The costs of drinking: comparative water dependency of sable antelope and zebra

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Abstract

Resource partitioning among the ungulate species occupying African savanna ecosystems has been well documented in relation to food resources and habitat features, but few studies have addressed how distinctions in surface water dependency contribute to coexistence. During the dry season surface water becomes restricted to a few perennial sources, while the food resources remaining at this time are also most limited in quantity, especially near water where animals congregate to drink. We compared the movement patterns to and from water of sable antelope *Hippotragus niger* and zebra *Equus quagga* herds in Kruger National Park (KNP), South Africa. Owing to distinctions in their digestive systems, we expected sable to drink less frequently than zebra, allowing sable to occupy regions further from surface water than zebra. Sable travelled to water at 2–4-day intervals, versus 1–2-day intervals for zebra. However, sable travelled *c*. 25% greater distances to water due to the location of their late dry season home ranges relative to perennial water sources; zebra home ranges were generally closer to water sources. Travelling 10–15 km to and from water substantially reduced time spent foraging and resting by both species on days when animals drank. Longer intervals between travel to water by the sable antelope herd enabled it to occupy regions of the landscape further from water than those heavily exploited by the more common grazers during the critical dry season months. By avoiding concentrations of other grazers, the sable also probably gained a reduction in predation risk, balancing the substantial costs in terms of time and energy associated with travel to water. Thereby the distinctions in water dependency of this relatively rare grazer facilitated its coexistence alongside more abundant grazers in the KNP.

Introduction

Distinctions in forage resources and habitat features contributing to the coexistence of ungulate species within African savannas have been well documented (Murray & Illius, 1996; Prins & Olff, 1998). Few studies have addressed how differences in surface water dependency could also promote spatial partitioning among these species. Grazers are generally more water dependent than browsers, because the moisture content of grasses commonly falls below 10% by the late dry season (Jarman, 1973; Kay, 1997). Over 80% of the biomass of grazing ungulates occurred within 5 km of water sources during the dry season in the Amboseli region of Kenya (Western, 1975). In Kruger National Park (KNP), South Africa, waterbuck *Kobus ellipsiprymnus* and buffalo *Syncerus caffer* were more strongly concentrated near water than wildebeest *Connochaetes taurinus* and zebra *Equus quagga* during the dry season, but little of the park area was >5 km from surface water (Redfern *et al*., 2003). Wild-

ebeest and zebra favoured artificial water points in the form of dams and drinking troughs supplied from boreholes, while buffalo and waterbuck concentrated more near rivers (Smit, Grant & Devereux, 2007). Locally rare tsessebe *Damaliscus lunatus*, sable antelope *Hippotragus niger* and roan antelope *Hippotragus equinus* tended to occur closer to artificial water points than rivers (Smit *et al*., 2007; Smit, 2011). The dry season concentration of abundant grazers near water intensifies forage depletion and accentuates resource competition among these species at a time of the year when both food and water resources are most limited.

The artificial water points in Kruger Park were provided partly with the aim of buffering the rarer antelope species against water restrictions affecting forage access during severe droughts (Pienaar, 1983; Gaylard, Owen-Smith & Redfern, 2003). Instead, these species declined severely when drought conditions drew an influx of more common grazers, particularly zebra, into the relatively dry northern section of the park where the rarer antelope mostly occurred,

attracting more predators (Harrington *et al.* 1999; Owen-Smith & Mills, 2006). Following recognition of the adverse consequences of excessive surface water provisioning, park managers greatly reduced the number of artificial water sources, especially in localities remote from pools in rivers. However, concern remained about the effects of water point closure on the three locally rare grazers.

Differences in water dependence among ungulate species may arise through the variety of physiological, morphological and behavioural mechanisms employed in the maintenance of temperature and water balance (Cain *et al.*, 2006). Because water in faeces and urine are major routes of water loss, species-specific differences in faecal moisture content, urine volume and osmolality contribute to water dependency. Due to higher digestive throughput of hindgut fermenters and continuing fermentation in the colon, equids generally produce large amounts of moist faeces (e.g. 60–70% water; Maloiy, MacFarlane & Shkolnik, 1979; Turner, Cizauskas & Getz 2010) compared with the relatively drier (40–50% water) faeces produced by most ruminants (Maloiy *et al.*, 1979; Woodall & Skinner, 1993). Antelope producing drier dung have longer large intestines and more surface area but smaller circumference of the proximal and distal colon than species producing wetter faeces (Woodall & Skinner, 1993). Urine concentrating ability is also generally lower in equids (1310–1545 mOsm kg^{-1} H$_2$O: Joubert & Louw, 1976; Brobst & Bayly, 1982) than in ruminants (2010–2638 mOsm kg^{-1} H$_2$O: Maloiy *et al.*, 1979).

Both sable antelope and zebra are described as being strongly water dependent, implying that they need to drink daily (Skinner & Chimimba, 2005). However, little data is available on the frequency of visits to water, or distances of the journeys undertaken.

Accordingly, our specific objectives were to (1) establish the intervals between journeys to water by these two species during the dry season; (2) determine the timing of these journeys; (3) establish the distance traversed, and hence energy costs, associated with such travel; (4) assess the time lost to feeding and other activities as a result. Because sable antelope produce dry faecal pellets, we expected them to need to drink less frequently than zebra, which have hindgut fermentation and accordingly produce somewhat moister faeces. This distinction should allow sable to occupy regions further from surface water than zebra, thereby alleviating competition between these two grazers. We did not consider buffalo, also a potential competitor for both food and water with sable, in our assessment of travel costs because the buffalo herd occupying our study area remained close to the river throughout the dry season, in conformity with the pattern typical of buffalo herds elsewhere in Kruger Park (Redfern *et al.*, 2003).

Methods

Study area

KNP covers almost 20 000 km^2 in north-eastern South Africa. Elevations range from 200 to 800 m. Our observa-
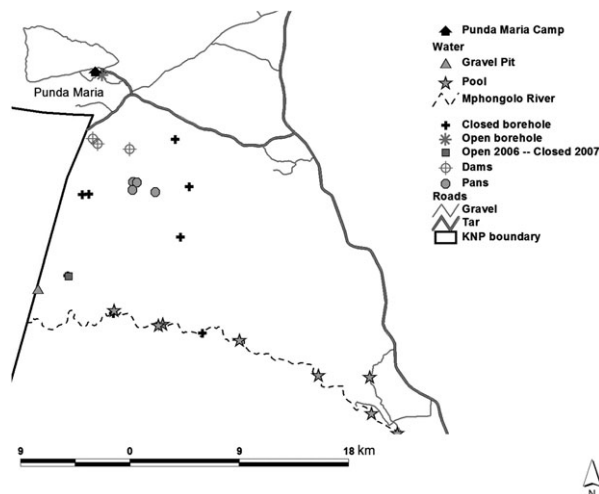

Figure 1 Punda Maria study area, Kruger National Park, South Africa, showing the location of all water points.

tions came from two localities. The Talamati area in central KNP is characterized by savanna woodlands with predominantly low bush willow trees (*Combretum* spp.). The Punda Maria area in northern Kruger has a more heterogeneous mix of bush willow and mopane *Colophospermum mopane* savanna woodlands. Annual rainfall (July–June) in the Talamati region during the 2004/2005 study period was *c*. 35% below the long-term (1960–2007) mean of 545 mm. The mean daily maximum temperature during the late dry season months (August–October) in 2005 was 30.6 °C (sd = 5.2). Annual rainfall recorded at Punda Maria camp was 32% above the long-term mean of 560 mm during the 2005/2006 rainfall year (July–June) and 25% below the mean during 2006/2007. Mean daily maximum temperature during the late dry season was 30.2 °C (sd = 4.2) during 2006 and 29.7 °C (sd = 4.9), during 2007. Only about 15% of the annual rainfall is received during the dry season (April–September) in both regions.

Water sources in the Talamati region included three borehole-supplied troughs plus a large dam in the nearby Manyeleti Game Reserve. In the Punda Maria study area, two earth dams as well as seasonal pools were dry by late August to early September each year. Thereafter, surface water remained only in perennial pools along the seasonal Mphongolo River in the south, a gravel pit near the western boundary fence, a drinking trough near the tourist camp, and during the 2006 dry season only, an additional trough supplied by a borehole (Fig. 1).

Frequency and timing of movements to water sources

Animal movements were tracked using global positioning system (GPS) collars transmitting location data through the GSM network. Collars were placed on two adult female sable representing two distinct herds in the Talamati area in November 2004. In May 2006, GPS collars were fitted on

three female sable within the sole sable herd remaining in the Punda Maria area, and on female zebra representing four distinct herds. In June 2007, a replacement collar was fitted on one of these female sable and collars were placed on two additional zebra herds in the Punda Maria area. The sable collars at Talamati supplied GPS positions for up to a year at 6-h intervals. Those placed on sable and zebra at Punda Maria supplied GPS fixes at 6-h intervals through 2006 and early 2007, interspersed with hourly records during periods of 3–7 days when foraging movements were monitored. From August 2007 onwards, all collars still operational provided hourly GPS fixes. One of the sable herds at Talamati and one zebra herd at Punda Maria had perennial water points within their dry season home ranges, so that distinct movements to and from water were not evident. Accordingly, our analysis of water movements was based on one sable herd at Talamati, and one sable herd plus five zebra herds at Punda Maria. Females of both species do not move independently of the herds to which they belong (Skinner & Chimimba, 2005). Frequency of water movements were assessed using both 6-h and hourly GPS data, whereas time and distance metrics were determined using only dates for which hourly GPS locations were available, because we could not accurately estimate timing or distance metrics with days with only 6-h GPS locations.

To identify movements to and from water sources, we plotted GPS positions in ArcView 3.2 (Environmental System Research Institute, Redlands, CA, USA) and created the daily movement paths by connecting all consecutive GPS locations for each animal using the Animal Movements extension for ArcView. Days during which animals travelled to water were characterized by a movement trajectory towards a known water source, followed by reverse travel towards the area from which the animals had come during the course of the same day. The time of initiation of these journeys was ascribed to the hourly interval in which movement in the direction of water had commenced, while the finish time was the hourly interval during which directional movement back was no longer evident. The time of arrival at water was the hourly interval when the journey reached its apex, while the departure time was the hourly interval during which return movement became apparent.

Distance costs of movements to water sources

We calculated the distance travelled during movements to water by summing the straight line distances between hourly GPS locations. The one-way distance between the start time and the arrival time at the water source represents the spatial separation between the water point and the location where the animal had been foraging. Round trip distances between the start time and the finish time represent the total travel cost to and from water. In addition, we calculated the total daily distance moved on days during which animals moved to water sources by summing the hourly displacement distances over the entire 24-h (midnight to midnight) period.

Time costs of movement to water sources

To assess the comparative time cost of movements to water, we distinguished three activity modes (resting, foraging and travelling) based on the hourly distance moved by identifying breakpoints in the log-frequency distribution of movement rates (Johnson et al., 2002; N. Owen-Smith, unpubl. data). For sable, we interpreted hourly displacement distances < 50 m as resting, 51–150 m as mixed resting and foraging, 151–600 m as foraging, 601–800 as mixed foraging and travelling, 801–1600 as mainly travelling and > 1600 m as solely travelling. For zebra, we interpreted hourly displacement distances < 50 m as resting, 51–150 m as mixed resting and foraging, 151–600 m as foraging, 601–800 m as mixed foraging and travelling, 801–1800 m as mainly travelling and > 1800 m as solely travelling, reflecting the slightly higher movement rate of zebra compared with sable. We assessed the accuracy of the distance categories used to define activity modes by plotting classified displacement distances across a 24-h period. Activity modes defined by rate of movement were consistent with daily activity patterns expected for grazers (e.g. peaks in movements classified as foraging occurred during the morning and late afternoon, and resting periods during the midday and nighttime periods); distance categories were also consistent with the rate of travel expected during foraging and movement activities (N. Owen-Smith, unpubl. data). We then calculated the number of hours within each day represented by each of the activity modes. To compare movement and time costs of water use days versus non-water use days, we randomly selected an approximately equal number of days during which animals did not move to water, and calculated the total daily movement distances and the number of hours for each day associated with each of the activity modes in the same way. Overall monthly time and distance costs associated with movements to water were estimated for each collared animal by calculating the proportional change in the average number of hours spent in each activity mode and the average total daily distances moved between use days and non-water use days, weighted by the proportion of water use days per month.

Statistical analyses

We used a parameter estimation approach for most statistical analyses, because we expected movement distances and the amount of time spent in each activity mode (e.g. resting, foraging) to differ between water use days and days when they did not move to water. Hence our goal was to estimate the magnitude of the difference in movement distances and time spent in each activity mode on water movement days versus non-water movement days. To estimate the distance and time costs to sable and zebra associated with accessing water sources during the late dry season, we calculated the mean difference and associated 95% confidence intervals comparing water movement days versus non-water movement days. We used contingency tables and χ^2 statistics to determine whether the distribution of water use intervals by

month differed between periods (i.e. 2006 vs. 2007 dry seasons) and species (i.e. sable vs. zebra). We performed all statistical analyses using SPSS 10.0.7 (SPSS Inc., Chicago, IL, USA)

Results

Frequency and timing of movements to water sources

During the 2005 dry season, journeys to water by the Talamati sable herd usually occurred at 3-day intervals, but occasionally at 4-day intervals (Table 1). All movements took place towards the dam in Manyeleti Game Reserve. The sable herd at Punda Maria travelled to water most frequently at 2- or 3-day intervals, but with 4-day intervals also recorded during the earlier stage of the less extreme dry season of 2006 (Table 1). Intervals between journeys to water tended to be shorter later in the dry season (for 2006, $\chi^2 = 8.51$, $P = 0.075$; for 2007, $\chi^2 = 26.08$; $P < 0.0001$). In August and September 2006, all movements were to pools in natural pans (Table 2), and thereafter to pools remaining in the river. In 2007, all water-related movements by the Punda Maria sable herd were towards the river (Fig. 2), apart from one journey towards a dam in early August. Following 36 mm of rainfall received during late September–early October 2007, no movements to water were evident until the end of October.

Zebra travelled to water more frequently than sable during both 2006 ($\chi^2 = 65.2$, $P < 0.0001$) and 2007 ($\chi^2 = 29.2$; $P < 0.0001$), undertaking journeys most commonly at 1–2-day intervals (Table 1). Three-day intervals occurred more frequently during the earlier months of the two dry seasons covered. Dams or pans were usually the water sources visited during August and September 2006 (Table 2). Zebra herds visited pools along the river as well as the gravel pit throughout the late dry season, and their use of these sources increased as the dry season progressed.

During 2007, visits to pans and dams by three collared zebra herds were restricted to August, with increasing use of pools in the river and gravel pit from September through early November. However, movements to water by zebra #280 were mainly to the borehole near the Punda Maria tourist camp and to the gravel pit (Fig. 2). No water movements by any of the collared zebra were evident during the weeks immediately following the rainfall received in early October 2007.

Sable commenced movements towards water at dawn, with 82% of the journeys initiated between 05:00 and 07:00 h. Sable mostly (68%) arrived at water sources between 08:00 and 12:00 h. Departure from water sources was evenly spread through the late morning and early afternoon (09:00–15:00 h). Sable generally arrived back in the vicinity of their normal home range between 19:00 and 23:00 h (75% of observations). Water movements began earlier in October–November, when sunrise occurred earlier, than in August–September. Mean overall time occupied by journeys to and from water, was 13.1 h (SD = 3.1 h).

Seventy-five per cent of all trips to water by zebra were initiated between 05:00 and 06:00 h. Peak arrival time at water occurred between 09:00 and 12:00 h. Zebra generally departed from water between 10:00 and 15:00 h, and had returned to their previous foraging areas between 18:00 and 20:00 h. Mean travel time for journeys to and from water was 13.2 h (SD = 2.4 h).

Distance costs of movements to water sources

Mean distance travelled to water sources by the Punda Maria sable herd was around 5 km (range 2–9 km) in 2006 and 8 km (range 2–14 km) in 2007, generating total round trip travel averaging 9 km (range 2–14) during 2006 and 16 km (range 9–22 km; Table 3) during 2007. Although the actual movement distances for the Talamati sable herd could not be assessed as precisely due to less frequent GPS

Table 1 Intervals between journeys to water sources by collared sable *Hippotragus niger* and zebra *Equus quagga* herds in the Talamati and Punda Maria areas of the Kruger National Park, South Africa during the dry seasons of 2005, 2006 and 2007

Animal	Period[a]	n[b]	Interval (days)				
			1	2	3	4	5
Sable-TAL[c]	Jun–Oct 2005	42	0	2	29	10	1
Sable-PM[d]	Aug–Nov 2006	34	4	11	10	9	0
Sable-PM	Aug–Nov 2007	27	5	10	10	1	1
Zebra 141	Aug–Oct 2006	83	73	10	0	0	0
Zebra 141	Aug–Sep 2007	32	10	18	4	0	0
Zebra 142	Aug–Oct 2006	58	33	19	6	0	0
Zebra 142	Aug–Nov 2007	37	21	15	1	0	0
Zebra 147	Aug–Nov 2006	44	6	33	5	0	0
Zebra 277	Aug–Nov 2007	29	8	19	2	0	0
Zebra 280	Aug–Nov 2007	35	4	29	0	0	0

[a]Excluding the period from 5 October until 29 October during which no movements to perennial water sources were detected.
[b]n is based on dates with hourly and 6-hourly GPS fix intervals.
[c]Sable in Talamati area.
[d]Sable in Punda Maria area.

Table 2 Proportional use of different water sources by sable antelope *Hippotragus niger* and zebra *Equus quagga* during the dry seasons of 2006 and 2007 in the Punda Maria area, Kruger National Park, South Africa

| Animal | Month | n | Water source | | | | |
			River	Pan	Dam	Gravel pit	Borehole
2006							
Sable	August	8		1.0			
	September	12		1.0			
	October	12	1.0				
	November	2	1.0				
Zebra 141	August	27	0.07	0.93			
	September	28	0.25	0.71		0.04	
	October	28	0.39			0.61	
Zebra 142	August	27	0.04	0.92	0.04		
	September	15	0.93				
	October	16	1.0				
Zebra 147	August	15	0.53	0.47			
	September	12	0.92	0.08			
	October	14	1.0				
	November	3	1.0				
2007							
Sable	August	9	0.90		1.0		
	September	12	1.0				
	October	1	1.0				
	November	5	1.0				
Zebra 141	August	17	0.24	0.24		0.52	
	September	15	0.73			0.27	
Zebra 142	August	13	1.0				
	September	19	1.0				
	October	1	1.0				
	November	4	1.0				
Zebra 277	August	10	0.70			0.30	
	September	14	1.0				
	October	2	1.0				
	November	3	1.0				
Zebra 280	August	14		0.47	0.06		0.47
	September	15					1.0
	October	2				0.50	0.50
	November	4				0.50	0.50
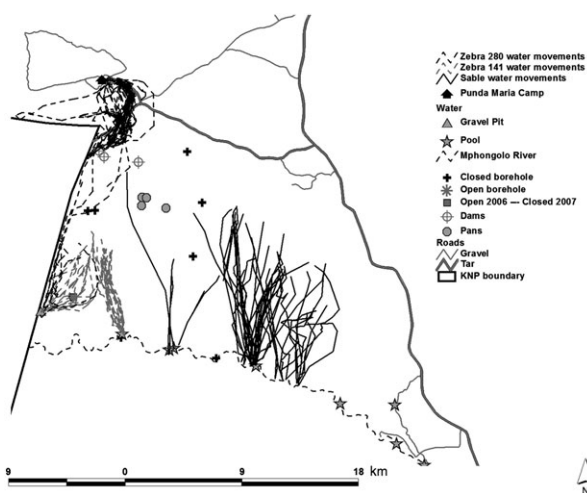
Figure 2 Movement trajectories of sable antelope *Hippotragus niger* and zebra *Equus quagga* herds 280 and 141 in the Punda Maria area, Kruger National Park during the late dry season of 2007.

locations, the distance between the core use area and the dam in the Manyeleti Game Reserve was *c*. 9 km. Mean travel distances to and from water sources by three of the four zebra herds at Punda Maria were a little less than those by the sable herd. Total daily travel distances by both sable and zebra were two to three times greater on days when journeys to water were undertaken than on other days (Table 4, Fig. 3).

Time costs of movement to water sources

Sable spent on average 4 fewer hours per day resting and 4.1 fewer hours foraging on days when movement to water occurred than on non-water movement days (Fig. 4). Time occupied by movement expanded correspondingly by *c*. 8 h during days involving travel to water.

Time costs associated with water movements by zebra varied among herds largely due to lower time costs for zebra #142 (Fig. 4). Based on the three zebra herds with more consistent time costs, zebra rested for an average of

Table 3 Mean (± SD) and range of one way and round trip distances (km) moved by sable antelope *Hippotragus niger* and zebra *Equus quagga* to water sources during the dry seasons of 2006 and 2007 in the Punda Maria area of Kruger National Park, South Africa

Animal	Period	n^a	One way distance moved to water sources (km)		Total round trip distance moved to water sources (km)	
			Mean (± SD)	Range	Mean (± SD)	Range
Sable	Oct–Nov 2006	5	5.3 (3.2)	1.9–9.4	10.4 (6.5)	3.3–16.9
Sable	Aug–Nov 2007	25	8.8 (3.1)	2.2–14.2	15.6 (4.3)	9.0–22.5
Zebra 141	Oct 2006	4	6.5 (1.6)	4.3–7.9	11.6 (3.1)	7.6–14.2
Zebra 141	Aug–Sep 2007	12	6.5 (1.1)	3.9–8.5	12.8 (1.4)	9.3–14.8
Zebra 142	Aug 2006	6	2.9 (1.5)	1.4–5.5	5.4 (1.8)	3.2–8.3
Zebra 142	Aug–Nov 2007	22	4.3 (1.9)	1.2–7.6	8.5 (3.5)	4.3–15.3
Zebra 277	Aug–Nov 2007	30	7.9 (2.4)	1.2–14.1	15.1 (3.3)	7.4–23.2
Zebra 280	Aug–Nov 2007	29	6.3 (3.2)	1.6–18.4	12.2 (3.9)	5.1–22.5

[a]n is the number of trips to water based only on dates for which GPS collars were set to record hourly GPS positions.
GPS, global positioning system.

Table 4 Total daily distances moved by sable antelope *Hippotragus niger* and zebra *Equus quagga* comparing days when journeys to water took place with days when no movement towards water occurred over the 2006 and 2007 dry seasons in the Punda Maria area, Kruger National Park, South Africa

Animal	No water movement		Including movement to water			
	Mean (km) ± SE[a]	Range (km)	Mean (km) ± SE	Range (km)	95% CI for mean difference	
Sable	5.0 ± 0.41	1.9–9.8	16.6 ± 0.94	3.3–27.1	9.6	13.7
Zebra 141	4.1 ± 0.78	1.6–10.9	12.9 ± 0.65	8.2–15.8	6.6	10.9
Zebra 142	5.5 ± 0.44	2.1–11.4	9.2 ± 0.70	4.2–17.1	2.4	5.1
Zebra 277	8.1 ± 0.78	2.6–16.7	16.1 ± 0.79	9.1–26.6	5.9	10.1
Zebra 280	5.1 ± 0.62	1.4–12.5	11.5 ± 0.87	4.5–25.3	5.0	7.8

[a]Based only on the number of trips to water based only on dates for which GPS collars were set to record hourly GPS positions.
GPS, global positioning system.
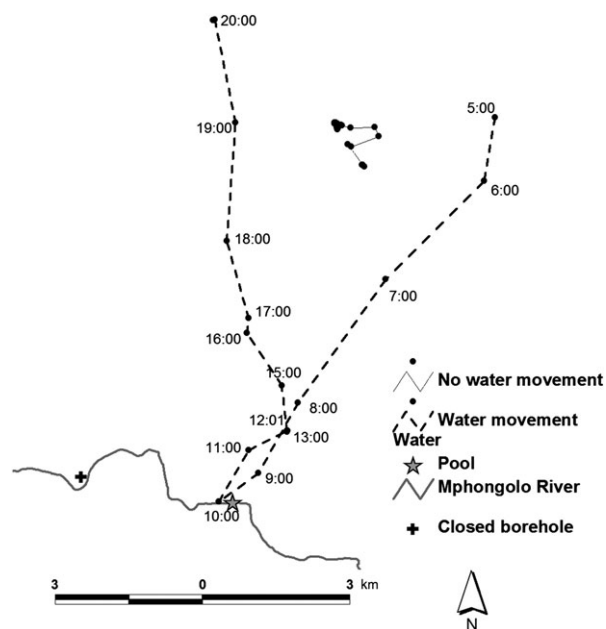
Figure 3 Movement trajectories of sable antelope *Hippotragus niger* in the Punda Maria area, Kruger National Park, comparing a water movement day (dashed line; 27 September 2007) and a non-water movement day (solid line; 25 September 2007).

2 h less per day and 3.3 fewer hours foraging on water movement days than on non-water movement days Fig. 4). Time occupied largely or entirely by moving amounted to almost 5.3 h more on days entailing travel to and from water.

Monthly time costs of water movement

The costs of water movements in reduced time for other activities calculated on a monthly basis were highest for sable during August and September when most movements to water occurred, amounting to a 12–16% decrease in resting time, 10–14% decrease in foraging time and 93–128% increase in travel time (Table 5). Monthly time costs for zebra varied among herds (Table 5). During August and September, zebra herds #277 and #280 spent 12–17% fewer hours per month resting, 10–15% fewer hours foraging and 45–100% more hours travelling. The home range of zebra herd #142 was closer to water, reducing time costs. Zebra herd #141 incurred the highest travel time cost because its home range was located farther from water.

Discussion

Contrary to statements made in the literature, neither sable nor zebra needed to drink daily. During the late dry season,
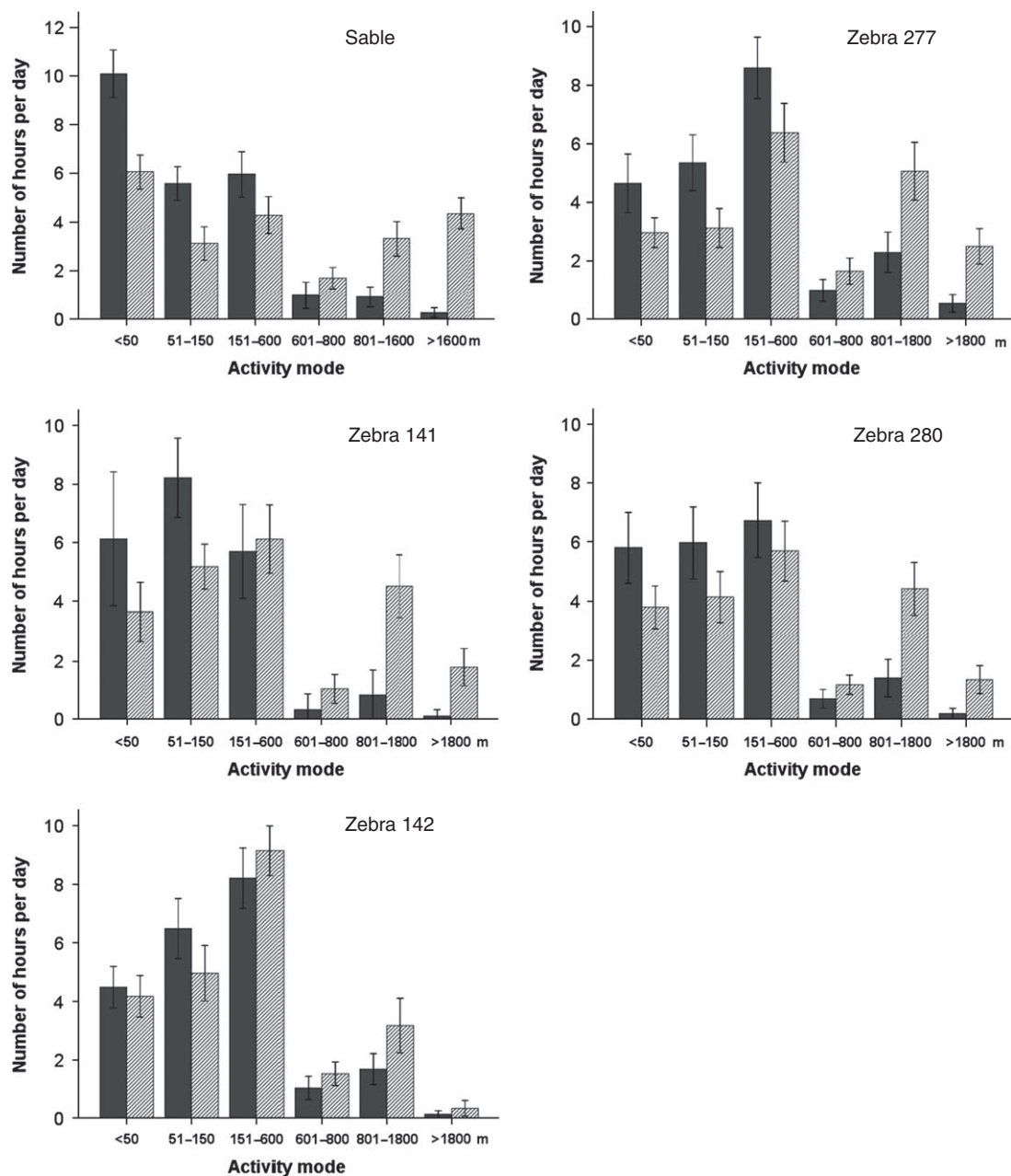
Figure 4 Average time occupied by different activity modes, distinguished by rates of movement, on days when journeys to water were undertaken compared with days when no such travel took place, for sable antelope *Hippotragus niger* and zebra *Equus quagga* in the Punda Maria region during the late dry season of 2007. Grey bars indicate days on which sable and zebra did not move to water sources; hatched bars represent days on which animals moved to water sources [<50 m – resting; 50–150 m – mixed resting and foraging; 151–600 m – foraging; 601–800 m – intermediate (i.e. foraging mixed with longer movements); 801–1600 m (sable), 801–1800 m (zebra) – mainly moving; and >1600 m (sable), >1800 m (zebra) – travelling]; error bars represent 95% confidence intervals.

sable travelled to water typically at 2–4-day intervals, substantially less frequently than the 1–2-day intervals recorded for zebra. The observed drinking frequency by zebra was consistent the drinking interval of 1–2 days documented by Young (1970) in KNP. However, zebra in Makgadikgadi and Nxai Pan National Parks, Botswana, visited water

sources only at 3–4-day intervals during the dry season (Brooks, 2005).

The amount of water consumed per animal per visit to a water source is almost identical for zebra and sable (4.7 vs. 4.6 L, respectively; Young, 1970). Because sable herds visited water sources less frequently than zebra, the amount of

Table 5 Proportional monthly change[a] in time and distance costs incurred by travel to surface water sources by sable antelope *Hippotragus niger* and zebra *Equus quagga* herds during the 2006 and 2007 dry seasons in the Punda Maria area of Kruger National Park, South Africa

Month	Sable	Zebra 141	Zebra 142	Zebra 277	Zebra 280
Resting time					
Aug 2006	−0.10	−0.35	−0.06		
Sep 2006	−0.16	−0.38	−0.03		
Oct 2006	−0.15	−0.36	−0.04		
Nov 2006	−0.03				
Aug 2007	−0.12	−0.22	−0.03	−0.12	−0.16
Sep 2007	−0.16	−0.20	−0.04	−0.17	−0.17
Oct 2007	−0.01		0.00	−0.02	−0.02
Nov 2007	−0.07		−0.01	−0.04	−0.05
Foraging time					
Aug 2006	−0.09	−0.16	−0.03		
Sep 2006	−0.14	−0.17	−0.02		
Oct 2006	−0.14	−0.17	−0.02		
Nov 2006	−0.02				
Aug 2007	−0.10	−0.10	−0.02	−0.10	−0.10
Sep 2007	−0.14	−0.09	−0.03	−0.15	−0.11
Oct 2007	−0.01		0.00	−0.02	−0.01
Nov 2007	−0.06		−0.01	−0.03	−0.03
Travelling time					
Aug 2006	0.83	3.88	0.65		
Sep 2006	1.29	4.16	0.38		
Oct 2006	1.25	4.02	0.39		
Nov 2006	0.21				
Aug 2007	0.93	2.44	0.31	0.45	0.91
Sep 2007	1.29	2.23	0.48	0.65	1.00
Oct 2007	0.10		0.02	0.09	0.13
Nov 2007	0.54		0.10	0.14	0.27

[a]Proportional change is the difference in distance or time incurred on water use days divided by the mean distance moved or time occupied on non-water use days, weighted by the proportion of water use days per month; positive numbers indicate additional time and distance costs, while negative numbers indicate time lost to other activities (i.e. resting and foraging) due to journeys to water sources.

surface water sable imbibed on a monthly basis during the dry season was only about half as much as for zebra. The difference in surface water needs between these two species is consistent with the distinctions in their digestive systems outlined in the introduction. Moreover, sable selected more strongly for patches retaining green grass during the dry season than zebra, enabling them to obtain somewhat more pre-formed moisture from forage (Macandza, 2009).

Travel to the few water sources remaining in the dry season represented a substantial cost in time as well as distance travelled, reducing the time available for foraging and resting for both species. Mean travel distance by the sable herd was about 25% greater than even for the collared zebra herds drinking at the river, because the areas where the sable foraged tended to be further from the river. However, the total time taken up by travel to and from water was almost identical for the two species (i.e. 13.1 vs. 13.2 h), because zebra tended to forage during the return journey while sable walked more persistently back towards their previous foraging area. Nevertheless, because sable drank less frequently than did zebra herds, their overall travel time cost calculated on a monthly basis was similar to that averaged across zebra herds, which visited water more

frequently but foraged on return journeys from water sources. High variability in time and distance costs among zebra herds was primarily due to the contrasting home range locations of two of the zebra herds relative to water.

Energetic costs of locomotion increase with distance travelled per day (Fancy & White, 1985). For example, Pennycuick (1979) estimated that wildebeest travelling 10 km per day utilise 8% of their net energy income on locomotion. Energetic costs of locomotion (above maintenance levels) for domestic herbivores on range conditions have been estimated as 9–14% for goats (Lachica, Barroso, & Prieto, 1997) and 9–17% for cattle (Brosh *et al.*, 2006) depending on seasonal variation in forage quality and daily distance travelled.

Our findings indicate that sable herds can forage in localities 5–9 km from water during the late dry season, contrary to reports that the distribution of sable is limited to <4 km of water sources (Wilson & Hirst, 1977; Ben-Shahar, 1990), but our results were consistent with the broad pattern reported for zebra (Western, 1975). However, the home range occupied by the sable herd at Punda Maria during the wet and early dry seasons was >14 km from the river that became the main remaining source of water for

drinking during the late dry season. Accordingly these animals shifted their home range to a location within 10 km of the river after seasonal pools in their wet season range had run dry. This range shift was made earlier during the drier year (in August 2007) than in the wetter year (only in September in 2006; Macandza, 2009). Zebra herds at Punda Maria also shifted their water use from ephemeral water sources to perennial sources (e.g. river, gravel pit) in September 2006 and in August 2007, but without a clear pattern in home ranges occupied (Macandza, 2009).

Journeys to water undertaken by the Talamati sable herd were exclusively towards a large dam on a river 9 km outside their typical home range, and not to drinking troughs available within the same distance. Travel to this dam only became possible following the removal of the boundary fence between KNP and Manyaleti Game Reserve around 1994. It seems likely that this small herd became established after this opportunity had opened.

The sable herd at Punda Maria did not use the gravel pit and made less frequent use of pools persisting in other artificial sources (i.e. small dams, or drinking troughs) during the dry season than did the collared zebra herds which is contrary to the conclusions of Smit *et al.* (2007) for sable antelope. Concentrations of zebra and other abundant water-dependent grazers that develop in the proximity of artificial water points may inhibit their use by sable either due to competitive interactions (Valeix *et al.*, 2008) or because large concentrations of prey species attract predators to the vicinity of the water holes (de Boer *et al.*, 2010; Valeix *et al.*, 2010).

Although maximum daily temperatures during the dry season months of September and October were frequently $> 35\,°C$, neither sable nor zebra travelled to and from water during the cooler nocturnal conditions. This is probably a response to the greater risk of predation by lions *Panthera leo* hunting predominantly at night when concealment is greater (Schaller, 1972). Although journeys towards water were generally initiated at or soon after dawn, arrival at pools generally took place only in the late morning. The hot conditions prevalent by then delayed the start of the return journey. This indirect cost from the risk of predation contributed further to the lost foraging time incurred, especially for sable, which generally did not forage until back within their home range. However, by travelling to water less frequently than zebra, sable may have lowered their encounter risk with lions during these journeys to some degree relative to zebra. By not foraging near the river, both sable and zebra avoided much overlap with the area subjected to heavy use by the large buffalo herd at Punda Maria during the dry season (Macandza, 2009).

Longer intervals between visits to water tolerated by sable antelope enabled it to occupy regions of the landscape further from water than those heavily exploited by the more common zebra and buffalo during the critical dry season months in our study area. By avoiding concentrations of these grazers, the sable also probably gained a reduction in the predation risk that they incurred, counteracting the substantial costs in terms of time and energy associated with travel to water. Thereby the distinctions in water dependency of this relatively rare grazer facilitated its coexistence alongside more abundant grazers in the KNP.

Acknowledgements

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