hence, the increased time spent moving during the drought and the drastically reduced amount of time spent on social activities (Figs. 1C and 2A, B) confirmed our prediction.

Food quality in Mahazat as-Sayd was clearly reduced during the drought period, with *Acacia*-trees being leafless and grass/herb species being not available at all (Cunningham, 2009a). It seems straightforward to predict increased foraging efforts under such

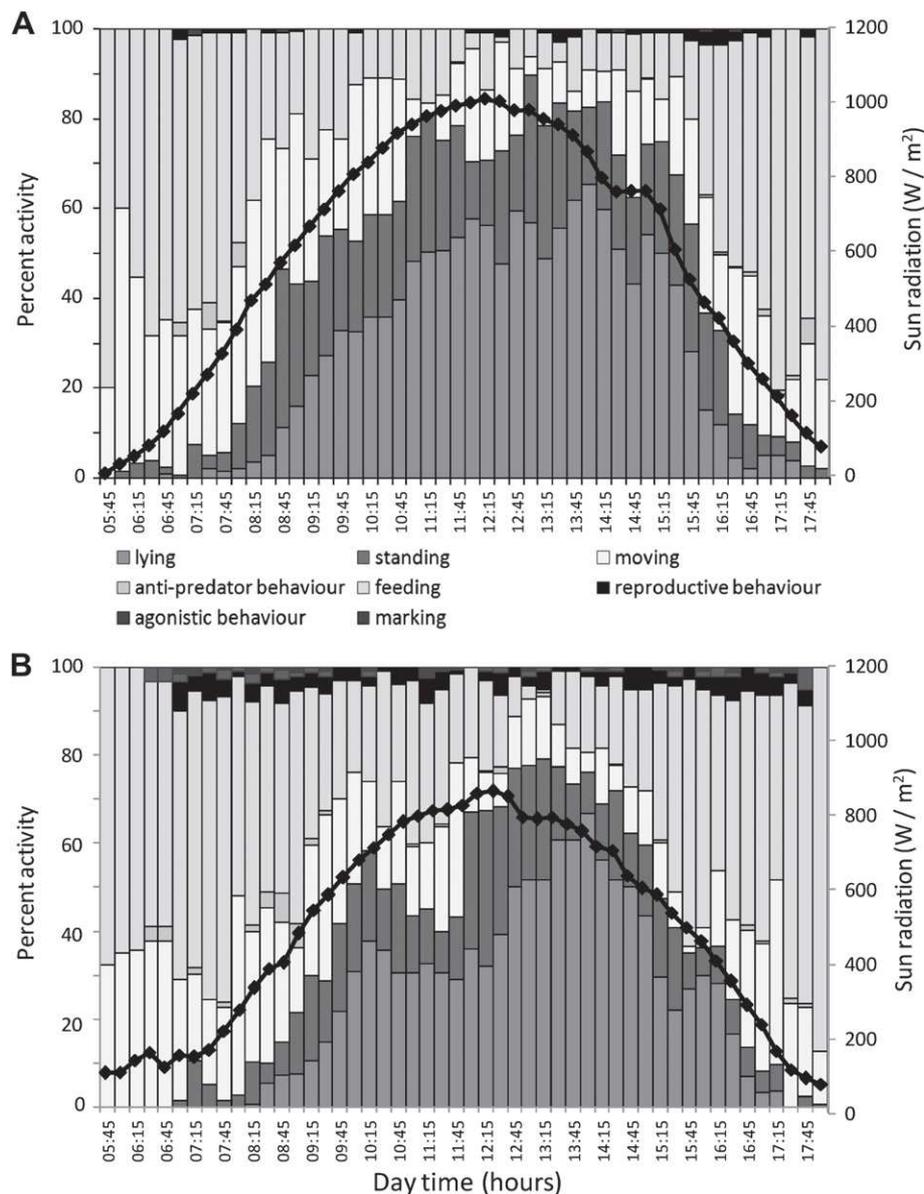


Fig. 2. Diurnal activity patterns of Arabian oryx in Mahazat as-Sayd Protected Area (A) during and (B) after the 2006/2007 drought period. Inserted values are means for sun radiation (W/m^2).

conditions, as more (low quality) plant material would need to be consumed. Contrary to our initial prediction, however, feeding was decreased, not increased. One the one hand, this pattern might simply be due to less food being available, so Oryx may have had fewer opportunities for actual food uptake. On the other hand, daily activity patterns (Fig. 2A, B) suggest that high temperatures restrict activity time during the drought period and increase the time spent resting (i.e., lying and standing). This additive negative effect of the drought, both in terms of reduced food availability and less time being available for feeding, apparently had a significant impact on social behaviours and especially reproductive activities and, therefore, on the reproductive success of Arabian oryx in the protected area. Reproduction in ungulates is typically timed to ensure that parturition occurs at a favourable time of the year to maximise offspring survival (Apio et al., 2009; Baharav, 1983; Skinner and van Jaarsveld, 1987). Species that inhabit arid areas with unpredictable environmental conditions display more opportunistic breeding patterns, with calves born over a more extended time period than

ungulates from mesic or tropical environments (Skinner and van Jaarsveld, 1987; Skinner and Louw, 1996; Vie, 1996).

4.3. Future perspectives

The impacts of global climate change are conventionally discussed in terms of changes in mean temperatures averaged over the year and over the globe, or for specific regions (MacDonald, 1999). Much less emphasis has been placed on anticipated changes in weather variability. Of particular interest are extreme events such as windstorms (e.g., Dodd and Dreslik, 2008; Spiller and Schoener, 2007), floods (e.g., Plath et al., in press), droughts (e.g., Holmgren et al., 2006; this study), etc. In the last decade, the number of catastrophic weather events was three times as great, and the cost to the world economies eight times higher than in the decade of the 1960s (MacDonald, 1999).

Generally, droughts can be accompanied by bush or forest fires that may cause extensive damage to both people and wildlife

(MacDonald, 1999). Droughts are also regularly accompanied by heat waves that have a direct effect on the health of wildlife populations (MacDonald, 1999). This may affect the viability of remnant or reintroduced populations, especially when they are small or face a number of other human-induced threats, such as hunting or habitat deterioration (Burkey, 1989; Robinson and Al Harbi, 2004; this study).

4.4. Implications for conservation management

Naturally migrating populations of ungulates respond to the negative effects of droughts by simply moving to another area, especially if rainfall is patchily distributed and/or other food-sources may be available elsewhere (e.g., Saiga (*Saiga tatarica*) in Kazakhstan: Bekenov et al., 1998; Goitred gazelle (*Gazella subgutturosa subgutturosa*) in Kazakhstan: Blank, 1985; Kingswood and Blank, 1996). This may not be possible for released animals in (fenced) sanctuaries (e.g., Blue wildebeest (*Connochaetes taurinus taurinus*) in Etosha National Park: Berry, 1997; Sand gazelle (*G. subgutturosa marica*) in Mahazat as-Sayd: Islam et al., 2010). The Arabian oryx in Mahazat as-Sayd Protected Area, is particularly susceptible to the negative effects of catastrophic climatic events, especially when their movements are restricted by a fence and when the population exceeds the estimated threshold carrying capacity 0.7 K (estimated as 300 individuals for our study area by Treydte et al., 2001).

Limited opportunities to follow localized rainfall—especially in conjunction with overpopulation (Cunningham, 2009b)—leads to overexploitation of locally available resources. Treydte et al. (2001), therefore, recommended removing an annual surplus of 15% of the total Oryx population in Mahazat as-Sayd Protected Area. Although no climate data were collected, the protected area of Uruq Bani ma-Arid in southern central Saudi Arabia also faced prolonged periods of drought, but Arabian oryx and Sand gazelles in that area are able to move freely and thus, follow localized rainfall events (Child and Grainger, 1990; NCWCD, 1987; Wachter and Robinson, 1999). Mass die-offs as reported from Mahazat as-Sayd were never observed in Uruq Bani ma-Arid; however, the role of increased hunting pressure due to the lack of a fence in the latter region needs to be evaluated in more detail.

4.5. Conclusions

Altogether then, a higher degree of connectivity of sanctuaries through corridors would be indicated in the case of Mahazat as-Sayd Protected Area (Reed, 2002), provided that human pursuit in such connecting areas is kept at a minimum. Since illegal hunting cannot be controlled outside the protected areas of Saudi Arabia, the only way to avoid catastrophic die-offs is to sustainably manage the ungulate population in Mahazat as-Sayd Protected Area and regularly remove surplus animals from the reserve (Cunningham, 2009b; Treydte et al., 2001).

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