

**INDICATORS OF ADAPTIVE RESPONSES IN HOME RANGE
UTILIZATION AND MOVEMENT PATTERNS BY A LARGE
MAMMALIAN HERBIVORE**

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ABSTRACT

GPS/GSM collars were fitted to females in two sable antelope herds occupying adjoining home ranges in the Kruger National Park in order to establish their movement responses to seasonally changing resource availability. This investigation formed part of a larger study aimed at identifying the factors responsible for the substantial population declines by this and other rarer antelope species in the protected area. To indicate responses to stressful periods during the seasonal cycle, we used the following measures: (a) proportion of locations outside the home range core, (b) displacement distances from day to day in foraging locations, and (c) extent of movement at night versus during daylight. Movements beyond the home range core were affected by excursions to water as well as foraging locations. When food and water availability became restricted during the dry season, one herd extended its range well beyond the core region favored during the wet season, while the other herd concentrated its space use more tightly within the core region, except during excursions to water. Journeys to water also affected the patterns shown by diel (24 h) displacements calculated between morning versus evening foraging locations. Diel displacement distances between evening locations were minimal when both food and water were plentifully available, and were greatest for one herd during the late dry season, but for the other herd when rainfall deficits occurred during a wet season month. Nocturnal movement showed a peak in the transition period between the dry and wet season when both resources were restricted and prevailing temperatures high. Hence, while these measures did indicate periods when resources became restricted, results revealed some of the complexities due to interactions between food and water availability. Findings also emphasised the limited extent of the landscape upon which sable depended for their resource requirements.

Keywords: animal movements, core area, GPS telemetry, home range, *Hippotragus niger*, water restrictions

INTRODUCTION

The home range represents the extent of the area normally covered by an animal in meeting its requirements for food, shelter, security, and reproduction (Burt, 1943; Jewell, 1966). The inverse of the area per animal is the number of animals per unit area. However, how space use by individual animals translates into population density depends on the number of animals sharing this range (i.e., the size of the social group) as well as on the overlap with the ranges covered by other individuals or groups (Owen-Smith, 1988). The limits to this area may be somewhat vague, being defined by what is "normal". Under some conditions animals may wander beyond their home range to seek requirements not available within the region normally traversed. Habitat conditions, available resources, and risks of predation vary from place to place within its limits, so that use may be concentrated within certain core areas or centers of activity, while other sections are infrequently visited. Resource availability and other conditions also vary seasonally, and under some conditions animals may migrate between distinct summer and winter (or benign and adverse season) home ranges. Seasonal variation is particularly influential for large mammalian herbivores, which depend on vegetation both as a food resource and for defining other habitat features (e.g., visibility affecting security against predation). Within the drier tropics and subtropics, seasons are governed largely by variation in rainfall, which is less predictable than the temperature conditions defining summer and winter in temperate latitudes. The extent to which animals cope successfully with conditions varying in space and over time through adjusting their movement patterns, time allocation, and diet selection ultimately determines their population performance. Furthermore, behavioral adjustments may reveal the onset of stressful conditions before the consequences for survival and reproductive output become manifested.

Our study was concerned with establishing the causes of the population declines shown by sable antelope (*Hippotragus niger*) and other rarer antelope species within South Africa's Kruger National Park (KNP; Ogutu and Owen-Smith, 2003). Sable numbers in KNP dropped from a peak of 2250 animals in 1987 to under 600 animals by 1996, with probably no more than 450 animals remaining currently. The sable antelope is a medium-sized (220 kg) grazer widely distributed through the savanna woodlands of south-central Africa, but never attaining high density levels. Sable form cohesive herds numbering from 10 to 50 or more females plus young, with adult males associated as temporary members of these herds (Estes and Estes, 1974; Grobler, 1974). Herds occupy fixed home ranges with limited seasonal displacements.

As part of this study, telemetry collars using the satellite-supported Global Positioning System (GPS) to record the locations of animals according to some pre-set schedule were placed on animals representing selected sable herds. These devices transmitted the location data through the GSM (cellular telephone) network to a website, from which it could be downloaded. We hoped through using this new technology to identify the habitat features limiting the distribution and abundance of sable antelope in the park, and how these animals coped with stressful conditions during the seasonal cycle when the availability of food and water resources became restricted.

In this article, we report findings from the first two collars that supplied reliable data on movement patterns over a complete year. These collars were placed to establish whether the GSM network reception in the central region of the park was adequate for data retrieval. For various reasons, there were no supporting field observations. Hence our assessment is restricted to what can be revealed by the remotely obtained location data alone. We seek to establish the extent to which meaningful behavioral indicators can be extracted from the movement patterns, extending the initial exploration of patterns in these data by Rahimi and Owen-Smith (2007). We evaluate the utility of three potential indicators:

1. EXTENSION OF MOVEMENTS BEYOND THE CORE AREA OF THE HOME RANGE

While food and water resources remain abundantly available, animals may restrict their movements to a core area providing all of their requirements (Owen-Smith, 1975; Kernohan et al., 2001). Deterioration of resource supplies within the core area may prompt animals to move more widely in search of better conditions. Hence we expected that an increased proportion of locations outside the core region favored under benign conditions would indicate the periods during the year when resource limitations become effective.

2. DIEL DISPLACEMENT DISTANCES

As forage declines in quality or abundance, animals should shift location more frequently, seeking areas with more favorable resources, unless conditions are so bad that there is little chance of finding anything better. There are obvious relationships with concepts of patch stay times and departure rules in foraging theory (Stephens and Krebs, 1986), except that responses are considered at broader spatial and temporal scales than formerly addressed. Displacement distances from day to day should indicate the extent to which animals searched more widely as resource availability diminished, as well as the energetic cost involved. More extensive movements also expose animals to a higher chance of wandering into a predator ambush (Lima and Dill, 1990), although some long moves could be made after contact with a predator. We expected that diel (24 h) displacement distances would lengthen as food became increasingly restricted over the course of the dry season.

3. EXTENT OF MOVEMENT AT NIGHT

High midday temperatures, radiant heat loads, and water restrictions may constrain the time available for foraging during daylight (Owen-Smith, 1998), causing animals to spend relatively more time foraging at night. Nocturnal foraging increases the risk of predation, because ambush predators like lions (*Panthera leo*) and leopards (*Panthera pardus*) hunt most actively at night. Food shortages may also pressure animals to engage in more risky nocturnal foraging (Sinclair and Arcese, 1995). We expected that nocturnal movements would peak in September and October, during the transitional period between the dry season and the wet season, when midday temperatures commonly exceed 35 °C and food remains in short supply.

MATERIALS AND METHODS

The GPS/GSM collars that we used were supplied by Africa Wildlife Tracking (<http://www.awt.co.za>). Observations from tracks and feeding signs of other sable bearing these collars indicate that most locations are accurate to within 2–3 m. The collar labelled AM1 was placed on an adult female sable in a herd numbering about 15 animals located to the northeast of Talamati tourist camp (24°34'S, 31°33'E), and collar AM2 on an adult female in a smaller herd numbering about six animals located to the northwest of Talamati camp. Because female sable are always associated with a herd, except for a short period after parturition before the calf becomes sufficiently mobile, the movements of these collared individuals are regarded as representing the movements of the herds of which they were members.

Collar AM1 delivered GPS locations from 26 November 2004 to 5 November 2005, while collar AM2 delivered from 26 November 2004 to 23 February 2006. Collar AM1 remained out of cell phone reception for most of the time, downloading stored data at long intervals when network contact was eventually established, while AM2 transmitted data more regularly. Because of the erratic network link, the schedule for recording GPS locations could not readily be changed from the initially supplied setting. Collar AM1 delivered locations twice daily at approximately 05:30 and 17:30, and similar settings applied initially to collar AM2. AM2 was re-set to deliver GPS locations at six-hourly intervals on 13 May 2005, at approximately 08:00, 14:00, 20:00, and 02:00. In early December 2005, these times shifted three hours earlier. This inconsistency in time settings needs to be born in mind when interpreting movement patterns. GPS fixes were missing for only 23 out of 686 points in time for AM1, while for collar AM2 52 out of 1437 fixes were missing, including one block spanning 19 days in December 2004.

The early morning and evening locations were regarded as representative of foraging activity, because large herbivores commonly rest during the midday and pre-dawn periods. Hence core areas within the home range and movements beyond them were assessed using only locations obtained during these prime foraging times. Core areas were identified from the 50% probability isopleth using the fixed kernel method in ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, California, USA) and Home Range Tools for ArcGIS (Rodgers et al., 2005), while the 95% isopleth was used to represent the outer limit to the home range, thus omitting occasional excursions beyond this area. The least squares cross-validation method was used to select the smoothing parameter. SigmaPlot 9.0 (Systat Software, Inc., San Jose, California, USA) was used to plot the utilization distribution of each herd. The core area favored during the green months (see below) was used as the basis for estimating the monthly proportion of locations outside of this core region. An isolated patch of concentrated use to the southeast by collar AM1 was excluded when estimating the core range, because it seemed to represent a period when the female bearing this collar remained away from the herd with a newly born calf.

Displacement distances showed a skewed distribution with an extended tail towards longer distances. Hence seasonal trends in diel displacements between foraging loca-

tions were assessed using median rather than mean values. Movement costs were assessed by summing the six-hourly displacements during the period when locations were obtained at this interval for herd AM2, and in this case the mean translocation distance was chosen as more representative of energy expenditures. Because 12-hourly displacements spanned varying proportions of the day and night, estimates of strictly nocturnal movement were restricted to the period when six-hourly fixes were obtained.

Monthly rainfall summaries were obtained from the four recording stations closest (<40 km) to the area occupied by these two sable herds. The wet season generally extends through the austral summer months of October to March, and the dry season from April through September. Because of the lagged influence of rainfall on vegetation, we grouped months into the green period from November to April, and the brown period from May to October.

RESULTS

HOME RANGE EXTENT AND UTILIZATION DISTRIBUTION

The two sable herds occupied adjoining home ranges separated by a gap not occupied by any other sable herd (Fig. 1). The annual home range extents estimated for these two

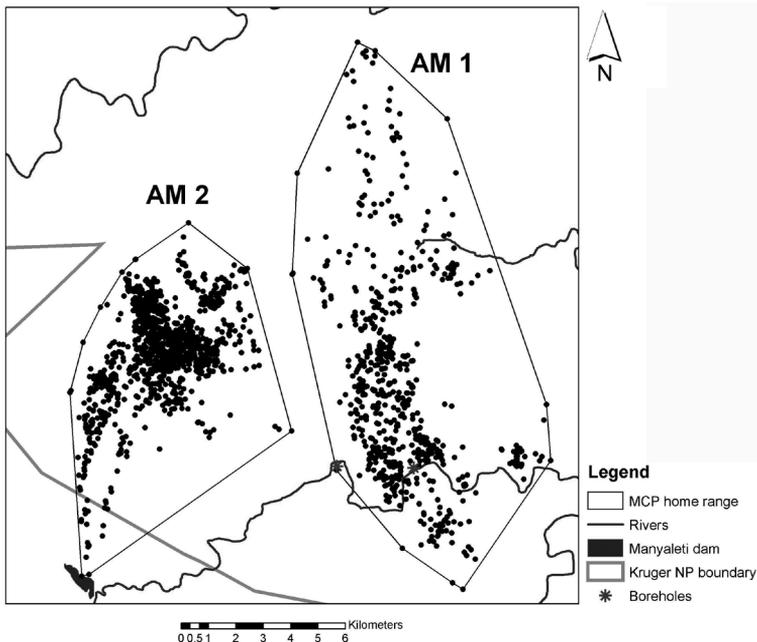


Fig. 1. GPS locations and minimum convex polygons enclosing the full annual home range extent for sable herds AM1 numbering about 15 animals (right, $N = 663$ locations from November 2004 to November 2005) and AM2 numbering about 6 animals (left, $N = 1385$ locations from November 2004 to February 2006) in the west-central region of Kruger National Park.

herds using the fixed kernel method were about 60% of those suggested by minimum convex polygons (Table 1). The core area defined by the 50% isopleth amounted to about 20% of the annual range defined by the 95% isopleth. Range estimates for the larger herd AM1 were almost twice as large as those for the smaller herd AM2. This was largely because herd AM1 extended its range northwards during the dry season (Fig. 2), while herd AM2 remained within approximately the same area year-round (Fig. 3).

Table 1
Annual and seasonal home range estimates (km²) for the two sable herds. Minimum convex polygon (MCP), 95%, and 50% kernel home-range estimates

	Herd AM1			Herd AM2		
	Annual	Green period	Brown period	Annual	Green period	Brown period
MCP	118	–	–	65	–	–
95% kernel	66.9	33.9	69.1	35.6	29.3	23.1
50% kernel	12.9	6.5	13.1	7.1	4.9	4.3

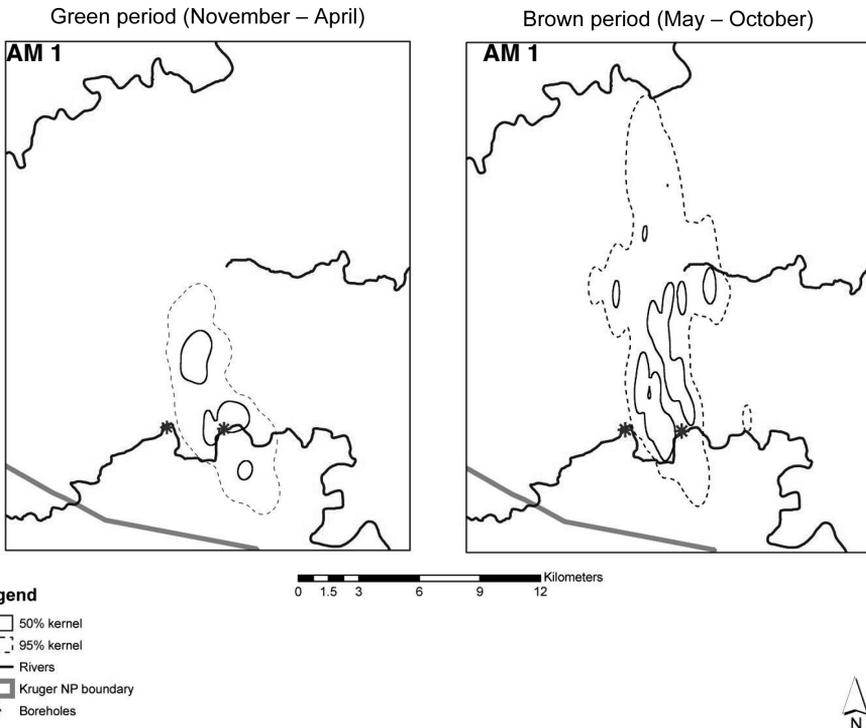


Fig. 2. Seasonal home range extents obtained by kernel smoothing of the GPS locations, showing 50% and 95% probability isopleths for sable herd AM1 (N = 274 locations for green period and 359 for brown period, representing foraging times of day from November 2004 to November 2005).

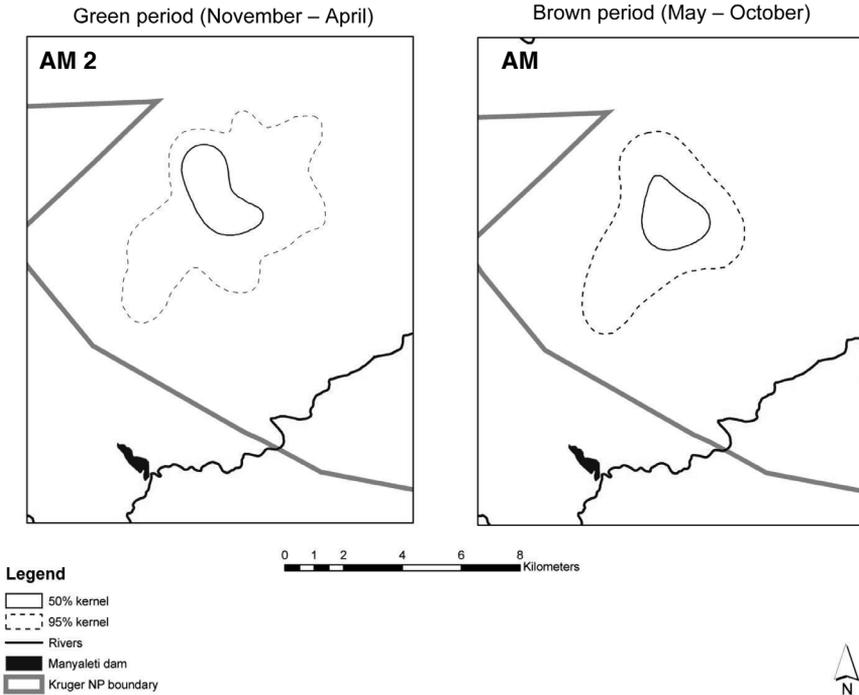


Fig. 3. Seasonal home range extents obtained by kernel smoothing of the GPS locations, showing 50% and 95% probability isopleths for sable herd AM2 ($N = 366$ locations for green period and 493 for brown period, representing foraging times of day from November 2004 to February 2006).

The annual utilization distribution of herd AM2 showed a single broad core area of use, while herd AM1 showed three locally distinct peaks within the region consistently used year-round as well as the northward extension of use (Fig. 4). The home range of herd AM2 also showed a corridor extending southwestwards in the direction of a dam on a seasonal river, evidently used as a source of water during dry periods. Surface water was available year-round in the southwest corner of the home range of herd AM1, from a borehole-fed trough close to the seasonal river passing through the southern region of its range.

EXCURSIONS BEYOND THE CORE RANGE

The proportion of locations within the core range remained around 60% for herd AM1 during the green months, except during February when the female bearing the collar stayed within a small area outside the core area for a period of about two weeks (Fig. 5). The February excursion, which probably represented the period while her new-

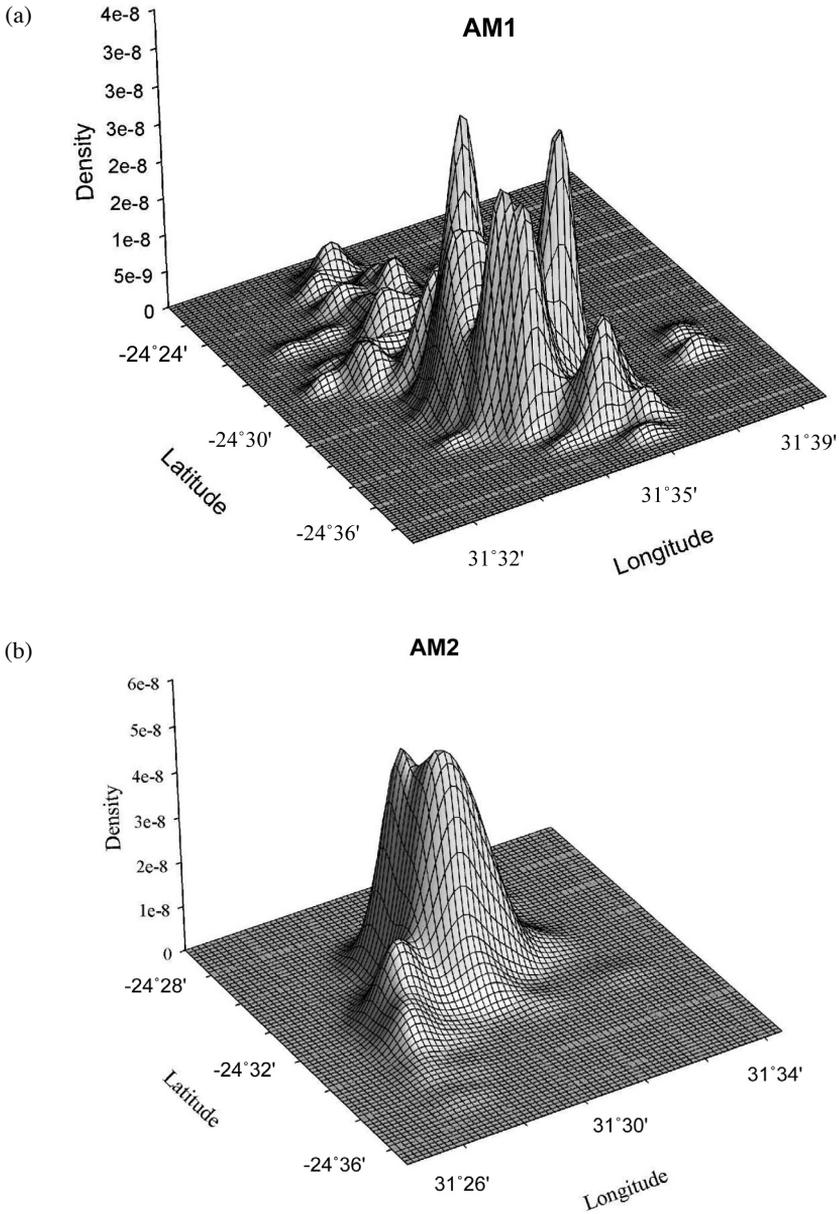


Fig. 4. Utilization distributions obtained by kernel smoothing of the annual GPS locations for (a) sable herd AM1 ($N = 274$ fixes for green period and 359 fixes for brown period, representing foraging times of day from November 2004 to November 2005) and (b) sable herd AM2 ($N = 366$ locations for green period and 493 for brown period, representing foraging times of day from November 2004 to February 2006).

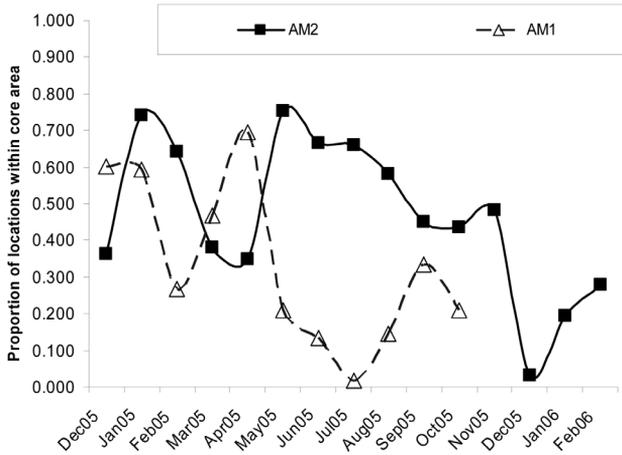


Fig. 5. Monthly variation in the proportion of GPS locations during the morning and evening foraging periods that fell within the 50% probability core area defined for the green period for sable herds AM1 and AM2.

born calf was lying out away from the herd, was terminated by a long move when she apparently rejoined the herd. Herd AM2 spent 50–75% of its time within the core range through most of the year, except during and following December 2005 after green-up of the grassland, when they moved farther afield. A drop in the use of the core area was evident for this herd through March–April, but with no indication of settlement by the collar-bearing female within a small area over the period when births were expected.

DIET DISPLACEMENT DISTANCES

The pattern revealed by diel (24 h) displacements depended on whether these were estimated between early morning or early evening locations, and also on the time of day when the GPS fixes were obtained. Estimated from early morning fixes, diel displacements for collar AM2 show a peak through August–September, but if derived from evening locations a peak in February 2005 was evident (Fig. 6). In both cases, peak movements were associated with times when excursions beyond the usual range in the direction of the dam used for drinking were shown. Journeys to water by this sable herd had evidently commenced by 08:00 when the early morning location of these animals was obtained from late May onwards. Earlier, during February, the animals were still in the course of the return journey when evening locations were taken around 17:30. Diel displacements estimated from evening locations through May–November indicated that this herd tended to remain close to their foraging area of the previous day despite the journeys to and from water. Diel displacements were at a minimum during January and May 2005 and February 2006, when there were no restrictions from either food or water availability.

A somewhat different pattern emerged for sable herd AM1, for which locations were obtained consistently around 05:30 and 17:30. In this case, the evening locations

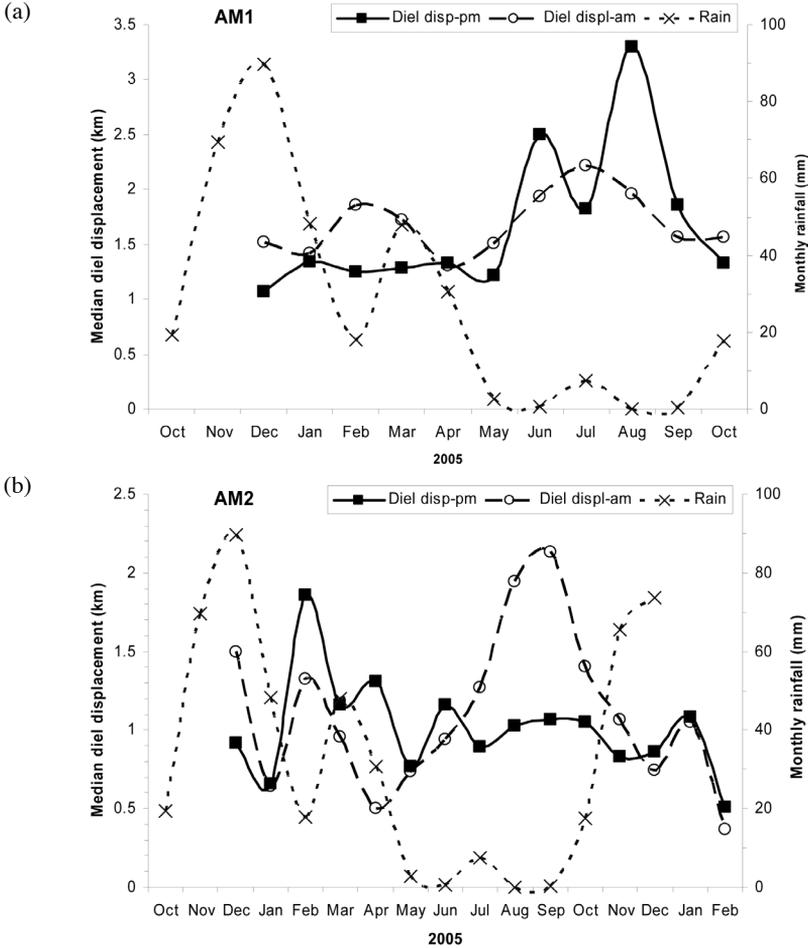


Fig. 6. Monthly median diel displacements calculated either between successive early morning or evening locations in relation to the monthly rainfall total, for (a) sable herd AM1, (b) sable herd AM2.

reflected a marked peak in diel displacements during the dry season from June through September, while shifts between morning locations likewise revealed a rise after May (Fig. 6). This herd showed no obvious excursions to water, which remained available within their home range. The rise in diel displacement distances in June reflected the extension of the home range into the northern section, and encompassed movements between this region and the southern wet season range, a pattern that continued through August. During September this herd confined its movements to within the southern section of the range, thereby lowering the median diel displacement. As for herd AM2,

Table 2

Median diel displacement distances (km) for the two sable herds averaged over the same periods. The period representing green conditions was extended through May from the monthly pattern shown in Fig. 7. Diel displacement distances in km were estimated either between successive early morning (a.m.) or early evening (p.m.) locations

Period	Herd AM1		Herd AM2	
	a.m.	p.m.	a.m.	p.m.
Green period (Dec.–May)	1.56	1.25	0.94	1.11
Brown period (May–Oct.)	1.85	2.16	1.54	1.04
Annual (Dec.–Oct.)	1.69	1.66	1.21	1.08

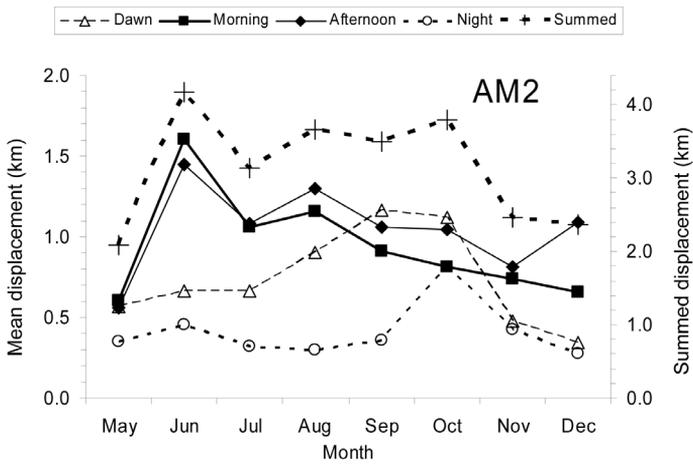


Fig. 7. Monthly mean six-hourly displacement distances at different times of day plus their summed daily total for sable herd AM2 between May and December 2005. Dawn = 0200–0800, morning = 0800–1400, afternoon = 1400–2000, night = 2000–0200.

elevated diel displacements, estimated from dawn locations, were evident in February 2005 when conditions were unusually dry.

However estimated, diel displacement distances were consistently much greater for the larger herd, AM1, than the smaller herd, AM2 (Table 2). Actual movement distances as indicated by the summed six-hourly displacements for herd AM2 during the dry season months from June through October remained almost double those shown in May or over November–December (Fig. 6).

DIURNAL VERSUS NOCTURNAL MOVEMENTS

Nocturnal movements could only be distinguished reliably for the period May–December 2005 when 6-hourly locations were obtained for collar AM2. Mean displacements entirely or mostly during daylight through the morning and afternoon periods were substantially greater than those mostly or entirely at night through the early dry

season months from June through August, but through September–October the dawn displacement between 02:00 and 08:00 exceeded that at other times of day (Fig. 7). The strictly nocturnal displacement between 20:00 and 02:00 rose to about double that shown in other months in October, the hottest month before the rains.

DISCUSSION

Although habitat features within the adjoining home ranges occupied by the two sable herds appeared very similar, the collared animals showed substantial differences in movement patterns. Some of the differences may have arisen because one herd was twice as large as the other. However, because its home range extent was also almost twice as large, this did not translate into much density difference. Other influences arose from the spatial location of perennial surface water. Herd AM2 needed to travel beyond its core range over a distance of 7 km to drink at times when water was no longer available within its home range. Such movements were made not only through the dry season months from June into October, but also from February to early April 2005 when low rainfall conditions prevailed during normally wet season months. Journeys to water were evidently made at 3-day intervals, and the herd returned to within its usual range between such excursions. Because these journeys generally took place during the course of the morning, they did not much affect the proportion of locations during the early morning and evening foraging periods that were within the home range, even on the days when travel to water occurred. Unlike herd AM2, AM1 extended its home range northwards for part of the dry season, a shift enabled by a water point in this region.

UTILIZATION DISTRIBUTED BEYOND THE HOME RANGE CORE

As expected, herd AM1 spent a much greater proportion of time outside the core regions of the home range it favored during the green months after the dry season had set in from May onwards. However, this was largely because of its use of the northern extension of its home range during this period. In contrast, herd AM2 concentrated its foraging activity more strongly in the core zone during the dry season months than for much of the wet season, apart from the regular excursions to water. Concentration of use within the core area was reduced during April 2005 after rain had ended the dry spell, and also from December 2005 onwards when resource conditions were favorable.

Accordingly, it seems that animals may adjust their range utilization in different ways to changing resource conditions. We expected that the sable would range more widely after resource availability had deteriorated in normally favored areas, seeking better conditions elsewhere. This is consistent with the pattern shown by herd AM1. The alternative is that benign conditions allow animals to move most widely, because resources are adequate everywhere. This interpretation is more consistent with observations on sable herd AM2.

Findings for other species suggest that grazers like white rhino (*Ceratotherium simum*; Owen-Smith, 1988) and African buffalo (*Syncerus caffer*; Ryan et al., 2006) expand their home ranges during the dry season seeking areas where grass still remains

green, while browsers like black rhino (*Diceros bicornis*; Goddard, 1967) and kudu (*Tragelaphus strepsiceros*; Owen-Smith, 1979) expand their ranges during the wet season to exploit the herbaceous "forbs" that become temporarily available at this time. The localities favored during adverse periods can be regarded as representing the key resource areas contributing disproportionately to supporting the population (Scoones, 1995; Illius and O'Connor, 1999). Seasonal ranging patterns may also be influenced by differences in the resources sought in different seasons if these resources also occur in different localities, with regard to both food and water.

Greater local resource depletion by the larger sable herd (AM1) might have contributed towards its need to move more widely when grass resources become non-renewing. On the other hand, the smaller herd (AM2) might have been restricted in size by the limited extent of key grass resources within its habitat region. Field surveys comparing the grassland composition in different zones of these home ranges are needed to distinguish which interpretation is better supported.

DIET DISPLACEMENTS BETWEEN FORAGING LOCATIONS

The interpretation of displacement distances between successive days by the two sable herds was complicated by travel to water. Journeys evidently commenced soon after dawn, and the animals only regained their preferred foraging range late in the afternoon, allowing for rest periods during the return journey. Accordingly, the pattern revealed by diel displacements depended on the time of day during which displacement distances were measured. Diel displacement distances calculated between evening locations, to exclude travel to water, became elevated during the dry season for herd AM1, but appeared greatest for herd AM2 during February 2005 when dry conditions prevailed during a normally wet season month. Nevertheless, the latter herd showed minimal day-to-day movement, however estimated, at times when resources were likely to be most plentifully available. The larger herd consistently showed greater diel displacements than the smaller herd, suggesting a cost of increased group size in the form of more frequent movements. Closer estimates of the actual distance travelled, obtained from the summed six-hourly displacements for herd AM2, remained almost twice as great during the dry season months as under more benign conditions, implying substantially elevated energetic expenditures in procuring both food and water.

Accordingly, our second expectation was supported. Sable travelled farther during the dry season, and when dry conditions prevailed during the normally wet season months, than when conditions were more benign. However, part of this greater travel was related to journeys to water rather than shifts between foraging locations. Wider movements from both causes imply greater energy expenditures, less daily time for foraging, and increased risk of encountering a predator.

MORE NOCTURNAL MOVEMENT

Greatest nocturnal movement was evident in October, the most stressful month through combining high temperatures with low food availability, for herd AM2. However, a more critical assessment of the amount of movement occurring during the hours

of darkness requires a shorter time interval between GPS locations than those supplied by these two sable collars.

WHAT DO THE SPACE USE PATTERNS REVEALED BY GPS TELEMETRY INDICATE?

The movement patterns and utilization distributions documented by GPS tracking show changing responses by these two sable herds to seasonal and within-season changes in both food and water resources. Diel displacement distances closely followed our expectation by increasing when resources were less readily available. The relative utilization of different sections of the home range showed less consistent patterns, with both expanded use beyond the core region and contraction within the core region evident at times judged to be stressful. We obtained some indication of greater movement during the more dangerous hours of darkness when both food and temperature conditions were most stressful, but a finer time resolution of GPS locations is needed for more insight into this response.

Nevertheless, despite occupying adjacent home ranges in regions with no obvious distinction in vegetation features, the two sable herds exhibited some unexpected differences in their response patterns. The obvious factor underlying these differences seemed to be the greater numerical size of the one herd, seemingly prompting greater movement through more rapid depletion of local resources. Ecological density did not differ between the two herds, because the smaller herd moved over a correspondingly smaller home range. We suspect that the smaller herd has split from the larger one to take advantage of the access to surface water provided by the dam enabled by the removal of the park boundary fence in 1994.

More generally, the GPS tracking revealed the relatively small sections of the landscape, as represented by the core sections of the home ranges, that were effectively suitable habitat for supporting the sable. What prevents other sable from exploiting the unutilized regions of the landscape remains unclear. Water is not a general limitation, because the park policy had been to develop a wide network of artificial water sources where natural supplies were inadequate, in the form of boreholes and dams (Redfern et al., 2003). Elevated predation pressure has emerged as the most likely factor contributing to the population declines by this and other rare antelope species in Kruger, at a time when habitat conditions were also stressful on account of low rainfall (Owen-Smith et al., 2005; Owen-Smith and Mills, 2006). We suspect that the foraging responses of the sable to cope with these conditions, both through wider movements and greater foraging during nocturnal hours, contributed towards accentuating the risk of predation.

The patterns shown by the GPS location records for these two sable herds obviously need to be augmented by similar data for other herds, and supported by field observations on the food resources sought by sable. Nevertheless, this preliminary assessment has revealed greater diel movements and an expansion of the range traversed during periods when food and water resources became limiting. These indicate both higher energetic costs in procuring food and water, and increased exposure to predation, at these times. Both aspects have implications for population trends. The advantage of the GPS technology is that we have been able to obtain these insights from a small remnant

of a declining population in a remote area and, apart from the placement of the collars, without the disturbance involved in direct observations on the animals.

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